



Do species display characteristic intraspecific levels of patchiness in a given habitat type? The case of intertidal seagrass macrobenthos

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Abstract

Intertidal macrobenthic assemblages associated with monospecific stands of *Zostera muelleri*, *Cymodocea serratula*, *Halodule uninervis* and *Halophila ovalis* seagrasses are known to display uniform spatial patchiness on the Moreton Bay coast of North Stradbroke Island, Queensland, as do those in *Z. capensis* in the Knysna estuarine bay, South Africa. Thirty-seven historical datasets of these macrobenthic assemblages were re-analysed to assess variation of local patchiness in each of the 18 most common individual assemblage components at each of these localities in terms of three metrics: overall patchiness (Lloyd's index of patchiness), levels of unoccupancy, and variation in abundance across occupied samples (Lloyd's index of mean crowding). Within-site patchiness was not caused by a restriction of individual species to specific subareas but by variation in their local density, particularly by the extent of unoccupied 'interstitial' spaces within patches. Especially in the more uniform Queensland conditions, the more common species occurred relatively widely across the whole locality; individual samples from which a given species was absent never themselves formed patches, the number of such samples conforming to points on truncated normal curves of the frequency of occurrence. Of the 36 species investigated, the two most abundant and widespread both in Queensland and in South Africa displayed significant or near-significant uniformity of levels of local patchiness, whilst five showed significantly uniform mean crowding and ten significantly uniform unoccupancy. This is the first demonstration that some species may display a characteristic level of patchiness in a given habitat type.

Introduction

Patchiness is the norm in biological systems; patchiness of the habitat, patchiness of resources, patchiness of organismal numbers (Wiens 1989; Kotliar and Wiens 1990). It also

occurs at all spatial scales such that patches are themselves patchy (Kotliar and Wiens 1990; Morrissy et al. 1992). These spatial patterns have been much studied in seagrass systems, particularly in relation to anthropogenically-induced habitat fragmentation (Bell et al. 2001; Rielly-Carroll and Freestone 2017). Some seagrass faunal characteristics do seem resistant to the effects of mosaic habitats, in some areas at least (Lefcheck et al. 2016), but even continuous and apparently uniform beds may support patchy macrofaunal assemblages both in terms of their occupancy and abundance (Kraan et al. 2009; Barnes and Hamylton 2019).

Recently, Barnes (2019a, 2020a) assembled data from a series of > 30 expanses of three species of dwarf-eelgrass from seemingly equivalent intertidal-flat habitats in sheltered bays in the cool-temperate north-west Atlantic, warm-temperate southern Indian Ocean, and subtropical eastern Pacific. The macrobenthic assemblages characterising all these beds of *Zostera* subgenus *Zosterella* [= *Nanozostera* in the 2013 revision of Coyer et al. (2013)] were found to display effectively the same low but significant level of patchiness, a Lloyd's index of 1.125 ± 0.054 (SD). Further, intertidal-flat beds of other seagrass genera (*Cymodocea*,

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Halodule and *Halophila*) were found to support macrofaunal assemblages with levels of patchiness that also fell within one standard deviation of the mean value for those in dwarf-eelgrass (Barnes 2020a). Assemblages from adjacent subtidal meadows and from high-level salt-marsh creeks, however, showed values outside this remarkably uniform range for intertidal beds (Barnes 2019a; Barnes and Claassens 2020).

Such metrics of macrofaunal assemblages are amalgamations of those of all the component species concerned, and these individual elements are known to display a range of dispersions from random to highly patchy at these sites (Barnes and Hamylton 2019). The present study, based on the subtropical eastern Pacific locality and, to a lesser extent, that in the warm-temperate southern Indian Ocean, sought to investigate the null hypothesis that patchiness of each of the more common component species of the benthic macrofauna at these locations, which together create systems with a uniform degree of patchiness, also display a characteristic level of patchiness that remains constant over time and local space. Since notions of patchiness have components of both distribution (presence/absence) and abundance (differential numbers when present) these two components were also investigated in parallel with overall levels of patchiness as determined by Lloyd's index.

Materials and methods

Twenty-seven historical datasets from the period 2009–2019 (see Online Appendix) are available for the seagrass macrobenthos associated with monospecific areas of four seagrass

species (*Zostera muelleri capricorni*, *Cymodocea serratula*, *Halodule uninervis*, and *Halophila ovalis*) along a 6 km stretch of the northwest Moreton Bay coast of North Stradbroke Island (Minjerribah), Queensland (Fig. 1); i.e. from Deanbilla (27° 30' 32" S, 153° 24' 33" E), Goompi (27° 29' 38" S, 153° 23' 54" E), Yerrol (27° 29' 02" S, 153° 24' 19" E), and Capembah (27° 28' 04" S, 153° 25' 19" E). These datasets generally comprised series of randomly located samples but those from Deanbilla also included spatially-explicit regular lattices with samples 0.3 m and 5.75 m apart. A further ten historical datasets from the period 2011–2016 (see Online Appendix) are also available for similar sized and to a degree equivalent intertidal extents of a fifth species, *Zostera capensis*, with macrofaunal samples taken at three points within a distance of 2.5 km across the marine-bay section of the Knysna estuarine system in South Africa's Western Cape (Fig. 1): Brenton (34° 03' 35" S, 23° 02' 07" E), Kingfisher (34° 03' 39" S, 23° 03' 09" E), and Steenbok (34° 03' 47" S, 23° 03' 25" E). Individual samples from Kingfisher were also spatially explicit, including some with a fixed interval of *c.* 6 m. Datasets from large (> 1 ha) areas were split into a number of smaller, non-overlapping sets where appropriate to yield a standard series of small local < 2000 m² sites. Full details of the sampling methodology at each site are given in the papers listed in Online Appendix.

