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The role of geomorphology in the distribution of intertidal rocky macroalgae in the NE Atlantic region

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ABSTRACT

It is known that rocky macroalgae distribution depends on several abiotic factors, but little attention has been given to geomorphological influences. This paper analysed the relation between geomorphological variables (active processes, coastal morphology, coastal orientation and lithology) and rocky intertidal macroalgae species at a local scale. Thirteen sites were sampled along the coast of Cantabria (North Spain) in order to obtain covers of macroalgae species. Multivariate analysis and logistic regression were applied, predicting the probability occurrence of macroalgae species as a response to the predictor geomorphological variables. Our results showed that coastal morphology and coastal orientation were the principal geomorphological factors explaining the structure of macroalgae communities. The most significant differences in substrate preferences were found between *Bifurcaria bifurcata*, that appears in wave-cut platforms oriented towards the east, and *Corallina officinalis*/*Ellisolandia elongata* and *Gelidium spinosum*, which are found in cliffs oriented towards the north and west. Although these variables help to characterise species distribution, their predictive value is still limited, possibly due to other factors influencing macroalgae. Thus, some of the geomorphological variables studied here are among the environmental factors that determined the distribution of intertidal macroalgae communities at a local scale, even if not always in a direct way.

1. Introduction

The successful protection and management of marine diversity, the assessment of anthropogenic impacts and the restoration of altered ecosystems rely largely on understanding the processes and factors that structure biological assemblages (Chapman, 1999). Thus, relationships between environmental factors and organisms need to be explored in order to recognise the key agents that determine the composition of communities and the distribution of species.

Several abiotic and biotic factors determine the distribution and structure of coastal benthic communities, depending on the main drivers of ecological processes and patterns at a spatial scale (Levin, 1992). At a global scale, temperature and solar radiation are mainly responsible for biogeographic differences (van den Hoek, 1982; Lüning, 1990; Ramos et al., 2014). At a regional scale, exposure to wave action, tidal range, salinity and nutrients, among other factors, may play a major role in the distribution and structure of intertidal communities (Kautsky and van der Maarel, 1990; Ramos et al., in press). However, at a local scale some of these variables do not vary significantly; therefore other factors, such as geomorphological characteristics and vertical height, seem to affect species distribution (Schoch and Dethier, 1996; Díez et al., 2003; Chappuis et al., 2014; Bermejo et al., 2015). On the other hand, changes also occur on a seasonal basis, since intra-annual fluctuations in the abiotic parameters (temperature, light and salinity) determines species reproduction and growth (Lüning, 1990; Raffaelli and Hawkins, 1996). In temperate seas, as the North coast of Spain, the period of maximum development for most seaweed populations is from late spring (June) to late summer (September), with seasonal episodic explosion of ephemeral species occurring in April–May (“naturally opportunistic species”) (Juanes et al., 2008). A study carried out in the Cíes Islands (NW Iberian Peninsula) concluded that geographical features and shore slope are among the factors that explain the differences in species assemblages and

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the tidal level at which each species is found (Troncoso and Sibaja-Cordero, 2011). A similar study in the Azores Islands showed that the agents that strongly influence community structure and determine major biotope separations are shore level and substratum type, as well as wave exposure (Wallenstein and Neto, 2006).

Focussing on geomorphological features, different variables may affect the sessile assemblages in different ways. The orientation (direction of the surface floor), slope and texture of the surface may cause differences in drainage, evaporation, sedimentation and shade, modifying the characteristic patterns of the intertidal zone (Lobban et al., 1985; Rinne et al., 2011). Roughness may also influence composition through indirect effects on herbivore activity (Jenkins et al., 2008). The type of substratum affects the retention of heat and water, which makes algae grow or survive better (McGuinness and Underwood, 1986; McGuinness, 1989), causing differences among assemblage structures and the covers of individual taxa of algae (Green et al., 2012). On the other hand, substratum nature could also affect turbidity, as it is high when the substrate is extremely soft (Dixon and Irvine, 1977). In general, the agents that cause the differences in assemblages can change in their intensity due to the geomorphology of the rocky coast (Bird, 2008).

In spite of the important role played by geomorphological characteristics in explaining patterns in the structure of rocky communities (e.g. Cerrano et al., 1998; e.g. Bavestrello et al., 2000), relatively little attention has been paid to the study of these types of interaction, except for those focused on the settlement of larval stages of fauna species depending on rock type (Fischer, 1981; Anderson and Underwood, 1994; Schiaparelli et al., 2003). Although seaweeds are among the most obvious and ecologically important components of rocky shore communities worldwide (Lubchenco et al., 1991), until now little has been known about the influence of substrate mineralogy and geomorphology on their distribution.

Given the important synergies found between geomorphology and macroalgae communities, a detailed study should be performed in order to test the specific effect of each geomorphological variable on rocky intertidal macroalgae species. In order to avoid noise caused by other abiotic factors, it will be appropriate to carry out such a study in a homogenous area based on meteo-oceanographic conditions. For this reason, the coast of Cantabria (North Spain) may be an optimal zone for this study, as it is considered a unique environmental typology at both European and regional scales (Ramos et al., 2012, 2014, in press). In addition, this coast shows geomorphology variability, allowing us to study the influences of different geomorphological factors.

This paper is aimed at testing whether geomorphological features influence the distribution and structure of rocky intertidal macroalgae communities. More specifically, the objective was to determine which geomorphological factors cause differences in macroalgae communities, at which level of community organisation these differences are caused, and the main species affected. This detailed study of seaweeds and their environment contributes to understand about the ecology and distribution patterns of these communities and, consequently, to the assessment and conservation of marine ecosystems.

