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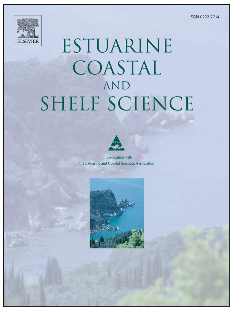

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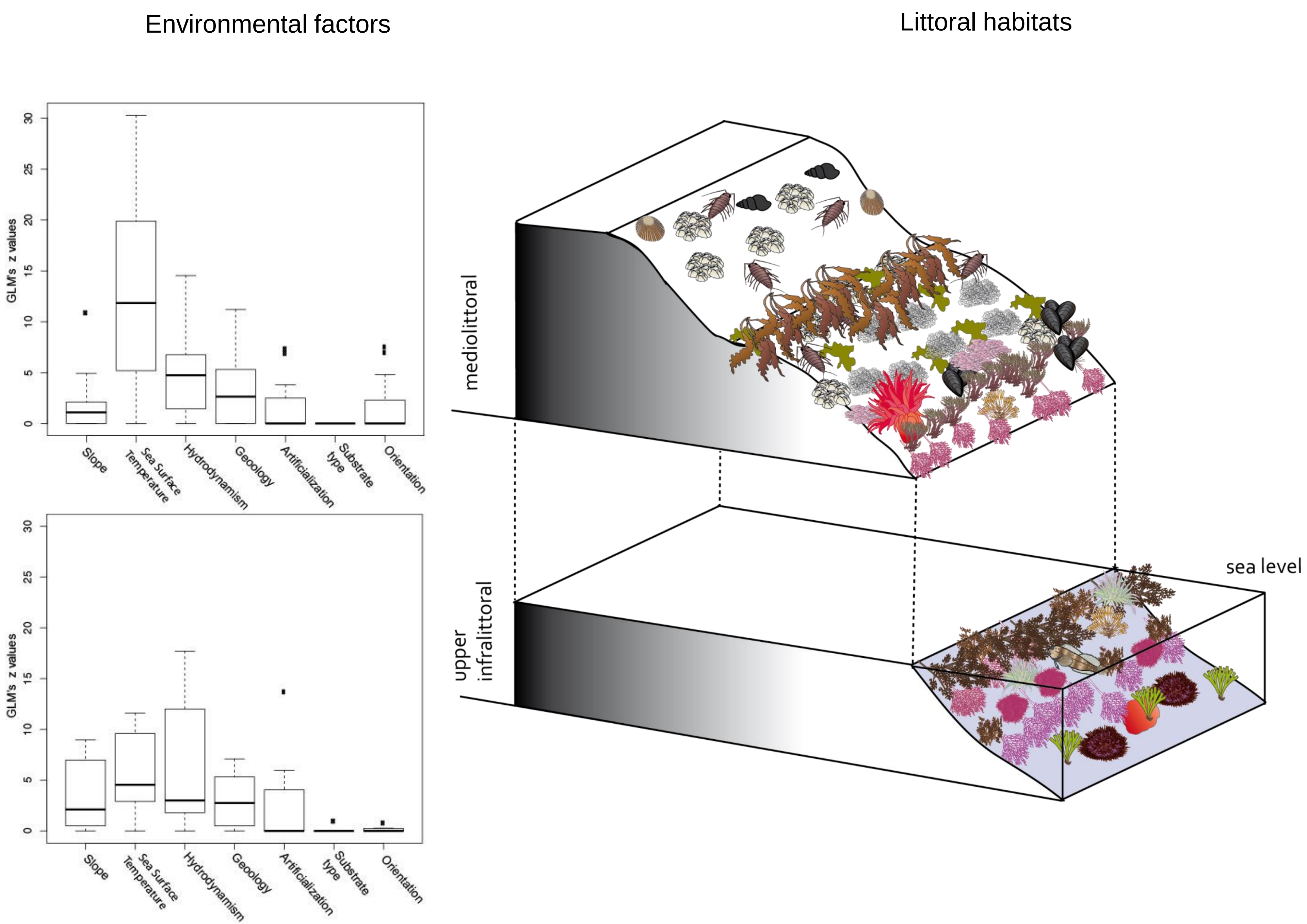

Environmental factors
Littoral habitats
GLM's z values
Slope
Sea Surface Temperature
Hydrodynamism
Geology
Artificialization
Substrate type
Orientation
mediolittoral
upper infralittoral
sea level

Life on the boundary: environmental factors as drivers of habitat distribution in the littoral zone

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Abstract

The boundary between land and sea, i.e. the littoral zone, is home to a large number of habitats whose distribution is primarily driven by the distance to the sea level but also by other environmental factors such as littoral's geomorphological features, wave exposure, water temperature or orientation. Here we explore the relative importance of those major environmental factors that drive the presence of littoral rocky habitats along 1100 km of Catalonia's shoreline (Spain, NW Mediterranean) by using Geographic Information Systems and Generalized Linear Models. The distribution of mediolittoral and upper infralittoral habitats responded to different environmental factors. Mediolittoral habitats showed regional differences drawn by sea-water temperature and substrate type. Wave exposure (hydrodynamism), slope and geological features were only relevant to those mediolittoral habitats with specific environmental needs. We did not find any regional pattern of distribution in upper infralittoral habitats, and selected factors only played a moderate role in habitat distribution at the local scale. This study shows for the first time that environmental factors determining habitat distribution differ within the mediolittoral and the upper infralittoral zones and provides the basis for further development of models oriented at predicting the distribution of littoral marine habitats.

