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Spatial variability of macrobenthic zonation on exposed sandy beaches

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ABSTRACT

We analysed the consistence of vertical patterns of distribution (i.e. zonation) for macrofauna at different spatial scales on four intermediate exposed beaches in the North of Portugal. We tested the hypothesis that biological zonation on exposed sandy beaches would vary at the studied spatial scales. For this aim, abundance, diversity and structure of macrobenthic assemblages were examined at the scales of transect and beach. Moreover, the main environmental factors that could potentially drive zonation patterns were investigated. Univariate and multivariate analyses revealed that the number of biological zones ranged from two to three depending on the beach and from indistinct zonation to three zones at the scale of transect. Therefore, results support our working hypothesis because zonation patterns were not consistent at the studied spatial scales. The median particle size, sorting coefficient and water content were significantly correlated with zonation patterns of macrobenthic assemblages. However, a high degree of correlation was not reached when the total structure of the assemblage was considered.

1. Introduction

Marine shorelines are boundary regions between oceans and continents. These intertidal boundaries experience steep environmental gradients that promote the development of distinct spatial structure of benthic assemblages (Schlacher and Thompson, 2013). The regular change of tides determines the duration of air exposure and thus, the abiotic stress related to temperature, desiccation, irradiance and salinity. Abiotic stress increases from the low to the high intertidal zone, where it exhibits its most extreme value (Valdivia et al., 2011).

Species are not equally distributed but occupy specific sections of the intertidal zone generating different faunal–floral belts across the intertidal. Studies focused in rocky shores have explored the vertical patterns of distribution of organisms (i.e. zonation) in response to the tidal gradient (e.g. Southward, 1958; Stephenson and Stephenson, 1949). These studies described ubiquitous broad-scale patterns of zonation that inspired many experimental studies about processes responsible for vertical distribution of populations on rocky shores (e.g. Hawkins et al., 1992; Underwood, 1985) showing the importance of biological (i.e. predation, herbivory, competition) and physical drivers in shaping intertidal zonation and improving our current understanding of the spatial distribution of organisms on rocky shores (Benedetti-Cecchi, 2001). Moreover, recent studies found that vertical variability and horizontal variability are comparable in magnitude at small spatial scale (10 s of cm) while horizontal variability is generally larger at scales of 100 s and 1000 s of m, pointing out the importance in considering both vertical and horizontal sources of variation to describe spatial patterns in the abundance of organisms (Benedetti-Cecchi, 2001; Valdivia et al., 2011).

Various attempts have been made to find similar universal zonation patterns on sandy beaches than those found on rocky shores. Defeo and McLachlan (2005) summarized macrofaunal zonation into 4 types: a) without a clear zonation; b) two zones (i.e. air breathers above the drift line and water breathers below; c) three zones, on the basis of the distribution of crustaceans (Dahl, 1952) and d) four zones, on the basis of physical properties of the beach, characterized by the movement and retention of interstitial water (Salvat, 1964). However, the question of whether a general biological zonation pattern exists on sandy beaches is still under debate (Brazeiro and Defeo, 1996; Raffaelli et al., 1991; Schlacher and Thompson, 2013). Recent studies support the existence of three biological zones on sandy beaches (Defeo and McLachlan, 2005; Schlacher and Thompson, 2013). Nevertheless, the number of biological zones depends on the beach type and so, reflective beaches present fewer zones than those dissipative (Defeo and McLachlan, 2005; Jaramillo et al., 1993).

In contrast with rocky shores, exposed sandy beaches are extremely dynamic environments inhabited by highly mobile species (McLachlan and Jaramillo, 1995). The mobility of beach species and the instability of substrate are considered as sources of variability in the biological zonation on sandy beaches and thus, high spatial variability on zonation patterns could be expected (Schlacher and Thompson, 2013). Despite the increasing number of studies about sandy beach macrobenthic

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assemblages, none has examined if biological zonation is consistent at a hierarchy of spatial scales. Investigating patterns of spatial variability of natural assemblages is a main and challenging goal of ecology (e.g. Underwood et al., 2000) and a key concept for basic and applied ecological issues, such as support assessments of anthropogenic impacts (e.g. Balestri et al., 2004) or the design of management and conservation measures (e.g. Benedetti-Cecchi et al., 2003). These issues are extremely important at sandy beaches, because they are exposed to increasing sources of anthropogenic disturbance (Schlacher et al., 2007). Therefore, the first objective of this study was to test if biological zonation, in terms of abundance, diversity and structure of macrobenthic assemblages is consistent at two different spatial scales: transect (10 s of m apart) and beach (kms apart). Considering the increasing evidence that spatial patterns in nature are scale dependent (Fraschetti et al., 2005; Wu and Loucks, 1995), the mobility of beach species and the instability of their substrate (McLachlan and Jaramillo, 1995; Schlacher and Thompson, 2013) we hypothesized that biological zonation on exposed sandy beaches will vary at the two studied spatial scales.

