Is spatial uniformity of soft-sediment biodiversity widespread and, if so, over what scales?

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ABSTRACT: Spatial variation in the components of faunal assemblages, but spatial uniformity of their biodiversity metrics, as described in 2013 for a seagrass bed in an estuarine bay in the warm-temperate Indian Ocean, is probably widespread in marine environments, and not restricted to seagrass habitats. Here, it is shown to occur across unvegetated siliceous sandflats as well as seagrass beds on a high-diversity but low-abundance subtropical island (North Stradbroke Island, Australia) in the South Pacific, and on a low-diversity but high-abundance cool-temperate island (Scolt Head Island, UK) in the North Atlantic. At the Australian locality, this uniform biodiversity but non-uniform faunal assemblage composistion were observed to extend over distances of at least 6.5 km in both habitat types. Unit areas as small as 0.0275 m^2 in each system supported a statistically invariant percentage of the total species pool of that system (i.e. the system's overall mean percentage constancy index at the spatial scale concerned). Further, assemblages in all localities showed very similar ranked species-constancy curves, even though the proportions of the total numbers comprised by the various species varied widely. It is therefore suggested that the factors structuring the macrofaunal assemblages in such soft-sediment habitats must be capable of promoting comparable systems of relative frequency of occurrence, regardless of local levels of faunal abundance and biodiversity.

KEY WORDS: Biodiversity · Macrobenthos · Patchiness · Sandflat · Seagrass · Spatial constancy · Spatial occurrence · Spatial uniformity

INTRODUCTION

The effects of spatial scale have long been recognised to be central to modern ecology (Levin 1992, Liebhold et al. 1993, Dray et al. 2012). Consequently, 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), including in the benthic macrofauna associated with intertidal and shallow water seagrasses (Bowden et al. 2001, Borg et al. 2010, Arponen & Boström 2012). Local spatial uniformity of assemblage biodiversity, however, has received almost no attention—although it has recently been demonstrated in an inter-

tidal seagrass *Zosterella capensis* bed in the Knysna estuarine bay, South Africa (Barnes 2013). As expected from earlier studies at this site (Barnes & Ellwood 2011a), various seagrass-associated macrobenthic species and their populations were highly variably distributed across a 1 ha area, with abundances of the individual dominants being significantly patchy, and composition of the macrofaunal assemblage being significantly non-uniform. Nevertheless, in marked contrast to the nature of the species' populations collectively responsible for generating the attributes concerned, the magnitudes and spatial dispersions of emergent features of that same assemblage exhibited spatial uniformity: per-unit-area values of species richness, species density and species diversity did

not differ significantly across the site or across spatial scales. Distribution of species density and species diversity through space was even statistically invariant. Arguments developed for temporal stability of biodiversity (e.g. Brown et al. 2001, Goheen et al. 2005) seemed broadly applicable to the spatial dimension at this site, suggesting that although apparently counterintuitive, it may be the varying assemblage composition that permits this spatial uniformity. There was no evidence, however, that the macrobenthic seagrass assemblage was competitively-structured with rigid niche-partitioning — a condition postulated to be necessary for temporal stability. Rather, the Knysna system appeared to be open, at non-equilibrium and below-carrying-capacity.

Using the same sampling and analytical methodology as at the South African site (Barnes 2013) for comparability, the present study tests hypotheses that such spatial uniformity is (1) a local phenomenon restricted to the specific 34°S warm-temperate Indian Ocean site previously investigated, and to stands of seagrasses, as well as (2) to very small areas of ca. 1 ha. This was undertaken by investigation of 2 further localities contrasting in their nature to that of Knysna and supporting expanses of unvegetated sand as well as seagrass beds. The first was a high-diversity but low-abundance subtropical South Pacific locality, at which earlier studies had produced results suggestive of spatially uniform levels of biodiversity (Barnes & Barnes 2011, 2012); the second was a low-diversity but very high-abundance cool-temperate locality in the northeast Atlantic. Further, unlike the system at Knysna, which was dominated mainly by a suite of infaunal polychaetes, strikingly different faunal and/or ecological groups were known to be dominant at the new localities investigated: an epifaunal clade-G truncatelloid microgastropod (sensu Criscione & Ponder 2013) in both the cool-temperate habitat types, an infaunal urohaustoriid amphipod in the subtropical sandflat, and a range of species (epi- and infaunal clade-I truncatelloids, a macrophthalmid crab, and a phoxocephalid amphipod) with no single overall dominant in the subtropical seagrass (Barnes & Barnes 2011, 2012, Barnes & Ellwood 2011b, 2012).

MATERIALS AND METHODS

Study sites and sampling protocols

Spatial distribution of soft-sediment macrobenthic abundance and biodiversity was surveyed primarily along the sheltered, subtropical Rainbow Channel
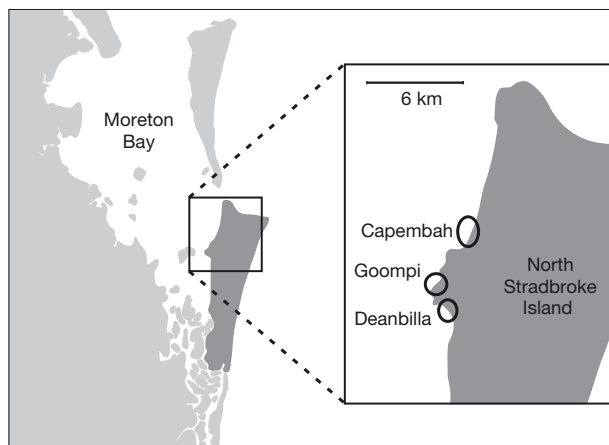