Keywords: mediolittoral, upper infralittoral, benthic assemblages, algae, seaweeds, regional scale.

1. Introduction

The littoral zone of seas and oceans is host to a rich array of biologically diverse and socio-economically important ecosystems (Martínez et al., 2007). Littoral species and habitats may show non-random distributions along the vertical axis perpendicular to the seashore. These distributions are mainly regulated by a strong gradient of environmental conditions, which results in a pattern known as zonation. Zonation is essentially driven by seawater availability (Stephenson & Stephenson, 1949; Lewis, 1964; Dayton, 1971; Foster, 1971; Ballesteros & Romero, 1988; Chappuis et al., 2014). Nonetheless, at wide geographical scales, other distribution patterns arise as a result of the uneven distributions of environmental factors like seawater temperature (van den Hoek, 1982; Breeman, 1988), wave exposure (Levin and Paine, 1974; Denny, 1985), shore slope (Whorff et al., 1995; Benedetti-Cecchi et al., 2000), salinity (Wallentinus, 1991), rock mineral composition (Bavestrello et al., 2000; Guidetti et al., 2004), nutrient availability (Arévalo et al., 2007), or biotic interactions among organisms (Dayton, 1971; Connell, 1972; Underwood & Jernakoff, 1984; Hawkins & Hartnoll, 1985; Janke, 1990; Menconi et al., 1999; Benedetti-Cecchi, 2000; HilleRisLambers et al., 2012). Additionally, species and habitats thriving on rocky shores regularly face anthropogenic pressures that lead to significant changes in their abundance and distribution patterns (e.g. Thompson et al., 2002; Thibaut et al., 2005; Smith et al., 2007; Airoldi & Beck, 2007; Mangialajo et al., 2008; Pinedo et al., 2013; Campbell et al., 2014), especially in densely populated areas (e.g. Ballesteros et al., 2007; Pinedo et al., 2007).

Only few studies have dealt with the distributions of littoral species and habitats at regional scales, and the information available mostly arises from observations (e.g. Stephenson & Stephenson, 1950, 1954; Underwood, 1981; Ballesteros & Romero, 1988; Blanchette et al., 2008; Ramos et al., 2014; Chappuis et al., 2014) and experiments (e.g. Lubchenco, 1980; Menge et al., 1999; Benedetti-Cecchi et al., 1999; Harley, 2003) at local scales. Nevertheless, an increasing number of studies aim to identify (Harley et al., 2006; Martínez et al., 2012; Bermejo et al., 2015) or predict (Huang et al., 2011; Martin et al., 2014) species and habitats distribution patterns across wide geographical areas. In all cases, sampling resolution seems to represent the limiting factor for pattern detection (Archambault & Bourget, 1996, Fraschetti et al., 2005; Tello & Stevens, 2010).

The Mediterranean is a tideless sea (Ballesteros & Romero, 1988) whose littoral zone (i.e. the boundary between terrestrial and marine domains) here is split into two different zones: the mediolittoral and the upper infralittoral (Ros et al., 1985). The mediolittoral zone harbours species and habitats that require or tolerate immersion but cannot thrive in permanent or semi-permanent immersion. The upper infralittoral zone harbours species and habitats that require permanent immersion although they can occasionally survive for short periods of time in emerged conditions. Algae, barnacles and limpets are unevenly distributed across the mediolittoral and infralittoral zones, usually making evident belts or habitats (Chappuis et al., 2014).

The main goal of this study is to identify the environmental drivers of the distribution of mediolittoral and upper infralittoral habitats at a regional scale (> 1000 Km coastline). We rely on a high-resolution GIS-based cartographic database of all littoral habitats found along 1100 km of shoreline in Catalonia (Spain, NW Mediterranean) (Mariani et al., 2014) and physical variables (e.g., substrate type, temperature, hydrodynamism, etc.) as proxies to describe the range of abiotic conditions that define the subsequent distribution of littoral habitats at a regional scale.

Specifically, we aim to (1) identify the subset of environmental variables driving the distribution of littoral habitats at a regional scale; (2) explore the relative importance of each variable in determining the habitat presence both in the mediolittoral zone and in the upper infralittoral zone, and (3) determine the relative importance of local factors (i.e. slope, orientation, geology, substrate type, wave exposure), regional factors (i.e. seawater temperature), and anthropogenic pressures (i.e. coastal artificialization) in shaping the distribution of littoral and upper infralittoral habitats.

