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

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A B S T R A C T

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,

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wind, water clarity, temperature and ice exposure; McQuaid, 1985; Kiirikki, 1996b; Reichert et al., 2008), biotic factors (e.g. competition [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 1100 km of shoreline.

2. Methods

2.1. Study site and sampling method

Catalonia is a Northwestern Mediterranean region situated in Northeastern 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., 2014). 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

Fig. 1. Location of the sampled transects along the Catalan coast (Northwestern Mediterranean).

wind action (very low, low, moderate, high and very high), substrate type (i.e. sandstone, calcareous rock, granite, metamorphic, conglomerate and cement), slope (in degrees but grouped into 5 categories: $0°–10°$; $10°–35°$; $35°–55°$; $55°–80°$; $>80°$) and orientation (8 categories: N; NE; E; SE; S; SW; W; NW) of each transect were recorded as qualitative environmental variables.

2.2. Statistical analysis

Cover abundances of phytosociological relevés were transformed to a more symmetric and fully numerical scale according to van der Maarel (1979). An analysis of similarities (ANOSIM, Bray−Curtis similarity, 999 permutations) was performed to test for significant differences between assemblages. Consequently, only significantly different assemblages were used throughout the study. In order to detect patterns, relevés were ordered using a Detrended Correspondence Analysis (DCA) with detrending by segments as data showed a clear unimodal response. Rare species were down-weighted and the DCA scatterplot showed height (m a.m.s.l.) fitted as a smooth surface. Correlation between the 1st DCA axis and height was tested with a linear regression model. The proportion of the variance accounted for by the environmental variables was explored using canonical multivariate analyses. As the gradient length obtained in the DCA (7.82 SD) was higher than would be the case for a complete species turnover (4.0 SD; Hill and Gauch, 1980) unimodal methods (Canonical Correlation Analysis, CCA) were used as non-linear responses were expected along such a gradient. A subset of significant environmental variables were determined by a forward selection (Legendre and Legendre, 1998) of environmental variables in the CCA ordination ($p = 0.05$; 999 Monte-Carlo permutations). ANOVA tests were run to test the significance of the CCA, the selected environmental variables and the CCA axis.

Patterns of a subset of 23 species were studied with more detail. Included species were the most frequent (see Electronic appendix A) and some other abundant species that dominate specific assemblages throughout the vertical gradient. First, species patterns were explored into the DCA scatterplot based on relevés.

The patterns of presence or absence of each species and their response to the environmental variables above mentioned were modeled with generalized linear model (GLM, McCullagh and Nelder, 1989) using the binomial distribution and a logistic link function. Both monotonic and unimodal responses were tested for continuous environmental data and the best model was selected based on ANOVA tests and AIC (Akaike's information criterion). The fit of the model (D^2) is calculated as the proportion (%) of explained deviance:

$$D^2 = (\text{null deviance} - \text{residual deviance})/\text{null deviance} \cdot 100$$

Finally, as the vertical gradient repeatedly appeared as important, the distribution of the 23 species were plotted along the height of the shore.

All statistical tests were performed with the software R version 2.12.2 (R Development Core Team, 2011) and CANOCO version 4.5 (ter Braak and Smilauer, 1998).

3. Results

3.1. Assemblages

A total of 750 relevés were recorded along the 143 transects, corresponding to 23 different assemblages and including a total of 174 different species or taxa (see Electronic appendix A). Each transect exhibited a variable number of assemblages (up to 11). Similarly, the number of species per relevé was variable and ranged from 1 to 31.

Significant differences are found among assemblages based on relevés data (ANOSIM Global R = 0.844, $p = 0.0001$). Pairwise tests show that all the assemblages differ among them with the exception of three assemblages dominated by: the limpet group *Patella* spp. (corresponding mainly to *Patella rustica*); the red alga *Polysiphonia sertularioides*; and the red algae guild *Pyropia elongata-P. sertularioides* ($p > 0.05$) that are hereafter merged into a single assemblage referred to as *Patella-Polysiphonia*.

