



Original Article

Intertidal zonation and latitudinal gradients on macroalgal assemblages: Species, functional groups and thallus morphology approaches



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ABSTRACT

Macroalgae are unavoidable biological elements when monitoring and assessing coastal environments. However, these tasks can be difficult to address because macroalgae a) present a high natural variability across a range of spatial and temporal scales, b) they imply a high sampling and laboratory processing effort and good taxonomical expertise (as they are a very diverse group of species), and c) there is insufficient knowledge about their structural and functional characteristics. This work addressed how the vertical (intertidal zonation) and horizontal (latitudinal gradient) variability of macroalgae assemblages are structured across continental Portugal, as well as how some surrogates for species-level biodiversity measures (namely functional groups and thallus morphology approaches) respond to such large-scale variability. Particularly, it was tested if intertidal zonation patterns are higher than fine-scale horizontal variation, and however, if vertical variation decreases along broad-scale horizontal variation. To do so, cover per species was taken (using a photographic and GIS methodological approach) from five sites located along the shoreline and along respective upper- mid- and lower-intertidal zones. The work findings include that both intertidal and latitudinal gradients impose deep structural changes on assemblages patterns. That is, broad-scale processes along Portuguese latitudes act as strongly as vertical stress gradients on assemblages patterns. Functional groups and thallus morphology approaches were useful to generalize the latitudinal assemblages patterns, where some groups emerge at the expense of others, and may improve biodiversity understanding and ecological synthesis. Because these surrogates decrease taxonomical expertise needs and can provide insight into the functional structure of macroalgal communities, their patterns founded may be particularly useful as reference data for further monitoring, so that shifts in such patterns might represent early warning surrogate approaches to detect environmental impact changes. Ultimately, to generate broader databases on rocky shore assemblages diversity (from species-level to functional groups and thallus morphologies approaches) can be useful for large-scale comparisons and for establishing ecological reference conditions, including for monitoring programs and environmental impact studies.

1. Introduction

Monitoring marine biodiversity of coastal areas is a key activity for conservation and management issues. However, the inherent spatial and temporal complexity and variability of coastal ecosystems will always present problems for meaningful biomonitoring (De Jonge et al., 2006). Difficulties related with the assessment of benthic communities, such as marine macroalgae thriving in intertidal rocky shores, include that a) they present a high natural variability across a range of spatial and temporal scales, b) they imply a high sampling and laboratory processing effort and good taxonomical expertise (as they are a very diverse group of species), and c) there is insufficient knowledge about

their structural and functional characteristics (Puente and Juanes, 2008).

In order to implement suitable monitoring programs and environmental impact studies, it is imperative to understand and quantify the magnitude of natural variability of macroalgal assemblages (Underwood, 1993; Chapman et al., 1995). Intertidal rocky shore systems are featured by vertical strong environmental stress gradients from the lower to the upper shore. Because of this, the spatial and temporal distribution of macroalgae assemblages is not homogeneous, but resultant from the effects of abiotic factors such as wave action, aerial exposure, irradiance, temperature ranges and time available for nutrient exchange, as well as of biotic factors such as competition,

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grazing, predation, facilitation and dispersal (Lobban and Harrison, 1994; Choi and Kim, 2004; Chappuis et al., 2014 and references therein). In spite of its heterogeneous distribution patterns, different species tend to occur at different intertidal levels, giving the idea of species vertical zonation (e.g. Araújo et al., 2005; Martins et al., 2008). The role of biotic interactions and abiotic factors in structuring intertidal assemblages patterns along its vertical gradient of stress has long been studied by many authors (see Araujo et al., 2005 and references therein; see Díaz-Tapia et al., 2013 and references therein). Nevertheless, different environmental factors emerge as the main drivers of ecological processes and patterns depending on the spatial scale (Levin, 1992; Willig et al., 2003). Actually, environmental factors variability influence assemblages' heterogeneity at different scales, ranging from local patchiness to variation along biogeographic gradients (e.g. Levin, 1992; Frascchetti et al., 2005; Tuya and Haroun, 2006). In larger geographical scales such as along latitudinal gradients, most species can vary in their ecology in response to large-scale environmental variability (Brown, 1984). For example, the sea surface temperature latitudinal gradient along Portuguese continental shores is translated in the overlapping distributions of macroalgal species of both boreal and Lusitanian origins (Lima et al., 2007). A large number of cold- and warm-water species have there their southern or northern distributional range edges (Ardré, 1971), while other species show latitudinal clines in abundance (Boaventura et al., 2002; Lima et al., 2007; Pereira et al., 2006). In this context, assemblages' vertical zonation patterns may vary along the coastline (horizontal variations) due to processes unrelated to vertical gradients (Chappuis et al., 2014). As broad-scale processes may add extra variability to the patchiness commonly observed at fine scales on rocky shores (Martins et al., 2008), it has been highlighted the need of more knowledge on how vertical variation (intertidal zonation) compares with horizontal variation measured at increasing spatial scales (in terms of sampling interval along the shoreline). Under this scope, recent studies have been focused on the variability of littoral assemblages at different spatial scales along shores (horizontal variation) taking or not taking into account the intertidal zonation patterns (vertical variation) (e.g. Araújo et al., 2005; Frascchetti et al., 2005; Martins et al., 2008; Burrows et al., 2009; Cruz-Motta et al., 2010; Valdivia et al., 2011; Veiga et al., 2012; Chappuis et al., 2014).