2. Materials and Methods

2.1 Study area

The coastline of Catalonia (Spain, NW Mediterranean Sea) stretches along 1100 km and is constituted of 39% natural rocky shores, 30% artificial hard-bottom shores (breakwaters, sea walls, jetties, etc.), and 30% beaches (see Mariani et al., 2014). Data on littoral habitat distribution and environmental variables were collected along the entire coast, concretely between 3º10'28.072"E, 42º26'17.619"N and 0º30'57.001"E, 40º31'26.302"N. In this study, only hard-substrate habitats (both natural and artificial) were considered. The Catalan littoral zone (from the supralittoral down to the upper infralittoral zone at -1 m, as defined by Chappuis et al., 2014) encompasses most of the Mediterranean littoral habitat diversity (Ballesteros et al., 2007; Mariani et al., 2014), thus providing an excellent opportunity to explore the relationships between habitat and the distributions of environmental variables.

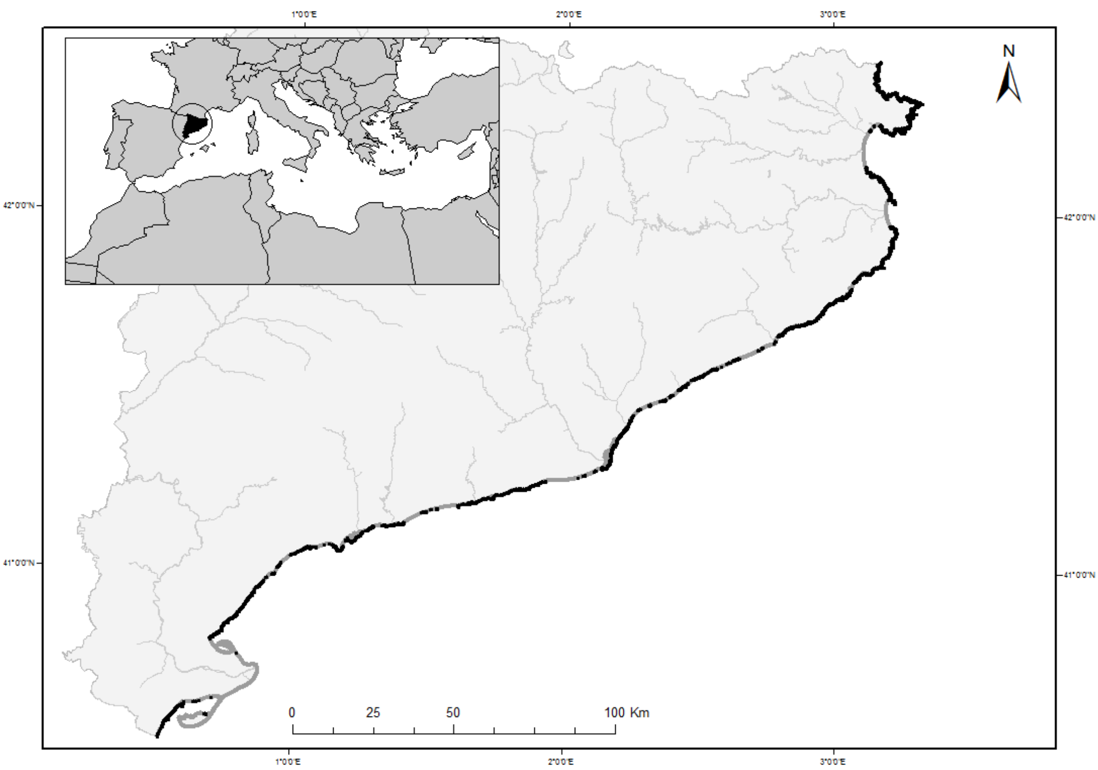

Figure 1. Coastline of Catalonia. Rocky and other hard-bottom shores are coloured in black.

2.2 Input data

2.2.1 Habitats

A habitat is here considered following the definition of the European Habitats Directive (92/43/EEC, see Mariani et al., 2014). The habitats were recognised in the field from their macroscopic biological features (i.e. the presence of dominant species; see Mariani et al., 2014), and corresponded to littoral habitats recognised by at least one of the three main classification schemes used in the Mediterranean Sea (CORINE Biotopes, EUNIS, and LPRE lists; see Ballesteros et al., 2014).

All littoral habitats distributed from the supralittoral to the upper infralittoral (0-1 m depth) zones were digitally mapped along Catalonia using the Cat-LIT methodology (Mariani et al., 2014), at 1:1500 scale. The minimal sampling unit was 10 m (Ballesteros et al., 2014; Mariani et al., 2014), thus the rocky coast was split into 15,934 segments. The coastline polyline layer contained all data about the habitat composition for each segment. Among all identified habitats, those that were widespread [e.g. habitats from the supralittoral zone and the upper mediolittoral zone dominated by lichens (*Verrucaria amphibia*), periwinkles (*Melarhaphe neritoides*, *Echinolittorina punctata*) and barnacles (*Euraphia depressa*, *Chthamalus* spp.) and those that were present in coast segments measuring less than 10 m (see exceptions in Mariani et al., 2014) were eliminated from the data set to prevent confounding statistical results. The final dataset included data on the distribution of 29 littoral habitats, 19 in the mediolittoral zone and 10 in the upper infralittoral zone (Table 1).