Fig. 1. Sampling sites along the northwest coast of North Stradbroke Island, Moreton Bay, Queensland, Australia

coast of North Stradbroke Island, within the Moreton Bay Marine Park, Queensland, Australia. Seaward of the mangrove belt, the intertidal zone supports 2 alternative habitat types (Barnes & Hamylton 2013): (1) beds of the seagrass *Zosterella capricorni* (often with admixed *Halophila ovalis*) forming part of the 180 km^2 seagrass system in the Bay (Roelfsema et al. 2013), and (2) unvegetated areas of the same substratum (fine- to medium-grained quartz sand) structured by the thalassinidean *Trypaea australiensis*. Two 5 × 5 m stations >250 m apart were established between low water neap (LWN) and mean low water (MLW) tides in both these seagrass and unvegetated-sand habitats at each of 3 sites (Fig. 1), distributed along a 6.5 km stretch of the shore from 27° 27′ 57″ S, 153° 25′ 21″ E to 27° 30′ 37″ S, 153° 24′ 39″ E. The stations Deanbilla and Goompi were ~2 km apart, while Goompi and Capembah were ~4 km apart (measured along the shoreline). Each station was sampled by 25 individual cores arranged quincuncially as 5 blocks of 5 (Fig. 2), exactly as was the case at Knysna. Using the terminology of Wiens (1989), this yielded a basic spatial sampling system of 0.0275 m^2 grain (core-block) and 0.1375 m^2 grain (station), and nested linear extents of 1 m, 5 m, 250 to 300 m, 2 to 4 km and 6.5 km. Each habitat type was therefore represented by 30 core-blocks (= 150 individual samples). All seagrass stations were located in regions of at least 75% cover within single continuous swards of seagrass, and >20 m from the margins of a bed to avoid potentially confounding variables such as percentage ground cover, patch size and proximity to edges (Irlandi 1994, Bowden et al. 2001, Tanner 2005). The unvegetated sand stations were likewise situated within large (>0.5 ha) blocks of bare sandflat >20 m
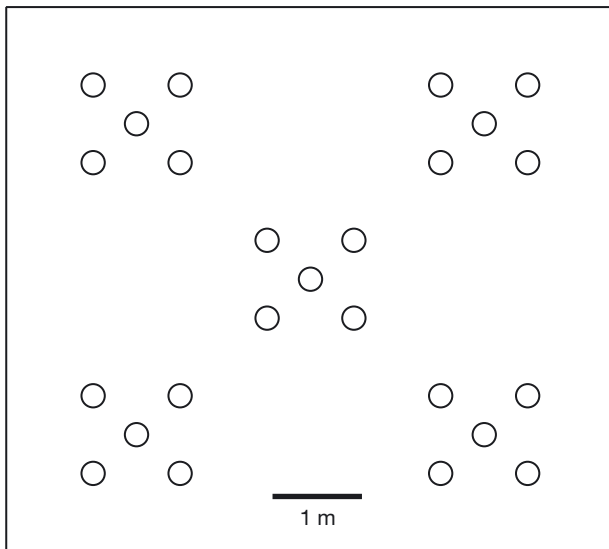
Fig. 2. Quincuncial arrangement of the 5 core-blocks, and the 5 core samples in each, within each station

away from the nearest seagrass. Sampling took place over a 10 wk period during the 2013 austral spring.

Seagrass sampling methodology was as previously carried out at Knysna (Barnes 2013), and unvegetated sand cores were treated similarly. Faunal individuals were identified to species wherever possible and were counted, with taxonomically intractable individuals being identified to morphospecies (Dethier & Schoch 2006, Albano et al. 2011). 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. sea-anemones) that had become detached from the seagrass leaves during sampling. One further species was excluded: the soldier crab *Mictyris longicarpus.* 'Armies' containing hundreds of soldier crabs emerge on the falling tide to march across the local sandflats, periodically tunnelling en masse just beneath the surface to feed (e.g. Webb & Eyre 2004). By chance, some sand samples therefore contained large numbers of these wandering crabs, whereas at another point in time or in an adjacent area they contained none. In these circumstances, exclusion of the crab from the dataset seemed most appropriate. All nomenclature is given as listed in the World Register of Marine Species (WoRMS; www.marinespecies.org).

The same procedures were also used to collect comparable (although less extensive) data on the same assemblage metrics from the macrobenthos of cool-temperate (1) intertidal seagrass *Zosterella noltei* and (2) associated stretches of unvegetated fine- to medium-grained quartz sandflat. This was conducted on the English North Sea coast at 2 stations, ca. 500 m apart at upper Cockle Bight on the leeward side of the Scolt Head Island National Nature Reserve, Norfolk (centred on 52° 59′ N, 00° 40′ E and 52° 59′ N, 00° 41′ E), a locality described by Barnes & Ellwood (2011b). At each station, 5 coreblocks randomly scattered across each habitat type were sampled between MLW and high water neap (HWN) tides over 4 wk during the boreal summers of 2012 and 2013.

Data analysis

Variation in composition of the macrofaunal assemblages across sites was assessed via PRIMER v6.1 (PrimerE: Plymouth Routines in Multivariate Ecological Research) using multivariate permutational analysis of variance (PERMANOVA) of S17 BrayCurtis similarities with fourth-root transformed data and 999 permutations. Compositional similarity between spatial sampling units within an individual habitat type was assessed both by the Bray-Curtis index and the Chao et al. (2005) modification of the Sørensen abundance-based similarity index that corrects for the effects of under-sampling (thereby substantially reducing the negative bias of the BrayCurtis, especially in species-rich assemblages). The upper abundance limit per sample for rare species was set at 5 for the Chao et al. (2005) index. Variability in global spatial structure (sensu Cooper et al. 1997, Perry et al. 2002) was then assessed from values of the same assemblage metrics as measured at Knysna (Barnes 2013), which were calculated from the totals for each core-block (and where appropriate for other spatial scales) using EstimateS v9.0.0 (Colwell et al. 2012, Colwell 2013). These metrics were overall faunal abundance, and a series of 4 indices quantifying diversity along linear scales of the 'effective number of species' (Jost 2006) according to the mean proportional abundances system of Hill (1973) (Table 1). EstimateS v9.0.0 was also used to estimate maximum species density (S_{max}) — on this occasion solely by the abundance coverage-based estimator. Normality was established by the Shapiro-Wilk test (Razali & Wah 2011).