Clear patterns are observed in the DCA scatterplot (Fig. 2). Both relevés and assemblages gradate from lower to upper height (infralittoral to supralittoral) along the first axis, as the isolines of the fitted height data show. Linear regression between DCA1 scores and height is significant and relatively high (R-squared = 63.1%, $p < 0.01$). Consequently, DCA1 is highly related to the vertical gradient. As observed in nature, different assemblages co-occur at the same height at different sites, which is shown along the second axis. For example, the assemblages dominated by the brown alga *Ralfsia verrucosa,* the red algae *Rissoella verruculosa* and *Nemalion helminthoides,* and the *Patella-Polysiphonia* guild occur at similar heights of the mediolittoral, always below the assemblage dominated by *Chthamalus* spp. and always above *Corallina elongata* (mediolittoral), *Cystoseira mediterranea* and *Mytilus galloprovincialis.* Generally, assemblages are consistent and appear in dense clouds even if limits might overlap. However, some assemblages, such as those dominated by the green alga *Ulva compressa,* the red algae *Gelidium pusillum* and *Ceramium ciliatum,* the brown alga *Cystoseira compressa* or the crustose coralline *Lithophyllum incrustans,* show a very high dispersion along the DCA scatterplot. Only one assemblage is found at the supralittoral stage, which contrasts with the high variation and assemblage diversity find around the 0 m a.m.s.l. (between the mediolittoral and infralittoral stages).

The Monte-Carlo permutation test selects a four variable model that accounts for a 9.8% of the total inertia or variation of the relevé data. The first and main selected variable is the height ($F = 59.504$, $p = 0.001$), which accounts for a 75.5% of the model inertia. Longitude (UTM-x coordinate, $F = 11.669$, $p = 0.001$) and latitude (UTM-y coordinate, $F = 5.758$, $p = 0.001$) are the 2nd and 3rd most relevant variables, respectively accounting for 14.6% and 7.2% of the model inertia. The last significant term of the model is the average transect slope ($F = 2.367$, $p = 0.001$), which accounts for only a 2.9% of the model inertia. Sampling date was also tested but was not significant ($F = 1.144$, $p = 0.206$).

The studied coastline stretches diagonally from NE to SW, consequently longitude and latitude coordinates are highly correlated (0.93 Pearson correlation, $p < 0.05$) and provide similar information. The CCA scatterplot performed with a reduced model of height and longitude as environmental variables is shown in Fig. 3.

Finally, only half of the selected variables are included as they explain more than 90% of the model inertia and the last three variable vectors point at the same direction. ANOVA tests on the CCA model ($p = 0.005$), on the first two axes (both $p = 0.005$) and on the two environmental variables included (both $p = 0.01$) are significant.

The first CCA axis account for a 4% of the canonical variance and relates to the height on the shore (see Fig. 3), in a similar way than DCA1 (Fig. 2). The second CCA axis is much less important as it accounts for a 1% of the canonical variance and relates to the longitude or NE—SW gradient (Fig. 3). Some assemblages (e.g. *Verrucaria-Euraphia, Chthamalus* spp., *Patella-Polysiphonia, Corallina elongata* ML and IL, and the algae guild *Halopteris-Padina-Dictyota*) are distributed along the whole coast. In contrast, some assemblages are typical from the northeast area (e.g. *Rissoella verruculosa, Nemalion helminthoides, Lithophyllum byssoides, Cystoseira mediterranea*) or the southwest area (e.g. *Ulva compressa, Gelidium pusillum*).

3.2. Species

Species patterns of abundance are shown in Fig. 4 using the plot of the previous DCA performed with the relevés (Fig. 2). None of the main species studied is distributed along the whole height gradient (which corresponds to DCA1) even if different patterns are shown. Some species exhibit narrow distributions along the height range and are often related to one or few assemblages (e.g. *Euraphia depressa, Nemalion helminthoides, Rissoella verruculosa, Cystoseira mediterranea* and *Padina pavonica*). In contrast, some species exhibit distributions that span along a large height range and are present at various assemblages (e.g. *Chthamalus* spp., *Perforatus perforatus, Lithophyllum incrustans, Mytilus galloprovincialis* and *Corallina elongata*).

