



Uniform functional structure across spatial scales in an intertidal benthic assemblage



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ABSTRACT

To investigate the causes of the remarkable similarity of emergent assemblage properties that has been demonstrated across disparate intertidal seagrass sites and assemblages, this study examined whether their emergent functional-group metrics are scale related by testing the null hypothesis that functional diversity and the suite of dominant functional groups in seagrass-associated macrofauna are robust structural features of such assemblages and do not vary spatially across nested scales within a 0.4 ha area. This was carried out via a lattice of 64 spatially referenced stations. Although densities of individual components were patchily dispersed across the locality, rank orders of importance of the 14 functional groups present, their overall functional diversity and evenness, and the proportions of the total individuals contained within each showed, in contrast, statistically significant spatial uniformity, even at areal scales <2 m². Analysis of the proportional importance of the functional groups in their geospatial context also revealed weaker than expected levels of spatial autocorrelation, and then only at the smaller scales and amongst the most dominant groups, and only a small number of negative correlations occurred between the proportional importances of the individual groups. In effect, such patterning was a surface veneer overlying remarkable stability of assemblage functional composition across all spatial scales. Although assemblage species composition is known to be homogeneous in some soft-sediment marine systems over equivalent scales, this combination of patchy individual components yet basically constant functional-group structure seems as yet unreported.

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1. Introduction

Beds of the dwarf-eelgrass *Zosterella* are a common feature of sheltered intertidal marine soft sediments from some 60°N to 48°S, especially outside the tropics (Green and Short, 2003). Such beds support a rich fauna of small epi- and infaunal invertebrates (Puttick, 1977; Connolly, 1997; Lee et al., 2001; Honkoop et al., 2008; etc.) in densities of up to some 80,000 ind m⁻² (Barnes and Elwood, 2011). Earlier work has shown that the distribution of each individual species across the beds is characteristically patchy, and the associations that together they form therefore vary spatially in composition (e.g. Barnes and Barnes, 2011; Barnes, 2013). Nevertheless, the number of species per unit area, even at very small

scales (0.0275 m²), has proved to be statistically uniform at each of the three localities that have been investigated in this respect, at 53°N, 01°E in the NE Atlantic, 34°S, 23°E in the SW Indian, and 27°S, 153°E in the SW Pacific Oceans (Barnes, 2014). This uniformity has been shown to be a direct consequence of random compositional nature, in which no species significantly influences the distribution of any other (Barnes and Ellwood, 2011; Barnes and Barnes, 2014). This, in turn, is probably a result of being maintained well below carrying capacity by the predation effected by the juvenile crustaceans and fish for which such seagrass beds serve as commercially significant nurseries (Valentine and Duffy, 2006; Moksnes et al., 2008; Lewis and Anderson, 2012). The precise uniform number of species present per unit area at each of these disparate localities was also relatively similar (i.e. within a range of 14–23 per 0.0275 m² sample) in spite of wide variation in size of the local species pools (from 30 to >160) and in overall levels of assemblage abundance (from <2,500 to >60,000 ind m⁻²) and Hill's N_1 α diversity (from <3 to >35) (Barnes and Henny, 2015). This

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constancy in number of species reflects the possession of similar ranked relative frequency of species occurrence curves at the three localities: under random assemblage conditions, different frequency of occurrence distributions yield different uniform species numbers per unit area (Barnes and Barnes, 2014). Finally, it is likely that the possession of similar functional diversities and a common set of dominant functional groups forming similar ranked functional-group occurrence curves are critical to the establishment of the shared frequency of taxon occurrence curves (Barnes and Hendy, 2015). As argued by Bremner et al. (2003) and McGill et al. (2006), amongst others, it is analysis of how components of ecological system function and the nature of the niches concerned that can elucidate many of their emergent assemblage properties.

Although several relevant aspects of the functional ecology of seagrass systems have received attention (e.g. Duffy et al., 2001; Plummer et al., 2012; Yamada et al., 2014), especially in the Baltic Sea (e.g. Bonsdorff and Pearson, 1999; Boström, O'Brien et al., 2006), many gaps in our understanding of these systems remain. Critically, the spatial phenomena of pattern and scale — arguably the central issue in ecology (Levin, 1992) — remain largely unaddressed (Pavoine and Bonsall, 2011; Yamakita and Nakaoka, 2011; Törnroos and Bonsdorff, 2012) even though functional and taxonomic diversity are generally acknowledged to be prime candidates for scale dependence (Ellingsen, 2001; Fonseca and Ganade, 2001). Spatial extent, i.e. size of the studied area (Turner et al., 1989), for example, is intimately involved in the potential roles of the main metacommunity processes structuring the ecology of organismal assemblages, and comparisons across several spatial extents are vital for our understanding of such structuring (Leibold et al., 2004; Josefson, 2009; Alahuhta and Heino, 2013). In this respect, Barnes and Hendy (2015) have shown that although neither functional diversity nor the subset of groups dominating the functional spectra nor the rank relative group occurrence curves varied significantly across a 6.5 km distance in a *Zosterella capricorni* bed in Moreton Bay, Queensland, there was considerable local variation (between points some 2 km apart) in the rank-order of importance of the individual component functional groups. The overall pattern remained the same whilst the components varied spatially, suggesting the existence of a fundamental structural system in seagrass beds. Studies to date of the spatial uniformity of ecosystem properties in these seagrass beds (e.g. Barnes, 2014), however, have ignored the precise geospatial locations of each data-point within a given sampling unit. Clearly, features may be uniform statistically whilst not being absolutely constant, and spatial autocorrelation is already known to be one source of local structural patterning in seagrass faunas (Barnes and Hamylton, 2013) as in other soft-sediment systems (McArdle and Blackwell, 1989). Does spatial autocorrelation occur in functional group structure and abundance, is it present across multiple spatial scales, and how does the variation that it creates fit into a uniformity paradigm?