2. Methodology

2.1. Study area

This study was carried out on the coast of Cantabria, approximately 200 km long, located in the north of the Iberian Peninsula (NE Atlantic). The Cantabrian Coast is divided into a series of pocket beaches and small inlets isolated between rocky headlands. Most of the coastline has quite stable cliffs, as they are formed by compact rocks, although some show clear signs of retreat (Rivas and Cendrero, 1992). The composition of the substrate is mainly massive and stratified cretaceous or carboniferous limestone, with some areas where Palaeozoic quartzite can be found. Waves on the Bay of Biscay approach mostly from the northwest with a mean significant wave height (Hs) of 1 m and a typical winter storm significant wave height of Hs ≈ 5 m. The tides are semi diurnal with a mean tidal range of 3 m and a spring tidal range of 5 m.

Within the intertidal area of the Cantabrian coast two clear levels can be distinguished according to macroalgae communities: the middle intertidal, dominated by *Corallina officinalis/Ellisolandia elongata* and accompanied by calcareous encrusters, *Caulacanthus ustulatus, Ceramium* spp., *Chondracanthus* spp., *Osmundea* spp., etc., and the lower intertidal, dominated by *Bifurcaria* spp. and accompanied by *Stypocaulon scoparium, Codium* spp., *Cladostephus* spp., various red small folioses, Champiaceae, etc. (Guinda et al., 2008; Ramos et al., in press).

2.2. Collection of data

In order to obtain biological data, field work was carried out during spring tides in April 2011 and May and June 2012 in 13 sites located along the coast of Cantabria (Fig. 1). We selected sites that covered as much geomorphological variability as possible in the study area. At each site, three transects perpendicular to the coast were selected, which were separated by 50–100 m and had a coverage of macroalgae greater than 50% (see detailed information about transects in Supporting Information, Table A1). A stratified sampling was carried out taking into account the characteristic zonation pattern of the study area previously described. In this way, each transect was divided into two zones: 1) Lower intertidal (belt of brown algae) and 2) Middle intertidal (belt of red algae). Three sampling stations of 50×50 cm were distributed at equal distances in each area. As such, 177 quadrats were sampled, 86 in the lower intertidal and 91 in the middle. Covers of macroalgae species were obtained by photo analyses as described in Ramos et al. (in press) because this is a good approach to relate physical factors to species distribution.

Geomorphological characteristics of the sampling sites were initially obtained by an analysis of the corresponding 1:50,000 Geologic Maps (Geological and Mining Institute of Spain, IGME). In some cases, additional field work was carried out to confirm uncertain data. For each sampling site, four geomorphological variables were considered: active processes, coastal morphology, coastal orientation and lithology, according to the definitions of the categories in Fig. 2.

2.3. Data analysis

The relationship between geomorphological features and intertidal macroalgae was analysed at three levels of organisation: community descriptive parameters, assemblage composition and species preferences. First, specific richness (S) and Shannon–Wiener diversity ($H' \log_2$) were calculated based on species cover in each sample. A one-way ANOVA test was carried out to prove whether differences in these indexes between geomorphological categories were statistically significant. Levene's test for equality of variances and a histogram plot to verify the normal distribution of the data had been performed. If variance was not homogenous after logarithmic transformation, a Kruskal–Wallis test was carried out.

As a second step, an ANOSIM test was applied to detect significant differences in assemblage composition among the geomorphological variables. Prior to the multivariate analysis, cover data was previously square root transformed and the similarity matrix was calculated using Bray–Curtis similarity coefficient.

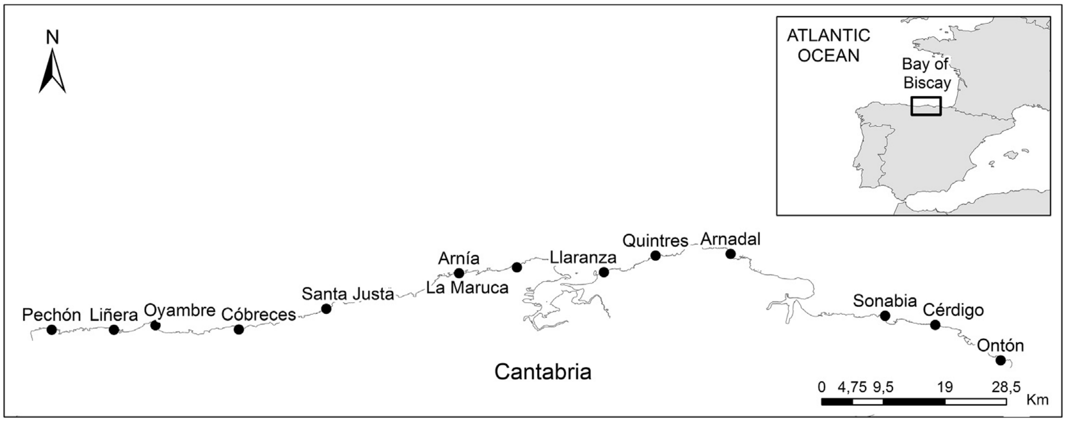

Fig. 1. Location of the 13 sampling sites along the coast of the Cantabria region (Bay of Biscay).