GLM results strongly support that height is the most important gradient factor for all the studied species (Table 1). The vertical gradient is always significant and explains high proportions of species variance, in some cases up to half the variance (i.e. *Euraphia depressa, Melarhaphe neritoides, Corallina elongata* and *Cystoseira mediterranea*). In contrast, longitude and latitude are significant for
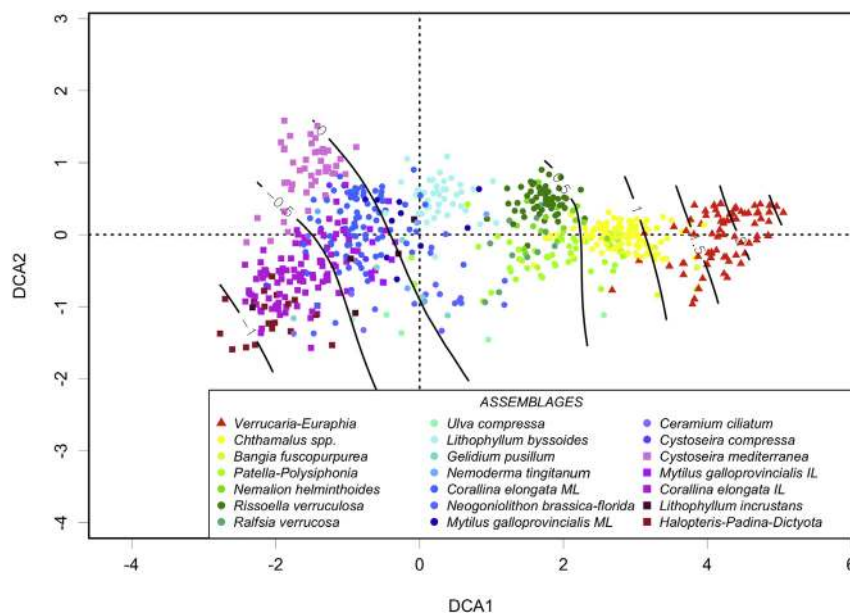

Fig. 2. Scatterplot of the Detrended Correspondence Analysis (DCA) based on relevés. The different assemblages are shown and height (m a.m.s.l.) is fitted into the plot as a smooth surface. Abbreviations: ML — mediolittoral; IL — infralittoral.
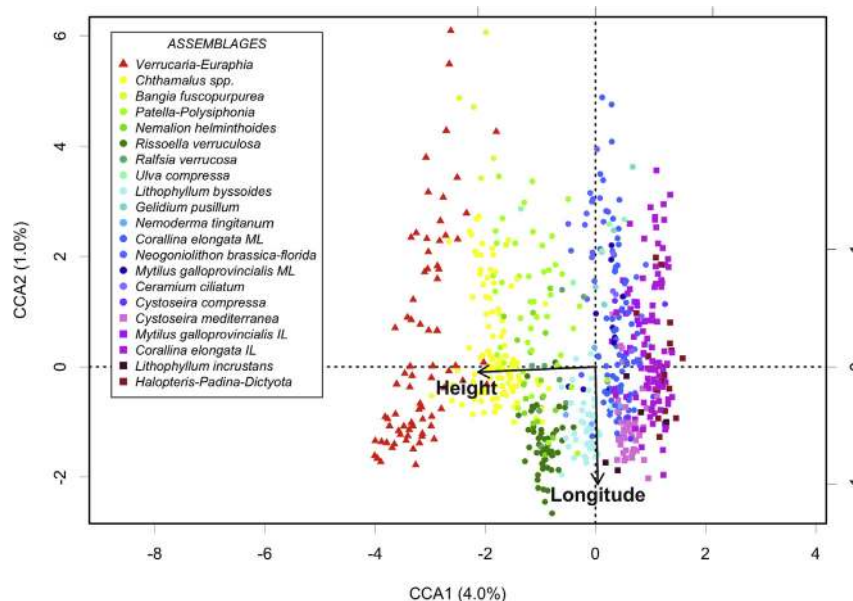
Fig. 3. Scatterplot of the Canonical Correspondence Analysis (CCA) based on relevés. The different assemblages are shown as well as the main environmental gradients selected by a Monte-Carlo permutation procedure. The scale on the right y-axis correspond to the abiotic variable vectors. Abbreviations: ML − mediolittoral; IL − infralittoral.

much less species and account for much smaller species variance. Only *Echinolittorina punctata* (with a distribution concentrated towards the southwest) shows similar values for height, longitude and latitude. Similarly, *Lithophyllum byssoides* exhibits relatively high proportions of variance explained by longitude and latitude (distribution concentrated towards the northeast) compared with height. In general, exposure and substrate explain low proportions of species variance. Slope and orientation explain even lower proportions of variance and only for a very few species. All species tested have unimodal response along the height gradient, but have either monotonic or unimodal responses along the longitude and latitude gradients.

