



## Microscale dispersion of intertidal seagrass macrofauna

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### ARTICLE INFO

#### Keywords:

Abundance  
Benthic ecology  
Coastal zone  
Microdispersion  
Microgastropods  
Moreton bay  
Patchiness  
Seagrass  
Spatial autocorrelation  
Spatial scale

### ABSTRACT

Previous studies of dispersion of intertidal seagrass-associated macrobenthos in subtropical Moreton Bay, Queensland, showed that patchiness characterised its assemblage abundance with scale-invariant magnitude across areas ranging from  $>8000$  to  $0.1 \text{ m}^2$ . Those studies were here continued across the smaller scales (down to  $0.014 \text{ m}^2$ ) arguably more relevant to the dominant 2–10 mm long animals, using 16 replicate blocks of  $5 \times 5$  contiguous  $0.0024 \text{ m}^2$  cores nested within the previously studied site. At microscales  $\geq 0.09 \text{ m}^2$ , the earlier congruence of conclusions derived from patchiness indices and spatial autocorrelation broke down. At  $>0.014 \text{ m}^2$ , adjacent points (cores) no longer together formed larger spatial units of related abundance (i.e. showed no autocorrelation), but point abundances were still highly disparate (as reflected in patchiness indices). Congruent indications of patchiness only manifested at  $0.014 \text{ m}^2$  spatial scales. Assemblage dispersion pattern was partly consequent on one microgastropod (*Pseudoliotia*) occurring superabundantly in scattered  $0.0024 \text{ m}^2$  hotspots.

### 1. Introduction

In any given habitat type, both all but rare individual animal species (and many of those as well) and overall animal abundance are distributed patchily across space (Wiens, 1989; Duffy, 2006; Magni et al., 2017). Indeed patchiness has been shown to prevail at virtually all spatial scales of study (Kotliar and Wiens, 1990; Morrisey et al., 1992; Underwood and Chapman, 1996; Kraan et al., 2009). In many cases this is because the presence and/or abundance of their food or other required resources, habitat availability, environmental drivers, etc. are themselves patchy and this imposes patchiness on those dependent on them. Patchiness, however, also seems an intrinsic property of animal populations and of the multi-species associations they form, even where there are no obvious external or behavioural causes of such a state (Lloyd, 1967; Kraan et al., 2009).

An example of this is provided by the intertidal seagrass macrofauna of areas in subtropical Moreton Bay/Quandamooka, Queensland, such as Deanbilla Bay, where the meadows lack the surface relief or macrograzer-control described by van der Heide et al. (2012) and Siteur et al. (2023). The assemblage of benthic invertebrates inhabiting one such intertidal dwarf-eelgrass bed (*Nanozostera sensu Sullivan and Short, 2023*) was recently studied via a regular  $16 \times 16$  grid of core samples, with rows and columns 5.75 m apart (Barnes and Laurie, 2018). The

whole macrofaunal assemblage, and most of the common individual species, were found to be patchy at scales from the almost 1 ha down to the  $33 \text{ m}^2$  area enclosed by unit square of four cores. This process was then repeated at the same season the next year by siting another regular  $16 \times 16$  grid of cores within a nested area equivalent to that  $33 \text{ m}^2$  of unsampled space, with the rows and columns now being only 0.3 m apart (Barnes and Hamylton, 2019). Again, the whole assemblage and most of its common species were found to be significantly patchy at all spatial scales within this much smaller area.

The level or magnitude of such patchiness, however, is known to vary with spatial scale (Rosenberg, 1974; Morrisey et al., 1992; Trifonova et al., 2022; etc.), and did so in some of the dominant assemblage components at this Moreton Bay site. The micro-brachyuran *Enigmoplax littoralis* and the burrowing polychaete *Malacoceros ?divisus*, for example, showed a pattern of decreasing patchiness with decreasing analytical scale, in the case of the worm down to random dispersion. What was therefore much more unexpected was that the level of patchiness of the whole assemblage was effectively the same right across the range of scales investigated (e.g. a Lloyd's index of patchiness,  $I_p$ , of 1.18 across 0.85 ha and of 1.16 across the nested  $23 \text{ m}^2$  site). Further, its magnitude was very similar to those recorded for the benthic macrofauna of equivalent intertidal beds of other *Nanozostera* species as far away as South Africa's Western Cape ( $I_p = 1.15$ ) and the European North

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<https://doi.org/10.1016/j.marenvres.2024.106385>

Received 29 December 2023; Received in revised form 30 January 2024; Accepted 31 January 2024

Available online 1 February 2024

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Sea ( $I_p = 1.14$ ) (Barnes, 2019a). Indeed, it was similar to the levels of macrofaunal patchiness recorded from equivalent intertidal beds of other seagrass genera: *Cymodocea* ( $I_p = 1.13$ ), *Halodule* ( $I_p = 1.11$ ) and *Halophila* ( $I_p = 1.14$ ) in Moreton Bay (Barnes, 2020). These are a series of faunal assemblages displaying very different overall densities (<2000 - >50000  $m^{-2}$ ), numbers of component species (<35 - >200) and taxonomic composition, and sampled to different extents (Barnes, 2019a).

The next logical analytical step in the analysis of patchiness at Deanbilla is therefore to look at even smaller spatial scales than hitherto, as close as it is practical to a continuous surface. The present study adopted the limiting state of a series of small contiguous cores with their centres only 0.06 m apart, such that 25 of them would fit into the unsampled 0.09  $m^2$  space between unit square of four samples in the Barnes and Hamylton (2019) study. Very little is known of spatial dispersions of benthic macrofauna at scales more usually deployed in relation to the meiofauna (e.g. Van Gaever et al., 2009), and more recently to the plankton (Robinson et al., 2021). Which spatial scales are most appropriate for the analysis of any given ecological system are often not clear (Urmy et al., 2022), but, arguably (Hope et al., 2020; Douglas et al., 2023), this is the scale particularly relevant to the microphytobenthos and to topographical features likely to affect the tiny (0.002–0.01 m long) polychaetes, malacostracans and gastropods that dominate the Deanbilla macrofauna. Understanding of processes operating at small scales can also help elucidate patterns at larger ones (Huston, 1999) and hence it was hoped that the results at these scales

would aid explanation of patchiness across the whole site. Therefore, in the present study a variant of the general procedure pioneered by Reise (1979) was used to investigate the null hypothesis that there was no change in level of seagrass macrofaunal patchiness at the smallest of workable spatial scales at Deanbilla.

## 2. Methodology

### 2.1. Study area, sample collection and processing

The study took place within Habitat Protection Zone 2 of the Moreton Bay Marine Park on the sheltered side of North Stradbroke Island/Minjerrabah in the same intertidal *Nanozostera muelleri capricorni* dwarf-eelgrass meadow studied earlier in Deanbilla Bay (Barnes and Laurie, 2018; Barnes and Hamylton, 2019); the 2023 sampled area being nested within that previously studied site (Fig. 1). Sampling was undertaken via 16 replicate blocks each of 5 x 5 touching cores, each core being of 0.0024  $m^2$  internal area and 0.1 m depth. Each block therefore was set within a 0.09  $m^2$  area, with the same sized area separating adjacent blocks (Fig. 2A). The whole series of blocks was positioned within a visually-uniform 4.5  $m^2$  with >65 % *Nanozostera* cover (sensu McKenzie, 2003), centred on 27°30'26"S, 153°24'31"E. All individual cores were spatially referenced. To minimise disturbance to a protected habitat, the component core tubes of each block were not fused together into one unit, inserted simultaneously and then dug out. Instead, first two rows of