Finally, the response of individual species to geomorphological variables was modelled. A preselection of the species was made through a SIMPER analysis. Then, a logistic model was carried out taking into account the categorical nature of the parameters studied in this paper (Ysebaert et al., 2002; Guanche et al., 2013). This statistical method measures the fitting quality by comparing the deviance ratio (Δdev) and the chi-square distribution (χ^2). Assuming a confidence level $\alpha = 95\%$, if $\Delta dev > \chi^2_{0.95\%,\ \Delta dev}$, the fitting quality of the parameter was significant. Once the parameters estimated for the models are known, the predicted probabilities *p* of the significant fittings were represented according to four categories: absent, low (0–33% probability of occurrence), medium (33–66% probability of occurrence) and high (66–100% probability of occurrence). Thereby, the graphical representation allowed us to visualise the probability of occurrence of each species, based on its relative abundance, according to geomorphological variables.

Assuming shore height as the main influencing factor in the distribution of species at this scale (Wallenstein and Neto, 2006; Chappuis et al., 2014), separate analyses were performed for each tidal level (lower and middle intertidal). Statistical analyses were carried out using the Statistica 6.0 program (ANOVA analysis), the package PRIMER-E (v.6 + PERMANOVA) (ANOSIM and SIMPER analyses) and Matlab R2011b (logistic model).

3. Results

A total of 65 different macroalgae taxa were recorded, 62 in the lower intertidal and 53 in the middle one (species list in Supporting Information, Table A2). The most widely represented phylum was Rhodophyta with a total of 47 taxa, followed by Ochrophyta with 14

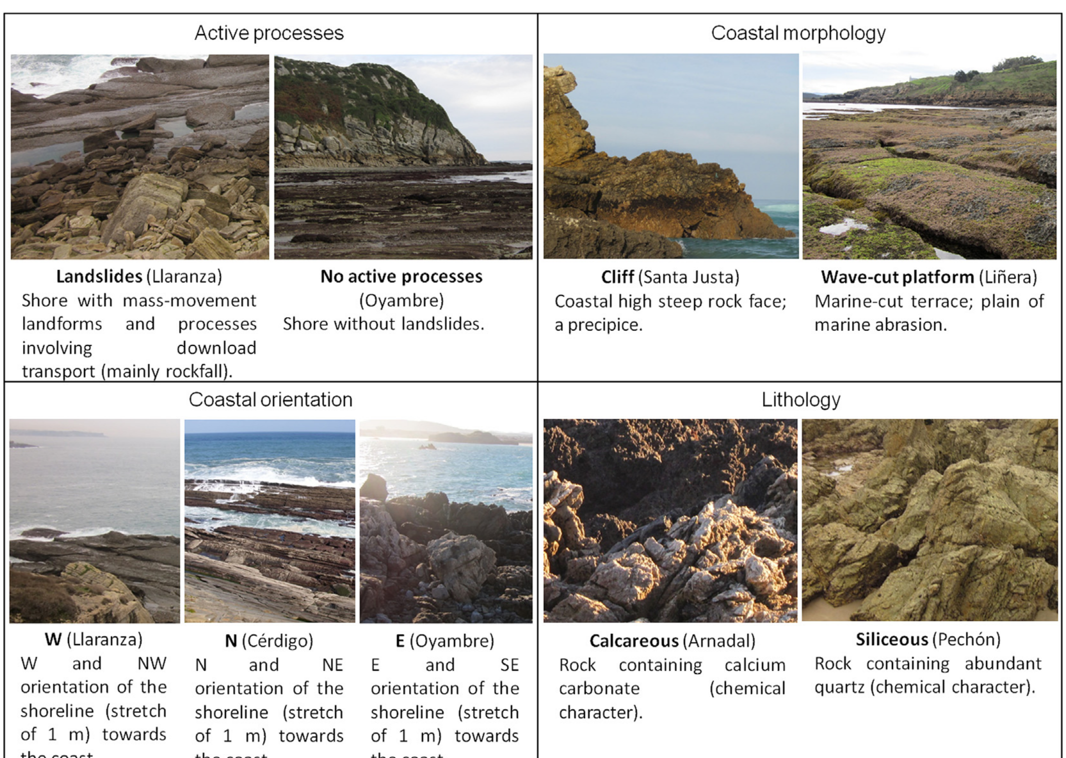

Fig. 2. Examples and description of the categories of geomorphological variables corresponding to different sampled sites.

and Chlorophyta with 4.

The specific richness index ranged from 7 to 19 per site with an overall mean of 14.5 in the lower intertidal, and from 9 to 16 with an overall mean of 11.6 in the middle intertidal. On the other hand, the Shannon–Wiener diversity showed a similar pattern, ranging from 1.2 to 2.5 per site with an overall mean of 1.8 in the lower intertidal, and from 0.6 to 1.8 with an overall mean of 1.2 in the middle one. According to ANOVA analysis (Table 1), specific richness and Shannon–Wiener diversity did not show significant differences within geomorphological variables in the lower intertidal, except in the case of diversity related to the lithology variable. As seen in Fig. 3, calcareous substrate presented higher diversity (1.9 mean value) than the siliceous (1.4 mean value), although the range of values was also broader in the first one. In the middle intertidal, both richness and diversity indices were significantly higher in areas without landslides (12.2 vs. 10.6 and 1.3 vs. 0.9, respectively). In this fringe, species richness was also significantly different between coastal orientations, presenting the highest number of species in the north orientation (13.8), the mean in the east (11.4) and the lowest one in the west (10.4).

Regarding assemblage composition analysis, although differences within most of the geomorphological variables were statistically significant, R values were in general very low in the ANOSIM test (Table 2). For this reason, we considered species composition to be remarkably different when $p < 1\%$ and $R > 0.2$. This way, the structure of the macroalgae communities could be considered different according to coastal morphology in the lower intertidal and to coastal orientation in the middle intertidal.