The vertical distribution of some relevant species along the coast height is shown in Fig. 5. Two main groups can be identified: a first one with species that were never found submersed (lower limit above 0 m) and that were differentially distributed along the shore height following the wetting gradient. These species were typically found at the supralittoral and mediolittoral stages. A second group is composed by species that stretched their distribution well underwater, some of them exhibiting their upper limit above 0 m where wetting is still very frequent, and other species that were unequivocally always submersed (upper limit at 0 m). Species tolerating immersion are classified following Grime (1977) strategies as opportunists, stress-resistants or competitors. The lower limit of submersed species usually went far beyond the lower limit of sampling of this study and extended deeper in the infralittoral stage, where sampling was not carried out. As species presence in an assemblage is represented only by a dot at the average height of the belt, some distributions that are in fact continuous seem broken in Fig. 5 (e.g. *Ceramium virgatum, Cystoseira compressa, Perforatus perforatus*).

4. Discussion

4.1. Zonation

Vertical zonation is clearly a consistent pattern at a regional scale within the considered biogeographical zone. In contrast, horizontal variation along the shore appeared to be a secondary distribution pattern for assemblages and species, less important and less defined than vertical zonation. Our multivariate approach based upon a well-distributed, large number of long transects showed beyond any doubt that the strongest and widest variation took place vertically along the shore. Our results suggest that horizontal variation exists at the same shore height, but only a few assemblages were found at a specific height along the whole shore. For example, 5 assemblages were found at 0.5 m depth involving different sites: *Chthamalus* spp.; *Ralfsia verrucosa; Rissoella verruculosa; Nemalion helminthoides*, and *Patella-Polysiphonia* guild. Nevertheless, this horizontal patchy distribution shown by few assemblages, which frequently share species, is too small to account for an horizontal spatial pattern that is stronger than the vertical one.

Studied assemblages are considered significantly different groups based on ANOSIM, but most of them show a strong gradation with height (horizontal axis at the DCA ordination). These results agree with findings by Boudouresque (1971) who accepted a continuity between associations and proposed associations to be considered as nodes within a continuum. The supralittoral stage, with only one assemblage described (*Verrucaria-Euraphia*), is the less diverse and more constant along the studied coast. Only few species extremely resistant to desiccation (e.g. *Euraphia depressa, Melarhaphe neritoides, Echinolittorina punctata, Verrucaria amphibia*) can survive at the supralittoral level where water availability is infrequent. Similarly, Martins et al. (2008) did not found significant variation at the upper shore community among Atlantic islands.