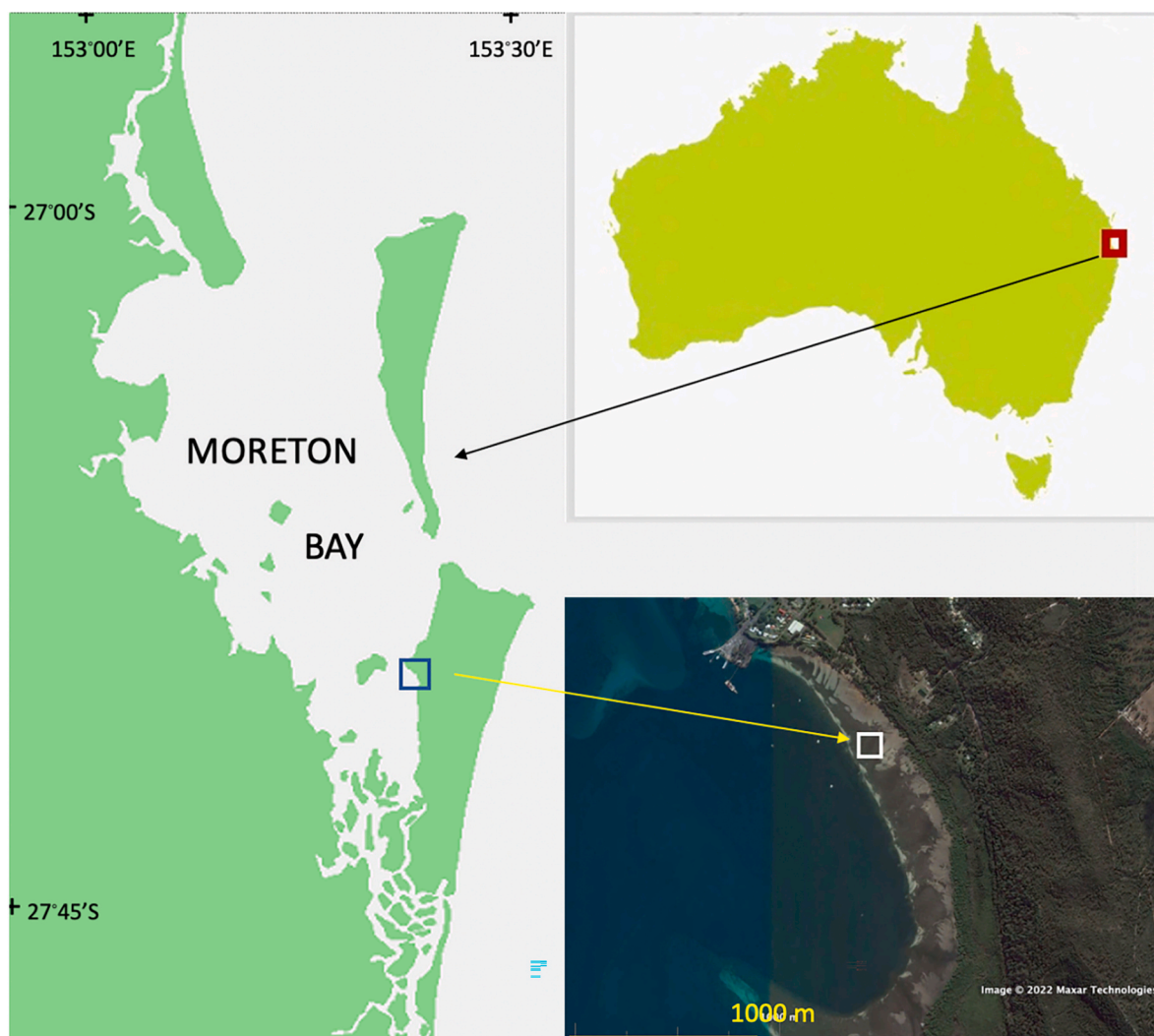
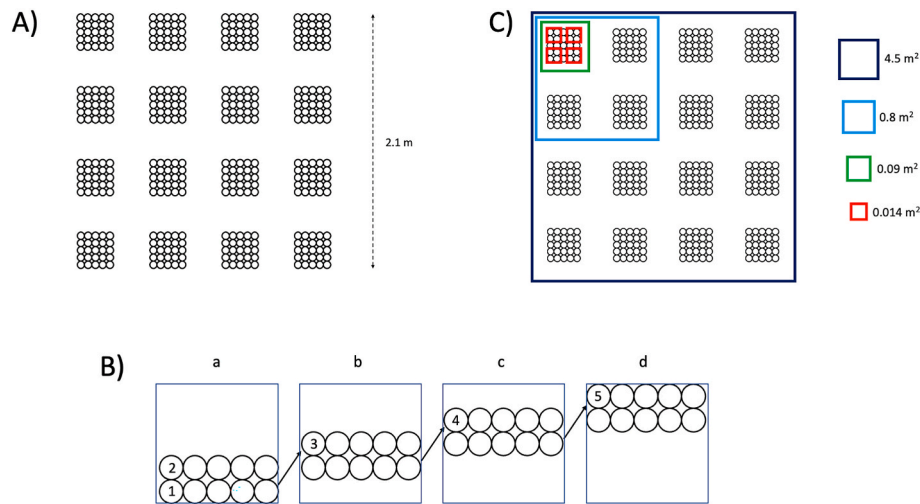


Fig. 1. Location of the Deanbilla Bay sampling site, Moreton Bay, Queensland (satellite image Google Earth Pro © 2022 Maxar Technologies).



**Fig. 2.** Sampling and analytical design. A. Lattice of 16 square core-blocks, each occupying  $0.09 \text{ m}^2$  area and comprising 25 contiguous and spatially-referenced  $0.0024 \text{ m}^2$  core samples; the whole lattice being set within  $4.5 \text{ m}^2$ . B. Sequential sampling system for the  $5 \times 5$  rows of cores comprising each block. C. Diagrammatic representation of spatial scales analysed.

five tubes were inserted contiguously into the seagrass bed as shown in Fig. 2B. Row 1 was then carefully harvested, core by core, and those tubes re-inserted to form row 3; the whole process then being repeated with row 2 leap-frogging 3 to form row 4, and likewise 3 becoming the final row 5 (Fig. 2B). There was no correlation between the sequence of samples collected in this manner and the number of macrofauna obtained per sample (Spearman  $R = 0.02$ ;  $P > 0.6$ ). The earlier patchiness data from the site at larger spatial scales had been collected using a  $0.0054 \text{ m}^2$  core tube; however in order to examine patchiness at very small scales the present data were necessarily obtained by means of considerably smaller diameter tubes. The measure of patchiness used (see below) is one known effectively to be independent of sample size (Lloyd, 1967) and indeed previous macrobenthic data from an equivalent intertidal *Nanozostera* bed in South Africa collected simultaneously using  $0.0015$ ,  $0.0026$  and  $0.0054 \text{ m}^2$  core sizes showed no effect of core grain size on the estimated values of assemblage patchiness (Barnes, 2016).

For consistency, collection and treatment of samples otherwise followed an identical procedure to the earlier studies at larger spatial scale at that site (Barnes and Laurie, 2018; Barnes and Hamylton, 2019). Cores were collected in the 2023 austral spring during daylight hours some 90+ minutes before the point of low tide whilst the substratum was still covered by  $> 20 \text{ cm}$  of water; all sampling being undertaken within the same small time window (10.00–14.00 h) to minimise any potential diel variation in epibenthic biodiversity and abundance (García-Trasviña et al., 2023). Material from each core was gently sieved through  $710 \mu\text{m}$  mesh, and then placed in a  $30 \times 25 \text{ cm}$  translucent tray over a light-emitting diode pad in which the living fauna was located by visual examination until no further animal could be observed. Immediately after each core-block collection, the resulting  $0.007 \text{ m}^3$  hole was refilled with local sediment from the adjacent sandflat, and after enumeration sampled animals were returned alive to the collection site.

The total number of macrobenthic animals in each core was established, together with those of some selected individual taxa. On the basis of the previous assemblage densities at the site of some  $2500 \text{ ind. m}^{-2}$  and because of the  $0.0024 \text{ m}^2$  size of the cores, an average number of animals per sample of only 6 was expected. Hence, few species were likely to occur with sufficient abundance and frequency to be suitable candidates for individual assessment of their patchiness. In the event, the most dominant species in previous years, *Calopia imitata* (a truncatelloid gastropod), proved unexpectedly rare ( $94 \text{ m}^{-2}$  versus  $\geq 400 \text{ m}^{-2}$  earlier), and only *Malacoceros ?divisus* (spionid polychaete), *Limnoporeia ?yarrague* (phoxocephalid amphipod), *Enigmoplax littoralis*

(macrophthalmid brachyuran) and *Pseudoliotia* spp (tornid truncatelloid) occurred in  $\geq 15 \%$  of samples, at overall densities of  $\geq 100 \text{ ind m}^{-2}$ , and in numbers  $\geq 1$  in at least several individual samples. Nevertheless, because of its importance at larger scales *Calopia* was also again included in analyses. Although more limited than previously, these taxa do constitute a representative range of the variation in patchiness across space observed earlier (Barnes and Hamylton, 2019). Nomenclature here is as listed in the World Register of Marine Species ([www.marinespecies.org](http://www.marinespecies.org)), accessed November 2023.

All core samples contained seagrass. Nevertheless, regardless of leaf-length and hence of percentage ground cover, individuals or groups of seagrass ramets are each surrounded by a zone of bare sediment, and this is especially obvious in the characteristically short-leaved intertidal stands (Barnes, 2020; Fig. 2; Park et al., 2021). It is well known that broad expanses of seagrass and of bare sediment often support macrofaunas of different composition, overall abundance, biodiversity and patchiness, and this typifies Moreton Bay (Barnes and Barnes, 2012; Barnes and Hamylton, 2013) to the extent that marked faunal change occurs across the precise  $0.1 \text{ m}$  boundary between seagrass bed and adjacent sandflat (Barnes and Hamylton, 2016). Whether this pattern extends to the composite ramet/bare-sediment situation *within* a bed is not known: earlier work at Deanbilla minimised any such possible effect by centering each sample on an individual seagrass ramet. At the very small spatial scales involved in the present work, however, any microtopographical patchiness and differential preferences of the seagrass-bed species for the specific microhabitats concerned could therefore influence overall patchiness (Roughgarden, 1977). Hence, its local magnitude was investigated at three nearby  $4.5 \text{ m}^2$  stations within the overall  $0.85 \text{ ha}$  2017–2023 study site by comparison of 20 replicate samples at each station centred on the local inter-ramet bare sediment and 20 centred on the individual seagrass ramets. Granted that the maximum distance between individual ramets was some  $40\text{--}50 \text{ mm}$ , an even smaller  $45 \text{ mm}$  diameter core tube ( $0.0015 \text{ m}^2$  area) was used. To place the nature of the inter-ramet sand fauna in context, a further 60 equivalent replicate samples were taken at the same tidal height beyond the margin of the seagrass in the adjacent sandflat.