Finally, the response of individual species to geomorphological variables was examined. Before describing these results, it has to be noted that only two sites along the coast of Cantabria are of a siliceous nature. Thus, relations between lithology and specific species have to be analysed with caution, without generalising the effects of this particular factor. The species preselected by SIMPER analysis were those needed to reach a 90% cumulative contribution to dissimilarity between categories, which were 12 in the lower intertidal. From these, *Codium tomentosum*, *Cystoseira baccata*, *Gelidium corneum* and *Ulva* spp. showed no significant relation with geomorphological variables, according to the increment on deviance with respect to the null model (Table 3a). On the other hand, *C. officinalis/E. elongata* was significant for all variables. As seen in Fig. 4, this taxa has a great probability of occurrence in high slope and siliceous substrates that were north and west oriented and lacked active processes. On the contrary, *Bifurcaria bifurcata* appeared mostly in wave-cut platforms of a calcareous chemical nature that were west or east oriented. Related to the coastal morphology, *Ceramium* spp. and *Gelidium spinosum* showed a high presence in cliffs areas. Regarding coastal orientation, *Ceramium* spp., *Falkenbergia rufolanosa* and *G. spinosum* presented a great probability of occurrence in areas oriented towards the north, while *C. ustulatus* mostly appeared in areas oriented towards the east. *Cystoseira tamariscifolia* and *S. scoparium* showed opposite relationships to active processes, with *C. tamariscifolia* appearing at sites with landslides. In the case of *S. scoparium*, however, probabilities have to be considered with caution because the maximum likelihood estimation did not converge even when the number of iterations increased. Finally, *G. spinosum* seemed to have a high probability of occurrence in siliceous substrates.

In the middle intertidal, 17 species were preselected by SIMPER analysis. Six species, *Cladophora* spp., *C. tomentosum*, *C. baccata*, *C. tamariscifolia*, *G. corneum* and *G. spinosum*, were not significantly related to geomorphological variables according to the logistic model (Table 3b). On the contrary, *Ulva* spp. was entered into the model for its significant relationship to active processes and coastal morphology, although Fig. 5 showed the broad tolerance of this cosmopolitan taxa for both variables. Several taxa exhibited a higher probability of occurrence where there are no landslides processes, such as *B. bifurcata*, *C. ustulatus*, *Ceramium* spp., *Lithophyllum incrustans* and *Osmundea pinnatifida*. *L. incrustans* showed a slightly higher probability of occurrence in cliffs substrates. For *Condracanthus acicularis* and *F. rufolanosa*, an increase in presence probability was observed in coasts oriented towards the north, whereas *C. officinalis/E. elongata* presented a high probability of occurrence along all orientations. Lithology variables did not present any significant relationship with species at this level.

4. Discussion

According to the results obtained, intertidal macroalgae distribution is partially related to geomorphological features at a local scale. This influence happens in different ways and with different intensities depending on the intertidal zone and the level of organisation analysed. In relation to species richness and diversity, slight differences were detected between most of the geomorphological factors. The assemblage composition seems to be partially determined by coastal morphology and coastal orientation, and several species (i.e., *B. bifurcata*, *C. officinalis/E. elongata*, *F. rufolanosa*, *G. spinosum*) showed preferences according to geomorphological characteristics.

This work provides an advanced and appropriate approach in the study of geomorphological features and seaweed distribution to improve knowledge about their relationship. The observational and descriptive method here applied seems to be highly relevant, as studies using artificial surfaces may be extremely misleading (McGuinness, 1989). On the other hand, sampling work performed during spring and/or summer avoids the influence of seasonal influences by obtaining their cumulative effect (Gaspar et al., 2012). In addition, the analysis of associations between the probability of

Table 1
ANOVA test (*p*) on the richness (S) and diversity (H) indices according to geomorphological variables. Kruskal–Wallis (KW) test applied when a non-parametric test was required.

		Lower intertidal				Middle intertidal			
		df	MS	*F*	*p*	*df*	MS	*F*	*p*
Active processes	S	1	11.07	0.61	0.437	–	–	4.66 KW	0.031*
	H	1	0.03	0.09	0.765	–	–	7.46 KW	0.006**
Coastal morphology	S	1	45.99	2.59	0.111	1	35.21	3.88	0.052
	H	1	0.48	1.76	0.178	1	0.27	1.09	0.299
Coastal orientation	S	2	23.47	1.31	0.276	2	90.45	12.03	0.000**
	H	2	0.48	1.76	0.178	2	0.42	1.72	0.184
Lithology	S	–	–	3.83KW	0.051	1	19.14	2.07	0.154
	H	1	2.81	11.40	0.001**	1	0.31	1.27	0.263

*$p < 0.05$, **$p < 0.01$.
KW: Kruskal–Wallis test statistic.