All these macrobenthic seagrass assemblages were located between mean low water and low water spring tide levels, and all were sampled using the same methodology, involving series of 30–80 individual core samples (average 56) per site, each of 0.0054 m² area and 100 mm depth, together with one further series of 256. Those from Moreton

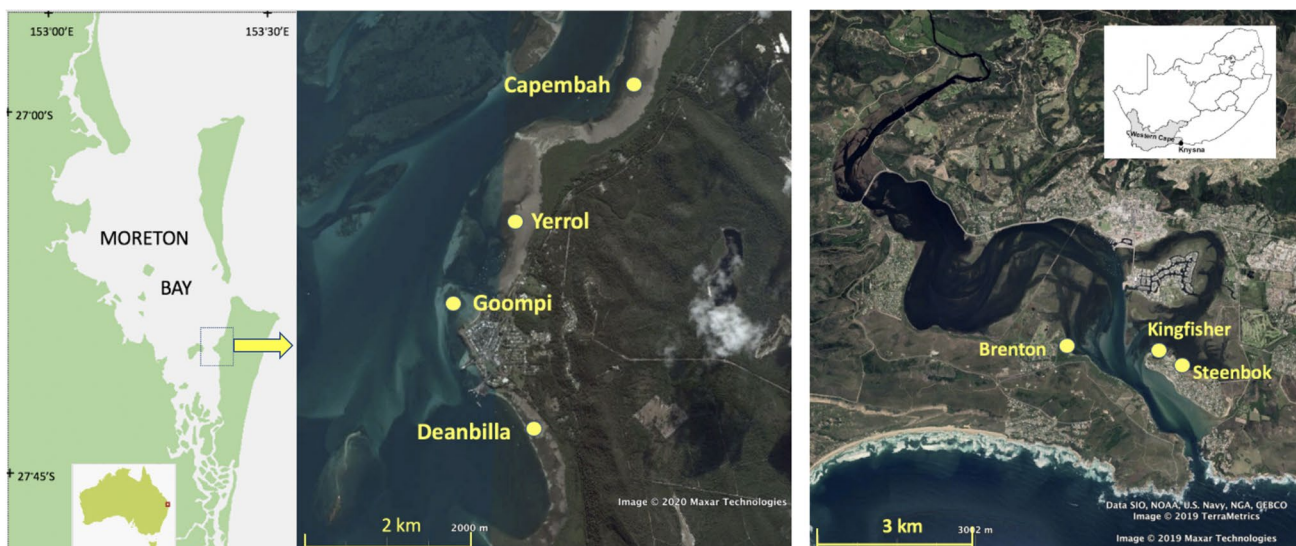


Fig. 1 Location of the study areas on North Stradbroke Island/Minjerribah, Moreton Bay, Queensland and in the Knysna estuarine bay, Western Cape, South Africa (Google Earth Pro satellite images)

Bay were sampled during the austral spring and those from Knysna in the austral summer. A total of 2279 such samples was analysed. All were from continuous swards of seagrass, were at least 10 m away from any interfaces with adjacent bare sediment, and were collected at low tide before complete tidal ebb whilst the substratum was still covered by at least 15 cm of water. Cores were gently sieved ('puddled') through 710 μm mesh on site. This sampling procedure collects the smaller (mostly < 5 mm) and more numerous members of the macrofauna that constitute the large majority of invertebrate biodiversity (Bouchet et al. 2002; Albano et al. 2011), though not the meiofauna nor much scarcer mega-fauna nor sessile animals attached to the seagrass leaves. Warwick et al. (2006) have shown that different patterning rules may apply to meiofauna and macrofauna, and likewise Davidson et al. (2004) and Leopardas et al. (2014) to sessile species. Sessile or semi-sessile species that had accidentally become detached from the seagrass leaves during sampling were therefore ignored.

Retained material from each core was: (1) placed in a large polythene bag of local seawater within which all seagrass was shaken vigorously to dislodge all but sessile animals; (2) then re-sieved and transported immediately to a local laboratory, and (3) there placed in a 30×25 cm tray over a light source in which the living fauna was located by visual examination using $3.5 \times$ magnifying spectacles until no further animal could be observed. Animals were identified to species level wherever possible, with all organismal nomenclature here being as listed in the World Register of Marine Species (www.marinespecies.org) (accessed June 2020). It should be noted, however, that the specific identity of several animals, especially amongst the Polychaeta and Peracarida, is questionable because of lack of relevant systematic studies in Queensland and South Africa. Such animals were treated as morphospecies, an operationally appropriate procedure to detect spatial patterns in numbers of species and their differential abundance (Dethier and Schoch 2006; Gerwing et al. 2020). The 18 most widespread and abundant of the species in both Moreton Bay and Knysna were each subjected to patchiness analyses.

All abundance data for individual species included unoccupied samples (i.e. zero values); occupancies are proportions of the total samples at a given site in which a species was present and, correspondingly, unoccupancies are those from which it was absent. Magnitude of patchiness was ascertained by spatial point pattern analysis of count data using Lloyd's index of patchiness (Lloyd 1967), the ratio of mean crowding (see below) to mean density, given by $I_p = [1 + (v - m)/m^2]$, where 'm' is the mean abundance across samples and 'v' is the associated spatial variance (Waters et al. 2012; Henriques et al. 2017). A Lloyd's index of 1 indicates a random distribution, whilst one < 1 suggests uniformity and > 1 patchiness. This index

has been demonstrated to yield equivalent results to those of the spatially explicit Moran's spatial auto-correlation index for intertidal dwarf-eelgrass macrobenthos (Barnes and Hamylton 2019). It is also independent of sample size over a wide range of areas, provided that the animals position themselves at random with respect to each other within a patch and that the patches are large relative to sample size (Lloyd 1967; Myers 1978). Granted that the core area was 0.0054 m^2 , it seems unlikely that macrofaunal patches were smaller than that; indeed it has previously been found that cores of 0.0015 , 0.0026 and 0.0054 m^2 spatial grain all produced the same value of the closely similar but differently-derived Morisita's I_δ index (Barnes 2016).