As was done previously (Barnes 2013), spatial dispersion of these metrics was assessed by Smith-Gill's (1975) standardised version of Morisita's (1959) index of patchiness (I_m). I_m was also used to test for departures from random of the dispersions of the individual species. I_m values from +0.5 to +1.0 indicate significant patchiness, and those from −0.5 to −1.0 signifi-

Table 1. Biodiversity metrics calculated per unit area

Symbol	Metric
N_0	Observed species density (sensu Gotelli & Colwell 2001); its reciprocal is the harmonic mean of the proportional abundances
N_1	Shannon exponential species diversity index $[\exp(-\Sigma p_i \ln p_i)]$; its reciprocal is a geometric mean of the proportional abundances
N_2	Simpson (inverse) species diversity index $[1 / \Sigma p_i^2]$; its reciprocal is the arithmetic mean of the proportional abundances
N_∞	The reciprocal of Berger-Parker dominance, i.e. the reciprocal of the proportional abundance of the most numerous species

Table 2. Indices of similarity between the macrofaunal assemblages within and between sites on North Stradbroke Island; both indices are derived from untransformed species abundances

	Chao et al. (2005)	Bray-Curtis
Between stations at a site: seagrass		
Capembah	0.871	0.369
Goompi	0.823	0.451
Deanbilla	0.980	0.559
Between stations at a site: bare sand		
Capembah	0.967	0.453
Goompi	0.766	0.366
Deanbilla	0.802	0.480
Between sites: seagrass		
Capembah vs. Goompi	0.919	0.524
Capembah vs. Deanbilla	0.925	0.616
Goompi vs. Deanbilla	0.881	0.614
Between sites: bare sand		
Capembah vs. Goompi	0.862	0.490
Capembah vs. Deanbilla	0.867	0.343
Goompi vs. Deanbilla	0.958	0.472

cant uniformity (at 1-tailed p = 0.025); values 0.5 units on either side of zero show no significant departure from random variation. Note that the terms 'uniformity' and 'constancy' are not used interchangeably here. As above, 'uniformity' refers to the even, regular, or if statistically significant, invariant dispersion of individual values (for example, of biodiversity metrics) through space; it is the obverse of 'patchy'. 'Constancy' refers to the frequency of occupancy or occurrence of a taxon in samples from a given area (e.g. Dengler et al. 2009), here measured as Cabioch's (1968) percentage constancy index (C).

RESULTS

Subtropical North Stradbroke Island

The 3 seagrass sites on North Stradbroke supported an observed total of 143 macrofaunal species (estimated true total 186) at an overall density of 2256 ind. m^{-2}, and with an overall effective number of species of 16 (N_2) to 37 (N_1). No single species attained >15% of total assemblage individuals, but 4 taxa each contributed >5%, together comprising 46% of the numbers (see Appendix). The assemblage was not uniformly distributed across the locality (PERMANOVA pseudo-F = 3.91, p <0.001), and showed low mean compositional similarities across the 3 sites and even between stations within a site (Table 2). Only a single species comprised ≥10% of the individuals at all 6 stations, although 10 other taxa (see Appendix) comprised >5% in at least 1 station. The dispersions of 12 of the 13 most abundant seagrass species (those each comprising >1% of the total) were significantly patchy (I_m > +0.501), as was overall faunal abundance (I_m = +0.5004).

In contrast, the bare sand assemblage at the same locality had an observed total of only 41 macrofaunal species (estimated true total 64), plus the excluded *Mictyris*, at an overall density of 1190 ind. m^{-2} and with an effective number of species of 2.4 (N_2) to 5.4 (N_1). A single species of urohaustoriid amphipod (see Appendix) overwhelmingly dominated the assemblage, being the most numerous animal at all 6 stations. Nevertheless, as in the seagrass, the bare sand assemblage was not uniformly distributed across the locality (PERMANOVA pseudo-F = 6.35, p <0.001), and showed similar low mean compositional similarities across the 3 sites and between stations within a site (Table 2). Only 1 other species contributed >5% to the total individuals (see Appendix). Of the 12 species each comprising >1% of the total individuals in the sand, the dispersions of 8 species (including the 3 most common) were significantly patchy (I_m > +0.508), as was overall faunal abundance (I_m = +0.508), although those of 4 species did not depart from random. Only the urohaustoriid had a value of C > 75%. Such major differentiation of adjacent seagrass and bare-sediment macrobenthos conforms to that described earlier from the same locality (Barnes & Barnes 2012, Barnes & Hamylton 2013).