## 2.2. Analyses

Spatial dispersion of animal numbers was analysed using two contrasting but complementary techniques.

### 2.2.1. Indices of patchiness

As advocated by Payne et al. (2005), Stanley et al. (2012), Rindorf and Lewy (2012), Henriques et al. (2017), etc., and as previously at the site (Barnes and Laurie, 2018; Barnes and Hamylton, 2019), the existence and magnitude of faunal patchiness was ascertained by the Lloyd (1967) index of patchiness ( $I_p$ ),  $1 + [(s^2 - m)/m^2]$ , where  $m$  is the mean number of individuals per unit sample and  $s^2$  the associated variance. Lloyd's  $I_p$  and equivalent indices are influenced by two separate and uncorrelated variables (Barnes, 2021): (i) proportion of absences of the organisms of interest from samples (i.e. their occupancy) and, where present, (b) variation in their abundance (i.e. mean crowding *sensu* Lloyd, 1967); low occupancy having a much greater effect on  $I_p$  than mean crowding [not inappropriately granted the usual meaning of patchiness; i.e. 'the quality of only existing or happening in some parts or situations' (<https://dictionary.cambridge.org/dictionary/english/patchiness#>)]. A general problem with the occurrence of zero-value samples, however, is the need to decide whether they lie within or outside the potentially inhabitable range of the organisms or assemblages in question (Bez, 2000). This difficulty was not considered to be apply to the habitat under study. Zero values hardly occurred in counts of the whole macrofaunal assemblage but did so in respect of those of the five individual target taxa (see above). For them, however, and as previously (Barnes and Hamylton, 2018), degrees of  $I_p$  patchiness were where relevant adjusted by the occupancy of each species at each of the component spatial scales affected to downplay the overwhelming effect of the number of zeros. Statistical significance of any departure from random distribution was determined by Monte Carlo simulation with 9999 iterations, using PAST v.4.11 (Hammer et al., 2001) and the expression  $n [(\Sigma y^2 - \Sigma y)^2 / (\Sigma y)^2 - \Sigma y]$ , where  $n$  = number of core samples and  $y$  = number of animals per sample, which is for all practical purposes identical to  $I_p$  (Lloyd, 1967).

The 4 x 4 grid of core blocks within a 4.5 m<sup>2</sup> area adopted permits analysis at nested scales down to 0.014 m<sup>2</sup> (Fig. 2C), and analysis of patch size down to 0.0024 m<sup>2</sup>. Organismal dispersion pattern in relation to spatial scale can be viewed and assessed in two different ways: *inter-areal* and *intra-areal*, i.e. patchiness can be reflected by variation (a) in the numbers of animals per sample *within* any given area (*intra-areal*) and/or (b) in the total number of animals present across or *between* replicates of that given area (*inter-areal*). Because of limitation of number of possible replicate large spatial-scale areas within any given study site (in the present case, the 4.5 m<sup>2</sup> one) and number of component replicate samples at small spatial scales (here the 0.014 m<sup>2</sup> one), in practice most studies within sites (including earlier work at Deanbilla) have been based mostly on one or other of these measures. Where possible both were included here. Change in degree of patchiness across spatial scales was assessed using the Taylor (1961) empirical power-law function,  $s^2 = \alpha m^\beta$ , in which  $\beta$  (the scaling exponent) was used earlier (Barnes and Laurie, 2018) to indicate direction of any alteration in pattern with changing numbers of individuals present (here consequent on changing analytical area); with  $\beta \approx 1$  indicating isometric scale-invariance of pattern regardless of the nature of that pattern and  $\beta > 1$  indicating decrease in patchiness with decrease in spatial scale; i.e. change towards randomness, or being 'scattered' in the preferred terminology of Reise (1979). [Note that, contrary to received wisdom,  $\beta$  does not indicate the nature of the dispersion pattern itself.]

### 2.2.2. Potential effects of inter-ramet bare sediment on seagrass bed faunal patchiness

Comparison of metrics of the two component system-compartments of seagrass ramet and inter-ramet bare sand used one-way ANOVA, with faunal patchinesses being assessed as above. In addition, multivariate comparison of their relative assemblage composition was undertaken, based on (a) untransformed abundance data and (b) standardised taxon abundances (i.e. all samples abundances adjusted to the same total to reflect solely differential taxonomic composition) using hierarchical clustering analysis of  $S_{17}$  Bray-Curtis similarity and one-

way ANOSIM via the PAST 4.11 software package (Hammer et al., 2001). Other analyses used Microsoft Excel for Mac 16.77 with the StatPlus:mac Pro 8.0.4 add-on.

### 2.2.3. Spatial analysis of autocorrelation

Secondly, patterns in locational dispersion of assemblage abundance were analysed by spatially-explicit autocorrelation techniques at both global and local scales: (i) the univariate global Moran's  $I$  statistic was calculated as an assessment of spatial autocorrelation in total assemblage abundance, assemblage abundance excluding *Pseudoliotia*, and in each of the five target species (section 2.1), across each nested spatial scale; and (ii) local Moran's  $I$  was assessed through a series of correlograms.

Global Moran's  $I$  was calculated to assess spatial association following a procedure based on the cross-product, which measures covariance of values for assemblage abundance at all possible pairs of cores sampled (Anselin, 1996). This yields an  $I$  statistic ranging from negative (-1) to positive autocorrelation (1), that is, the tendency of assemblages sampled closer together in space to be similar to one another. Statistical significance of the resulting global Moran's  $I$  was evaluated via a randomisation approach in which it was compared to a reference distribution generated by Monte Carlo simulation with 999 iterations, with an associated pseudo-significance level ( $P$ -value) (Anselin, 1995).

Local Moran's  $I$  was also calculated for a series of distances ('distance classes') from each point or core sample within the lattice, following the same formulation as employed by Hamylton and Barnes (2018). This local-scale approach was also based on cross products (i.e. the product of the difference between two stations a given distance apart and the overall neighbourhood mean). It was calculated as a local statistic that iteratively compared all point pairs within a neighbourhood, then grew the neighbourhood in order to construct a correlogram, which plotted the index as a function of linear distance between points, expressed as a 'distance band', i.e. a binned range of distances between point pairs within the sampled lattice. At each distance class, only those point samples that fell within a particular distance band were included as pairs for calculation of local Moran's  $I$ , such that variation in autocorrelation could be evaluated as a function of distance between points (stations) across the sampled lattice.

## 3. Results

### 3.1. Patchiness as determined by Lloyd's $I_p$ index

Overall assemblage density was within the range observed at the same time of year during earlier studies (2290-2600 m<sup>-2</sup>), i.e. 2320 m<sup>-2</sup> with a mean 5.6 animals sample<sup>-1</sup>, a maximum of 33, and a minimum of 0 (in 2% of samples) (Figs. 3 and 4). All values of assemblage  $I_p$  obtained from intra-area and inter-area data, and from inter-ramet and ramet comparisons, were within the range 0.95-1.96. Those of the intra-core-block areas were particularly variable: 1.02-1.96 for the whole macrobenthic assemblage, and 0.98-1.27 excluding *Pseudoliotia*. This microgastropod proved markedly patchy at such a level that it affected that of the whole fauna at some spatial scales, even though in total it only comprised 10% of assemblage numbers. Numbers of *Malacoceros* and *Enigmaplax* were negatively correlated at the spatial level of core block (Spearman  $R = -0.59$ ;  $P < 0.02$ ); no correlation coefficient exceeded ( $\pm$ )0.12 at the level of the individual cores.

Patchiness at the 2023 spatial scales of the whole assemblage and of the five target species assessed in the earlier studies at larger scale are displayed in Table 1. That of the whole assemblage is given both with and excluding the *Pseudoliotia* data for the reason given above. *Malacoceros* continued its random dispersion pattern seen at larger scale, and *Enigmaplax* continued its decline in patchiness with decrease in spatial scale (Barnes and Hamylton, 2019). Otherwise there was no evidence of any change towards a random dispersion at microspatial scale, and the