It should be noted that Lloyd's I_p although termed an index of patchiness is actually an index of dispersion; values of such an index that indicate significant departures from random are dependent on the total number of individuals in the dataset, which will vary from species to species and across sites. Hence significant departures from random in the direction of patchiness per se cannot be inferred from any specific value of the index, although all such values will be > 1 . Besides the calculation of the I_p index itself, two metrics influencing it were also assessed in parallel: (a) proportion of unoccupied samples (unoccupancy); and (b) variation in abundance where present (i.e. across only occupied samples) using Lloyd's domain-free index of mean crowding (I_c), the mean number of neighbours per individual per unit area, where $I_c = m + (v/m - 1)$ (Lloyd 1967; Wade et al. 2018). Within-site spatial location of unoccupied samples was also assessed in two large Deanbilla datasets, both derived from lattices of 16×16 samples, located within (a) 0.85 ha and (b) a nested 23 m^2 subarea. Spatial dispersion of unoccupied samples was assessed by nearest-neighbour analysis of spatially explicit data, with the Donnelly (1978) correction for rectangular edge effects (the minimum number of such samples was $47 = 18\%$ of the total). Potentially confusingly, in contrast to Lloyd's I_p , nearest-neighbour $R > 1$ suggests a uniform dispersion, 0 random, and < 1 one that is clustered or patchy.

All calculations were carried out in Microsoft Excel for Mac 16.37 with the StatPlus:mac Pro 7.1.1 add-on, or via PAST 3.24 (Hammer et al. 2019). Correlations were assessed as nonparametric Spearman's rank (S_r) or parametric Pearson's product-moment coefficient (P_c) as appropriate; and statistical significance of any uniformity of values of patchiness, mean crowding or (after logit transformation) unoccupancy was determined by Monte Carlo simulation with 9999 iterations, yielding a relatively conservative estimate of significant departure from random.

Results

The 18 species from each locality included in this study comprised $\approx 75\%$ of the total seagrass macrobenthic animals sampled. All correlations between the abundances of individual species at each locality were weak ($S_r \leq 0.3$), and there was no correlation between I_p value and number of core samples at a site (Moreton Bay: $S_r = -0.09$; $P > 0.15$. Knysna: $S_r = 0.05$; $P > 0.5$) or variation in I_p with year of sampling (Moreton Bay: ANOVA $F_{7,231} = 0.88$; $P > 0.5$. Knysna: $F_{5,129} = 1.65$; $P > 0.15$). The I_p values of the known and presumed epifaunal species (largely the gastropod molluscs) were significantly larger than those of the known and presumed infaunal species (principally polychaetes and decapods) (Moreton Bay: ANOVA $F_{1,241} = 21.05$, $P < 0.00001$. Knysna: ANOVA $F_{1,132} = 9.90$, $P = 0.002$). Two genera, the gastropods *Alaba* and *Nassarius*, were common to both localities, and average values for the mean and variance of I_p for the *Nassarius* species were effectively identical: 5.26 and 19.50 for *N. burchardii* in Moreton Bay and 5.28 and 20.30 for *N. kraussianus* at Knysna (ANOVA $F_{1,19} = 0.00004$, $P > 0.995$). Those for *A. difformis* in Moreton Bay and *A. pinnae* at Knysna were also very similar (3.77 and 5.82 versus 4.09 and 6.85; ANOVA $F_{1,12} = 0.05$, $P > 0.8$) notwithstanding a considerable difference in their abundances (means of > 65 versus < 15 ind m^{-2}).

Of the 18 dominant Moreton Bay species, six were always significantly patchy whilst the other 12 each varied from being randomly distributed to significantly patchy across the different sites. All species occurred across the whole locality through a wide range of spatial scales but with considerable variation in local abundance; the spatial dispersion of a representative species is illustrated in Fig. 2. Their spatial patterns, however, were not in the form of restrictions to species-specific local areas (i.e. geographical ‘patches’). Absences were only from scattered samples (as illustrated in Figs. 2 and 3) and for the more abundant species the number of unoccupancies all conformed to expectation based on truncated normal distributions of frequencies of occurrence (Fig. 4). Using the full (16 \times 16 sample) spatially-explicit datasets from Deanbilla, in no species did unoccupied core samples form spatial clusters within sites (i.e. display values of nearest-neighbour $R < 1$). In all species, individual unoccupied samples were dispersed across the sampled areas of 0.85 ha and 23 m^2 either randomly (R not differing significantly from 1; $z < 0.6$; $P > 0.3$) or uniformly ($R > 1.4$; $z > 8$; $P < 0.0001$). Uniform dispersions, reflecting the regular pattern of the sampling stations, characterised those, such as *Longiflagrum* and *Eriopisella*, with numerous unoccupancies ($> 50\%$ of the total samples). The dispersion of

