Journal of Experimental Marine Biology and Ecology 314 (2005) 79–97

Journal of
EXPERIMENTAL
MARINE BIOLOGY
AND ECOLOGY

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Contrasting spatial heterogeneity of sessile organisms within mussel (*Perna perna* L.) beds in relation to topographic variability

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Received 26 March 2004; received in revised form 1 September 2004; accepted 14 September 2004

Abstract

We examined the spatial heterogeneity in three sessile rocky shore organisms, the mussel *Perna perna*, the barnacle *Octomeris angulosa* (Sowerby) and the red alga *Gelidium pristoides* (Turn.) at a range of continuous local scales along horizontal transects within mid- and upper mussel beds of South African shores. We also examined the relationships between variability of organisms and topographic features (rock depressions, slope, aspect), and between mussel, barnacle and algal variability over the same scales. To estimate spatial heterogeneity, we analyzed scaling properties of semivariograms using a fractal approach. Relationships between different variables at the different scales were examined by cross-semivariograms. Spatial dependence of *P. perna* variability increased with spatial dependence of topographic variability, so that scaling regions of mussel and topographic distributions corresponded well. This relationship often improved with larger local scales (mussel cover increased with depressions, steeper slope and aspect towards waves), while at smaller spatial scales, variability in mussel cover was less well explained by variability in topography. The variability of the barnacle *O. angulosa* exhibited spatial dependence, even on topographically unstructured shores. In contrast, the distribution of the alga *G. pristoides* revealed high fractal dimensions, showing spatial independence on topographically unstructured shores. Algae also showed a very strong negative relationship with mussels at most local scales, and a negative relationship with barnacles in upper zones, especially at larger local scales. Barnacles may show clear spatial dependence because of hydrodynamics (at larger local scales) and the need to find a future mate in close proximity (at smaller local scales), while algae may show a strong negative relationship with mussels because of competition for space.

Keywords: Algae; Barnacles; Fractal dimension; Intertidal distribution; Mussels; Rocky shores; Spatial dependence

1. Introduction

While variability is a general term indicating changes in the value of a variable, heterogeneity refers to the structure in variability across different

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doi:10.1016/j.jembe.2004.09.010

spatial scales, which may be categorized as patchy, uniform or random (Kolasa and Rollo, 1991; Ettema and Wardle, 2002). Spatial dependence is a concept dealing with the similarity between data points as a function of spatial separation (lag) between them (Legendre, 1993; Ettema and Wardle, 2002). Since spatial independence is a basic assumption in many statistical tests, and since spatial dependence can often be detected in ecological systems (Palmer, 1988; Wiens, 1989), the importance of the assessment of spatial heterogeneity at different scales becomes apparent. Thus, the design of a field experiment may be facilitated or complemented by first studying spatial heterogeneity of an organism.

High variability in abundances of organisms at spatial scales within and among shores has been found in many intertidal studies (e.g., Morrisey et al., 1992; Lindegarth et al., 1995; Harris et al., 1998; McKindsey and Bourget, 2000; Lawrie and McQuaid, 2001; Benedetti-Cecchi et al., 2003). Because these studies have examined variability across local (within shores: cm–m scales) meso (between shores: km scales) or regional (between regions: 10s–100s km scales) scales, the variability of organisms within shores has usually been estimated at only one or two small scales simultaneously. Thus, while the structure of the spatial variability has been studied across local to regional scales in these studies, this structure has not been analyzed within small scales. The intertidal studies that have quantified spatial structure in the variability of organisms at a range of within-shore scales have mainly been from soft-bottom habitats (e.g., Hall et al., 1994; Kostylev, 1996; Hewitt et al., 1997, 2002; Kostylev and Erlandsson, 2001), with only a few from rocky shores (Underwood and Chapman, 1996; Johnson et al., 1997; Guichard et al., 2000; Erlandsson and McQuaid, 2004). Relationships between spatial dependence in the distribution of an organism and of other organisms or of habitat features is commonly studied in plant, soil, freshwater and plankton ecology (Seuront and Lagadeuc, 1998; Dale, 2000; Schmid, 2000; Ettema and Wardle, 2002), but not on rocky shores, exceptions being Guichard et al. (2000) and Erlandsson and McQuaid (2004).

Nested heterogeneity, i.e., multiple scales of patchiness, with smaller patches or gradients integrated into larger ones, may occur because several physical and biological factors or processes that influence distribution patterns operate and interact at different characteristic spatial scales (Wiens, 1989; Sugihara and May, 1990). For example, hydrodynamics, substratum type and surface topography are important in the settlement and recruitment of marine invertebrates (Denny, 1987; Barry and Dayton, 1991; Booth and Brosnan, 1995; Abelson and Denny, 1997), especially for the aggregation of some barnacle species at smaller scales (LeTourneux and Bourget, 1988; Lemire and Bourget, 1996; Harvey and Bourget, 1997; Bourget and Harvey, 1998; Hills et al., 1999).

Mussel beds provide secondary space and microhabitats for a wide diversity of associated benthic species (Suchanek, 1985; Sebens, 1991; Lintas and Seed, 1994; Kostylev, 1996), generally because of their high architectural and horizontal complexity (Sebens, 1991; Kostylev et al., 1997; Snover and Commito, 1998; Commito and Rusignuolo, 2000). At within-shore scales, intertidal mussel beds can appear spatially homogeneous (80–100% cover), with distinct gaps often created by strong waves (Paine and Levin, 1981; Denny, 1987). On other shores, however, mussel abundance within beds may be very patchy. Some studies of intertidal mussel distribution over a large range of continuous local scales have found that there is often spatial dependence of this variability, with higher spatial heterogeneity at smaller local scales and several natural scaling regions of the spatial variability (Kostylev and Erlandsson, 2001; Erlandsson and McQuaid, 2004).

On rocky shores in southern Africa, the distribution of mussels varies markedly with the spatial scale considered, both at a regional scale between the west and the east coasts (Harris et al., 1998) and between shores within a region (Lawrie and McQuaid, 2001). Wave-exposed shores exhibit larger sizes, higher mortality and higher growth rates than sheltered shores (McQuaid and Lindsay, 2000; McQuaid et al., 2000). There is also high, unpredictable variability (especially in recruitment) at within-shore scales (Lawrie and McQuaid, 2001). This variability reveals strong spatial dependence in the density of adults at a range of within-shore scales (Erlandsson and McQuaid, 2004), while spatial dependence of recruitment variability increases with recruit size. Macroalgae and barnacles may compete with mussels for