Mediolittoral Habitats	**Code**	**% (16098 points)**	**% (1000 points)**
Mediolittoral *Corallina elongata*	Cor elo ML	84.3	82
Mediolittoral *Mytilus galloprovincialis*	Myt gal ML	50.9	47.3
Rissoella verruculosa	Ris ver	47.9	41.3
Lithophyllum byssoides	Lit bys	34.9	30.5
Gelidium pusilum/Gelidium crinale	Gel pus/Gel cri	12.9	14.1
Ulvales	Ulv	8.0	10.2
Ralfsia verrucosa	Ral ver	7.7	9.1
"Trottoir" (*Lithophyllum byssoides* rim)	Trottoir	7.2	6.4
Polysiphonia sertularioides	Pol ser	6.4	7.3
Ceramium spp./ *Osmundea* spp.	Cer Osm	4.5	6.2
Ceramium ciliatum	Cer cil	4.2	4.2
Lithophyllum cf.*vickersiae*	Lit vic	3.9	3.6
Nemoderma tingitanum	Nem tin	2.8	2.7
Neogoniolithon brassica-florida	Neo bra	2.8	3.4
Bangia atropurpurea	Ban fus	0.8	1
Hildenbrandia rubra and *Phymatolithon lenormandii*	Hil Phy	0.7	0.8
Dendropoma petraeum	Den pet	0.5	0.5
Mediolittoral *Lithophyllum incrustans*	Lit inc ML	0.4	0.4
Pyropia elongata	Pyr elo	0.3	0.3
Infralittoral Habitats	**Code**	**% (16098 points)**	**% (1000 points)**
Infralittoral *Corallina elongata*	Cor elo IL	64.9	62.4
Cystoseira mediterranea	Cys med	28.4	23.5
Photophilic algae	PA	24.1	26.1
Infralittoral sciaphilic *Corallina elongata*	Cor elo SIL	4.6	4.7
Infralittoral *Lithophyllum incrustans*	Lit inc IL	2.6	2.7
Sciaphilic algae	SA	1.2	1
Infralittoral *Mytilus galloprovincialis*	Myt gal IL	1.0	1.2
Cystoseira caespitosa	Cys cae	1.0	1
Pterocladiella capillacea	Pte cap	0.2	-
Sabellaria alveolata	Sab alv	0.1	-

Table 1. List of the habitats studied. Each habitat is named after the principal species that characterizes it. Different frequencies of habitats occurrence for data sets of 16098 points and 1000 points are presented.

2.2.2 Environmental variables

Data on environmental parameters relative to substrate features (slope, orientation, and geology), substrate type, coastal artificialization, wave exposure (hydrodynamism), and seawater temperature were obtained from different sources (Table 2).

Slope and orientation (relative to the cardinal points) of the coast were obtained from a Digital Elevation Model (DEM) created with a LiDAR detection method by the Institut Cartogràfic de Catalunya (ICC). The DEM was in raster format with pixel resolution of 2×2 meters. Slope and orientation were calculated with a surface spatial analysis tools in ArcGis. Slope was classified into five categories and orientation into eight levels (Table 2).

The geological features of the rocky shore (i.e. the mineral composition) were provided by the Institut Geològic i Cartogràfic de Catalunya (IGCC, www.igc.cat) at 1:50.000 scale. Five different categories were considered: sedimentary (calcareous, lutite, graywake), plutonic (mostly granitic), metamorphic (schists), mineral (quartz and barite), and artificial.

Eight substrate types were recognized in situ for each coastal segment: continuous rock, partially emerged rock (without supralittoral zone), submerged rock (lacking supralittoral and mediolittoral zones), natural boulders, artificial boulders (breakwaters), concrete walls, and caves.

Information on coastal artificialization [i.e. whether a substrate was natural or artificial (man-made)] was obtained from the CARLIT data set (see Ballesteros et al., 2007) at a scale of 1:1000 (Table 2).

Data on wave exposure were estimated using the Downscaled Ocean Waves model (DOW) (Camus et al., 2013), with a resolution of 0.01 degrees latitude and 0.008 degrees longitude, along the shore. The mean, maximum, and minimum wave height values were calculated for a dataset of 3091 points along the coat and corresponding to a time frame of ten years (1998 to 2008) (Table 2).

Daily mean Sea Surface Temperature (SST) from January 2003 to December 2010 was obtained from satellite measurements performed by the MODIS (aqua) sensor system (http://oceancolor.gsfc.nasa.gov/), available as “Ocean Level-2” HDF data by NASA's Goddard Space Flight Center. We considered only high-quality temperature readings (flag values of 0 or 1), and we discarded less reliable readings (flag values of 2 or 3) (see Serrano et al., 2013). Over the SST study period, the mean annual temperature and mean annual 90th and 10th percentiles were determined for 200 points along the Catalan coastline.