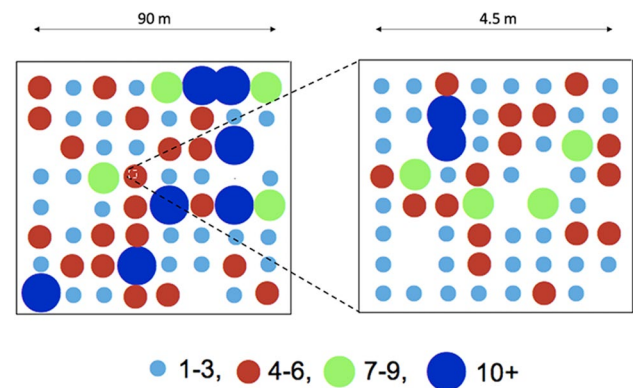


Fig. 2 Spatially-explicit diagram of the abundance of a representative member of the Moreton Bay seagrass macrofauna, the benthic amphipod *Limnoporeia*, across a large (0.85 ha) block of seagrass at Deanbilla (from the data of Barnes and Laurie 2018), and within a small (23 m^2) subarea nested within that larger block (data of Barnes and Hamylton 2019). Abundances are displayed as total numbers in blocks of four 0.0054 m^2 cores, a notional distance of 11.5 m apart (for 0.85 ha) and 0.6 m (for 23 m^2). Overall abundance was 144–200 m^{-2} (close to average density for the commoner species); I_p at 0.85 ha = 1.37 and at 23 m^2 = 1.28, in each case significantly patchy at $P < 0.001$

unoccupancy in one species, however, depended on the spatial resolution of the analysis. In *Eriopisella*, decreasing the resolution by four [i.e. from the original 256 samples to 64 (each comprising a block of 4 individual cores, as in Fig. 3)] decreased the value of R at the larger 0.84 ha site from 1.5 ($z = 9.1$; significantly uniform at $P < 0.0001$) to 0.87 ($z = -1.4$; almost significantly patchy at $P = 0.08$).

Table 1 sets out the mean value (together with associated variance) for each of the three patchiness metrics for each of the 18 dominant species across the various Moreton Bay sites. The two most abundant and widespread species across the whole locality, both with a $> 70\%$ occupancy and between them with 35% of the 22,200 macrofaunal animals, were the tiny macrophthalmid crab *Enigmaplax littoralis* and the truncatelloid microgastropod *Calopia imitata*. Both these, together with the snapping-shrimp *Alpheus*, showed a uniform level of patchiness across all sites ($P < 0.01$), *Enigmaplax* with a mean I_p of 1.19 and *Calopia* one of 2.07. Eight species, including the *Enigmaplax*, *Calopia* and *Alpheus* above, showed significantly uniform levels of unoccupancy across sites ($P < 0.05$), and four displayed a similarly uniform degree of mean crowding. Three (*Calopia*, *Limnoporeia* and *Alpheus*) showed uniformity in two of the three measures of patchiness, and one (*Enigmaplax*) in all three, whilst eight did not display uniformity in any measure. Values of I_p were significantly correlated with those of unoccupancy in half of the 18 species ($S_r > 0.40$, $P < 0.05$), and those of I_p with I_c in seven ($S_r > 0.45$, $P < 0.05$), I_p being significantly correlated with both unoccupancy and I_c in four (all gastropods). I_p values of

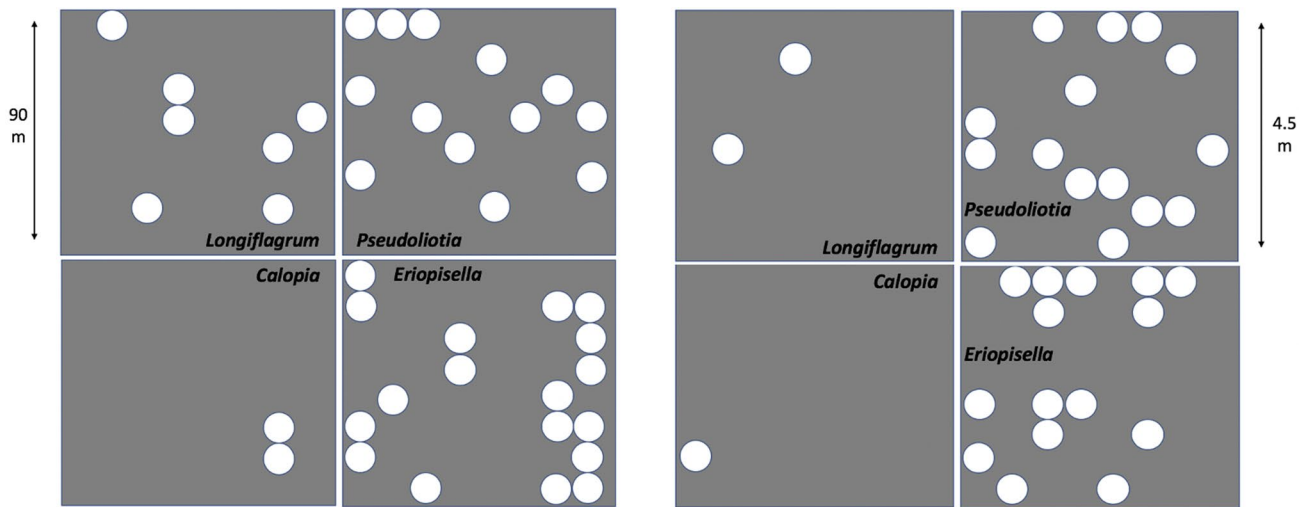


Fig. 3 Spatially-explicit distribution of unoccupancies (indicated by the white circles) of four representative species at two spatial scales at the Deanbilla site in Moreton Bay [from the data of Barnes and

Laurie (2018) and Barnes and Hamylton (2019)]. As in Fig. 2, each datapoint is the total of four 0.0054 m² core samples

two of the more numerous species, the infaunal crustaceans *Enigmaplax* and *Longiflagrum*, were correlated with those of I_c ($S_r > 0.45$, $P < 0.05$) but not unoccupancy; indeed, the only infaunal species to show a correlation between I_p and unoccupancy was the polychaete *Armandia* ($S_r = 0.74$, $P < 0.01$). Values of I_p across the sites were negatively correlated with a species' abundance at them ($P < 0.05$) for *Armandia* ($S_r = -0.75$), *Smaragdina* ($S_r = -0.57$), *Calopia* ($S_r = -0.44$) and *Alaba* ($S_r = -0.83$) (and *Tricolia* approached this state with $S_r = -0.61$, $P = 0.06$), and positively so for *Circulus* ($S_r = 0.73$) ($P < 0.05$). In addition, values of I_p in *Dasybranchus* were negatively correlated with the total numbers of macrobenthos at the various sites ($S_r = -0.67$; $P < 0.05$). Pearson product-moment correlation revealed particularly strong linear relationships between the I_p values of the dominant microgastropods and of *Enigmaplax* ($P < 0.005$): positive between *Calopia* and *Enigmaplax* ($P_c = 0.55$) and between *Circulus* and *Pseudoliotia* ($P_c = 0.83$); negative between *Enigmaplax* and both *Pseudoliotia* ($P_c = -0.53$) and *Circulus* ($P_c = -0.87$), and between *Calopia* and *Circulus* ($P_c = -0.89$). An equally strong relationship occurred between the I_p values of *Limnoporeia* and *Dasybranchus* ($P_c = 0.84$).