Nevertheless, in spite of this significant spatial patchiness in both abundance and composition of the macrofaunal assemblages (no species being significantly uniformly distributed in either habitat), the levels per core-block of the 4 assemblage biodiversity metrics all showed uniform dispersions (i.e. neg-

Table 3. Magnitude and spatial dispersion of overall values per core-block of emergent assemblage biodiversity metrics (N_0 … N_∞; see Table 1 for details) across the sampled seagrass and unvegetated-sandflat habitats on North Stradbroke Island in the South Pacific, and on Scolt Head Island in the North Atlantic. The equivalent earlier seagrass data from Knysna in the southern Indian Ocean (from, or from the data of, Barnes 2013) are included for comparison. Magnitudes are given as means ± SE; dispersion patterns as standardised Morisita's indices (I_m), of which values shown in bold indicate significant uniformity at p < 0.025; those in italics, whilst also showing uniformity, indicate no significant departure from random variation at p = 0.05

Locality Habitat	N_0 Magnitude	I_m	N_1 Magnitude	I_m	N_2 Magnitude	I_m	N_∞ Magnitude	I_m
N Stradbroke								
Seagrass	22.73 ± 0.65	**−0.5001**	14.36 ± 0.59	*−0.302*	9.78 ± 0.51	*−0.230*	4.82 ± 0.25	**−0.517**
Bare sand	7.23 ± 0.28	**−0.532**	4.11 ± 0.31	*−0.325*	3.16 ± 0.28	*−0.315*	2.12 ± 0.16	**−0.555**
Scolt Head								
Seagrass	14.30 ± 0.76	**−0.501**	2.42 ± 0.22	**−0.524**	1.66 ± 0.13	**−0.592**	1.45 ± 0.90	**−0.620**
Bare sand	13.10 ± 0.48	**−0.504**	2.70 ± 0.25	**−0.519**	1.91 ± 0.16	**−0.558**	1.31 ± 0.06	**−0.759**
Knysna								
Seagrass	20.71 ± 0.39	**−0.506**	14.83 ± 0.32	**−0.506**	11.60 ± 0.31[a]	**−0.509**[a]	6.09 ± 0.21	**−0.518**

[a]These values differ from those given in Barnes (2013) in that they were calculated from overall species totals for each core-block, rather than on the basis of rarefied subsets of the reference samples

ative values of I_m) across the locality, and for N_0 and N_∞, the degree of uniformity was significantly invariant across both the seagrass and the unvegetated sediment (Table 3). No biodiversity metric was (even insignificantly) patchily dispersed. Hence, uniformity of these biodiversity metrics occurred across a distance of at least 6.5 km, each core-block containing the overall mean constancy percentage ± a small standard error (seagrass 15.9 ± 0.45 %; bare sand 17.6 ± 0.69; SE <4 % of the mean) without any variation from site to site (1-way ANOVA; $F_{2,27}$ < 2.17, p > 0.13). In the seagrass, variation in abundance and in the biodiversity metrics did not depart from normality (W > 0.95, p > 0.33) but all metrics did so in the bare sand (W = 0.77 to 0.92, p < 0.04) (Fig. 3). Spatial variation in the diversity indices N_1 and N_2 was greater than in N_0 and N_∞, and did not depart from random. This larger scatter of the species diversity data was consequent on the combination of patchy abundance and very high levels of constancy shown by the most abundant species in each habitat. In the bare sand, it was due to the pattern of distribution of the urohaustoriid (I_m = +0.521; C = 97 %). In coreblocks where that amphipod was particularly abundant, levels of species diversity were very low, and vice versa (Spearman's r > −0.85, p ≪ 0.0001). This created a bimodality in the sandflat data in which the 12 core-blocks forming the lower diversity group in Fig. 3C,D (e.g. mean N_1 = 2.3) averaged 42 urohaustoriids per core-block (out of a total of 51 faunal individuals), whereas the 18 core-blocks in the higher diversity group (e.g. mean N_1 = 5.3) supported an average of only 7 urohaustoriids (in which they formed

only 21 % of the individuals). There was, however, no difference between the mean numbers of species in the 2 sandflat core-block groups (Mann-Whitney p = 0.55), so that N_0 was unaffected. Likewise in the seagrass, the proportion of faunal individuals in a coreblock comprised of the 2 most abundant microgastropods, for example, varied from 0.05 to 0.59 (I_m = +0.508; C = 100 %), and this proportion impacted inversely on levels of the diversity indices (Spearman's r > −0.37, p < 0.05).

