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Vertical zonation is the main distribution pattern of littoral assemblages on rocky shores at a regional scale

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Vertical variation in the distribution of rocky shore assemblages is greater than horizontal variation, as shown by univariate and multivariate analysis performed with data obtained along 1000 km of shoreline and covering from the upper supralittoral to the upper infralittoral zone (−1 m). Consequently, vertical littoral zonation is a consistent pattern at a regional scale within the same biogeographical zone. While their distribution varies at the same shore height, marine species and assemblages from rocky shores show a specific vertical sequence known as zonation. A key question in ecology is how consistent is zonation along large spatial scales. The aim of this study is to show distribution patterns of littoral assemblages at a regional scale and to identify the most relevant abiotic factors associated to such patterns. The study is based on a detailed and extensive survey at a regional scale on a tideless rocky shore. Benthic macroflora and macrofauna of 750 relevés were described along the vertical axis of 143 transects distributed across the shoreline of Catalonia (NW Mediterranean). The Detrended Correspondence Analysis (DCA) first axis is highly related to the height on the shore: species, relevés, and assemblages grade from lower to upper height (infralittoral to supralittoral). As observed in nature, different assemblages co-occur at the same height at different sites, which is shown along DCA second axis. The abiotic variables that best explain the assemblage distribution patterns are: height (75% of the model inertia), longitude (14.6%), latitude (7.2%) and transect slope (2.9%). The Canonical Correspondence Analysis (CCA) first axis is related to height on the shore and explains four times more variance than CCA second axis, which is related to the horizontal gradient. Generalized Lineal Model (GLM) results show that height on the shore is the factor explaining most of the variance in species presence. Most studied species show distribution patterns related to latitude and longitude, but always in a much smaller proportion than to height.

1. Introduction

The distribution of organisms is not homogeneous but changes according to abiotic and biotic factors. Zonation can be defined as the distribution of species and communities along environmental gradients. The natural layering of ecosystems along altitude in mountain regions is well known (e.g. Daubenmire, 1943; Hagvar, 2005; Hemp, 2006) but zonation also occurs in freshwater (e.g. Spence, 1982; Machena, 1988) and marine environments (e.g. Logan et al., 1984; Abbiati et al., 1987; Rodil et al., 2006). Littoral rocky shores are in the transition between terrestrial and marine environments, but because of water movement associated with tides, waves and spray, the transition is not abrupt but gradual. A strong environmental stress gradient occurs perpendicular to shore related to desiccation, temperature and irradiance, which exhibit their most extreme values towards the upper limit of the littoral zone. The distribution of organisms along this vertical gradient in a specific spatial sequence is known as littoral zonation. This pattern has long been studied (e.g. Wahlenberg, 1812; Baker, 1909; Zaneveld, 1937; Ballesteros and Romero, 1988) and it is considered universal by some authors (Mokyevsky, 1960; Barnes and Hughes, 1999).

The vertical distribution of littoral assemblages and species has been extensively studied in relation to abiotic factors (e.g. waves, wind, water clarity, temperature and ice exposure; McQuaid, 1985; Kiirikki, 1996b; Reichert et al., 2008), biotic factors (e.g. competition

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[Bulleri et al., 2002; Mangialajo et al., 2012], grazing [Underwood and Jernakoff, 1981; Thomas, 1994], predation [Underwood and Jernakoff, 1981], facilitation [Erlandsson et al., 2011], dispersal [Burrows et al., 2009]) and the interaction between abiotic and biotic factors (Underwood and Jernakoff, 1981).

However, zonation patterns may vary along the coast due to processes unrelated to vertical gradients. Furthermore, different factors emerge as the main drivers of ecological processes and patterns depending on the spatial scale (Levin, 1992; Willig et al., 2003). Consequently, in recent times studies have focused on the variability of littoral assemblages and species at different spatial scales along shores either influenced (Burrows et al., 2009; Cruz-Motta et al., 2010; Valdivia et al., 2011; Veiga et al., 2013) or not influenced by tides (e.g. Abbiati et al., 1991; Menconi et al., 1999; Fraschetti et al., 2005; Cruz-Motta et al., 2010). These studies show that the distribution of species and assemblages along the horizontal axis (i.e. parallel to the sea surface) is important at different scales, from fine-scale (10s of cm) to broad scales (100s or 1000s of km). Among possible relevant causes for patterns and distributions along the shore (horizontal variation) there are abiotic factors, such as changes in topography of the substratum (Underwood, 2004), physical disturbance (e.g. changes in wave exposure, Schoch et al., 2006; Tuya and Haroun, 2006) and coastal geomorphology (Schoch and Dethier, 1996), and biotic factors such as whiplash (frond sweeping by canopy-forming seaweeds, Kiirikki, 1996a), variations in grazing and predation activity (Rilov and Schiel, 2011) and variation in recruitment (Reaugh-Flower et al., 2011). At the global scale, Cruz-Motta et al. (2010) related distribution patterns of assemblages to photoperiod, temperature and rainfall.