In respect of the 18 dominant species across the ten Knysna datasets (Table 2), five were always significantly patchy whilst the other 13 each varied from being randomly distributed to significantly patchy dependent on site. There, no species showed a significantly uniform level of patchiness across all sites, although the polychaetes *Simplisetia erythraeensis* and *Prionospio sexoculata* (the two most abundant and widespread species at Knysna, together comprising 18% of the total individuals and both with occupancies > 60%)

approached this state at $P = 0.06$ – 0.07 . Those two, together with the annelids *Scoletoma tetraura* and tubificid sp., and the crustaceans *Cyathura estuaria*, *Danielella edwardsii* and ?*Cylindroleberis*, however, were significantly uniform across sites according to the Smith-Gill (1975) standardised Morisita index ($P < 0.05$). Only two species, *Danielella* and gastropod *Nassarius*, showed significantly uniform levels of unoccupancy across sites ($P < 0.05$), and only one (the polychaete *Orbinia angrapequensis*) displayed a similarly uniform degree of mean crowding. Values of I_p and unoccupancy were significantly correlated within four of the 18 species, three epifaunal and one infaunal ($S_r > 0.65$, $P < 0.05$), and those of I_c , and I_p were significantly correlated within two of them, both epifaunal ($S_r > 0.76$, $P < 0.05$). Values of I_p across the sites were negatively correlated with a species' abundance at them in *Exosphaeroma* ($S_r = -0.67$) and *Melita* ($S_r = -0.93$) (and approached this state in *Nassarius* with $S_r = -0.61$, $P = 0.06$), and were positively so for *Danielella* ($S_r = 0.79$) ($P < 0.05$). The only particularly strong Pearson correlation ($P < 0.005$) of between-species I_p values was that between *Nassarius* and *Orbinia* ($P_c = 0.97$).

Discussion

Most investigation of 'patchiness' in intertidal marine soft sediments, from Bassindale and Clark (1960) through to Kotta and Möller (2009) and Schenone and Thrush (2020), has reported individual benthic species or associations of species to occur in discrete geographical patches that may overlap with those of other species to varying extents, forming a mosaic or harlequin system in contrast to the classic

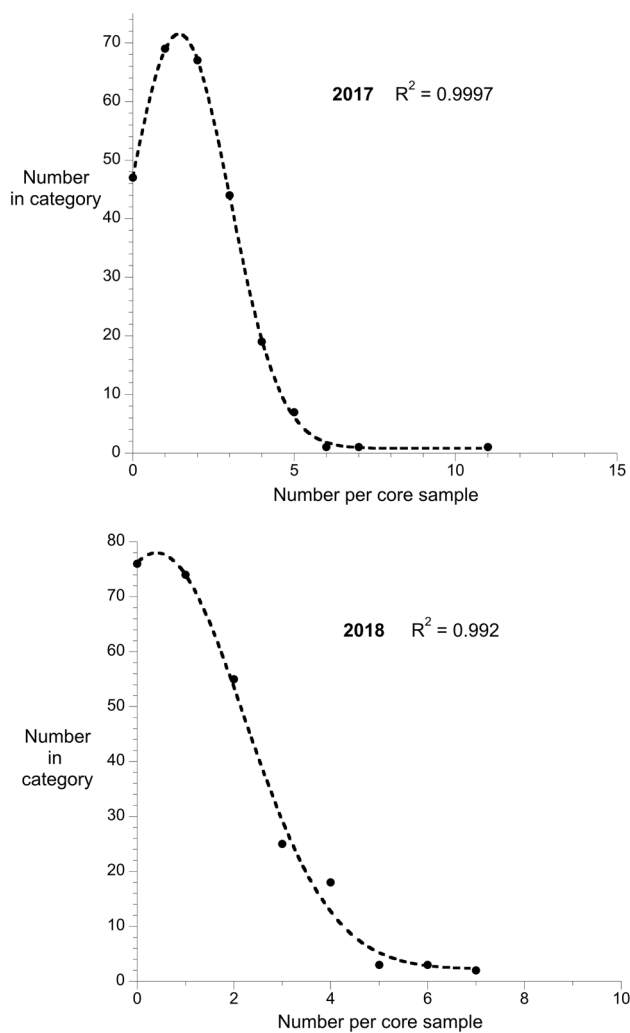


Fig. 4 Plots of the frequency of different numbers of individual *Enigmaplax* per core sample, one of the most numerous species at the Deanbilla site, across an area of 0.85 ha in 2017 and across a nested subarea of 23 m² in 2018, showing the fitted truncated-normal curves. In each case the number of zero values is no more than would be appropriate in such a distribution granted the mean value [from the data of Barnes and Laurie (2018) and Barnes and Hamylton (2019)]

