Estuarine, Coastal and Shelf Science xxx (2013) 1–12

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Multi-scale spatial variability in intertidal benthic assemblages: Differences between sand-free and sand-covered rocky habitats

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A R T I C L E I N F O

Article history:
Received 19 March 2013
Accepted 10 August 2013
Available online xxx

Keywords:
biodiversity
sediments
spatial variations
intertidal environment
assemblage structure
rocky shores

A B S T R A C T

The presence of high loads of sediment is often thought to be negatively associated with sessile species living on rocky reefs, leading to assemblages with low alpha diversity (average species richness) and beta diversity (heterogeneity). Here we examine the effects of sand deposition on rocky assemblages by contrasting the multivariate composition, spatial variation and alpha diversity between sand-free assemblages and assemblages covered by sand. The assemblage composition differed markedly between sand-covered and sand-free reefs, supporting the idea of that sedimentation is one of the major physical factors influencing the structure of benthic assemblages. More surprisingly, our findings suggest that sand-covered assemblages have greater spatial variation in terms of multivariate dispersion at small spatial scales (from metres to 100s of metres) than sand-free assemblages. No differences were detected between the two habitats in average species richness and Shannon diversity, whereas sand-covered assemblages were found to be taxonomically more diverse. Thus, the effects of sedimentation on the diversity of assemblages from rocky shores remain unclear and further investigation is needed to clarify its structuring role in combination with other environmental factors.

1. Introduction

The successful management and protection of biological diversity, the assessment of anthropogenic impacts and the restoration of altered ecosystems rely largely on understanding the processes and factors that structure assemblages (Chapman, 1999; Anderson et al., 2005; Terlizzi et al., 2007). Causal relationships between influential factors, ecological processes and subsequent distribution of species need to be explored by experimental research (Underwood et al., 2000), but quantifying the range of natural variation of assemblages may help to identify which physical and biological factors are most relevant to be explored first under an experimental approach (Underwood and Chapman, 1996; Menconi et al., 1999; Coleman, 2002). Thus, research efforts have increased recently to provide a more in-depth knowledge of assemblage heterogeneity for a broad variety of habitats (Benedetti-Cecchi, 2001; Pérez-Ruzafa et al., 2007; Smale et al., 2010). In particular, marine benthic assemblages have been found to be highly variable across different scales of time and space (Coleman, 2002; Fraschetti et al., 2005).

With regard to intertidal systems, ecologists have devoted special attention to examining patterns of variation along the vertical gradient imposed by tidal cycles. The role of biotic interactions and physical factors in structuring intertidal assemblages along this gradient of stress has long been studied (Dayton, 1971; Schonbeck and Norton, 1980; Moreno and Jaramillo, 1983; McCook and Chapman, 1993; Jenkins et al., 1999). By contrast, along-shore variation has received far less attention despite the fact that it might be greater than vertical variation, depending on the spatial scale (Benedetti-Cecchi, 2001; Valdivia et al., 2011). In recent years, studies on horizontal heterogeneity have quantified variability across multiple scales of space, increasing knowledge of the processes that regulate species distribution from fine (patchiness) to broad spatial scales (Menconi et al., 1999; Johnson et al., 2001; Coleman, 2003; Denny et al., 2004).

The physical factors traditionally explored as sources of variation in intertidal assemblages include seawater temperature, salinity, wave exposure and intertidal height (Stephenson and Stephenson, 1949; Underwood, 1978; Druehl and Green, 1982; McQuaid and Branch, 1984; Josselyn and West, 1985). However, despite the large role that sedimentation plays in modifying coastal

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http://dx.doi.org/10.1016/j.ecss.2013.08.019

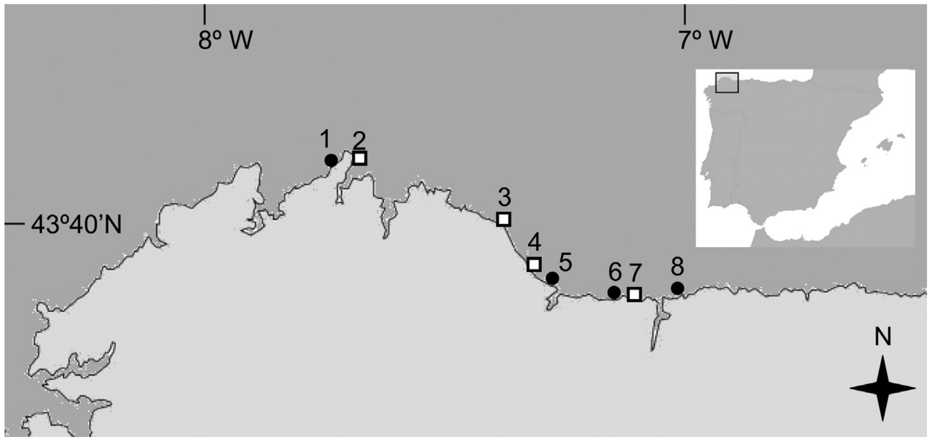

Fig. 1. Map of the study area showing the sampling locations on the northwestern coast of the Iberian Peninsula: 1) Picón, 2) Bares, 3) Burela, 4) Peinzás, 5) Llas, 6) Catedrales, 7) Rinlo and 8) Serantes. Unshaded squares and shaded circles correspond to sand-free and sand-covered reefs, respectively.