It is relevant to question how consistent are zonation patterns along the shore despite horizontal variations. Apart from general ecological considerations, recognizing patterns such as the clumped distributions of organisms along the environmental gradients above mentioned is ultimately important to implement monitoring practices aimed at the conservation of species and habitats. However, very few studies focus on either vertical and horizontal variation or their relationships (Benedetti-Cecchi, 2001; Fraschetti et al., 2005; Martins et al., 2008; Valdivia et al., 2011). Results depend on the height of the shore studied and on the type of statistical analyses employed (univariate or multivariate). For instance, significant variation was detected in lower and mid-shore assemblages, but not on the upper shore at large scales (among the Azores islands; Martins et al., 2008). Univariate analysis show similar or larger horizontal than vertical variation, which contrasts with multivariate analyses that indicate that vertical variation is larger than horizontal variation at fine scales but smaller than that found at broad scales (Benedetti-Cecchi, 2001; Valdivia et al., 2011). Nevertheless, all of this literature studying both vertical and horizontal variation is based on hierarchical designs and consequently only samples a reduced number of shore heights and sites along the coast. Furthermore, they usually focus on few abundant species or types of organisms overlooking the less visible taxa (Rilov and Schiel, 2011).

Littoral species and assemblages at the same shore height vary along the coast, but zonation at every site is evident (e.g. Little and Smith, 1980; Ballesteros and Romero, 1988; Thomas, 1994). Thus, a key question is how consistent is zonation along large spatial scales? Here, the aims are: 1) to show distribution patterns of littoral assemblages and species at a regional scale, and 2) to identify the most relevant abiotic drivers associated to such patterns. The hypothesis is that zonation is the main distribution pattern of littoral assemblages and species. The study is based on a detailed but also extensive survey at a regional scale on a NW Mediterranean rocky shore, which is heterogeneous regarding exposure, substrate type and slopes. Both benthic macroflora and macrofauna are used as descriptors characterizing well-established assemblages (dominated by well definable species or species guilds) along the vertical littoral gradient of 143 transects distributed across about 1000 km of shoreline.

2. Methods

2.1. Study site and sampling method

Catalonia is a North-western Mediterranean region situated in North-eastern Spain. The Catalonian coastline stretches along about 1100 km and is formed by 39% of natural rocky shores, 30% of artificial hard-bottom shores (breakwaters, sea walls, jetties…) and 30% of beaches (Mariani et al., submitted for publication). Despite the fact that tides are imperceptible in this area, wave splash and changes in sea level mainly associated to atmospheric pressure operate vertically allowing organisms to extend upwards, far beyond the zero sea-level (Ballesteros and Romero, 1988; Ballesteros, 1992).

Along the coast, 143 hard-bottom sites were sampled (Fig. 1), both natural rocky shores and man-made structures such as breakwaters and jetties. Sites were selected to cover a wide range of physical conditions along the coast, notably the shore height, location, exposure, substrate type, slope, and orientation (see below). Considering the rocky coast only, the average distance between transects was about 3.7 km. The whole sampling took three years, from May to July of 2010, 2011, and 2012, at the annual period of maximum algal development (Ballesteros, 1988b, 1991a,b, 1992). Except for a few sampling repetitions mainly due to bad meteorological conditions, all transects were visited only once.

At each site, which was located using a GPS (European Datum 1950, UTM Zone 31N), a vertical transect was placed from the higher point reached by any marine organism (e.g. the lichen *Verrucaria amphibia* or the small periwinkle *Melarhaphe neritoides*) to the upper infralittoral (−1 m a.m.s.l.) through the mediolittoral level. The lower limit of each transect was arbitrarily established since an assessment of deeper assemblages was beyond the scope of the present study. The upper limit depended on the shore profile and the presence of characteristic marine species, thus the transect length ranged from about one (shores where rocks did not reach the supralittoral level) to 12 m.

Along each transect, specific assemblages dominated by conspicuous species or species guilds were recognized as homogeneous belts, following a bionomical approach (Abbiati et al., 1987; Morri et al., 2004). Assemblages were named after the dominant species of the belt, which mostly have annual life cycles (Ballesteros, 1991a, 1992). Heights on the shore of the upper and lower limits of the belts were measured and each belt assemblage was characterized through phytosociological relevés (plots). All visible flora and fauna (sessile and vagile) comprised within each belt of approx. 2 m. wide was recorded using a Braun-Blanquet cover-abundance scale (Braun-Blanquet, 1964) that has been already used to quantify the abundance of littoral flora and fauna (Molinier, 1960; Sales and Ballesteros, 2009, 2010). When necessary, specimens were removed and later identified in the laboratory. Organisms were identified to species level, only a few difficult taxa were classified to higher taxonomic levels (genus or family). A relatively large area was sampled (2 m wide) to avoid small-scale variation due to patchiness and microhabitats (e.g. Underwood and Chapman, 1996; Valdivia et al., 2011).

Seven relevant environmental variables were studied. Mean belt height on the shore and location (longitude and latitude) were recorded as quantitative variables. Degree of exposure to wave and wind action (very low, low, moderate, high and very high),