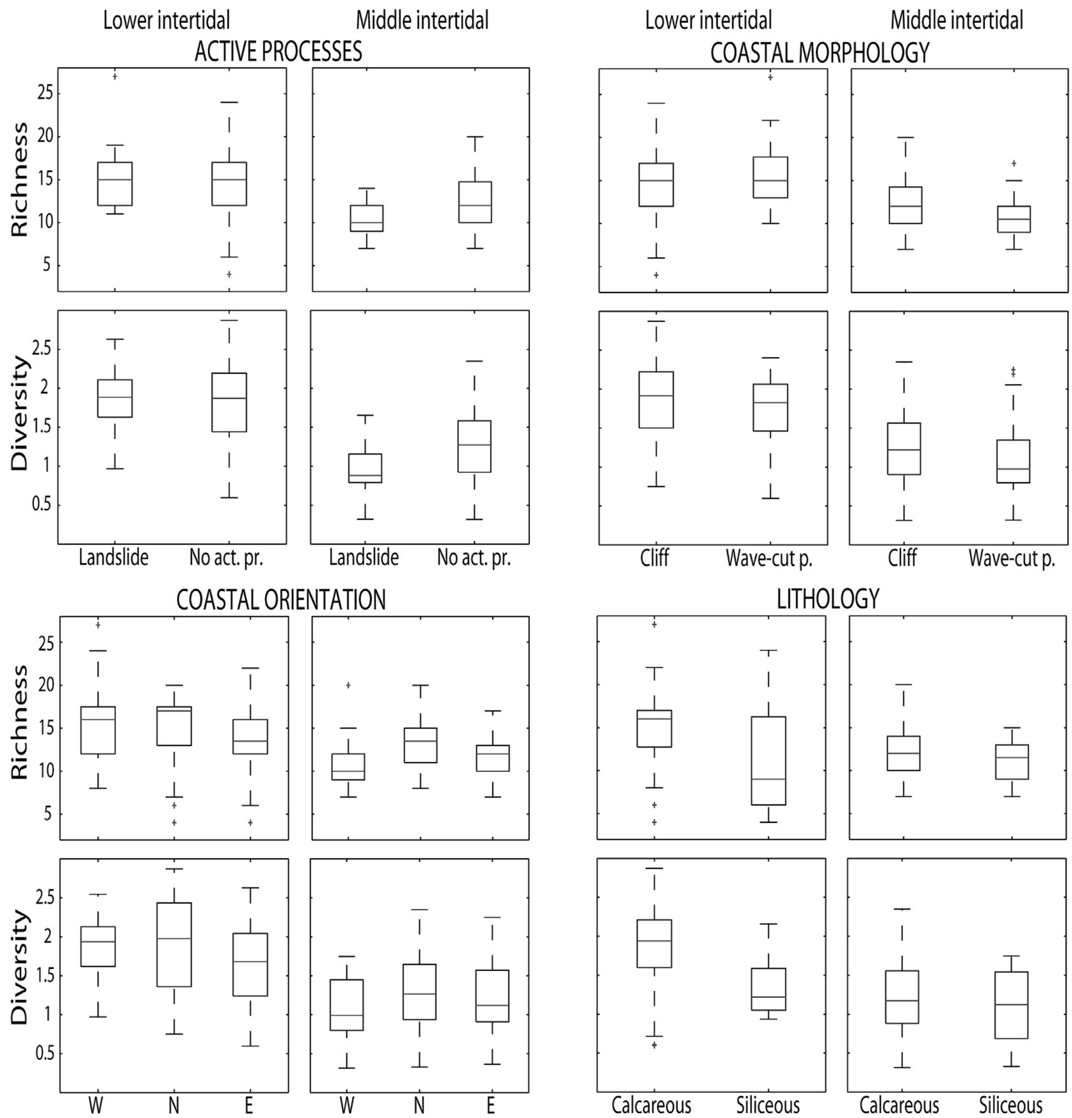

Fig. 3. Box plots of species richness and Shannon Wiener diversity for each category of geomorphological variables. The middle line in the box is the median, the lower and upper box boundaries mark the first and third quartile. The whiskers are the largest and smallest observed values that are not statistical outliers (values more than 1.5 interquartile range), which are represented by a cross. No act. Pr.: No active processes; Wave-cut p.: Wave-cut platform.

occurrence of marine species and abiotic environmental variables by logistic regression may generate robust predictions of distribution, even if the mechanisms or processes that explain the effect of the type of substratum on the abundance of sessile species in marine habitats are not known (Ysebaert et al., 2002; Ellis et al., 2006). According to McGuinness (1989), the reasons for these effects are not clear, but may include differential grazing by invertebrates or differential retention of spores, water or heat.

Table 2
Results of global and pairwise test (R and *p*) from ANOSIM for differences among geomorphological variables.

Global test		Lower intertidal		Middle intertidal	
		R	*p* (%)	R	*p* (%)
Active processes		0.10	3.2*	0.00	46.1
Coastal morphology		0.24	0.1**	0.12	1.2*
Coastal orientation		0.17	0.1**	0.21	0.1**
Lithology		0.14	1.8*	−0.07	81.9
Pairwise test					
		Lower intertidal		Middle intertidal	
		R	*p* (%)	R	*p* (%)
Coastal orientation	E, W	0.11	0.3**	0.13	0.2**
	E, N	0.21	0.1**	0.19	0.1**
	W, N	0.17	0.1**	0.21	0.1**

*p (%) < 5, **p (%) < 1.

In general, species richness and Shannon–Wiener diversity indexes did not show strong patterns related with geomorphological features. Active processes in the middle intertidal were the only variable significantly related to both richness and diversity indexes, as these indexes were higher in areas without landslides. Active processes (i.e., boulder of different sizes) could create a more heterogeneous habitat with higher diversity and richness because of an intermediate disturbance effect. But, in this case, the explanation could be that disturbance caused by active processes, results in reduced diversity by causing mortality and recruitment inhibition of less tolerant species and/or enhancing the spatial dominance of a few tolerant space-monopolising species (Schiel et al., 2006).