Greater assemblage and species diversity, continuity and overlap are found at the mediolittoral and infralittoral stages. Actually, the variation among assemblages located around the average sea level (0 m a.m.s.l.) is the largest along the vertical zonation. Consequently, if only this narrow section of the whole fringe is taken into account, horizontal variation among sites with different assemblages may be greater than the variation among adjacent belts. This pattern has been shown by several authors who focused their research on a tiny fringe between 0 and 0.4 m in the NW Mediterranean Sea (Benedetti-Cecchi, 2001; Fraschetti et al., 2005). Reducing the coast height rank analyzed, the number of sampling
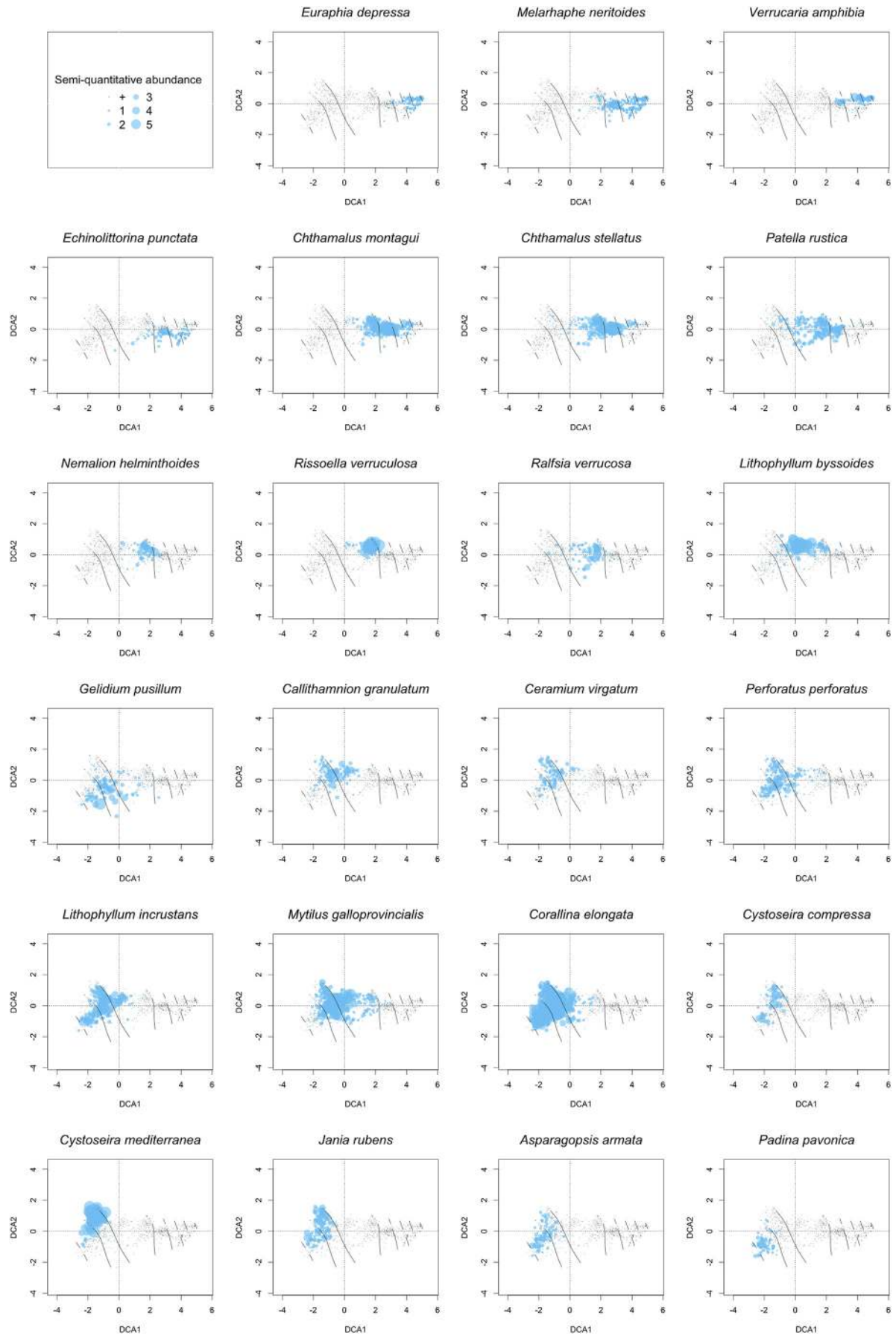
Fig. 4. Distribution patterns of species in the DCA plot of the relevés. Species presence in each relevé is shown with a blue dot of proportional size to the Braun-Blanquet cover abundance. The more dots overlapping, the brighter is the blue.

Table 1
One variable Generalized Linear Models (GLM) for species. Presence/absence data of species fits a binomial distribution and both, monotonic and unimodal, responses were tested for continuous environmental data (only the best fitted response is shown in the table, based on ANOVA tests and AIC). The fit of the model (D^2) is calculated as the proportion (%) of explained deviance (D^2 = (null deviance − residual deviance)/null deviance 100). Models were tested with ANOVA and only significant results are shown (gray results indicate $0.05 > p > 0.01$ and black results indicate $p < 0.01$).

D^2 (%)	Height	Latitude (x)		Longitude (y)		Exposure	Substrate	Slope	Orientation
	Unimodal	Monotonic	Unimodal	Monotonic	Unimodal				
Eur dep	46,5								
Ver amp	40,0	4,6			4,4		2,4		3,0
Mel ner	54,2								
Ech pun	21,8		20,6		22,0	3,3	10,4		3,5
Cht mon	23,2								
Cht ste	15,6		1,7		0,8		1,5		
Pat rus	19,1				0,5	1,4		1,5	
Nem hel	16,2				2,2	3,5	3,3		
Ris ver	23,2	6,9			7,1	2,4	8,9		3,5
Ral ver	16,3		1,9		1,9	1,9			
Lit bys	13,3	9,8			9,3	6,0	3,2		2,5
Gel pus	16,0	1,3		1,0			3,9		2,9
Cal gra	19,6				0,9	8,1	2,2		
Cer vir	21,4					4,2			
Cys com	26,8		3,9	2,7			5,3		
Per per	27,2		6,1	6,7			3,5		
Lit inc	28,1	3,3		4,7			4,1		2,4
Myt gal	18,8			3,9					
Cor elo	48,4								
Cys med	44,7	3,0			3,7	2,4			
Jan rub	36,8	3,8			3,6	2,6	2,8		
Asp arm	35,6	5,1			4,9			2,0	
Pad pav	36,6		3,4		2,4	4,5	3,7	2,6	