zonal pattern on rocky shores. The occurrence of benthic species is patchy and their abundance then varies within each such patch. Indeed, several studies have sought to correlate the presence of such specific patches with biological or physical features of the habitat (e.g. Kotta and Möller 2009; Yamada et al. 2014; Jelinski 2015). In the systems under consideration here, at least at the spatial scales investigated, the occurrence of few if any component species seems patchy in that sense. Most species in the Moreton Bay beds are distributed throughout the localities from scales of kilometres down to ones of < 1 m² (Barnes and Hamylton 2019), and up to 10 of the 12 most numerous faunal elements could occur in a unit 0.0054 m² sample. Spatially-explicit sampling across a 1 ha area at Deanbilla in Moreton Bay,

for example, showed no spatial separation of inhabited and non-inhabited blocks of habitat. Experience elsewhere also suggests that at least amongst *Zostera* epifauna, patterns experienced at scales of a few metres do not differ from those in areas several kilometres apart (Whippo et al. 2018). This may indicate an important role of seagrass as an agent of biological habitat amelioration in a manner similar to that discussed by Moore et al. (2007) for intertidal algal beds (see, e.g., van Katwijk et al. 2016).

The results also strongly indicate that the degree of patchiness of some individual species, like that of the whole macrobenthic assemblage to which they belong (Barnes and Laurie 2018; Barnes and Hamylton 2019), is effectively constant across local space and overtime periods of a decade. Values of patchiness indices are dependent on quadrat size (Steenweg et al. 2018); those reported here, however, are all of the same grain (0.0054 m²), one appropriate for the size of animals concerned, and cannot have had bearing on the results other than yielding small mean values of density per unit sample with the consequent high probability of chance unoccupancies. The species under study were the relatively numerous ones that characteristically also show correspondingly high levels of occupancy (He and Gaston 2003). Relatively rare species are not a major element of the Knysna fauna, but they are in Moreton Bay seagrass (Barnes 2014). Not all species with low occupancies display small population densities though, and there is a wide range in abundance of such species. In Moreton Bay, species with very low occupancy (e.g. < 10%) such as the vitrinellid microgastropod *Circulus cinguliferus* may achieve the highest local density of any member of the macrobenthos, at 37 in a single 0.0054 m² sample. By virtue of their rare but superabundant hotspots, overall they form one of the most abundant assemblage components. Other species with similarly low occupancies, however, remain at very low density and some have never been recorded in excess of 1 per 0.0054 m² (Barnes 2019b). It may be significant that the two most abundant and most frequently occurring animals, *Enigmaplax* and *Calopia* in Moreton Bay and *Simplisetia* and *Prionospio* in Knysna, were the ones to show the largest degree of spatial uniformity of dispersion pattern.

Although neither Moreton Bay nor Knysna seagrass appeared a mosaic system, the occurrence of scattered unoccupancies within inhabited blocks was a major influence on the level of macrofaunal patchiness, the greater degree of correlation between I_p and unoccupancy than between I_p and I_c indicating a more important role than that of variation in non-zero density. In a companion study of the interspecific relationship between abundance, occupancy and patchiness within seagrass assemblages (Barnes 2020b), it was also found that whilst Lloyd's I_p and unoccupancy were strongly correlated, Lloyd's I_p and I_c were more poorly so and in several cases the correlation was not statistically significant.

Table 1 Patchiness metrics (Lloyd's index of patchiness I_p and Lloyd's index of mean crowding I_c , mean m and variance v ; and % unoccupancy, mean m and coefficient of variation cv) for 18 intertidal benthic seagrass macrofauna across 27 sites in Moreton Bay, Queensland

	I_p		I_c		% Unoccupancy	
	m	v	m	v	m	cv
ANNELIDA						
<i>Armandia cf lanceolata</i> ($n=11$)	3.75	7.13	0.99	0.50	77.4	0.18
<i>Dasybranchus caducus</i> ($n=11$)	1.47	1.00	0.43	0.06	71.8	0.23
<i>Malacoceros cf reductus</i> ($n=8$)	1.77	3.02	0.87	0.24	54.3	0.38
<i>Spio blakei</i> ($n=4$)	1.71	0.85	0.86	0.07	60.6	0.24
OSTRACODA						
? <i>Archasterope</i> sp. ($n=7$)	6.29	43	1.25	0.60	83.8	0.12
PERACARIDA						
<i>Longiflagrum caeruleus</i> ($n=19$)	3.57	6.93	3.14	5.86	58.5	0.28
<i>Limnoporeia cf yarrague</i> ($n=19$)	2.22	1.67	1.62	0.57	55.7	0.29
<i>Eriopisella moretoni</i> ($n=12$)	3.06	3.12	1.58	0.87	71.1	0.19
DECAPODA						
<i>Alpheus papillosus</i> ($n=13$)	1.28	0.30	0.43	0.03	72.5	0.11
<i>Enigmaplax littoralis</i> ($n=27$)	1.19	0.05	1.78	0.58	29.4	0.45
GASTROPODA						
<i>Calthotia fragum</i> ($n=6$)	2.72	3.60	0.41	0.05	85.1	0.06
<i>Tricolia fordiana</i> ($n=10$)	3.01	5.66	0.63	0.14	81.8	0.11
<i>Smaragdia souverbiana</i> ($n=14$)	2.41	2.50	0.36	0.02	84.5	0.09
<i>Alaba difformis</i> ($n=6$)	3.77	5.82	0.56	0.03	84.3	0.12
<i>Calopia imitata</i> ($n=24$)	2.07	0.26	6.66	11.2	25.4	0.58
<i>Pseudoliotia</i> spp. ($n=27$)	7.04	22	7.34	31	71.3	0.13
<i>Circulus cinguliferus</i> ($n=10$)	29.37	449	8.00	97	93.0	0.04
<i>Nassarius burchardi</i> ($n=11$)	5.26	19.5	1.23	1.44	79.2	0.21

Significant spatial uniformity of values (Monte Carlo simulation at $P < 0.05$) are indicated by bold type. *NB* The different datasets were collected for different purposes and not all enumerated all 18 species; further, where numbers of a given species at a site were all either only 0 or 1 per sample that species was discounted; n therefore indicates the number of available datasets of each species