Many studies have stated that physical features of the beach control the benthic assemblages structure, especially on exposed beaches (McLachlan and Dorvlo, 2005; Schlacher et al., 2007). Once again in contrast to rocky shores, biological drivers seem to play a minor role in shaping patterns of distribution for macrobenthic assemblages on exposed sandy beaches (Defeo and McLachlan, 2005). The autoecological hypothesis states that assemblages in such environments are structured by the independent responses of individual species to the physical environment whereas biological interactions are minimal (McLachlan and Dorvlo, 2005). However, recent studies found that macrobenthic assemblages on exposed beaches are not primarily structured by physical drivers but, for a complex set of physical, chemical and biological drivers (Cisneros et al., 2011). Particularly, different biological zones across the intertidal of sandy beaches seem to be mainly related to sediment water content (Allen et al., 2010; Defeo and McLachlan, 2005; Jaramillo et al., 1993). The second objective of the present study is to explore if different environmental variables have some influence on the zonation of macrobenthic assemblages.

2. Materials and methods

2.1. Study area

This study was conducted on four sandy beaches in the North Portuguese coast (Fig. 1; Table 1). In this area the tidal regime is semi-diurnal, with the largest spring tides of 3.5–4.0 m. Coast is largely straight and exposed to the wave action, being the dominant swell directions W and NW and the most common wave height 1.5–2 m, with maximum values about 7 m. Moreover, the studied area is subjected to a seasonal upwelling that provides nutrients and increases the primary production in the water column (Lemos and Pires, 2004).

2.2. Sampling design

Sampling was done during low spring tides between 7th and 10th of September 2010 (one beach per day). A three-factor sampling design was used to assess the consistence of the tidal level effect on vertical patterns of distribution of macrobenthic organisms in terms of abundance, diversity and structure of assemblages at different spatial scales. The largest spatial scale was that of beach, which included four levels: Moledo, Âncora, Cabedelo and Ofir, spaced between kms and 10 s of kms apart from each other (Fig. 1; Table 1). At each beach, four transects, 10 s of ms apart, were established along a perpendicular line to the shoreline between the high and low water marks. Each transect

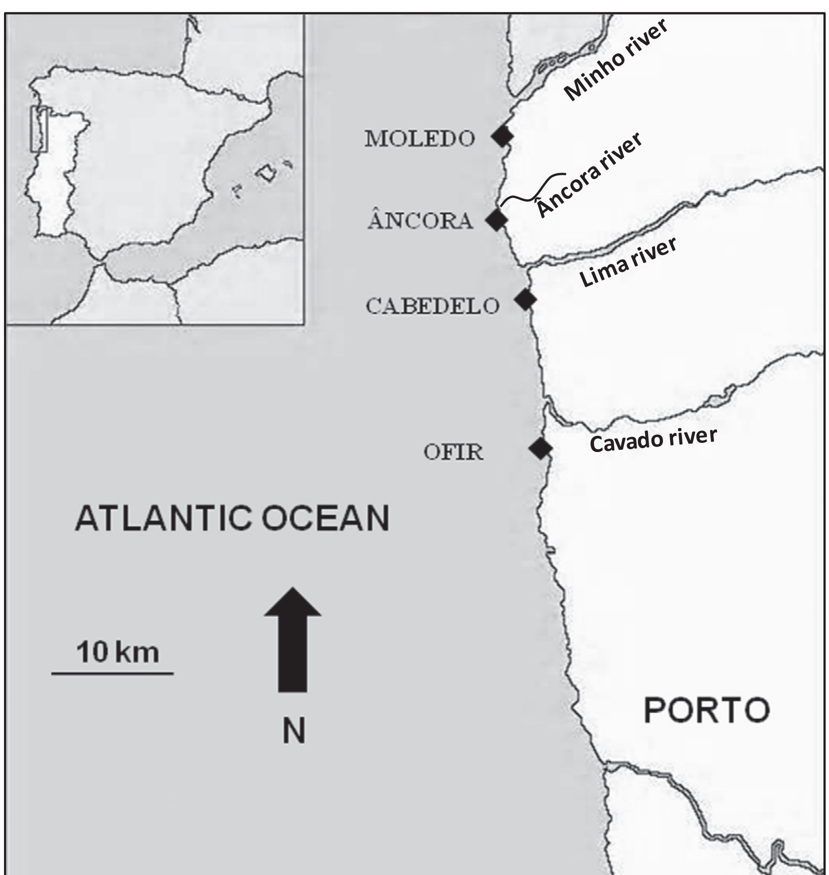

Fig. 1. Map of the Portuguese coast indicating the location of the 4 sampled beaches.