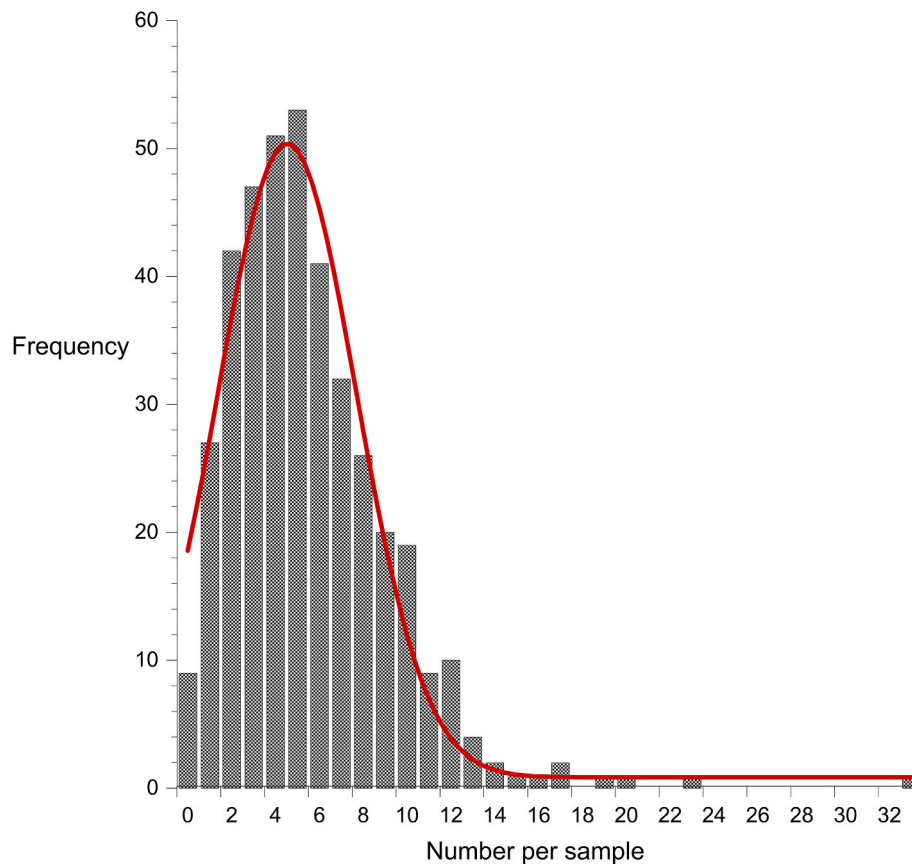


Fig. 3. Frequency of different numbers of macrofaunal animals per unit  $0.0024 \text{ m}^2$  sample across the whole sampling lattice ( $n = 400$ ).  $R^2$  of fitted normal curve 0.97.

values of assemblage patchiness at the smallest scales continued the effectively constant level of patchiness seen across all previously studied scales (Fig. 5) that was not related to scale in any way (Spearman  $R < 0.05$ ;  $P > 0.8$ ). There was a marked correlation of 0.70 ( $P < 0.0001$ ) between the numbers of truncatelloid microgastropod mesograzers per core and the total number of animals (microgastropod numbers comprised 15 % of that total), and an even stronger one between the numbers of *Pseudoliotia* in each core block and the values of core-block assemblage  $I_p$  (Spearman  $R > 0.87$ ;  $P \ll 0.0001$ ). *Pseudoliotia* was mainly responsible for 11 out of the 24 abundance hotspots (a hotspot being defined as supporting  $\geq 12$  animals  $\text{core}^{-1}$ , see Fig. 3); on that basis there being 0–5 such hotspots per core block. There was no correlation between values of assemblage  $I_p$  and number of samples on which it was based (Pearson  $R = 0.03$ ;  $P > 0.8$ ).

Nevertheless, the scaling exponent  $\beta$  of Taylor's power law was greater than 1 both at the microscales of this study and over the whole range of scales investigated at Deanbilla to date (Fig. 6), indicating a general trend of decreasing patchiness with decreasing scale of analysis, albeit a small one. This is also suggested by the intra-area patchiness within each of the replicate core-blocks. Dispersion in one quarter of those individual blocks did not depart from random, and would have been so in a further 44 % had it not been for *Pseudoliotia* (Fig. 7), notwithstanding that abundance across those blocks was significantly patchy (Table 1). Dispersion within each  $0.8 \text{ m}^2$  sub-area (i.e. quarters of the whole site) were all significantly patchy, however, with ( $I_p$  1.12–1.30;  $P < 0.001$ ) or excluding ( $I_p$  1.11–1.18;  $P < 0.002$ ) the *Pseudoliotia* data.

The faunas of the inter-ramet and ramet microhabitat compartments within the seagrass bed were significantly different (ANOSIM  $R = 0.16$ ,  $P < 0.0001$ ; PerMANOVA  $F = 7.3$ ,  $P < 0.0001$ ). However, that in the inter-ramet sand was much more similar to that of the seagrass ramet

samples (a Bray-Curtis similarity of 50 %) than it was to the sand of the adjacent flats (Bray-Curtis similarity of only 10 %). The inter-ramet areas thus supported an impoverished version of the seagrass ramet fauna, differing in that the most characteristic and abundant local seagrass species such as *Enigmaplax* and *Limnoporeia* were rare between the ramets (ANOVA  $F_{1,118} > 8$ ,  $P < 0.005$ ). There was no significant difference in the abundance of *Malacoceros* (ANOVA  $F_{1,118} 1.4$ ;  $P > 0.2$ ), however, whilst only mobile subsurface polychaetes (e.g. *Aglaophamus*, *Armandia* and *Goniada*) were more abundant in the inter-ramet sediment. As would be expected in sand vs seagrass comparisons, the inter-ramet sand supported the lower abundance (in the ratio of 1: >2.5; one-way ANOVA  $F_{1,118} 33$ ,  $P < 0.0001$ ) and fewer species (ratio of 1: >2.0; one-way ANOVA  $F_{1,118} 27$ ;  $P < 0.0001$ ) per unit area. It should be noted that like other seagrass systems elsewhere (e.g. Muller et al., 2023), few, if any, of the most characteristic species in the Moreton Bay seagrass are actually restricted to that habitat. They are also known from other local soft-sediment systems, although not the immediately adjacent intertidal sandflats. The dominant *Calopia* and *Pseudoliotia* at Deanbilla, for example, are two of the five most abundant and two of the three most frequent gastropods in/on the sediments flooring Moreton Bay (Rachello-Dolmen, 2013). Across the small spatial scales under study, overall the inter-ramet sand supported an assemblage displaying less patchiness in its local abundance than the seagrass (mean  $I_p$  1.09 vs 1.23); all ramet sites showing significant patchiness ( $P < 0.0001$ ), whilst two of the three individual inter-ramet sand ones did not depart from randomness ( $P > 0.07$ ) and the third was only significantly patchy at  $P = 0.02$ .

### 3.2. Spatial analysis of autocorrelation

Global Moran's  $I$  statistics indicated a general absence of spatial

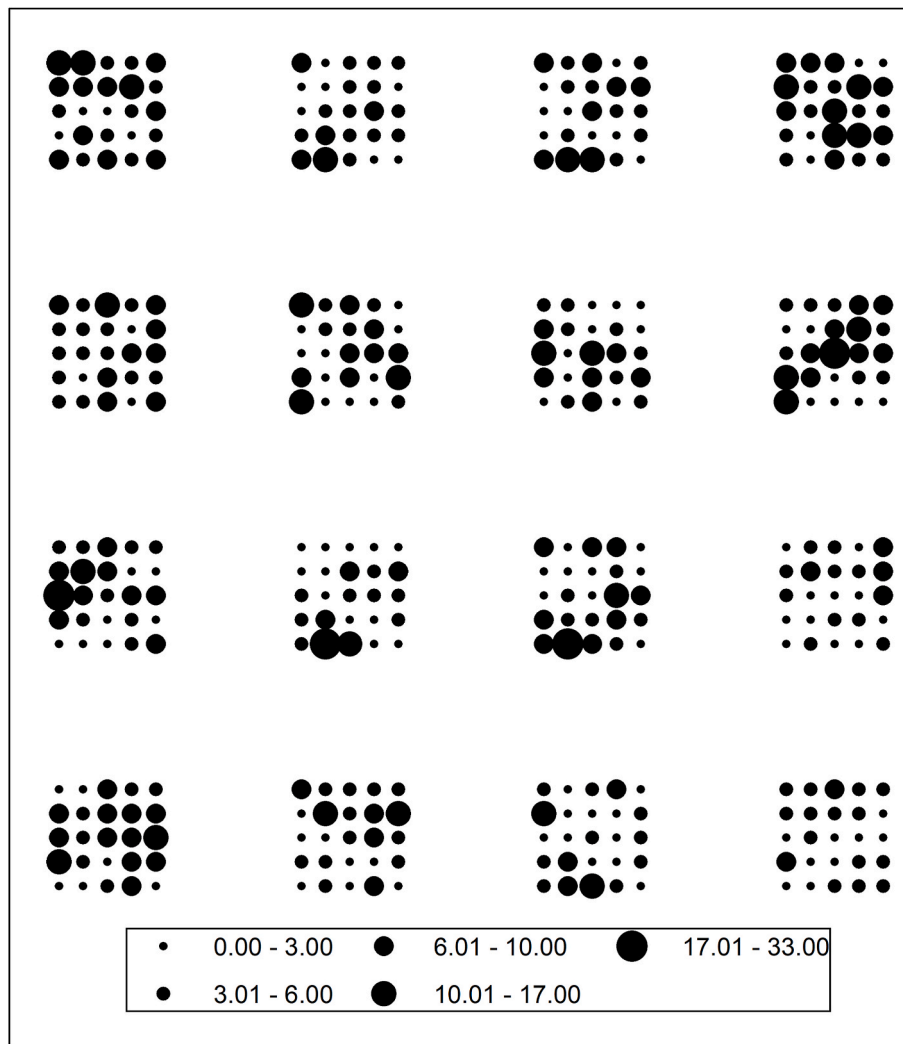


Fig. 4. Spatial distribution of whole assemblage counts of macrofaunal animals per unit 0.0024 m<sup>2</sup> sample across each of the 16 replicate core blocks ( $n = 400$ ).

