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Spatial homogeneity of benthic macrofaunal biodiversity across small spatial scales

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ABSTRACT

Spatial heterogeneity of biodiversity has been extensively researched, but its spatial homogeneity is virtually unstudied. An intertidal seagrass system at Knysna (South Africa) known to display spatially homogeneous macrobenthic species density at scales $\geq$0.0275 m^2 was re-investigated at four smaller spatial grains (0.0015 m^2 - 0.0095 m^2) via a lattice of 8 $\times$ 8 stations within a 0.2 ha area. The aim was to investigate the null hypothesis that spatial homogeneity of species density is not a fixed emergent assemblage property but breaks down at small spatial grains within given spatial extents. Although assemblage abundance was significantly heterogeneous at all spatial grains investigated, both species density and functional-group density were significantly homogeneous across those same scales; observed densities not departing from those expected on the basis of independent assortment. Spatial homogeneity is therefore an emergent assemblage property within given spatial extents at Knysna and probably at equivalent sites elsewhere. Equivalent species density in South Africa, Australia and the UK at spatial grains <0.03 m^2, however, is a scale-related sampling artefact, as may be temporal homogeneity of species density at Knysna over a 3 year period, but close similarity in shape of their species occupancy distributions remains unexplained.

1. Introduction

Number of benthic macrofaunal species per unit area has been shown to display statistically significant homogeneity across space in three intertidal seagrass systems (Barnes, 2013a, 2014); notwithstanding that, as is typically the case (Morrisey et al., 1992; He and Gaston, 2000; Ysebaert and Herman, 2002; Honkoop et al., 2006; etc), individual component species were distributed patchily and overall assemblage composition was consequently heterogeneous over small spatial scales. These three systems span a range of climatic and geographical zones, from the very high abundance (>60,000 ind m^2) but species-poor (<35) cool-temperate European North Sea, through the low abundance and moderately diverse warm-temperate Knysna estuarine bay in the South African Indian Ocean, to very low abundance (<2500 ind m^2) but species-rich (>140) Moreton Bay in the subtropical Australian Pacific.

The benthic macrofauna of these contrasting habitats does, however, share the common feature of stochastic assemblage composition across distances of <1 km (Barnes and Ellwood, 2011a, b; 2012a). The reason for this has not been investigated, but it may be that they are held well below carrying capacity by the top-down pressure of predation, especially from those juvenile nekton that use seagrass beds as nursery areas (O'Brien, 1994; Heck et al., 2003; Verweij et al., 2006; McDevitt-Irwin et al., 2016). Top-down control occurs widely in seagrass systems (Burkholder et al., 2013; Ebrahim et al., 2014), and it has frequently been observed that protection of seagrass mesograzers and other similarly-sized macrobenthic prey from microcarnivorous fish and crustacean predators results in significant increases in their numbers (Moksnes et al., 2008; Lewis and Anderson, 2012; Reynolds et al., 2014). Certainly, the macrobenthic abundances of <4000 ind m^2 characterising the Knysna and Moreton Bay sites seem very much lower than would be expected to be supportable by the available productivity (Barnes, 2013a). If maintained at low population densities, interspecific interactions between species will be minimised, and spatial homogeneity of species number per unit area ('species density' *sensu* Gotelli and Colwell, 2001) is then precisely what would be predicted in habitats lacking significant environmental gradients (Barnes and Barnes, 2014a). It will occur wherever the component species are

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distributed independently of each other, regardless of the nature of their relative frequencies of occupancy (= 'occurrence', 'incidence' or 'constancy') (Colwell and Hurtt, 1994; Barnes and Barnes, 2014a).

Spatial scale of analysis, however, greatly influences ecological metrics (Jumars, 1975; Wiens, 1989; Levin, 1992; Chase and Knight, 2013) including dispersion patterns (Turner et al., 1989; Pech et al., 2007; Mysak et al., 2013); and measures of species density are by their nature scale-specific (Whittaker et al., 2001; Gray, 2002). Further, the effect of generalist predators of the type possibly maintaining the random assortment of prey species may itself vary with spatial scale of analysis (Thrush, 1999), with knock-on effects on the spatial distribution of the prey. The seagrass macrofaunal homogeneity indicated above referred specifically to a spatial grain of 0.0275 m^2 although, as is inherent in uniform dispersions, it is also likely to apply across larger scales within the same spatial extent as well. Thus in the absence of evident environmental gradients, Barnes and Barnes (2011) recorded an effectively constant macrofaunal species density of 53 (±1.5) per 0.24 m^2 along 6 km of Moreton Bay seagrass shoreline in spring 2009, and one of 84 (±3.7) per 0.80 m^2 was found along the same coast four years later (from the database of Barnes, 2014). Further, spatial homogeneity does not apply only to taxonomically defined assemblages, since Barnes and Hamylton (2015) have found it in the proportions of the seagrass macrofaunal individuals occurring in each of the various component functional groups (*sensu* McGill et al., 2006; Violle et al., 2007) over spatial scales of 4000 m^2. To date, most attention has been focussed on these relatively large sampling scales (Pringle, 1984; Hewitt et al., 1998; Hortal et al., 2006; Yamakita and Nakaoka, 2011), and very little information is available across arguably more meaningful scales of <0.02 m^2 over which many potential ecological interactions are likely to operate for the sizes and degrees of mobility of the species under study (Huston, 1999; and see Collins and Glenn, 1997; Attrill et al., 2000).

