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Seagrass macrofaunal abundance shows both multifractality and scale-invariant patchiness

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ABSTRACT

Spatial patterns of abundance of the whole macrobenthic assemblage and of its 10 most numerous species were examined across hierarchically nested scales within a 0.85 ha area of intertidal seagrass in subtropical Moreton Bay, Queensland. Multifractality characterised the assemblage and all ten dominant species across those scales (*c.* 33, 130, 530 & 2115 m^2), with patchiness of assemblage numbers and those of at least some dominants exhibiting scale-invariance. The system displayed several abundance peaks, 12% of stations accounting for 88% of total variance, with many individual dominants showing a series of non-overlapping 'hot-spots'. Scale invariance and multifractality occurred notwithstanding low levels of species interaction consequent on maintenance at very low density. This suggests that critical self-organisation cannot be responsible for such patterning. Contrary to received wisdom, coefficient β of Taylor's power-law cannot form an index of aggregation, although it does indicate direction of change in dispersion pattern with changing numbers.

1. Introduction

Natural habitats are mosaics of patches (MacArthur, 1972; Wiens, 1989; Grünbaum, 2012) and seagrass beds are no exception (Duffy, 2006). Indeed, their botanical simplicity, ease of access and sampling, and, often, markedly contrasting faunal ecology to that of adjacent areas of unvegetated sediment have rendered them an ideal system for the study of the effects of such habitat patchiness on the associated macrobenthic fauna (Eggleston et al., 1998; Healey and Hovel, 2004; Maciá and Robinson, 2005; McCloskey and Unsworth, 2015; Henderson et al., 2017). Changes in the biodiversity and abundance of seagrass macrofaunal assemblages across patch systems with differing environmental characteristics are commonplace (e.g. Barnes and Ellwood, 2012a; Barnes, 2017a; Magni et al., 2017), but patchiness of species richness, or indeed its absence (Barnes, 2016; Boyé et al., 2017), also occurs in areas where systematic environmental variation appears to be lacking. This can be more instructive in aiding understanding of the causes and drivers of benthic biodiversity patterns (Chang and Marshall, 2016). However induced, such heterogeneous distribution of individual species is of critical macro-ecological importance, being for example the primary cause of the rate of distance-decay phenomena (species turnover inducing a loss of assemblage similarity over distance), whilst actual levels of assemblage similarity are primarily influenced by relative species abundances (Anderson et al., 2005; Morlon et al., 1999).

Faunal patchiness, like virtually all ecological phenomena in marine soft-sediment habitats, is well known to be affected by spatial scale (Morrisey et al., 1992; Underwood and Chapman, 1996; Kraan et al., 2009). Therefore the processes likely to be involved in creating patchiness cannot be understood without an appreciation of how it varies across the scales concerned (Underwood et al., 2000). Variation in seagrass assemblage composition across space has been investigated in these terms, including that of the benthic macrofauna (Omena and Creed, 2004; Barnes and Barnes, 2011; Barnes and Ellwood, 2012b; Magni et al., 2017). How such compositional variation then affects emergent assemblage properties, including overall abundance, however, remains unclear, and measurement of variability in organismal abundance followed by elucidation of the underlying causes has been identified as a major goal in ecology (Denny et al., 2004; Dal Bello et al., 2015).

The effect of changing spatial scale on the patterns in which intertidal soft-sediment faunal abundance is dispersed, whether of individual species or of whole assemblages, has also received some attention, with seemingly rather variable results. Thus Barnes and Barnes (2011) and Chertoprood and Azovsky (2013) found that the dominant individual benthic species in Queensland *Zostera* (*Zosterella*) *capricornia*

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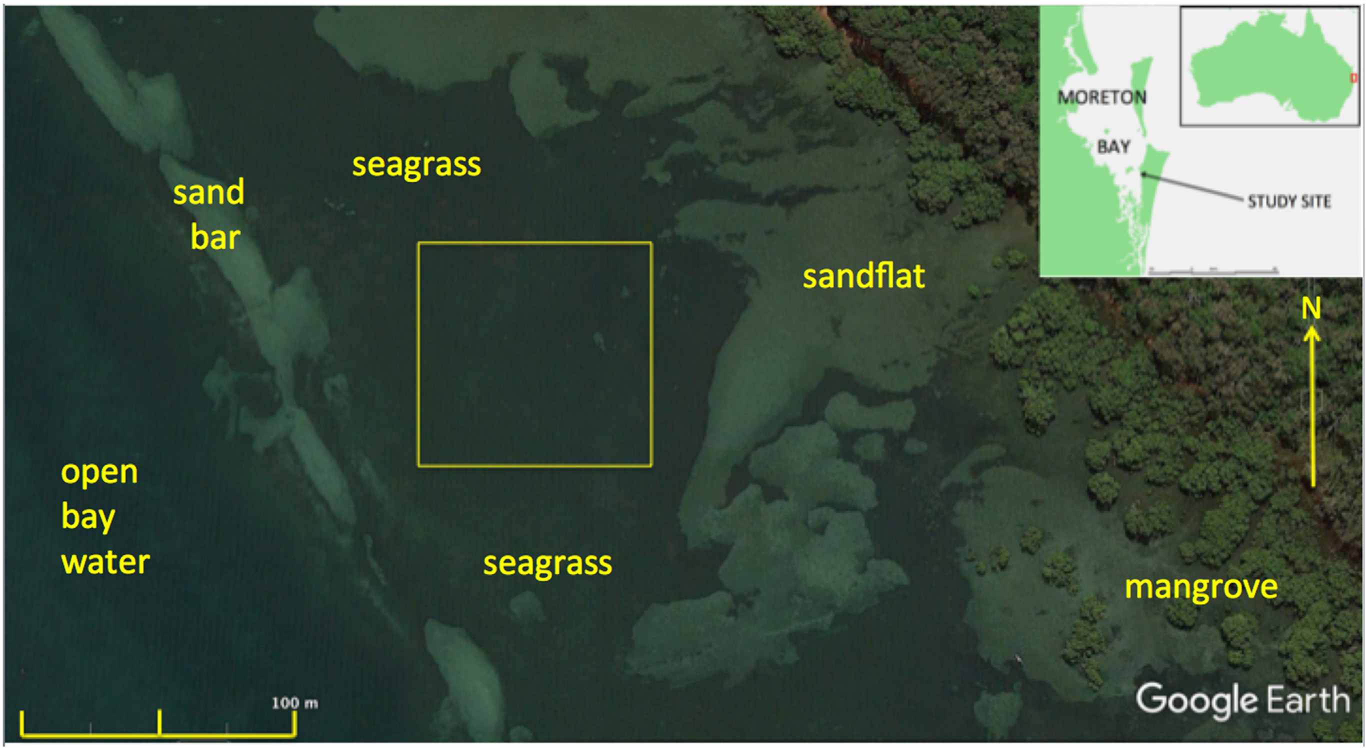