Table 1

Intra-area patchiness within the whole 4.5 m<sup>2</sup> site and inter-area patchiness across the replicate microscale 0.09 and 0.014 m<sup>2</sup> subareas for the whole macrobenthic assemblage and five representative component taxa. Total assemblage patchiness is given both including and excluding from the dataset the extremely patchy *Pseudoliotia*. Significant patchiness, as indicated by Monte Carlo simulation and as measured by Lloyd's  $I_p$  (adjusted for occupancy as relevant for the individual species) is indicated by asterisks: \* $P < 0.05$ , \*\*\*\* $P < 0.0001$ ; ns indicates a dispersion not differing from random.

	4.5 m <sup>2</sup>	0.09 m <sup>2</sup>	0.014 m <sup>2</sup>
Whole assemblage	1.27****	1.02****	1.12****
Whole assemblage (excluding <i>Pseudoliotia</i> )	1.11****	1.02****	1.06****
<i>Malacoceros ?divisus</i>	0.92 <sup>ns</sup>	1.09*	1.06 <sup>ns</sup>
<i>Limnoporeia ?yarrague</i>	1.69****	1.46****	2.06****
<i>Enigmaplax littoralis</i>	1.27****	1.03 <sup>ns</sup>	1.15*
<i>Pseudoliotia</i> spp.	3.20****	1.64****	2.27****
<i>Calopia imitata</i>	1.57****	1.69****	1.77****

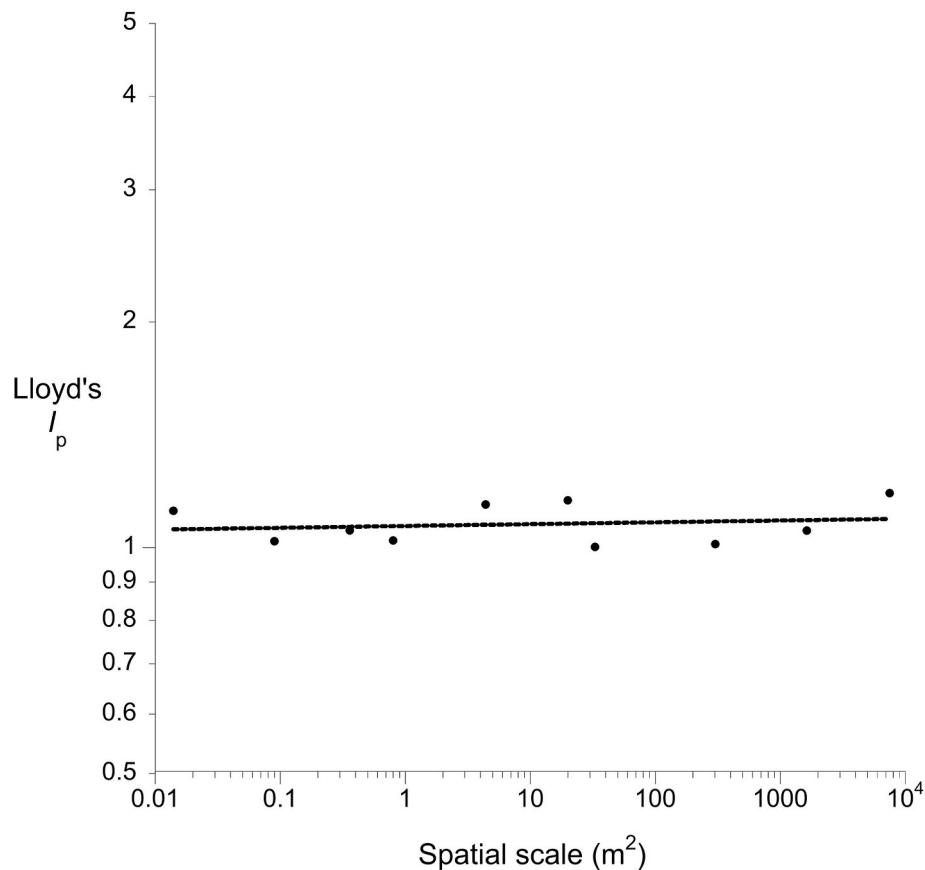
autocorrelation; i.e. 16 of the 21 Moran's  $I$  statistics calculated did not exceed 0.1 at each of the nested spatial scales (0.014, 0.09 and 4.5 m<sup>2</sup>) for total assemblage abundance, for assemblage abundance excluding *Pseudoliotia*, and for the five target taxa (Table 2). The exceptions to this were weak statistically significant positive autocorrelation detected with the global univariate Moran's  $I$  at the smallest spatial scale (0.014 m<sup>2</sup>) both for total assemblage abundance (0.18,  $P < 0.001$ ) and

assemblage abundance excluding *Pseudoliotia* (0.18,  $P < 0.001$ ), and, to a lesser extent, for *Limnoporeia* (0.13,  $P < 0.006$ ) and *Calopia* (0.11,  $P < 0.006$ ), the latter also showing weak autocorrelation at the 0.09 m<sup>2</sup> scale (0.10,  $P < 0.001$ ). Assemblage hotspots (i.e. with  $\geq 12$  animals core<sup>-1</sup>) were randomly distributed across space (Moran's  $I -0.04$ ;  $P > 0.5$ ).

Similar patterns were revealed by the correlograms (Fig. 8), which showed generally low Moran's  $I$  values calculated across all distance bands for all species, with the exception of the values for total assemblage abundance and assemblage abundance excluding *Pseudoliotia* across the smaller distances bands (i.e. between adjacent core samples).

#### 4. Discussion

Unlike earlier studies of the site at larger spatial scales (Barnes and Laurie, 2018; Barnes and Hamylton, 2019), conclusions drawn from spatially-explicit and non-spatially-explicit techniques differed quite markedly at areal scales  $>0.014$  m<sup>2</sup>. In general, use of Lloyd's  $I_p$  index mostly indicated continuation of the same level of assemblage patchiness that characterised larger spatial scales, albeit with variation when calculated inter-areally or intra-areally and with increasing incidence of non-departures from randomness. Spatial autocorrelation analyses, however, largely suggested a lack of significant assemblage patchiness at the studied  $>0.014$  m<sup>2</sup> microscales. The two approaches were in agreement, however, that *Calopia*, *Limnoporeia* and the whole assemblage minus the *Pseudoliotia* data were patchy at all spatial scales, and

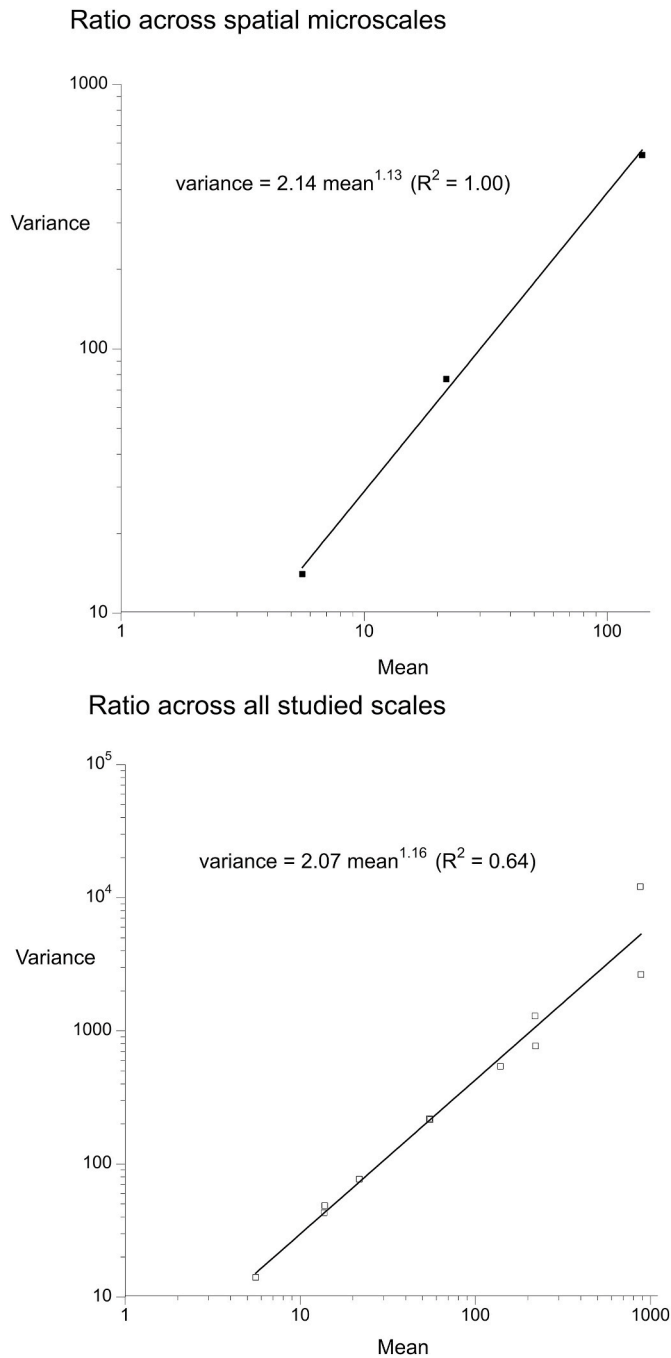


**Fig. 5.** Degree of intra-areal patchiness of the whole macrofaunal assemblage across all studied spatial scales at the Deanbilla Bay site (i.e. in 2017, 2018 and 2023) as assessed by Lloyd's  $I_p$ , earlier data being recast and represented only in this format. Data within areas of 7500 to 33 m<sup>2</sup> are from 2017; within 20 to 0.4 m<sup>2</sup> from 2018; and 4.5 to 0.014 m<sup>2</sup> are from 2023; when the same scale was assessed on more than one occasion (i.e. 4.5 m<sup>2</sup> in 2018 and 2023) the value presented is the mean. The fitted power curve has a scaling exponent of only 0.0024.