Cool-temperate Scolt Head Island

In contrast to the subtropical locality, the seagrass stations on the North Sea coast supported an observed total of only 30 macrofaunal species (estimated true total 34), but their combined density was >60 000 ind. m^{-2}. The overall effective number of species was also very low (N_1 = 2.5; N_2 = 1.6), with only 3 species together comprising more than 90 % of total assemblage numbers (these 3 were also the only ones each to contribute >4 % to the total), although 9 taxa had values of C > 75 % (see Appendix). The bare sand assemblage statistics were very similar, with an observed total of 29 macrofaunal species (estimated true total 36) at a combined density of 37 700 ind. m^{-2}. The effective number of species was 1.8 (N_2) to 2.8 (N_1). The same 3 dominant seagrass species (see Appendix) were also the only ones each to contribute >4 % of sandflat faunal numbers, where together they comprised more than 92 % of the sand total. The same 3 species, together
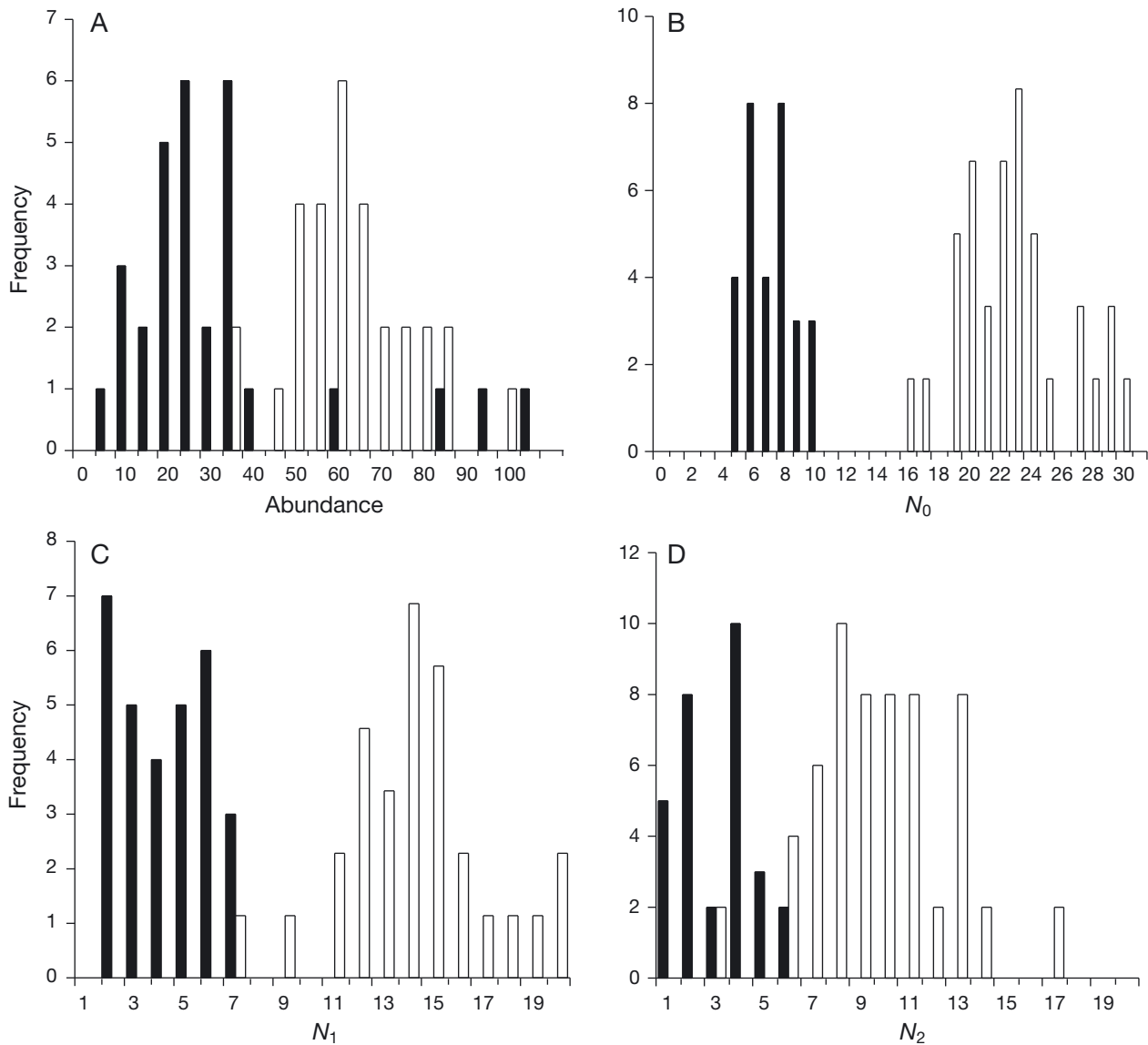
Fig. 3. Frequency distribution across the North Stradbroke Island seagrass (open bars) and unvegetated sandflat (black bars) of the magnitude per core-block of representative metrics: (A) faunal abundance (in bins of 5 ind.), (B) observed species density (N_0), (C) N_1 species diversity, and (D) N_2 species diversity. N_∞ showed equivalent patterns (see Table 1 for an explanation of the diversity indices)

with one other, were also the only ones in which $C >$ 75%. The 69% of the overall Scolt Head species that were common to both habitat types comprised 99.7% of the total faunal numbers. Such minor differentiation of the macrobenthic assemblages of *Zosterella* and of the adjacent bare sediment appears to be the typical state in the North Sea (e.g. Polte et al. 2005, Bouma et al. 2009).

Neither the macrofaunal assemblages of the seagrass nor those of the bare sandflat, however, were uniformly distributed across the area (PERMANOVA pseudo-$F > 11$, p < 0.001), although compositional similarities of untransformed data from within each

habitat were relatively high: 0.735 (Bray-Curtis) or 0.981 (Chao et al. 2005) in respect of the seagrass, and 0.725 (Bray-Curtis) or 0.973 (Chao et al. 2005) for the bare sand. Further, the 6 (sand) or 7 (seagrass) most abundant species in each habitat type (those each comprising >1% of the total, and together 98% of the individuals) all had significantly patchy distributions ($I_m > +0.501$ in all cases), as also did overall faunal abundance (seagrass $I_m = +0.502$; sandflat $I_m = +0.504$).

Nevertheless, as on North Stradbroke, and in spite of this patchiness in both individual species and entire macrofaunal assemblages, levels per core-
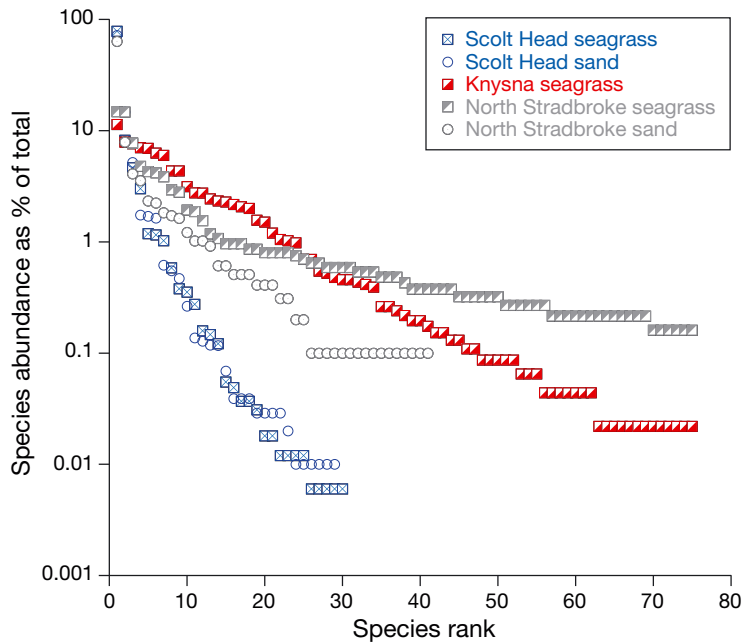
Fig. 4. Ranked species abundance curves for the various macrofaunal assemblages sampled on North Stradbroke and Scolt Head Islands (squares = seagrass; circles = unvegetated sand). The curve for the Knysna seagrass (data from Barnes 2013) is also included for comparison. Only the 75 most abundant species are shown for the North Stradbroke seagrass assemblage