Variables	Levels	Layer geometry	ID	Units	Source
Temperature	Average Sea Surface Temperature	Points	SST mean	ºC	MODIS
	P90 Sea Surface Temperature	Points	SST P90	ºC	MODIS
	P10 Sea Surface Temperature	Points	SST P10	ºC	MODIS
Hydrodynamism			Hydro	meters	DOW
	Average wave height	Points	hmean	meters	DOW
	Minimum wave height	Points	hmin	meters	DOW
	Maximum wave height	Points	hmax	meters	DOW
Orientation			Ori	qualitative	DEM
	North	Raster	N	qualitative	DEM
	NorthEast	Raster	NE	qualitative	DEM
	East	Raster	E	qualitative	DEM
	SouthEast	Raster	SE	qualitative	DEM
	South	Raster	S	qualitative	DEM
	SouthWest	Raster	SW	qualitative	DEM
	West	Raster	W	qualitative	DEM
	NorthWest	Raster	NW	qualitative	DEM
Slope			Slope	degrees	DEM
	0º - 10.8º	Raster	1	degrees	DEM
	10.8º - 22.8º	Raster	2	degrees	DEM
	22.8º - 45.1º	Raster	3	degrees	DEM
	45.1º - 68.2º	Raster	4	degrees	DEM
	68.16º - 87.8º	Raster	5	degrees	DEM
Geology			Geo	qualitative	IGCC
	Metamorphic	Polygons		qualitative	IGCC
	Mineral	Polygons		qualitative	IGCC
	Plutonic	Polygons		qualitative	IGCC
	Sedimentary	Polygons		qualitative	IGCC
	Artificial	Polygons		qualitative	IGCC
Artificialization			Arti	qualitative	CARLIT
	Natural	Polyline	N	qualitative	CARLIT
	Artificial	Polyline	A	qualitative	CARLIT
Substrate type		Polyline	Subs	qualitative	CAT-LIT

Rock	Polyline	2	qualitative	CAT-LIT
Rock without supralittoral	Polyline	3	qualitative	CAT-LIT
Natural rocky boulders	Polyline	4	qualitative	CAT-LIT
Harbour docks	Polyline	5	qualitative	CAT-LIT
Breakwaters	Polyline	6	qualitative	CAT-LIT
Caves	Polyline	8	qualitative	CAT-LIT
Concrete walls	Polyline	9	qualitative	CAT-LIT
Underwater rocks	Polyline	10	qualitative	CAT-LIT

Table 2. List and description of the environmental variables studied. A detailed explanation on the variable source and the calculation method are provided in the text.

2.3 Spatial data processing

The coastline layer, which included data on habitat distributions and substrate type, was converted into a point layer dataset with an ArcGis data management tool, where points were spaced 10 m from each other, to match the habitat data resolution.

In order to perform the statistical analysis, all the layers carrying environmental variables were overlapped and joined into the habitat layer in ArcGis. Different spatial tools were applied to combine all layers, depending on whether the layer was a vector or a raster. Within the vector layers, a closest spatial joint analysis was performed between the habitat dataset and all the other vector layers (exposure, geology, SST, and artificialization). An extraction spatial analysis with a bilinear interpolation was performed for the slope and orientation rasters. Nevertheless, deviations of overlapping values of all environmental variables were revised and corrected when necessary. This layer-by-layer procedure and particularly the continuous validation from expert knowledge used to generate the final database allowed minimising possible generation and propagation of errors deriving from uncertainty problems (e.g. different sensors, extrapolation from unknown parameters, different interpolations etc. see Leung, 2010). Finally, a layer of 16,098 points with biological and environmental information was obtained. Data processing for all environmental variables is summarized in Figure 2. The projection system European Datum 1950 UTM Zone 31N was used. All spatial analysis and spatial data processing were performed in ArcGIS 10.1 (©ESRI).