Fig. 1. Study location, including a Google Earth Pro image centred on 27°30′26″S,153°24′30″E in Habitat Protection Zone 2 of the Moreton Bay Marine Park, showing topography at low tide of the investigated stretch of North Stradbroke Island intertidal seagrass and the region sampled by the lattice of 16 × 16 evenly spaced stations. Image © 2017 DigitalGlobe (*nb* the image dates from 2003; the two small bare patches in the north-east quadrant are no longer there).

beds and in White Sea soft sediments, respectively, showed random dispersion across relatively small spatial extents (or when at low population density) and only occurred patchily when assessed across larger sampling areas (or when present at high densities). In marked contrast, however, the ecologically equivalent species at relatively low densities across seemingly similar *Z.* (*Zosterella*) *capensis* beds in South Africa each showed patchy distribution across all spatial extents investigated (1 m - > 1 km) (Barnes, 2010, and see Schabenberger and Gotway, 2004). Very little work has been devoted to whether such patches of different species coincide in space or whether they are complementary, although relevant data have been collected at some sites since the 1950s (Bassindale and Clark, 1960; Edwards et al., 1992). In some instances total macrofaunal abundance per unit area has been shown not to vary significantly across local space (e.g. Barnes, 2013; Lefcheck et al., 2016), suggesting that individual species patches tended to cancel each other out. In other cases, however, marked spatial heterogeneity in overall macrofaunal abundance has also been observed in seagrass beds (as well as in adjacent areas of bare sand), notwithstanding that homogeneous species density and diversity characterised the same systems (Barnes, 2014, 2017b). Where no significant differences occur across space in the number of assemblage individuals in unit sample (Barnes, 2013), this, by definition, will result in scale-invariant area-abundance relationships. But is this also the case for animal numbers in spatially heterogeneous seagrass systems?

In this study we focus on a range of relatively small spatial scales within which some populations of soft-sediment macrobenthic species have been demonstrated individually to show fractal-like patterning, i.e. within 1 ha (Azovsky et al., 2000; Warwick et al., 2006). As is emphasised below, although (mono)fractal analysis may be appropriate for the study of two dimensional systems (e.g. presence/absence data), it is not so for systems exhibiting greater complexity, in which a single fractal dimension is insufficient to describe their dynamics; for example those involving spatial variation in abundance as well as in occurrence. These require multifractal analyses (Harte, 2001). In the present context, it needs stressing that in the ecological literature, the main characteristic of (mono)fractal systems usually emphasised is their spatial self-similarity; multifractality, however, implies no such scale invariance.

In an attempt to understand the manner in which per-unit-area abundance of a whole macrofaunal seagrass assemblage is patterned spatially, and to investigate whether the degree of patchiness itself varies across scales, the present research was therefore conducted via the use of indices of patchiness and, for the first time on a macrobenthic faunal assemblage, multifractal analyses. These were undertaken within a single 0.85 ha seagrass bed of homogeneous visual appearance (i.e. lacking unvegetated patches or areas differing in apparent percentage cover) and without obvious environmental gradients. The bed concerned, however, was one already known to support significantly patchy distributions of individual dominant faunal taxa and patchy overall per-unit-area animal abundance (Barnes, 2014; Barnes and Hamylton, 2015).

2. Methods

2.1. Study area and sampling protocol

Macrofaunal sampling was conducted over a period of 9 weeks during the 2017 austral spring at a site at the southern end of the Rainbow Channel coast of North Stradbroke Island (aka Minjerribah) within the relatively pristine Eastern Banks region of the oligohaline, mesotidal, subtropical Moreton Bay Marine Park, Queensland (Dennison and Abal, 1999; Gibbes et al., 2014). The lower portion of the intertidal zone of this coast supports seagrass beds dominated by dwarf-eelgrass, *Zostera* (*Zosterella*) *capricorni* [*Nanozostera capricorni* in the recent revision of the Zosteraceae by Coyer et al. (2013)] but also with some *Halophila ovalis* and *Halodule uninervis* (Young and Kirkman, 1975; Abal et al., 1998). The precise site investigated, centred on 27°30′26″S, 153°24′30″E in Deanbilla Bay, was a *c.* 125 × 200 m block