Species abbreviations: Eur dep − *Euraphia depressa*; Ver amp − *Verrucaria amphibia*; Mel ner − *Melaraphe neritoides*; Ech pun − *Echinolittorina punctata*; Cht mon − *Chthamalus montagui*; Cht ste − *Chthamalus stellatus*; Pat rus − *Patella rustica*; Nem hel − *Nemalion helminthoides*; Ris ver − *Rissoella verruculosa*; Ral ver − *Ralfsia verrucosa*; Lit bys − *Lithophyllum byssoides*; Gel pus − *Gelidium pusillum*; Cal gra − *Callithamnion granulatum*; Cer vir − *Ceramium virgatum*; Cys com − *Cystoseira compressa*; Per per − *Perforatus perforatus*; Lit inc − *Lithophyllum incrustans*; Myt gal − *Mytilus galloprovincialis*; Cor elo − *Corallina elongata*; Cys med − *Cystoseira mediterranea*; Jan rub − *Jania rubens*; Asp arm − *Asparagopsis armata*; Pad pav − *Padina pavonica*.

sites, the taxonomical resolution or using different statistical analysis may lead to results that show wider horizontal than vertical variation (e.g. Benedetti-Cecchi, 2001; Valdivia et al., 2011). Possible causes accounting for this horizontal variation may be the result of the interplay of several factors such as wave exposure, temperature, geomorphology, runoff waters and even anthropogenic pressures (Ballesteros et al., 1984, 2007; Ballesteros, 1992; Pinedo et al., 2007).

However, even if height appears as the main driving factor, it has no direct effect on species and assemblages. In fact, many abiotic and biotic variables, which may directly affect species distribution and interactions, co-vary along with height. Specifically, height encompasses long-term exposure conditions to waves (wetting gradient), wind and insolation, which are pivotal factors for zonation of species and assemblages (e.g. Baker, 1909; Kiirikki, 1996b).

4.2. Species distribution patterns

Most studied species show distribution patterns related to latitude and longitude, but always in a much smaller proportion than to height (only *Echinolittorina punctata* shows almost equal values). Species that are present along the whole studied shore, such as *Euraphia depressa*, *Melaraphe neritoides*, *Chthamalus montagui* or *Corallina elongata*, show no relation to latitude and longitude (as their distribution showed no particular pattern along the coastline).

Weak relationships are found for the other environmental variables. Most studied species presence show low or no relationship with shore exposure, as studies from other regions have detected (Thomas, 1994; but see; Christofoletti et al., 2011). In contrast, assemblages and species abundance seem to respond better to exposure (Schoch et al., 2006; Garcia et al., 2011; Zamprogno et al., 2012; Williams et al., 2013), a factor that can also modulate vertical

zonation (Reichert et al., 2008). The species with the strongest relationships with exposure, *Lithophyllum byssoides* and *Callithamnion granulatum*, are more frequent in strongly exposed shores. *L. byssoides* often forms bio-concretions called *trottoirs* at low mediolittoral rocks with high hydrodynamism and slopes close to 90° (Pérès and Picard, 1964; Gili and Ros, 1985). Some specific small influences of substrate type on species presence are found but in general the relationship is weak, as found by McQuaid and Branch (1984). One exception is the red alga *Rissoella verruculosa* which is common over granite and schist but scarcely found growing on calcareous rocks as already reported in several studies (Ollivier, 1929; Feldmann, 1937; Pérès and Picard, 1964; Ballesteros, 1991b). Even if the relationship between slope and the studied species presence is weak, slope is important for *L. byssoides* trottoirs that are mainly present over cliffs or steep shores.