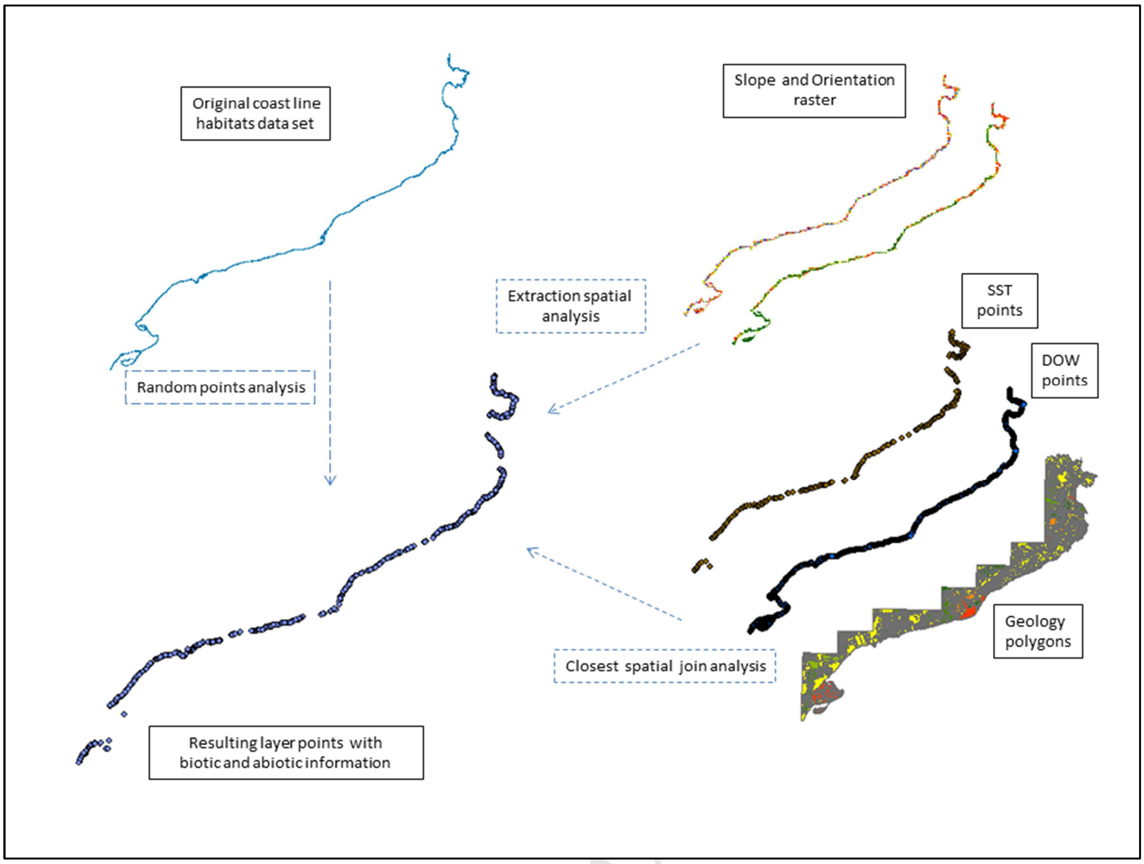

Figure 2. Spatial data processing diagram. Rectangles of solid line correspond to layer name and geometry, rectangles with dashed line correspond to spatial processing. See the text for details.

2.4 Statistical analysis

The four quantitative variables were tested for multi-collinearity based on Pearson's rank correlations (r>0.7). This resulted in a subset of three uncorrelated variables: mean and minimum wave heights and mean SST. The uncorrelated quantitative variables and all the qualitative variables were included in the analysis.

The availability of seawater and environmental variables tested (e.g. wave exposure, seawater temperature, slope) may have differential effects among the habitats of the mediolittoral and the upper infralittoral zones. Consequently, they were analysed separately.

Generalized Linear Models (GLM, McCullagh & Nelder, 1989) were developed to describe the relationship between the distribution of habitats and environmental variables using the entire dataset (16,098 points). Specifically, we performed logistic regression models assuming a binomial distribution with a logistic link function. The best model for each habitat, among the candidate models, was selected with the *glmulti* function (in the glmulti R package; Calcagno, 2013), and based on AIC values. Selected models were further analysed and the significance of the variables included was tested with Likelihood Ratio Test. The significant z values of the models were used for the interpretation of the relationships between variables (habitat vs. environmental variables). The fit of the model (D^2) was calculated as the proportion (%) of explained deviance:

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

To show the relative importance of each variable in the models, the mean and the dispersion of the significant z values (percentile 5% and 95%), both for the mediolittoral and upper infralittoral zones, were plotted in a boxplot diagram.

Presence/absence habitat data were analysed by a non-metric multi-dimensional scaling (nMDS) based on the Bray-Curtis similarity index to visualize spatial patterns. To simplify the computing effort and only for the multivariate analyses, the dataset was reduced to a lower resolution. For this aim, the layer was resampled in ArcGIS obtaining a matrix of 1000 points (one point every 120 m) along the coast. The subset was considered representative of the database, as the habitat occurrence frequencies matched between datasets (see Table 1). A bioenv analysis (in the vegan R package; Okasen et al., 2013) was performed to investigate the relationship between habitats and environmental variables, and to identify the subset of variables showing the maximum correlation with habitats dissimilarity. Those variables with maximum correlation from the bioenv analysis were projected in the nMDS with *ordisurf* function (in the vegan R package; Okasen et al., 2013).

All statistical tests were performed with the R software (R Development Core Team, 2011).

3. Results

The results of the logistic regression models are summarized in Tables 3 and 4. The variability explained by the environmental variable models for the mediolittoral habitats ranged between 5.2% and 72.6% (Table 3). The highest values were shown by the habitat of mediolittoral caves dominated by the encrusting red algae *Hildenbrandia rubra* and *Phymatolithon lenormandii* (72.6%), the habitat dominated by the encrusting red alga *Neogoniolithon brassica-florida* (50.0%), and the habitat dominated by the erect red alga *Rissoella verruculosa* (47.2%). The lowest values were shown by *Mytilus galloprovincialis* beds (5.2%), mediolittoral *Corallina elongata* turfs (11.5%), *Lithophyllum incrustans* barrens (14.6%), and *Nemoderma tingitanum* crusts (15.2%). D^2 overall ranged between 20 and 40% for the rest of habitats (Table 3).

The variability explained by the environmental variable models for the upper infralittoral habitats ranged between 8.8% and 70.2% (Table 4). The highest value was shown by the reefs of *Sabellaria alveolata* and the lowest by the algal beds of *Cystoseira caespitosa*. D^2 ranged between 9% and 36% for the other habitats (Table 4).