Both these inter- and intraspecific results, therefore, highlight the need to differentiate conceptually between those unoccupied samples that represent non-frequented areas between inhabited spatial patches and those that are scattered within inhabited areas, not least those necessarily so because of prevailing population density. An animal like a small amphipod measuring some 8×3 mm will occupy an area of some 25 mm^2 , and a density of such a species of some 200 m^{-2} will take up only 0.5% of the available space (the mean density of the ten most abundant species across the Moreton Bay locality, excluding the two relatively super-abundant *Calopia* and *Enigmaplax*, was 250 m^{-2}). On average, a 0.0054 m^2 core will capture one individual of such an animal, and hence a considerable number of unoccupancies are to be expected. Clearly, in such circumstances, gross patterns of dispersion are dependent on whether the unoccupied samples are themselves clumped. The same is, of course, true in virtually all animal populations, including at much greater scales amongst the largest and most aggregated of animals: there are spaces between individual elephants in a herd as well as between elephant herds.

Although the Moreton Bay and Knysna sites showed broadly the same pattern, there were differences between them. In particular, the levels of both Lloyd's I_p and unoccupancy were considerably less uniform across the South African estuarine bay. In part, this may be a reflection of marked differences in the macrobenthic assemblages characterising the two intertidal seagrass systems. That in Moreton Bay is a low-density and high species-richness assemblage, whilst that at Knysna supports almost twice the density but less than half the species, and, notwithstanding the general paradigm that seagrass beds are dominated by epifauna (Bouma et al. 2009) as they are indeed in Moreton Bay, the intertidal beds investigated in Knysna were infauna dominated. Nevertheless, such differences do not appear to affect overall levels of macrobenthic assemblage patchiness, which have proved remarkably uniform across all types of intertidal seagrass sward (Barnes 2019a, 2020a). There are however other, and probably more important, differences. The Knysna sample was considerably smaller (10 sites and 602 cores versus 27 sites and 1677 cores), and many of the values from Knysna that closely approached, but did not attain, $P < 0.05$

Table 2 Patchiness metrics (Lloyd's index of patchiness I_p and Lloyd's index of mean crowding I_c , mean m and variance v ; and % unoccupancy, mean m and coefficient of variation cv) for 18 intertidal benthic seagrass macrofauna from ten sites within the marine embayment section of the Knysna estuarine bay, South Africa

	I_p		I_c		% unoccupancy	
	m	v	m	v	m	cv
ANNELIDA						
Tubificid oligochaete ($n=7$)	1.66	0.32	0.55	0.22	71.4	0.18
<i>Simplisetia erythraeensis</i> ($n=10$)	1.75	0.39	4.41	10.14	31.2	0.64
<i>Scoletoma tetraura</i> ($n=5$)	0.97	0.04	0.75	0.22	60.3	0.27
<i>Caulleriella capensis</i> ($n=10$)	2.74	1.66	3.80	4.61	54.9	0.31
<i>Orbinia angrapequensis</i> ($n=6$)	0.95	0.34	0.56	0.11	57.9	0.31
<i>Paradoneis lyra</i> ($n=5$)	2.65	1.41	1.44	2.71	82.1	0.13
<i>Prionospio sexoculata</i> ($n=8$)	1.72	0.14	2.78	3.06	40.1	0.60
? <i>Pseudofabricia capensis</i> ($n=5$)	5.87	61	1.71	1.49	68.8	0.32
OSTRACODA						
? <i>Cyindroleberis</i> sp. ($n=8$)	2.27	0.49	1.42	1.17	67.4	0.17
PERACARIDA						
<i>Cyathura estuaria</i> ($n=8$)	1.44	0.32	0.96	0.18	60.0	0.28
<i>Exosphaeroma hylecoetes</i> ($n=9$)	4.10	34	2.47	4.56	55.5	0.42
<i>Cymadusa filosa</i> ($n=8$)	1.28	0.39	0.65	0.39	68.9	0.21
<i>Melita zeylanica</i> ($n=7$)	5.62	28	3.63	15	65.7	0.37
<i>Paramoera capensis</i> ($n=5$)	1.98	0.79	1.49	1.97	67.5	0.14
<i>Grandidierella ?lutosa</i> ($n=8$)	4.04	4.20	1.32	0.42	79.1	0.17
DECAPODA						
<i>Danielella edwardsii</i> ($n=8$)	1.47	0.31	1.03	0.37	62.0	0.23
GASTROPODA						
<i>Alaba pinnae</i> ($n=8$)	4.09	6.85	1.84	4.28	74.8	0.34
<i>Nassarius kraussianus</i> ($n=10$)	5.28	20.3	3.83	5.67	70.0	0.22

Significant spatial uniformity of values (Monte Carlo simulation $P < 0.05$) are indicated by bold type. NB The different datasets were collected for different purposes and not all enumerated all 18 species; further, where numbers of a given species at a site were all either only 0 or 1 per sample that species was discounted; n therefore indicates the number of available datasets of each species

are likely to have been significant with larger numbers of individuals and/or sites. The locality itself was also much smaller, more enclosed by land, and more spatially diverse in its local ambient environments. All three sets of Knysna sites were, like those in Moreton Bay, large expanses of marine tidal flat, but, although close together, that at Brenton was relatively open and exposed along the main longitudinal channel, that at Kingfisher was partly sheltered in the mouth of a subsidiary channel, and Steenbok was even more sheltered within a saltmarsh-enclosed channel between an island and the mainland (see Fig. 1). Although this does not impact on overall levels of assemblage patchiness (Barnes 2019a), it might be expected that such local variation in habitat features might differentially affect individual species; it certainly does so with respect to species composition of the assemblages (Barnes and Claassens 2020), and two of the Knysna species are known significantly to change their degree of patchiness along a local environmental gradient (Barnes 2019c).