block of the 4 biodiversity metrics were all significantly invariant across both habitat types (Table 3); each metric in each habitat type (including overall abundance) conformed to a single normal distribution (all p > 0.1). Each core-block again contained the overall mean constancy percentage ± a small SE: 47.7 ± 2.5% in the seagrass and 45.2 ± 1.7% in the unvegetated sand. In both the seagrass and bare sandflat, values of all 4 biodiversity metrics were even significantly uniform at the level of the individual core sample ($I_m < -0.516$) — the scale at which maximum spatial variability occurs at the site (Barnes & Ellwood 2011b).

General features of assemblage structure

Ranked species abundance curves are displayed in Fig. 4. Both Scolt Head habitats fell on the same line, but otherwise the sampled localities (including that at Knysna sampled earlier) show clear differences in organisational features related to relative abundance. Most, however, are of the concave form characteristic of Hughes' (1984) dynamic model for benthic marine assemblages and/or of Magurran & Henderson's (2003) composite log-normal/log-series model. As is typical of both these models, there is an 'excess' of rare species (Magurran & Henderson 2003). In the most speciose locality (the North Stradbroke seagrass), this excess corresponded to an abundance of <10 ind. m^{-2}, and this density was used below approximately to distinguish non-rare and rare species. In contrast to their divergent relative abundances, the rank order of per core-block species constancies (Fig. 5A) shows a basic similarity of form. This similarity is rendered even more evident by restriction of the data to the non-rare species component, and by expressing the individual species constancies in an exactly analogous form to those of Fig. 4; i.e. as proportions of the total non-rare species-constancies (the sum of the non-rare constancy indices at a locality) (Fig. 5B). With the partial exception of the depauperate North Stradbroke bare sand (with its few non-rare species), the curves for each locality clustered tightly together. The 15 highest-C species from all 3 seagrass localities and from the Scolt Head bare sand all comprised an average of 5.1 ± 0.5% (range = 4.24 to 6.15%) of the total summed constancies of their assemblages; there was no significant difference between those from Knysna and from North Stradbroke (Tukey's HSD; p = 1.0) or between those from the 2 Scolt Head habitats (Tukey's HSD; p = 0.71).

Across the various assemblages, the per core-block mean constancy percentage in both seagrass and bare sand correlated both with local mean assemblage density (Pearson's r = 0.92, p = 0.03) and with the local percentage of non-rare species (Pearson's r = 0.93, p = 0.02), mean C equalling 59 ± 4% of the non-rare component. But there were no significant correlations between mean C and any other assessed metric, including size of the local species pool (all p > 0.2).

DISCUSSION

The North Stradbroke and Scolt Head localities studied, together with the Knysna estuarine bay investigated earlier (Barnes 2013), are all sheltered, intertidal expanses of siliceous sand with some admixed silt. That apart, however, their ecological and environmental features display many contrasts: the localities are distributed across a wide latitudinal range; they are geographically far apart and located
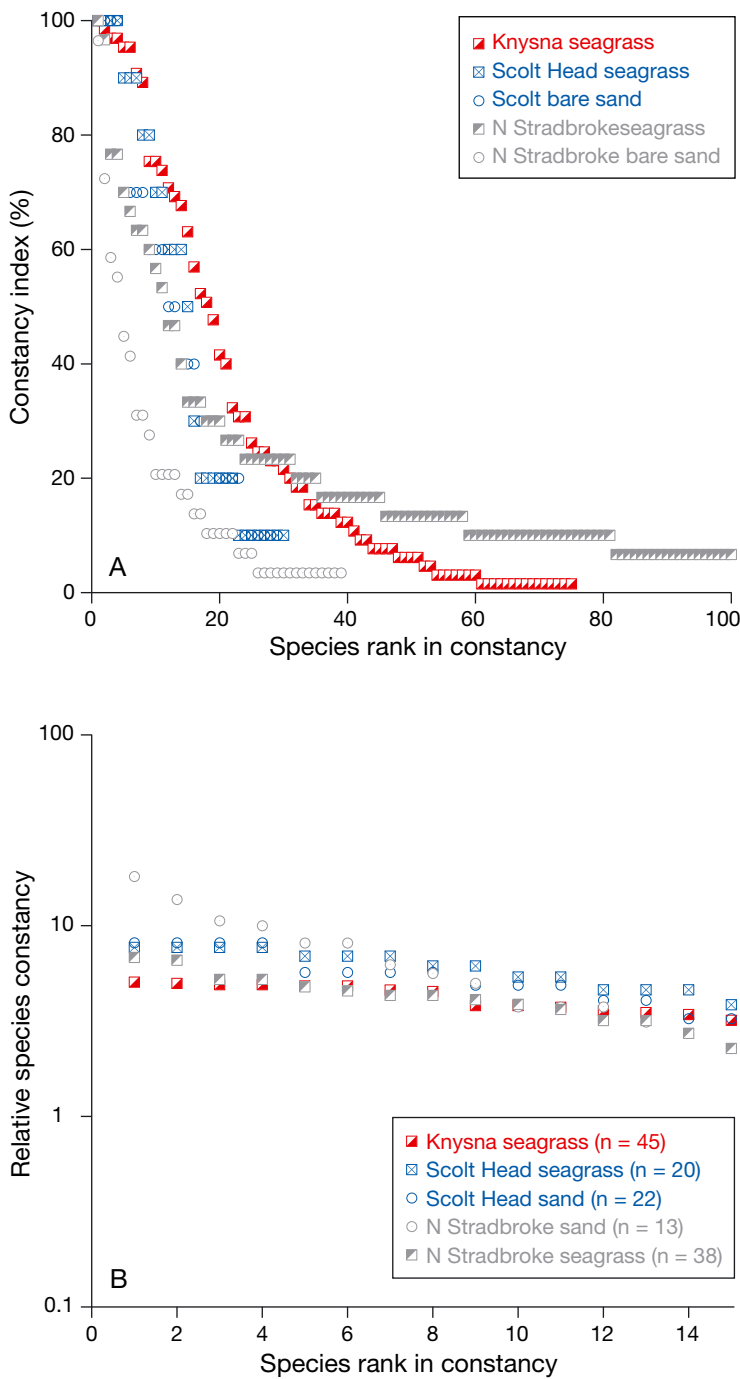
Fig. 5. Ranked species constancy curves for the various macrofaunal assemblages sampled on North Stradbroke and Scolt Head Islands (squares = seagrass; circles = unvegetated sand). The curve for the Knysna seagrass (data from Barnes 2013) is also included for comparison. (A) Ranked percentage frequency of occurrence curves for each assemblage. Only the 100 highest-C species are shown for the North Stradbroke seagrass assemblage. (B) Curves for the non-rare species component as percentages of the total non-rare species-occurrences, with only the 15 highest-C species at each locality shown (numbers in the non-rare category indicated in parentheses)