that *Malacocerus* and *Enigmaplax* continued their earlier-established trends at larger spatial scales to lesser patchiness and ultimately random dispersion with decrease in scale. Clearly, complicating factors in analysis of the situation at Deanbilla were present due to the gaps between core blocks within the 4.5 m<sup>2</sup> sampling lattice, and the hit-and-miss consequence of superabundance in spatially limited and randomly scattered hotspots on estimates of patchiness magnitude. Nevertheless, although each is much used to quantify patterns of spatial dispersion, these data illustrate that Lloyd's  $I_p$  and equivalent dispersion indices on the one hand, and Moran's  $I$  on the other are concerned with different aspects of the spatial arrangement of sets of data points. Dispersion indices examine whether the points are distributed randomly across space, whereas spatial autocorrelation takes the location of the points as granted and addresses the question of whether the variate values are scattered randomly about those points (Sakai and Oden, 1990). The contrast in conclusions from the two forms of assessment are a reflection of the nature of spatial inequalities of levels of abundance, particularly in relation to their areal extent. Macrofaunal abundances in the individual cores were certainly disparate, equivalent to a range of 0–13750 m<sup>-2</sup>, and it is this disparity that is reflected in the values of Lloyd's  $I_p$ . But there was little or no significant tendency for adjacent cores to support similar abundance and hence to form larger patches, as reflected by the lack of spatial autocorrelation within and across the core blocks. Areas of high abundance ('patches') were at the scale of (or less than) 0.014 m<sup>2</sup>, in considerable measure because of the microscale aggregation of *Pseudoliotia*. This snail also exemplified the contrast between conclusions drawn from spatial autocorrelation and from patchiness indices at microspatial scales. As a result of occurring partly in the form of dense but areally very small, scattered clumps, it scored no

or hardly any significant autocorrelation at >0.014 m<sup>2</sup> but nevertheless marked patchiness in abundance, and it was an important influence on dispersion of the whole assemblage. This, of course, leads to a general question: how should dispersions of this type, e.g. as shown in Fig. 9, be described; are they significantly patchy or not? Here, we take the view that because in that diagram numbers are clearly clumped or aggregated, they can legitimately be considered 'patchy'.

One of the most evident features of the patchiness of the Deanbilla seagrass assemblage across the whole range of spatial scales investigated from 2017 to 2023 was indeed the major role in its generation played by certain truncatelloid microgastropods, especially the 2 mm long *Calopia*, <3.5 mm *Pseudoliotia* and <6 mm *Circulus*. In fact, if these are excluded from the databases, the patchiness of the remaining fauna was at a lower and unvarying (although still significant) level across the time period, equal to an  $I_p$  of 1.12. It was variation in the numbers of the microgastropods at Deanbilla that led not only to the higher overall values of patchiness than at most of the other sites that have been investigated (Barnes, 2021) but also to such variation in its local magnitude as occurred. In particular, the vitrinelliform *Pseudoliotia* and *Circulus* are notable for having shown extremely clumped distributions throughout the study; although *Calopia* did also display a hotspot of >50 per 0.01 m<sup>2</sup>, nine times background levels. Both *Pseudoliotia* and *Circulus* had low rates of occupancy, averaging some 25 % and 7 % respectively. But where they did occur they could do so in staggering numbers, up to 110 per 0.01 m<sup>2</sup>. These are very large densities for such a subtropical system, although in the cool-temperate North Sea the equivalent truncatelloid microgastropod *Peringia ulvae* has achieved more than ten times that density (Smidt, 1951). Not all individual microgastropods were located in such clumps, however. Over the course of this study, some 65 % of the



**Fig. 6.** Taylor's power-law relationship between mean and variance of the total numbers of macrofauna at the 2023 microspatial scales of assessment, and across all those spatial scales investigated between 2017 and 2023. Exponent  $\beta$  being 1.13–1.16 indicates a small tendency towards a lesser degree of patchiness at smaller spatial scales.

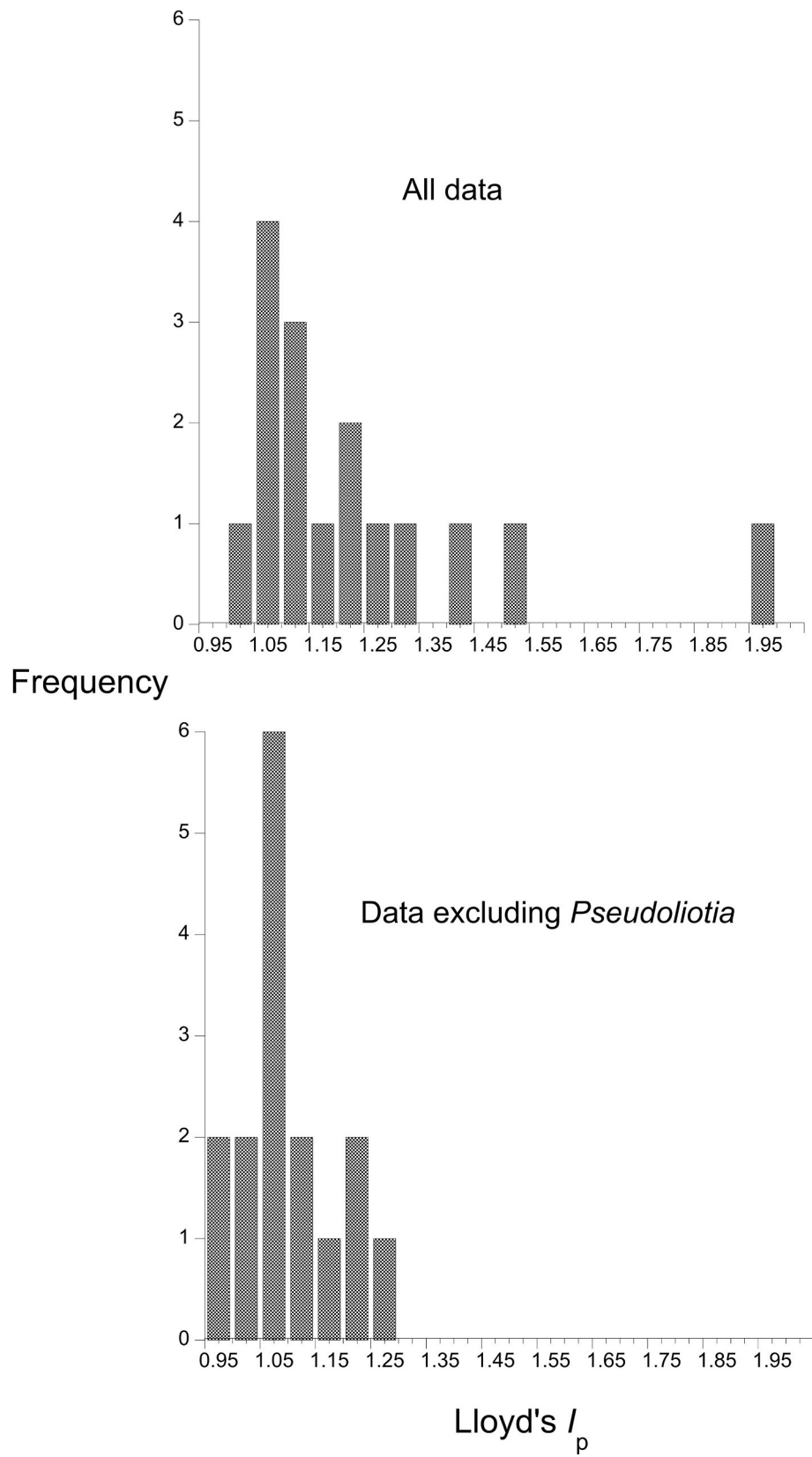
*Pseudoliotia*, for example, occurred in densities  $<800 \text{ m}^{-2}$ , more or less equivalently to *Enigmaplax*; only the remaining 35 % were located in dense aggregations of  $>800 - 10830 \text{ m}^{-2}$  (mean value  $2000 \text{ m}^{-2}$ ).