The variables that show significant differences according to the composition and structure of the communities, coastal orientation and coastal morphology, seem to be associated with other factors that ultimately determine species distribution. Coastal orientation

Table 3
Fitting diagnostics for different geomorphological variables in the lower (a) and middle (b) intertidal, including the rate of change on deviance (ΔDev) and the chi-square distribution assuming a confidence level $\alpha = 95\%$ (χ^2).

	Active processes		Coastal morphology		Coastal orientation		Lithology	
	ΔDev	χ^2	ΔDev	χ^2	ΔDev	χ^2	ΔDev	χ^2
a) Lower intertidal								
B. bifurcata	0.36	7.81	44.89[a]	7.81	17.98[a]	12.59	20.02[a]	7.81
C. ustulatus	–	–	2.56	7.81	13.08[a]	12.59	–	–
Ceramium spp.	6.31	7.81	8.30[a]	7.81	16.16[a]	12.59	9.33[a]	7.81
C. tomentosum	1.45	7.81	2.17	7.81	9.99	12.59	6.55	7.81
C. officinalis/E. elongata	18.19[a]	7.81	26.28[a]	7.81	27.97[a]	12.59	10.97[a]	7.81
C. baccata	–	–	–	–	9.09	12.59	–	–
C. tamariscifolia	11.47[a]	7.81	4.84	7.81	7.35	12.59	–	–
F. rufolanosa	6.49	7.81	–	–	20.65[a]	12.59	2.13	7.81
G. corneum	3.58	7.81	3.97	7.81	6.14	12.59	5.45	7.81
G. spinosum	5.35	7.81	8.54[a]	7.81	24.31[a]	12.59	16.58[a]	7.81
S. scoparium	9.57[b]	7.81	4.34	7.81	11.35	12.59	2.22	7.81
Ulva spp.	6.01	7.81	4.93	7.81	6.83	12.59	5.34	7.81
b) Middle intertidal								
B. bifurcata	29.92[a]	21.03	–	–	15.13[a]	12.59	–	–
C. ustulatus	22.62[a]	21.03	0.43	7.81	9.61	12.59	12.24	7.81
Ceramium spp.	30.16[a]	21.03	2.54	7.81	10.34	12.59	4.09	7.81
C. acicularis	–	–	–	–	15.43[a]	12.59	–	–
Cladophora spp.	–	–	–	–	–	–	0.81	7.81
C. tomentosum	–	–	–	–	9.43	12.59	–	–
C. officinalis/E. elongata	20.33	21.03	1.31	7.81	17.60[a]	12.59	3.33	7.81
C. baccata	–	–	–	–	2.24	12.59	–	–
C. tamariscifolia	–	–	–	–	4.40	12.59	–	–
F. rufolanosa	–	–	–	–	14.73[a]	12.59	–	–
G. corneum	–	–	–	–	2.17	12.59	–	–
G. spinosum	–	–	–	–	10.31	12.59	–	–
L. incrustans	54.7[b]	21.03	19.9[a]	7.81	–	–	7.67	7.81
O. pinnatifida	16.08[a]	21.03	1.51	7.81	–	–	–	–
S. scoparium	17.73	21.03	6.82[a]	7.81	7.35	12.59	1.45	7.81
Ulva spp.	27.67[b]	21.03	9.73[a]	7.81	3.31	12.59	8.29	7.81

[a] ΔDev > χ2.
[b] ΔDev > χ2 but maximum likelihood estimation did not converge.

is related to the exposure to wave action of a particular area. This geomorphological factor is especially related to assemblage composition in the middle intertidal, which can also be related with exposure because the smashing and tearing effects of waves reach a zenith in this zone (Nybakken, 1997). A similar work carried out by Wallenstein and Neto (2006) in the Azores Island showed that wave exposure is more important at the mid-littoral level, as was observed here with coastal orientation. On the other hand, coastal morphology is related to the slope of the substrate. Slope indirectly affects macroalgae distribution by affecting the types of flows and sediment deposition (Díez et al., 2003). Both slope and exposure have been mainly studied because of their relationship with intertidal macroalgae (e.g. Sousa, 1984; Lüning, 1990; Wallenstein and Neto, 2006; Rinne et al., 2011; Spatharis et al., 2011; Troncoso and Sibaja-Cordero, 2011).

In spite of our expectations, active processes that affect richness and diversity do not present differences in the assemblage composition. This may be explained by the particular species that vary, as most are rare species with a low cover (e.g., *Apoglossum ruscifolium, Gymnogongrus crenulatus, Heterosiphonia plumosa, Nitophyllum punctatum, Polysiphonia* spp. and *Pterosiphonia* spp.). As such, the absence of this species in places with landslides causes the decrease in specific richness and Shannon–Wiener diversity indices, even though it does not modify the general structure of the communities, as the keystone species and those with a higher cover remain similar.

Regarding specific species, *C. officinalis/E. elongata* showed a higher probability of occurrence in coasts orientated towards the west and north. This preference may be related to the elevated exposure to wave action of these orientations, as *C. officinalis/E. elongata* is an articulated calcareous taxa theoretically adapted to cope with exposed conditions and usually much more abundant in open coasts (Fernández and Niell, 1982; Puente and Juanes, 2008; Spatharis et al., 2011). This difference is especially marked in the lower intertidal, because in the middle intertidal *C. officinalis/E. elongata* is so abundant that it shows a high cover along the entire coast. On the other hand, *C. officinalis/E. elongata* and *G. spinosum* showed higher probabilities of occurrence in cliffs than in wave-cut platforms, in accordance with observations related to the slope of the substrate in the nearby coast of Asturias (Fernández and Niell, 1982). There are other species, such as *Ulva* spp, which show a cosmopolitan character, appearing throughout the study area without any preference for specific substrates.