in different oceans; and they are dominated by different taxa. Two are unvegetated, whilst 3 support dense beds of seagrasses, each dominated by a different species (albeit all of the dwarf-eelgrass *Zosterella*). On Scolt Head, there was little faunistic difference between the assemblages of vegetated and unvegetated areas, whereas the equivalent North Stradbroke pairings supported macrofaunas contrasting markedly in abundance, diversity and nature — one with a large epifaunal component and the other entirely infaunal. Scolt Head is fully marine, whilst the Knysna site is in the mouth of an estuary. Three of the sites were overwhelmingly dominated by a single species (contributing 64 to 78 % of total numbers), whereas 2 were characterised by a considerable number of co-dominants, with no species comprising >15 % of individuals. The localities also span wide ranges in known total numbers of macrofaunal species (i.e. 30 to >160), species diversities (e.g. N_1 values of <3 to >26), and mean faunal density (i.e. <1000 to >60000 ind. m^{-2}) (NB the effect of density on dispersion shown by Taylor 1961), and their ranked species abundance curves indicate clear differences in assemblage structure in that respect (see Whittaker 1965, Hughes 1986, Tokeshi 1990).

Granted these marked contrasts, it is then all the more remarkable that their emergent assemblage attributes all show exactly the same pattern. On the one hand, as would generally be expected (e.g. Morrisey et al. 1992), (1) the populations of individual species and the macrofaunal assemblages as a whole showed patchy abundances at each locality, (2) all assemblages varied in absolute and relative composition through space, and (3) their biodiversity metrics varied in magnitude from locality to locality. On the other hand, however, no per-unit-area biodiversity metric that was derived from any of these same assemblages varied significantly through space within a given locality, the N_0 and N_∞ metrics always being significantly invariant (on North Stradbroke over distances of up to 6.5 km), and the N_1 and N_2 metrics being significantly invariant at 3 of the 5 localities. None of the localities showed significant departure from similarity of overall form across space in spite of great variability of the component populations and species.

These 5 macrobenthic assemblages now shown to display spatial uniformity of biodiversity metrics do have in common, however, that they are likely to be below carrying capacity as a result of predation (Reise 1985, Valentine & Duffy 2006, Lewis & Anderson 2012). The conclusion that given levels of biodiversity are being maintained by predatory prevention of competitive exclusion, however, may be overly simplistic (Chesson & Huntly 1997). Coexistence can be promoted wherever niche differences cause species to limit their own populations more than they can limit those of others, although unfortunately very little is known of the niches of most of the species concerned, including even numerically dominant ones. None of the dominant Stradbroke seagrass species, for example, has been the subject of autecological work, and the majority have only been known scientifically since 1995 or are still undescribed species. But there are several other mechanisms that could contribute to the stability of biodiversity in systems without competitively induced resource partitioning (Chesson 2000). Frequency-dependent predation (Holt & Lawton 1994), for example, can be as much a stabilising mechanism as resource partitioning. Alternatively, dispersal leading to mass effect dynamics within metacommunities can be a powerful equalising mechanism, evening out local variations (e.g. Pulliam 1988, Hubbell 1997).