Lewis and Stoner (1981), however, have compared overall macrofaunal species density values obtained using different small-sized cores (0.009 m^2, 0.005 m^2 and 0.002 m^2) to sample the same total area of seagrass sediment (0.14 m^2). They found that core size did not affect assessment of overall species density nor their species accumulation curves, although the estimated population densities of various individual species did vary. But data are lacking on whether homogeneity of species density per unit sample or subarea (when it occurs at all) is only manifest above a threshold spatial grain, as may be the case with other soft-sediment phenomena (Thrush et al., 2001), and if so what the critical grain size may be. Analytical grain should always be consistent with the information content of the data (Elith and Leathwick, 2009) and the smallest of potential grain sizes may contain little information (few individuals and even fewer species). Unfortunately, although heterogeneity has spawned a voluminous literature (Ritchie, 2009; Stein et al., 2014), emergent homogeneity has received almost none, except in respect of regularly repeated patterning (e.g. Rietkerk and van der Koppel, 2008). Patchiness may occur through an effectively infinite range of nested spatial extents (Kotliar and Wiens, 1990; Marquet et al., 1993; Azovsky et al., 2000). Does its converse, homogeneity of number per unit area, when present show a comparable pattern, at least at relatively small spatial scales, notwithstanding the apparent general inverse relationship between patchiness and grain within fixed-sized extents (Francis and Klopatek, 2000; Lepczyk et al., 2007)? It was therefore the purpose of the present study to investigate the null hypothesis that spatial homogeneity of species density is not a fixed emergent assemblage property but breaks down at small spatial grains within given spatial extents. This was done by revisiting one of the systems in which homogeneity had previously been demonstrated to occur at a scale of 0.0275 m^2 (Barnes, 2013a) and by re-sampling it at a series of smaller spatial grains. The same data set also permitted investigation of the equivalent null hypothesis relating to spatial homogeneity of density of the component functional groups. *N.B.* Confusingly, 'spatial uniformity' and equivalent terms have been used in the literature with reference to two contrasting parameters; i.e. to describe both dispersions in which the observed values of a spatial variable are too regular to be a result of chance (as in Jumars, 1975; Barnes, 2014), and, conversely, distributions in which all possible values of a variable occur with effectively the same probability or frequency (e.g. Jetz and Rahbek, 2001). To avoid such potential confusion, the term 'spatial homogeneity' is used here to refer to statistically significant spatial regularity or evenness of numbers per unit area (*sensu* Calow, 1998; Perry et al., 2002; Van der Koppel et al., 2005).

2. Materials and methods

2.1. Study area and protocol

Spatial distribution of macrobenthic abundance and biodiversity was surveyed over 6 weeks of the 2015–16 austral summer in the 5 ha intertidal seagrass bed at Kingfisher Creek Bay within the warm-temperate Knysna estuarine system, part of South Africa's Garden Route National Park (Fig. 1). The sampled region was in the centre of the bed at approximately mean low water tidal level and was set within the same specific area investigated previously at larger grain and it was re-sampled at the same time of the year (Barnes, 2013a). Cape dwarf-eelgrass, *Zosterella capensis*, was the sole seagrass species present. A nested sampling design of the type used earlier (i.e. as recommended by Morrisey et al., 1992; Ghertsos et al., 2000), is not possible at the smallest spatial scales. Instead, as advocated by Fortin (1994) and Cole et al. (2001), data were collected from a two-dimensional lattice. This comprised 64 individual 1 m^2 stations in a 8 × 8 grid, with 8 stations separated by intervals of 0.2″ latitude (i.e. *c.* 6 m) in a transect down the shore and with each such transect replicated 8 times across the shore at intervals of 0.2″ longitude (i.e. *c.* 5 m), as determined by means of a hand-held GPS + GLONASS unit; the four corners of the 0.2 ha sampled area being 38.2″S/08.5″E, 38.2″S/09.9″E, 39.6″S/08.5″E, and 39.6″S/09.9″E (all 34°03′S/23°03′E).

A core sample of each of three different grain sizes — 0.0015 m^2 (4.4 cm diam.), 0.0026 m^2 (5.8 cm diam.) and 0.0054 m^2 (8.3 cm diam.) — was taken from within each station to a depth of 10 cm; most benthic macrofauna in seagrass beds being known to occur in the top few cm of sediment (e.g. 98% in the top ≤5 cm in the studies of Lewis and Stoner, 1981; Klumpp and Kwak, 2005). Such samples will collect the smaller and most numerous members of the macrofauna that constitute the large majority of invertebrate biodiversity (Gaudêncio and Cabral, 2007; Albano et al., 2011), though not the scarcer megafauna or deeply-burrowing species. For each spatial grain, the analysed database was then not a fixed total area sampled (*c.f.* Lewis and Stoner, 1981 above) but a fixed number of samples (64) except in one case (see below). Although not strictly comparable, combining the samples taken from each station permitted the additional scale of 0.0095 m^2 to be included in analyses. All samples were collected immediately after tidal ebb from the area of shore concerned, and were gently sieved through 710 μm mesh on site. Retained material from each core (i) was placed in a large polythene bag of seawater within which all seagrass material was shaken vigorously to dislodge all but sessile animals and then discarded (except as specified below); (ii) was then re-sieved and transported immediately to a local field laboratory, and (iii) was there placed in a 30 × 25 cm white tray in which the living fauna was located by visual examination, continuing until no further animal could be seen during a 3 min