As previously mentioned, *C. officinalis/E. elongata* is the clear dominant taxa in the middle intertidal, while in the lower intertidal there seem to be two opposite communities, one dominated by *B. bifurcata* and another by *C. officinalis/E. elongata* and *G. spinosum* (Puente, 2000; Araújo et al., 2005). The first community appears in wave-cut platforms, oriented towards the east and of a calcareous chemical nature, while the second one appears in siliceous cliffs oriented towards the north and west. The relation between lithology and specific species could be inaccurate as only two sites along the coast of Cantabria are of a siliceous nature. This is the case of *G. spinosum*, which shows a preference for siliceous substrates, while, conversely, increase from the west (mostly siliceous shore) to the east (mostly calcareous shore) along the Iberian Peninsula (Anadón, 1983; Gorostiaga et al., 2004). On the other hand, the possible effect of calcareous encrusting macroalgae (e.g., *L. incrustans*, *Mesophyllum lichenoides*) has to be taken into account. These species may create a biological substrate of a calcareous nature

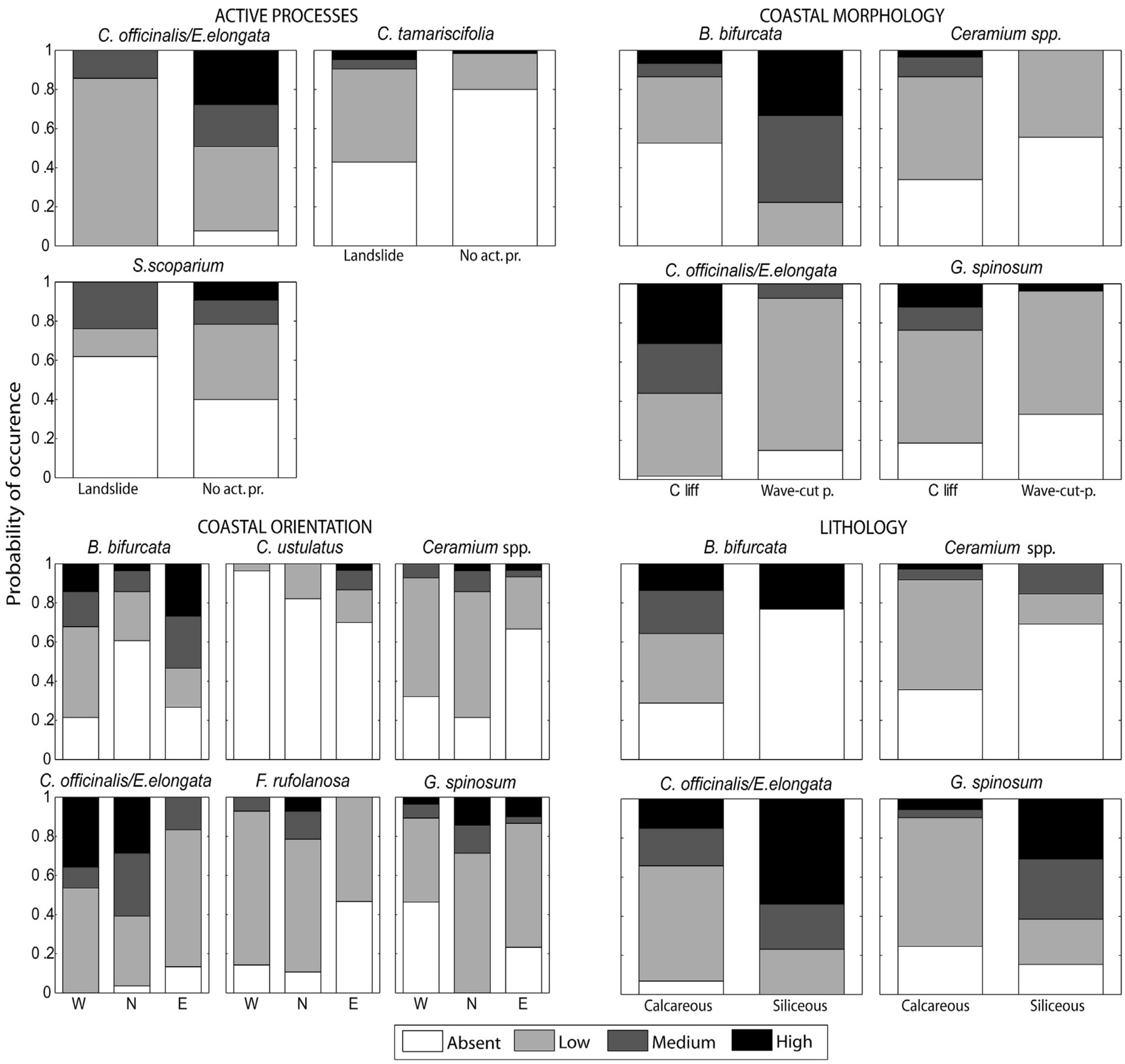

Fig. 4. Probability of occurrence of each species conditioned to geomorphological variables (active processes, coastal morphology, coastal orientation and lithology) in the lower intertidal. No act. Pr.: No active processes; Wave-cut p.: Wave-cut platform.

where epiphytic species are able to grow.