Causality of the common features that the Moreton Bay and Knysna localities do show can only be speculative.

Patterns of low but statistically uniform levels of patchiness across considerable areas and periods of time, however, suggest structuring processes capable of operating over those same scales. Processes operating over such scales must also control the overall very low macrofaunal density in the seagrass ($\approx 2,500$ ind m^{-2} in Moreton Bay and $4000+$ ind m^2 at Knysna), *c.f.* mean levels of $> 40,000$ m^{-2} ecologically-equivalent and similarly-sized animals in areas of the temperate *Zostera* (*Zosterella*) *moltei* seagrass beds of Arcachon Bay in Atlantic France (Blanchet et al. 2004) and $> 60,000$ m^{-2} in those of southern North Sea shores (Barnes and Ellwood 2011). Bottom-up process certainly operates in seagrass ecosystems, perhaps particularly those in relatively oligotrophic areas in which seagrass productivity increases in response to nutrient enrichment (York et al. 2018). There is also clear evidence that nektonic predators may be limited by the availability of their macrobenthic prey (Saulnier et al. 2020). Unfortunately there has been little study of the microphytobenthic productivity upon which most of the seagrass macrobenthos feed across a wide range of latitude (Hope et al. 2020), although it seems clear that

productivity of the seagrass itself increases towards the tropics (Duarte and Chiscano 1999; Vergés et al. 2018). On the assumption that microphytobenthic productivity follows that of the associated seagrass, the marked mismatch between macrobenthic abundance and the productivity supporting it suggests a much greater importance of top-down control. The results of this study, therefore, could be taken to provide further support to the proposed important predatory role of wide-ranging animals such as the juvenile nekton that use such areas as nurseries (Whitfield 2017, 2020; Lefcheck et al. 2019). Particularly in warmer climates (Freestone et al. 2020), these juvenile nekton opportunistically consume prey items by optimal foraging (Beseres and Feller 2007) and leave, by chance, only the occasional hot-spot of small invertebrate abundance (Beal et al. 2018; Barnes and Hamylton 2019). These types of the area may have served such a nursery role ever since the Devonian (Gess and Whitfield 2020). Few studies, however, have sought to link spatial patterns of potential benthic prey with those of their nektonic (or other) predators (Saulnier et al. 2020), and effectively nothing is known of the population dynamics of the potential prey items in Moreton Bay or Knysna.

In Moreton Bay, dominant crustaceans like *Enigmaplax* may well be the preferred prey of many of the relatively small predators that roam over the meadows at high tide (see e.g. Morrison et al. 2014), and at Knysna the camptandriids *Danielella* and *Paratyloidiplax* may fill much the same role there as related macrophthalmid *Enigmaplax* in Queensland. The dominant gastropod in Moreton Bay, *Calopia*, although a shelled mollusc and hence not a type of prey item generally regarded as preferred in such habitats (e.g. Reynolds et al. 2018), does have a particularly thin shell and might not be as unpalatable as most other gastropods seem to be (e.g. Vinson and Baker 2008; Sieben et al. 2011). The locally dominant Knysna gastropods have much stronger shells, and that may account for the very great abundance of *Alaba pinniae* (a mean 30,000 m⁻²) in subtidal areas there (Barnes and Claassens 2020) despite these being highly accessible to potential nektonic predators. As above, the low overall assemblage densities at Moreton Bay and Knysna generally suggest very heavy mortality of the small animals that dominate the macrobenthos, with mortalities at least equivalent to those documented by Reise (1985), Bachelet and Yacine-Kassab (1987), Beal et al. (2018), etc. in the cooler temperate North Atlantic. Nevertheless, nuanced relationships between the prey items appear to remain: it is not an unselective blanket reduction in density. Thus whilst circumstances leading to maximum patchiness of the two most dominant Moreton Bay species *Enigmaplax* and *Calopia* could well be similar, there is a strong negative relationship between I_p patchiness of *Enigmaplax* and that of the subdominant *Pseudoliotia*. Of the various

microgastropods, and in marked contrast to *Calopia*, for its size *Pseudoliotia* has a thick, heavy shell bearing surface sculpture of a type suggested by Vermeij (1974, 1978) to discourage consumption. The same is true of its fellow vitrinellid *Circulus*. If that is the case, however, relative immunity from predation clearly has not resulted in numerical dominance over the putatively edible *Calopia*. Polychaetes such as those that dominate the intertidal Knysna seagrasses are little exploited by fish in the similar nearby Swartvlei estuary (Whitfield 1988), although apogonids, gobiids, sillaginids, sparids and terapontids have all been recorded to feed on the types of worms known to inhabit seagrass beds (Kanou et al. 2005; D'Souza et al. 2009). However, what affects the spatial patterns of distribution and abundance of benthic polychaetes appears poorly understood.

The indications in the results of this study of differential levels of patchiness of epifaunal and infaunal species, and the broadly contrasting patterns of relationship between overall patchiness and unoccupancy between sites and lifestyles, seem particularly worthy of further investigation for the light that they may spread on the causes of patchiness in general. Given the extensive ecosystem services provided by seagrass beds (De los Santos et al. 2020) and their global decline since the 1930s (Connolly et al. 2020), understanding the nature and causes of macrobenthic patchiness within them could be of great importance to their conservation. Granted the small size of the animals concerned, it would also be most instructive to investigate their spatial dispersion at very small spatial intervals, i.e. equivalent to the studies on dispersion of mudflat polychaetes pioneered by Reise (1979).

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Compliance with ethical standards

Conflict of interest The author declares no conflicts of interest.

Ethical approval All applicable international, national and/or institutional guidelines for sampling, care and experimental use of organisms for the study were followed and all necessary permissions and approvals were obtained in respect of the original collections of the data.

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