Now, in order to capture macroalgal assemblages' variability and relate it with their environment, its biodiversity assessment usually relies on proxy measurements such as assemblages' structural components (species richness, composition and abundance) based on species-level taxonomical identifications. However, to enumerate all species is time-consuming, labor-intensive, and a task requiring expertise so that extrapolative and other techniques will always be sought to optimize biodiversity assessment efficiencies. For example, surrogates of species richness and species diversity can be focused on identifying higher taxa levels (e.g. genera or families) as a surrogate of total community richness or diversity (Magierowski and Johnson, 2006; Konar and Iken, 2009). Furthermore, wanting to have an ecosystem approach to marine monitoring and management, the importance of developing methods to investigate ecological functioning is receiving increasing attention (e.g. Bremner et al., 2006). However, there is a lack of knowledge regarding the functional structure of benthic communities and the relationship between the functional structure and gradients of environmental change (Paganelli et al., 2012). Thus, in order to a) reduce the time and resources consumed in identifying species-level taxa and to b) provide insight into the functional structure of macroalgal communities, macroalgal species can be grouped into different functional groups based on their ecological and morphological attributes (Litter and Litter, 1980; Steneck and Dethier, 1994; Balata et al., 2011). Particularly, certain patterns of macroalgal growth forms have been linked to certain levels of environmental disturbance, where a link between morphological habit and ecological role or function has been suggested (e.g. Littler and Littler, 1980; Littler and Littler, 1984).

Macroalgae' functional-form groups (Steneck and Dethier, 1994) have been widely used, categorizing species differing in morphological features (e.g., filamentous, corticated, leathery among seven others), and where these form-based features are supposedly linked to different ecological functions. Moreover, biological traits, in the sense of well-defined measurable properties of organisms, usually measured at the individual level and used comparatively across species (McGill et al., 2006), may be seen as well as a surrogate measure of the (species-level measured) biodiversity. Orfanidis et al. (2011) assigned macroalgal species into five ecological status groups (ESG), based on different traits (morphological, physiological and life history), which responded along eutrophication gradients. Particularly, macroalgal trait-based thallus morphologies (encompassing different ESG, which categorizes species as filamentous and leaf-like, fleshy, calcareous upright and calcareous and non-calcareous crusts or thick; Orfanidis et al., 2011) may also be used to represent the functional structure of the macroalgal community. However, the use of surrogate measures implies that the relationship between the assemblage structure considering species and considering the surrogate is consistent in space (Colwell and Coddington, 1994). These assumptions have, however, rarely been examined explicitly (Smale, 2010; Rubal et al., 2011; Veiga et al., 2012). Under these scopes, the objective was to study how different functional groups (FG; Steneck and Dethier, 1994) and macroalgal trait-based thallus morphologies (TM; Orfanidis et al., 2011) respond to the natural varying intertidal zonation patterns and latitudinal gradients along Portuguese continental shores. Particularly, we hypothesize that 1) the variability of macroalgal assemblages' structure (cover per species) at vertical gradients (intertidal zonation) is higher than the variability at small-scale horizontal gradients (among transects within each study site); but also, and however, that 2) the assemblages vertical variability will be lower (or will decrease) with increasing broad-scale horizontal gradients (along sites located along different Portuguese latitudes) and 3) the patterns of FG and TM founded along such above mention Portuguese natural gradients will be useful as reference data for further monitoring, so that shifts in such patterns might be useful as early warning surrogate approaches to detect environmental impact changes.

2. Material and methods

2.1. Study area

Five study sites depicting macroalgal assemblages thriving in intertidal rocky shores were selected along the Portuguese continental coastline, distancing apart from each other in about 150 km (Fig. 1). Viana do Castelo (41° 41.911'N; 8° 51.229'W; sampled in June 2013) and Buarcos (40° 10.054'N; 8° 53.269'W; sampled in July 2012) sites are within a coastal area with wave-exposed conditions, sea surface temperature (SST) values around 15–15.5 °C, a dissolved inorganic nitrogen (DIN) and a dissolved inorganic phosphorous (DIP) reference value of 4.3 µM and 0.31 µM, respectively; Ericeira (38° 58.460'N; 9° 25.264'W; sampled in September 2014) and Queimado (37° 49.258'N; 8° 47.626'W; sampled in August 2013) sites are within a coastal area with moderately wave-exposed conditions, SST values around 15.5–16.5 °C, a DIN and a DIP reference value of 2.5 µM and 0.18 µM, respectively; Arrifes (37° 4.581'N; 8° 16.573'W; sampled in August 2013) site is within a coastal area with wave-sheltered conditions, SST values around 16.5–17 °C, a DIN and a DIP reference value of 2.3 µM and 0.23 µM, respectively (Bettencourt et al., 2004; Santos et al., 2012; Cabrita et al., 2015). All selected sites present considerable extensions of irregular rocky platforms and where considered a priori as having minor anthropogenic pressures, none of them showing evidences of any particular pressure.

2.2. Sampling design and data production

At each study site, the intertidal rocky shore was sampled along

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