It appears that although geomorphological variables help to characterise species distribution, their predictive value is still limited. This could be explained by the influence of other variables on setting distribution patterns, such as biological interactions, which are of great importance at this local scale and also vary depending on the intertidal level. In the middle intertidal, the physical environment and grazing cause changes in algal composition, while in the lower intertidal, competition for space and light by the various algae are the dominant interactions that structure communities (Nybakken, 1997). In addition, the interactive effects of different factors on the structure of communities are important. Caution is needed when generalising about the effects of one variable alone; for example, orientation and surface composition may interact with each other and/or with other factors, influencing the composition of epibiota communities (Glasby, 2000). Thus, future efforts should be made at a larger scale in order to detect both the individual and the interactive effects of all biological and physical factors, including geomorphological ones, in species pattern distributions.

In conclusion, the geomorphological variables studied show a relation with intertidal macroalgae patterns at a local scale. However, these variables do not seem to be the most determining agents because in most cases they are related to other factors that ultimately define the distribution of species in the different levels of the intertidal. Regarding descriptive parameters, specific richness is related to the orientation of the coast, and this index together with diversity is related to active processes in the middle intertidal. The structure assemblage varies according to coastal morphology in the lower intertidal and to coastal orientation in the middle level. Finally, several species show substrate preferences, such as *B. bifurcata* that appears in wave-cut platforms oriented towards the east, or *C. officinalis/E. elongata* and *G. spinosum*, which are found in cliffs oriented towards the north and west. In any case, the knowledge obtained here about the relationships of species with environmental factors will be helpful for decision-making on the management and conservation of natural resources, offering a means to predict the composition and structure of sustainable systems over space and time (Richardson and Berish, 2003).

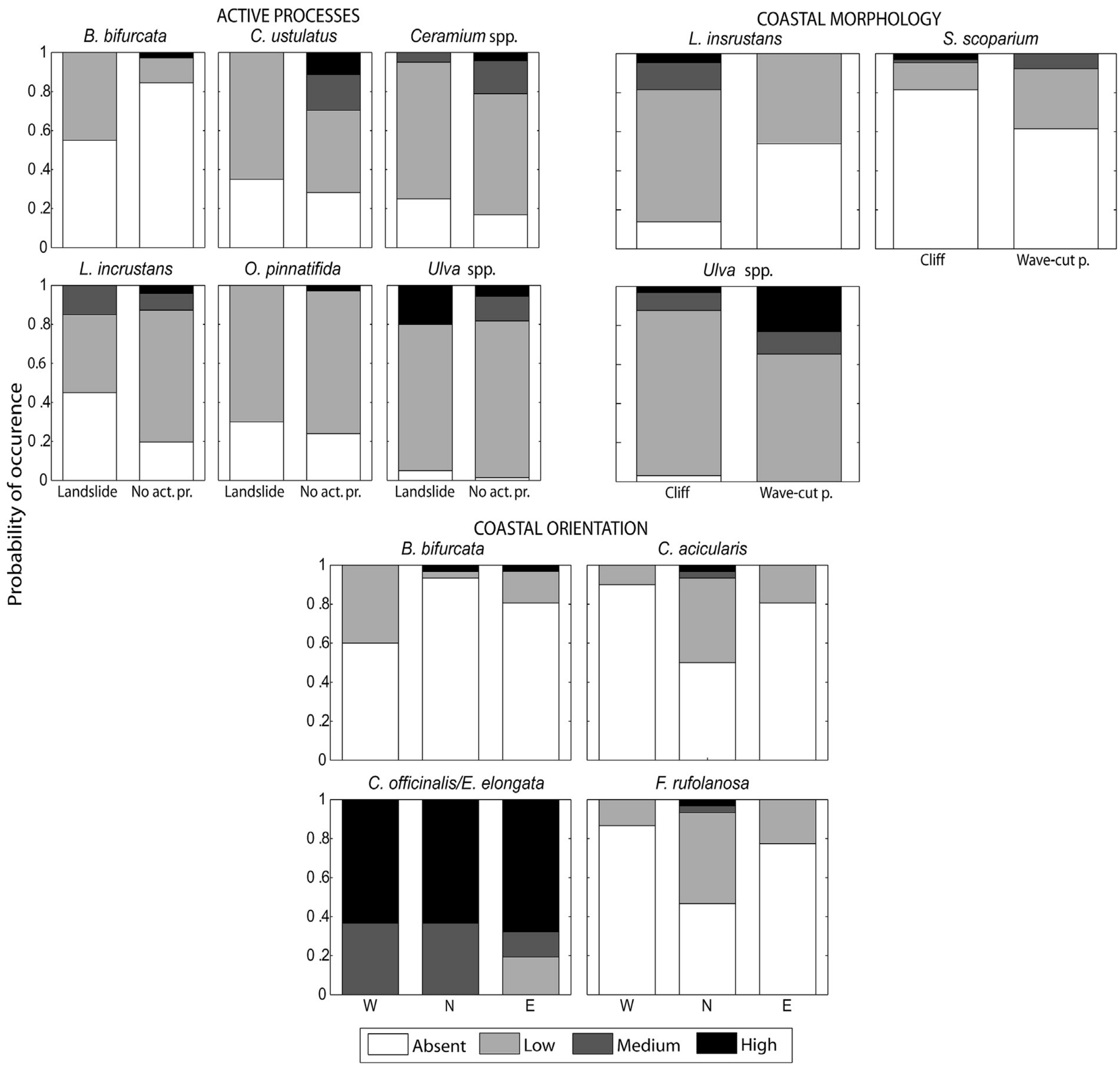

Fig. 5. Probability of occurrence of each species conditioned to geomorphological variables (active processes, coastal morphology and coastal orientation) in the middle intertidal. No act. Pr.: No active processes; Wave-cut p.: Wave-cut platform.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ecss.2015.10.007.

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