The same phenomenon of high microgastropod-induced patchiness was recently described across three warm-temperate estuaries in South Africa (Barnes et al., 2024) where *Nanozostera capensis* assemblages dominated by truncatelloid and/or cerithioid microgastropods showed  $I_p$  values of 1.74–1.95, whereas in sites not so dominated  $I_p$  values were 1.05–1.10. As at Deanbilla, in circumstances where microgastropods did dominate, the other members of the *N. capensis* fauna displayed relatively low and less variable though still significant  $I_p$  values ( $\leq 1.20$ ). In

one region of the South African systems the cerithioid *Alaba pinnae* averaged  $>400$  per  $0.01 \text{ m}^2$  (Barnes et al., 2022). Such marked differences in microgastropod abundance in Deanbilla, South Africa and the North Sea may result from the latitudinal variation in predation intensity discussed by Freestone et al. (2019) although relatively few predators seem to consume shelled gastropods (Reynolds et al., 2018).

Why should these microgastropods achieve such high levels of patchiness as to structure that of the entire assemblages of which they are part, but not necessarily a large part (15 % of the Deanbilla total in 2023)? In respect of Deanbilla, *Pseudoliotia* and *Circulus* are very similar in shell and bodily form (vitrinelliform gastropods form "one of the most extreme cases of shell convergence" known; Sasaki, 2008: 171), as indeed is a third truncatelloid *Sigaretorinus*, present less frequently, and a fourth, *Teinostoma*, recorded from Moreton Bay but not (yet) at Deanbilla. So much so that, until recently, all four genera were placed in the same family (although each is now accommodated in a separate one). Nothing is known of the ecology of the relatively common and widespread *Pseudoliotia*, although between them its 45 species range right across the Indo-West Pacific (Rubio and Rolán, 2018). What is nominally the same species of *Circulus* as at Deanbilla, however, is known to occur commensally in the burrows of decapod and stomatopod crustaceans in Japan (Goto and Sato, 2021), as are other *Circulus* species in Florida (Bieler and Mikkelsen, 1988); *Sigaretorinus* is also a commensal in those of stomatopods and of the echiuran worm *Listriolobus*, whilst *Teinostoma* is a commensal of axiidean crustacean burrows (Morton, 1988; Goto et al., 2014). Burrow commensalism not only accounts for their highly clumped spatial dispersions but also for their high local densities by virtue of exploitation of the vertical plane in the sediment. However, there are no suggestions in the literature that *Pseudoliotia* is an equivalent commensal, although the vitrinelliform shell shape can at least partly be associated with a lifestyle in burrows (Goto et al., 2021), and inhabiting burrows at least facultatively would certainly explain its dispersion pattern. Indeed, other members of its family are known (e.g. *Cochliolepis parasitica*) or suspected (e.g. *Ovini petalius*) commensals (Goto and Sato, 2021; Goto et al., 2021). Plentiful potential crustacean host burrows are certainly available in the local seagrass beds, i.e. those of axiidean (*Trypaea*) and caridean (*Alpheus*) decapods and of a number of types of stomatopod; and re-examining the pooled data of Barnes and Laurie (2018) and Barnes and Hamylton (2019) there was a highly significant correlation between the presence of *Alpheus* in a core sample and the abundance of *Pseudoliotia* ( $R = 0.30$ ;  $P \ll 0.00001$ ). The number of *Pseudoliotia* hotspots was of the order of a maximum  $15 \text{ m}^{-2}$  which would also indicate the density of supporting burrows if they only achieve large numbers when commensal. Unfortunately, what little is known of *Pseudoliotia*'s biology has not hailed from ecological work: Rubio and Rolán (2018: 113) comment that most species "have been studied from empty shells and so information on the habitat ... is wanting, or is unreliable", and more generally, Sasaki (2008: 171) notes that "the problem with biological studies in this group is the difficulty in finding live specimens". According to Beechey (2023), Australian *Pseudoliotia* species are "most commonly seen as bleached white shells in beach washup" but have been collected "on seagrass and other substrates ... and under rocks and debris in sheltered bays and estuaries", although no shell collectors seem to have looked below the sediment surface. No rocks or piles of macroscopic debris were present on the surface of the Deanbilla sediment. In the present study its numbers associated with seagrass ramets were much larger than in the inter-ramet sediment, but no *Pseudoliotia* hotspot was included in that dataset.

There is a further mystery relating to *Pseudoliotia*. It appears to be represented in the Deanbilla seagrass by at least three species, *P. micans*, *P. speciosa* and *P. axialis* (and maybe also *P. gowlandi*), all in the same '*micans* group' of closely related species within the genus (Rubio and Rolán, 2018). This is itself an unusual phenomenon, other local microgastropod genera being represented by only a single species (Barnes, 2019b). All share the same highly clumped dispersal pattern although all may also occur in the same  $0.0024 \text{ m}^2$  sample. Do they only coexist

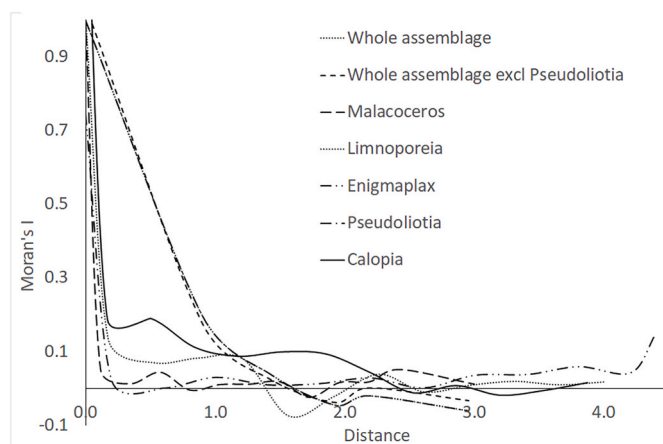


**Fig. 7.** Variation in intra-area patchiness of the whole macrofaunal assemblage *within* each of the sixteen replicate 0.09 m<sup>2</sup> core-blocks, including and excluding the extremely patchy *Pseudoliotia*, as assessed by Lloyd's  $I_p$  and with statistical significance as indicated by Monte Carlo simulation.  $I_p$  values < 1.08–1.10 do not depart from random dispersion; those > 1.10 are all significantly patchy. The mean value (including *Pseudoliotia*) was  $1.23 \pm 0.24$ . Spatial variation in *Pseudoliotia* numbers was solely responsible for faunal patchiness in 7 of the 12 patchy blocks. Note that dispersion *across* the same replicate core-blocks was significantly patchy (Table 1).

**Table 2**

Univariate global Moran's *I* measure of spatial autocorrelation within the whole 4.5 m<sup>2</sup> site and inter-area autocorrelation across the replicate microscale 0.09 and 0.014 m<sup>2</sup> subareas: the whole macrobenthic assemblage including and excluding from the dataset the extremely patchy *Pseudoliotia*, and five representative component taxa. Significant autocorrelation, as indicated by a randomisation simulation formed by 999 permutations of spatially random layouts using the same data values, is indicated by asterisks: \**P* < 0.05, \*\**P* < 0.01; \*\*\**P* < 0.001; *ns* indicates a dispersion not differing from random.

	4.5 m <sup>2</sup>	0.09 m <sup>2</sup>	0.014 m <sup>2</sup>
Whole assemblage	-0.002 <sup>ns</sup>	0.016 <sup>ns</sup>	0.18***
Whole assemblage (excluding <i>Pseudoliotia</i> )	-0.002**	0.04**	0.18***
<i>Malacoceros</i> ? <i>divisus</i>	-0.002 <sup>ns</sup>	0.03 <sup>ns</sup>	0.07*
<i>Limnoporeia</i> ? <i>yarrague</i>	-0.002***	0.04**	0.13**
<i>Enigmaplax littoralis</i>	-0.002 <sup>ns</sup>	-0.003 <sup>ns</sup>	0.004*
<i>Pseudoliotia</i> spp.	-0.002 <sup>ns</sup>	0.01 <sup>ns</sup>	0.08*
<i>Calopia imitata</i>	-0.002**	0.1***	0.11**



**Fig. 8.** Moran's *I* correlograms based on whole assemblage and individual species sub-fractions (as indicated in the legend) for distance classes, within the full lattice.

because their mesograzers trophic level is maintained well below carrying capacity (Barnes, 2017), most likely by predation (Nowicki et al., 2018; Freestone et al., 2019)? Do the autecologies of the various species differ; perhaps even are they commensals of different species?

This potential manner of generating overall patchiness is, however, restricted to Deanbilla. The abundant microgastropods inducing high levels of patchiness in equivalent South African *N. capensis* beds are almost certainly not burrow commensals and they occur at high occupancies (of up to 100 %), and neither are all microgastropod-dominated seagrass systems especially patchy, e.g. that investigated in *N. noltei* meadows in the British North Sea (Barnes and Ellwood, 2011) where the patchiness of the (sole) microgastropod species and of the remaining fauna were identical, notwithstanding that the microgastropod comprised 93 % of the faunal individuals. The reasons for these contrasting states are as yet unknown, but there are no clear relationships between overall patchiness in the systems concerned and microgastropod abundance or occupancy.