In the mediolittoral zone, “Trottoir” *(Lithophyllum byssoides* rim) and *Ralfsia verrucosa* crusts were found along steep shores with high wave exposures, and low water temperatures. While *Lithophyllum byssoides* rims were best associated with calcareous substrates, *Ralfsia verrucosa* crusts were found preferentially on both granitic and calcareous rocks, also on artificial substrates. The habitats of *Rissoella verruculosa* and *Lithophyllum byssoides* cushions were associated with low temperatures, moderate slopes on shores highly exposed to wave action, preferably over plutonic rocks. Furthermore, *Rissoella verruculosa* was negatively correlated with coastal artificialization. The habitats of *Nemoderma tingitanum* and *Lithophyllum* cf. *vickersiae* were also associated with low temperatures and moderate slopes on exposed shores. Moreover, *Nemoderma tingitanum* did not show any geological preference regarding the substrate. In contrast, the habitat dominated by *Lithophyllum* cf. *vickersiae* seemed to prefer natural, sedimentary substrates. The mediolittoral habitat of *Corallina elongata*, was associated with low temperatures, but did not show any relationship with other variables. The habitat characterized by *Polysiphonia sertularioides* was present on moderately exposed, artificial, steep shores with high water temperatures. The habitat characterized by *Neogonioliton brassica-florida* and *Dendropoma petraeum* was present on shores with moderate slopes and hydrodynamism, but high water temperature. These environmental conditions were associated also with the distribution of the mediolittoral mussel beds, although the total variance explained was very low. The habitats of *Hildenbrandia rubra* and *Phymatolithon lenormandii*, *Gelidium* spp., *Ceramium ciliatum*, and *Ceramium – Osmundea*, which showed strong association with moderately exposed shores and high water temperatures, had no relationship with slope. Coastal steepness and high seawater temperatures were strongly related to the presence of barrens of *Lithophyllum incrustans*. The habitat dominated by *Ulva* spp. and *Cladophora* spp. (as Ulvales in Table 3) showed no particular preference for any substrate, either artificial or natural, but preferred sites with high seawater temperatures with no preference for slope, wave exposure or geomorphology. The habitat dominated by *Bangia fuscopurpurea* was indifferent to steepness, and was associated with all types of exposed substrate, artificial and both plutonic and sedimentary. Finally, high water temperature was the only variable shown by the best model fit for the habitat dominated by the red alga *Pyropia elongata.* Only seven habitats showed a significant relationship (either positive or negative) with orientation. One exception was the *Lithophyllum byssoides* rim, which was negatively associated with south-east and south-west orientations.

In the upper infralittoral zone, all sciaphilic habitats, those dominated either by *Corallina elongata* or by *Plocamium cartilagineum* and *Schottera nicaensis* were mostly present on steep shores, with low seawater temperature, and strong hydrodynamism. Furthermore, these habitats appeared both on plutonic and sedimentary substrates. The upper infralittoral habitat dominated by *Corallina elongata*, seemed to prefer sites with moderate to high slopes and strong hydrodynamism, and its presence was abundant over granites. The habitat of *Pterocladiella capillacea* was present on steep slopes, and with low water temperatures. Low water temperatures were positively related to habitats dominated by *Cystoseira caespitosa* and *Cystoseira mediterranea,* regardless of any particular slope. In the case of the habitat of *Cystoseira mediterranea*, high wave exposure and natural granitic substrates were associated to its presence. Upper infralittoral barrens of *Lithophyllum incrustans* seemed to prefer sites with low water temperature and low wave exposure. In contrast, the only upper infralittoral habitats that preferred sites with high water temperatures were *Sabellaria alveolata* reefs and mussel beds. The first one appeared on sheltered shores, the second on exposed ones. The presence of photophilic algae seemed to be unrelated to any level of slope, but it was associated with low wave exposures. There was a weak association between the orientation and the distribution of upper infralittoral habitats. Nevertheless, the presence of *Cystoseira mediterranea* stands was positively associated with south-oriented shores.

Different combinations of environmental variables were selected in the models to explain each individual habitat occurrence. Water temperature, slope, wave exposure, and geological features were selected for most of the habitats and showed the highest contributions both for mediolittoral and upper infralittoral habitats. More specifically, water temperature showed the greatest contribution to mediolittoral habitats models, followed by hydrodynamism (wave exposure), geology, artificialization, and slope (Fig. 3a). In the upper infralittoral habitats, hydrodynamism showed the greatest contribution, followed by water temperature, slope, geology and artificialization (Fig. 3b).

The bioenv analysis showed that mean water temperature and substrate type were the variables explaining the highest dissimilarity between habitats, i.e. 30% for the mediolittoral zone and 25% for the upper infralittoral zone.