Species exhibit different upper and lower distribution limits along the vertical gradient (Fig. 5) as found by Sibaja-Cordero and Vargas-Zamora (2006). Several species are never found underwater suggesting that they are not able to withstand permanent immersion. It could be due to the physiological inability of being permanently submersed or because they are outcompeted or predated by other species when submersed. However, the strictly supralittoral to mediolittoral species show different upper shore distribution limits. It is not possible to disentangle whether the upper limits of species distributions are the results of abiotic or biotic factors (such as competition or predation), although there is evidence of increasing desiccation resistance for those species attaining higher upper distribution limits (Little and Smith, 1980; Lubchenco, 1980). Two different strategies seem to be operating for those organisms that are able to grow just above and below the mean water level. On one side there are opportunists, such as some members of the Ceramiales and *Gelidium pusillum*, that grow fast when conditions are suitable and disappear when abiotic factors do
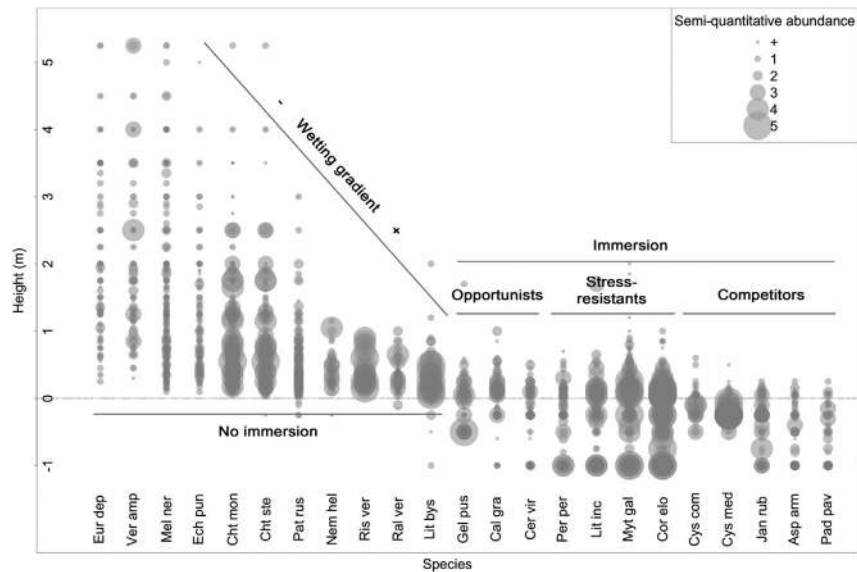
Fig. 5. Species distribution along the vertical gradient (height in meters). Species presence in each relevé is shown with a gray dot of proportional size to the Braun-Blanquet cover abundance. The more dots overlapping, the darker is the gray. See Table 1 for species abbreviations.

not allow maintenance of populations (e.g. long periods of low water level; Ballesteros, 1992) or they are outcompeted/grazed when conditions do not allow them to grow so fast. A second strategy is that of stress-resistant species that are able to grow and remain for a long period of time in harsh conditions (Grime, 1977). That is the case of red algal crusts (e.g. *Lithophyllum incrustans*), branching corallines showing heterotrichy (e.g. *Corallina elongata*; Littler and Kauker, 1984; Ballesteros, 1988a) or *Mytilus*. Finally, competitors (Grime, 1977) such as *Cystoseira mediterranea* are not capable to withstand the high unpredictability associated to the mediolittoral stage and only thrive below the water level or just above, where water availability is almost always guaranteed. However, even these species that are found almost always submersed but close to the surface have a higher resistance to desiccation than species thriving only underwater (Delgado et al., 1995), since prolonged periods of low water levels caused by high atmospheric pressure can eventually occur (Ballesteros, 1989, 1992).

5. Conclusions

Multivariate and univariate analyses show that there is a strong, well-defined pattern in the distribution of littoral assemblages and species along the vertical axis (height). Despite the physical heterogeneity of the shore, the variation range of such pattern is overall larger than that recognizable horizontally at a wide regional scale within the same biogeographical zone. Thus, vertical zonation is the main distribution pattern of littoral assemblages and species in Northwestern Mediterranean rocky shores. A trustworthy, easy recognizable order of appearance of species and communities along the vertical axis in a shore may help classify habitats when monitoring or managing practices are to be implemented.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ecss.2014.05.031.

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