environments, its potential influence on the structure of rocky assemblages has been rarely studied until recently (but see Daly and Mathieson, 1977; Littler et al., 1983; Airoldi et al., 1995). In recent years there have been some studies on the effects of the increase of anthropogenic sediment loads in rocky coastal assemblages (Airoldi, 2003 and references therein), which has been reported as a major threat to marine biodiversity on a global scale (United Nations Environment Programme, 1995). By contrast, the role of natural sedimentation in the structure of benthic assemblages has received little attention (but see e.g. Daly and Mathieson, 1977; Taylor and Littler, 1982; Littler et al., 1983; Airoldi and Hawkins, 2007; Anderson et al., 2008b). The two approaches to the study of sedimentation in regard to benthic assemblages agree in that sedimentation affects the composition and distribution of rocky coast organisms, but they present contrasting views regarding its effects on diversity. The prevalent opinion is that high sediment loads related to anthropogenic activities are detrimental to the overall diversity of rocky coast organisms (Airoldi, 2003 and references therein), but some authors support the hypothesis that the natural presence of sediments promotes species diversity (Littler et al., 1983; McQuaid and Dower, 1990). However, a multiple-scale approach comparing the relevant spatial-scales of variation in diversity between sand-covered and sand-free rocky assemblages has never been attempted. Indeed, the issue of scale has rarely been addressed in research into the impacts of sedimentation on rocky coast assemblages (Airoldi, 2003).

Descriptive studies of rocky intertidal assemblages from the Atlantic coast of the Iberian Peninsula have shown differences in composition between sand-free and sand-covered rocky assemblages (e.g. Miranda, 1931; Ardré, 1970; Pérez-Cirera, 1976; Pérez-Cirera and Maldonado, 1982; Bárbara, 1994; Bárbara et al., 1995; Díaz-Tapia and Bárbara, 2005). However, quantitative data on spatial patterns of distribution of organisms are scarce (Boaventura et al., 2002; Cremades et al., 2004; Araújo et al., 2005; Díez et al., 2009). In addition, all these studies are focused on sand-free rocky habitats, while there are no previous quantitative studies of sand-covered assemblages, even though they are commonly distributed along the Atlantic coastline of the Iberian Peninsula (see Díaz Tapia et al., 2011).

This study assessed differences in spatial patterns of variability in multivariate structure and diversity between sand-free and sand-covered rocky assemblages. We use a hierarchical design to quantify the magnitude of variation attributable to each of several spatial scales at each of the two habitats. The use of nested hierarchical sampling designs to examine both univariate and multivariate response variables at multiple spatial scales has led to a greater appreciation of the importance of scale in ecology (Underwood and Chapman, 1996; Fraschetti et al., 2005). These designs provide unbiased, independent, rigorous quantitative measures of variability at predetermined spatial scales with a view to testing structured hypotheses (Underwood and Chapman, 1996; Terlizzi et al., 2007). Specifically, we address 3 main questions: (1) do sand-free and sand-covered rocky assemblages differ in terms of multivariate structure and alpha diversity (species richness, Shannon and Taxonomic Distinctness measures); (2) are patterns of variability in assemblage structure and diversity dependent on spatial scale, and (3) are sand-free rocky assemblages spatially more heterogeneous than sand-covered assemblages?

2. Methods

2.1. Study area

The study area extends for approximately 100 km along the northern Galician coast in northwestern Spain (43°33′ N to 43°47′ N and 006°56′ W to 007°48′ W; Fig. 1). This is an open coast exposed to a large fetch where swell comes mainly from NW (38%) and WNW (29%), with mean significant heights (Hs) of 3 and 2.5 m, respectively (Puertos del Estado, 2013). It consists mostly of rocky substratum interrupted irregularly by the presence of rias and beaches. Tides are semidiurnal with a spring tidal range of up to 3.8 m, and the sea surface temperature ranges from 11 °C to 18 °C (Bárbara et al., 2005). The flora falls within warm-temperate NE Atlantic subregion 1 (WNE1) according to the phytogeographical scheme proposed by Hoek and Breeman (1990).

2.2. Collection of data and sampling design

Sampling was conducted from July to August 2010. Two different habitats at the low intertidal level (between 0.4 m and 1.2 m above MLWL) were selected for this study: sand-free and sand-covered rocky platforms. The former consists of rocky shores located at least 100 m apart from sandy beaches. The latter are rock outcrops on sandy beaches constantly covered by a sand layer (>1 cm thick) which is trapped within algal turfs. Sampling locations were randomly selected along a stretch of coastline about 100 km long, from a set of locations with comparable environmental conditions: N-NE-facing pristine open coastal shores exposed to strong wave action, with stable substrata (continuous bedrock and large blocks), smooth surfaces and slight to moderate