In order to gain a better understanding of the causes of the remarkable similarity of emergent assemblage properties across disparate seagrass sites and assemblages, the first object of the present study was to investigate the extent to which these emergent functional properties are scale related by testing the null hypothesis that functional diversity and the suite of dominant functional groups in the *Zosterella*-associated macrofauna at the Queensland locality above are robust structural features of such a seagrass assemblage and do not vary across local space. A second, though related, object was to explore the precise spatial meaning of 'uniformity' of emergent assemblage properties by collected data from a lattice of spatially referenced points. Because variation in intertidal marine soft-sediment density appears to be most marked at scales in the order of 0.25–100 m² (Olabarria and Chapman,

2001; Ysebaert and Herman, 2002; Barnes and Ellwood, 2012), the spatial scales investigated were centred on those values.

2. Methods

2.1. Study area, sample collection and processing

Macrofaunal sampling was conducted over a period of 11 weeks during the 2014 austral spring at Deanbilla Bay, an area of seagrass previously studied by Barnes and Barnes (2012), Barnes and Hamylton (2013) and Barnes (2014) on the sheltered Rainbow Channel north-western coast of North Stradbroke, a large (27,400 ha), sand-dune, false barrier island (*sensu* Pilkey, 2003) located in the relatively pristine Eastern Banks region of the shallow, oligohaline, mesotidal, subtropical Moreton Bay Marine Park, Queensland (Dennison and Abal, 1999). In the specific area sampled, centred on 27°30'26"S, 153°24'31"E and straddling MLW tide level, the beds were predominantly of *Z. capricorni* with *Halophila ovalis*, and were sited roughly in the middle of a virtually uninterrupted 25 + km long seagrass belt (Roelfsema et al., 2009). Typically in such intertidal conditions, dwarf-eelgrass plants are of the small morphological forms characteristic of shallow areas (Young and Kirkman, 1975), and that was especially so at the Deanbilla site, many leaves being <5 cm long. In consequence, although occurring at the same high shoot density as at other local sites (see Barnes and Hamylton, 2013), percentage ground covers were only in the range 40–65% (*sensu* McKenzie, 2003).

As previously (Barnes, 2013, 2014), each station was a block of five individual 55 cm² cores arranged quincuncially with a distance of 1 m between pairs of corner cores to represent a notional area of 2 m². An 8 x 8 lattice of such stations, with a distance of 0.3" of both latitude between each row (i.e. c. 9.4 m) and longitude between each column (i.e. c. 8.3 m), was used to sample a rectangular plot of 0.4 ha within the bed (Fig. 1), with its diagonals c. 25° off alignment with the water-line and the long axis of the shore. Individual stations were positioned via a hand-held GPS + GLONASS unit (with a stated accuracy of 3 m). This design made possible analysis across nested spatial scales of ≈0.005, 2, 250 and 1000 m² within the 0.4 ha locality (Fig. 1). Individual cores were only of 10 cm depth because most benthic macrofauna in seagrass is known to occur in the top few mm of sediment (e.g. 98% in the top 5 mm in the study

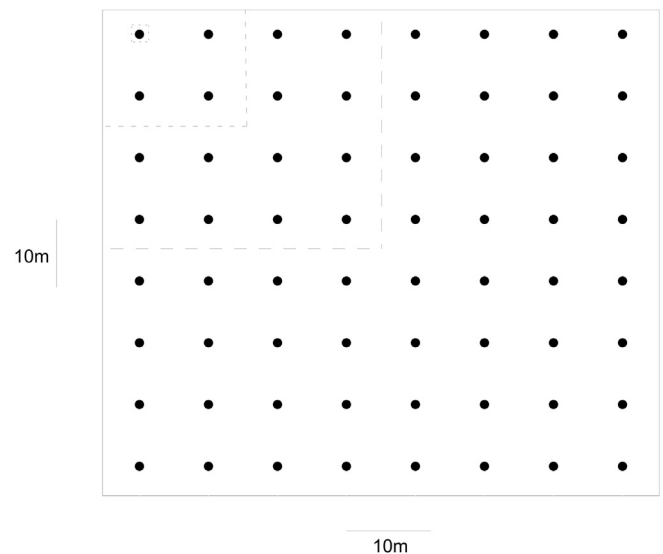


Fig. 1. Diagrammatic representation of the sampling lattice and of the nested spatial scales of 2, 250, 1000 m² within the 0.4 ha locality.

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