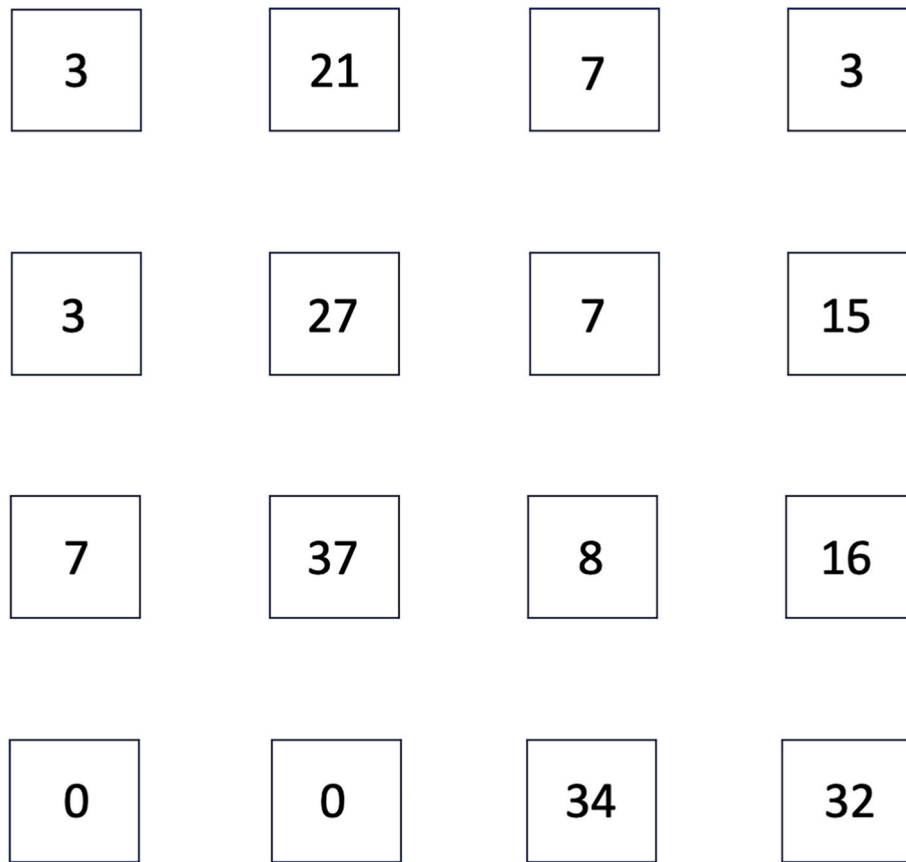
Nevertheless, as seen in South Africa, Queensland, and the North Sea, it is not just the microgastropods that are patchily dispersed; 13 of the 24 Deanbilla hotspots, for example, did not include high densities of *Pseudoliotia*. Seemingly no other study has investigated patchiness of a whole benthic marine macrofauna across these small to micro-spatial scales, and therefore there is no other body of work available to compare with the present results, and as yet little evidence to help explain small-scale dispersion patterns. Indeed, the only other really comparable study is that in the intertidal North Sea by Reise (1979) who used an array of contiguous cores in a 0.24 × 0.24 m block, amongst other strategies, to

investigate the dispersion of five polychaete species. Three of them were clearly patchy; one, that displaying least abundance, was randomly dispersed ('scattered'); and the final one was likewise distributed in a scattered or even regular pattern. He suggested that their micro-spatial biology was related to their feeding behaviour, as has also been proposed for soil nematodes (Quist et al., 2017). Polychaetes in subtidal St Margaret's Bay, Nova Scotia, have also been sampled across a range of scales down to <10 cm by sets of contiguous subsampling from much larger box cores by Volckaert (1987), although the particular focus there was variation in individual species with depth off the coast. The target infaunal polychaete representing this group at Deanbilla was the large, burrow-dwelling and surface-feeding spionid *Malacoceros*, and perhaps comparably to Reise's 'territorial' burrow-dweller (*Hediste*), at spatial scales below some 20 m<sup>2</sup> its dispersion did not depart from random, except that in one instance it too was regular (Barnes and Hamylton, 2019; present study). In terms of the other 2023 target species at Deanbilla, no information is yet available on the feeding behaviour of *Enigmaplax* (other than that it is likely to be an atypical macrophthalmid since it does not possess spooned-tipped chelae), but if *Limnoporeia* is a typical phoxocephalid it will be a highly mobile and active predator of meiofaunal and juvenile macrofaunal animals (Oliver et al., 1982) and may aggregate in areas of prey abundance.

Overall, it is no surprise that the Deanbilla seagrass fauna was patchy at spatial scales from 8000 down to 0.014 m<sup>2</sup> (Kotliar and Wiens, 1990; Berg, 2012; Robinson et al., 2021; etc.), but the relative uniformity of the degree of patchiness of the whole assemblage across those scales is unexpected because of known spatial variability in benthic assemblages and habitat features (Chapman et al., 2010; etc.), and even more unexpected is the close similarity of the uniform Deanbilla value with those of other intertidal seagrass macrofaunal assemblages across the globe. Although the Deanbilla fauna is unlikely to be a random subset of the local species pool (Sommerfield et al., 2009), earlier work has shown the individual faunal components within the local seagrass systems there and elsewhere to be independently and randomly assorted spatially (Barnes and Barnes, 2014; Barnes, 2017), and it has been argued that independently patchy spatial distributions generally enhance stability of many-species dynamics (Hanski, 1994). This might include the factors influencing levels of assemblage patchiness.

The consequent lack of biological interactions such as competition could also impact on individual dispersion patterns. Random dispersion is rare in nature and some have even questioned whether it really occurs at all (e.g. Reise, 1979), let alone whether non-departure from Poisson is indicative of randomness (Hurlburt, 1990) or indeed whether departure from it actually does indicate non-randomness (Young and Young, 1990). At face value, however, it has been noted in several studies of individual marine macrobenthic species besides some of those studied here (Angel and Angel, 1967; Volckaert, 1987; Susintowati et al., 2019; etc.). Density dependence can affect spatial dispersion (Brush and Harte, 2021) and randomness may be particularly associated with low densities (Taylor et al., 1978). At the level of the whole assemblage, the wide range of densities across which the same level of patchiness is manifested (Barnes, 2019a, 2021), however, suggests that no effect of density is operating at sites such as Deanbilla, and the densities of the randomly dispersed *Enigmaplax* and *Malacoceros* in 2023 were at the same level as across the larger scales assessed in 2017 and 2018 when their dispersals were patchy. The caveat here is that the small size of the 2023 individual core samples and the low densities of some of the species inevitably ensured that for them high frequencies of zero and unity scores occurred, and such was the case for *Malacoceros*. It was also the case for *Limnoporeia*, however — both species displayed exactly the same proportion of zero + unity scores — and that amphipod did not show randomness at any scale, neither from spatial-autocorrelation nor dispersal-index assessment.

Many areas of ignorance in the spatial patterning of individual and associations of species obviously remain at Deanbilla and elsewhere. But it is clear that further progress in the understanding of patchiness in



**Fig. 9.** Does this pattern of numbers of *Pseudoliotia* in each of the various 0.09 m<sup>2</sup> core blocks, with a mean to variance ratio of 1 : 11.7, display 'patchiness' or not? It shows a significant level of non-spatially-explicit Lloyd's  $I_p$  (Table 1), but no significant value of spatially-explicit Moran's  $I$  (Table 2). Because of the evident clumping or aggregation of individual animals, here we consider dispersion patterns like this to display patchiness, notwithstanding the lack of spatial autocorrelation.

seagrass-associated systems, especially at very small spatial scales, is likely to need greater knowledge of the ecology of the dominant component species. For the seagrass beds of Moreton Bay, this means of *Enigmaplax*, and particularly of *Calopia* and *Pseudoliotia* about which all that is known is their numbers per unit area, their levels of occupancy, and that they numerically dominate the fauna of the *Nanozostera* beds along the Rainbow Channel shores of North Stradbroke Island in both those respects (Barnes, 2017). They are assumed to be grazers of microphytobenthos, epiphytic algae and 'detritus', as are most microgastropods (Fong et al., 2018), but even that is not certain.

### Funding

LB received a Moreton Bay Research Station Sibelco Student Grant, otherwise this research did not receive any specific funding from agencies in the public, commercial, or not-for-profit sectors.

### CRediT authorship contribution statement

**R.S.K. Barnes:** Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Conceptualization. **Sarah M. Hamylton:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis. **Liz Borburgh:** Writing – review & editing, Investigation.

### Declaration of competing interest

The authors declare that they have no known competing financial

interests or personal relationships that could have appeared to influence the work reported in this paper.

### Data availability

Data uploaded to stated Open Science Framework repository

### Acknowledgements

RSKB and LB are indebted to the Quandamooka Yoolooburrabee Aboriginal Corporation and the Quandamooka Aboriginal Land and Sea Management Agency for permission to carry out fieldwork within the native-title area of the Quandamooka People, and to the Queensland Parks and Wildlife Service for permission to sample in a Habitat Protection Zone of the Moreton Bay Marine Park under permits MPP19-002133 and P-MPP-100245398. The study was conducted from the Moreton Bay Research Station, Dunwich, and we thank its staff especially Martin Wynne for their hospitality, support and assistance; and likewise in that regard we are most grateful to Sheridan Rabbitt and Ian Tibbetts of UQ's Centre for Marine Science. RSKB also thanks Lily Cottrell for her help collecting the seagrass-ramet vs inter-ramet sediment data.

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