Nevertheless, although mechanisms such as source-sink population dynamics, niche-related species sorting, may account for maintenance of overall levels of species richness and abundance within metacommunities (Cottenie 2005, Holyoak et al. 2005), they would not seem likely to be responsible for the remarkable uniformity of local-scale biodiversity metrics displayed across relatively large areas within each of these soft-sediment systems. Not only did all core-blocks in each system effectively support the same percentage of the total biodiversity present in that system (i.e. without significant local variation about the locality's overall mean constancy at the spatial scale concerned), but the species in all systems showed very similar ranked constancy curves, even though the proportions of the total numbers of the various species varied widely. Therefore, whatever the forces structuring this common aspect of these systems are, they must be capable of producing similar systems of relative frequency of species occurrence regardless of the local magnitude of overall assemblage abundance and biodiversity. Although the number of relatively abundant species varied from assemblage to assemblage, all except the North Stradbroke sandflat contained several species with very high constancies, as did the Knysna seagrass investigated earlier (Barnes 2013). In the 3 equivalent *Zosterella* seagrass systems, these represented a wide range of major taxa even at a single station, as well as several different feeding guilds (including predators, deposit feeders, suspension feeders and micrograzers). The precise taxa represented at each locality were not the same, but even within a single seagrass bed the most constant animals in different areas can belong to different major taxa. It is tempting to consider these different combinations as ecological alternatives, perhaps capable of exploiting subtly different local resource spectra, and/or as balanced suites of complementary species (Loreau 2000), between them capable of exploiting the main categories of resources available in an intertidal *Zosterella* bed (Duffy et al. 2003, Moore et al. 2004, Heck & Valentine 2006). Accordingly, the individual components of a suite might well occur in due proportion to the frequency of those resource categories, and the uniformity of macrofaunal assemblage metrics could then simply reflect the basic similarity of the types of resources likely to be available in any seagrass meadow. There is, however, no evidence that the dominant species at each locality are ecologically equivalent, although in part this could be because effectively nothing is known of the niches occupied by many.

Unfortunately, although much effort has been directed to understanding what the shapes of different rank species-abundance curves can tell us about the processes structuring a given ecological system (Tokeshi 1993, Belyea & Lancaster 1999, McGill et al. 2007, Weiher et al. 2011), ranked species-constancy curves have not been quantitatively examined for general patterns (Jenkins 2011). Those presented here in Fig. 5A comprise (in some) a small shoulder, reflecting the group of high-C species ('core' species in Hanski's 1982 core-satellite terminology), and a generally exponentially declining group of low-C (or 'satellite') species. They are, therefore, equivalent to the unimodal to very weakly bimodal frequency models with dominant satellite-species modes of Tokeshi (1992, his Fig. 4d,f,g) and McGeoch & Gaston (2002). After an analysis of 24 terrestrial and freshwater datasets, Jenkins (2011) suggested 2 possible ecological explanations for this type of curve. Firstly, recruitment limitation, also as a result of large-scale disturbance; and secondly, strong biological structuring due to competition or generalist predation, the latter coupled with faunal components that are either resistant to such predation (the high-C core species) or vulnerable to it (the low-C satellite

species). Neither explanation is without its problems in the present context. Recruitment via dispersal has been argued to be a strong force within seagrass meadows (see Barnes 2013), and there were no barriers to dispersal across the sites investigated; further, the precise habitats studied here — all within legally protected areas with relatively little wave action — did not show signs of large-scale disturbance, and might be expected to have shown such signs were they disturbed either naturally or anthropogenically. Although control of seagrass assemblage abundance and species richness by generalist predation is usually considered to be the norm (see above), it seems unlikely that the small, fragile species forming the high-C core component at the present sites (i.e. thin-shelled microgastropods, oligochaetes, a <10 mm diameter crab, etc.) are resistant to predation, and that this explains their high-C status. Indeed, work elsewhere (e.g. Reise 1985) has shown species of this size and nature to be highly susceptible to generalist predators. Further, these types of explanations may address differences between various potential types of rank species-constancy curves (see Jenkins 2011, their Fig. 1) but not why systems with very different ecological features should show such similar relative rank-constancies, and indeed uniformity of assemblage metrics across individual sites. Clearly, there is much more to learn of the ecological forces producing spatial uniformity.

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Appendix. The most numerous and widespread species in the various macrofaunal assemblages

North Stradbroke Island

(1) Seagrass species contributing >5% to overall abundance:
Enigmaplax littoralis (14.9%), *Calopia imitata* (14.7%), *Pseudoliotia* spp. (*P. micans*, *P. speciosa*, *P. axialis* and *P. gowlandi*) (together 9.0%) and *Limnoporeia* sp. (7.8%)

(2) Seagrass species with constancies >5% in at least 1 station (species marked * have values of *C* > 75%):
* *Enigmaplax littoralis* (>10% at all stations), * *Calopia imitata*, * *Pseudoliotia* spp., * *Limnoporeia* sp., * *Alpheus* spp., *Malacoceros cf indicus*, *Armandia intermedia*, *Onuphis holobranchiata*, *Paracalliope* sp., *Longiflagrum caeruleus* and *Leptochelia opteros*

(3) Sandflat species contributing >5% to overall abundance:
Urohaustorius mertungi (64%)

(4) Sandflat species with constancies >5% in at least 1 station (species marked * has a value of *C* > 75%):
* *Urohaustorius mertungi* and *Mysella vitrea*

Scolt Head Island

(1) Seagrass species contributing >5% to overall abundance:
Peringia ulvae (78.4%), *Tubificoides benedii* (8.2%) and *Pygospio elegans* (4.6%).

(2) Seagrass species with values of *C* >75%:
Peringia ulvae, *Tubificoides benedii*, *Pygospio elegans*, *Abra tenuis*, *Macoma balthica*, *Eteone longa*, *Fabricia stellaris*, *Littorina saxatilis* and *Carcinus maenas*

(3) Sandflat species contributing >5% to overall abundance:
Peringia ulvae (72.1%), *Tubificoides benedii* (14.8%) and *Pygospio elegans* (5.2%)

(4) Sandflat species with values of *C* >75%:
Peringia ulvae, *Tubificoides benedii*, *Pygospio elegans* and *Abra tenuis*