The results of the nMDSs revealed how mediolittoral habitats were differently distributed across the temperature gradient (Fig. 4a). This pattern was not so evident for the upper infralittoral habitats (Fig. 4b). Regarding substrate types, natural continuous rock was positively associated with several habitats (rims and cushions of *Lithophyllum byssoides*, *Rissoella verruculosa*, *Ralfsia verrucosa*, and *Cystoseira mediterranea*). Breakwaters were associated with mediolittoral and infralittoral habitats of *Corallina elongata*. Caves were always associated with habitats of *Hildenbrandia rubra* and *Phymatolithon lenormandii* in the mediolittoral zone and sciaphilic habitats in the upper infralittoral zone. The other habitats did not display any preference for a particular substrate type (Fig. 4a,b).

Mediolittoral Habitats	Models with z values	D²
H. rubra and *P. lenormandii*	-3.4 sedimentary, +2.6 SST average, +2.08 h average	72.6%
N. brssica-florida	+14.98 SST average, -8.05 h min, +2.21 h average, +2.2 slope3	50.0%
R. verruculosa	-29.68 SST average, +22.9 plutonic, -21.9 sedimentary, -4.5 slope5, +3.2 h average, -2.8 slope 4, +2.7 Arti N	47.2%
D. petraeum	+6.8 SST average, +5.2 h averge, -4.7 h minimum, +2.3 slope3, +2.2 slope2	41.5%
P. sertularioides	+21.3 SST average, -7.5 h minimum, +6 h average, +5.8 slope3, +4.3 slope4, -3.8 Arti N, +2.3 O	39.2%
Ulvales	+11.7 SST average, +9.96 artificial, +7.3 Arti N,-5.8 haverage, +5.4 plutonic, +5.9 sedimentary, -4.02 slope3, +3.4 NO, +2.1 O, -3.3 h minimum, +1.96 NE	23.2%
"Trottoir"	+22.2 sedimentary, +18.5 h average, +13.5 slope 4, +13.1 slope3, +11.4 slope5, -11.97 SST average, +10.6 hminimum, +5.5 slope2, -2.9 SE, -4.1 SO	35.3%
Gelidium spp.	+30.3 SST average, - 7.6 h minimum, +6.4 plutonic, -3.95 artificial, +2.9 h average	33.6%
C. ciliatum	+18.4 SST average, +7.3 h average, -5.5 h minimum,+ 2.8 O, +2 SO	29.6%
R. verrucosa	+14.2 h average, +12.9 h minimum, +11.2 sedimentary, +9.4 slope5, +8.7 artificial, +5.2 slope4, +5.05 slope3, +3.8 plutonic, -2 SST average	29.1%
L. byssoides	-25.1 SST average, +15.4 h average, +12.8 h minimum, -10.9 sedimentary, +9.9 plutonic, +2.9 mineral, 2.6 slope2, -2.3 slope5	25.0%
B. fuscopurpurea	+5.9 artificial, +4.05 h average, -3.2 slope3, +2.7plutonic, +2.3 sedimentary	24.5%

L. cf *vickaersiae*	-13.9 SST average, +6.8 sedimentary, -3.9 slope4, +2.8 Arti N, -2.7 slope5, -2.6 slope3	21.9%
P.elongata	+5.2 SST average	21.6%
Ceramium sp./*Osmundea* sp.	+16.7 SST average, +5.7 artificial, +3.2 plutonic, +2.9 sedimentary, -2.9 h minimum, -2.4 SE	20.4%
N.tingitanum	+9.8 plutonic, -9.6 SST average, +4.6 h minimum, -3.9 slope4, -3.8 slope3, -3.3 slope2, +3.2 artificial, +3.7 sedimentary, +2.5 Arti N	15.2%
L. incrustans ML	+5.4 slope5, +3.2 SST average, -2.04 slope2	14.4%
C. elongata ML	-19.9 SST average, -7.1 artificial, -6.9 Arti N, -3.6 sedimenatry	11.5%
M. galloprovincialis ML	+9.4 h average, +7.8 SST average, +7.6 h minimum, +3.8 slope2, +2.4 slope3, +2.02 SE	5.2%

Table 3. Selected GLMs for mediolittoral habitats. D^2 is the explained deviance of the model considering all significant variables. The z value is the Wald statistic for testing the null hypothesis that the corresponding regression coefficient is zero. The z value sign shows the relation (positive or negative) between the variable and habitat presence. Only z values with significant p values (Pr(>|z|)) were considered and presented in the table.

Infralittoral Habitats	Models with z values	D²
S. alveolata	-4.7 h average, +3.3 SST average	70.2%
Sciaphilic *C. elongata*	+12.9 sedimentary, +11.2 slope5, +9.3 slope4, -9.6 SST average,+8.9 plutonic, +8.4 slope3, +7.5 h average, +3.03 h minimum, +2.3 slope2, +2.2 mineral	36.3%
P. capillacea	-2.9 SST average, +2 slope4, -2 plutonic	26.4%
C. mediterranea	+14.9 plutonic, +14.4 h average, -11.7 slope3, -11.6 SST average, -11.5 slope4, +9.6 h minimum, -7 slope5, -5.7 slope2, +4.05 Arti N, -4.2 NO, -2.8 artificial, +2.25 S, +2 mineral	22.6%
M. galloprovincialis	+7.4 SST average, +2.5 h average, -2.5 h minimum, -2.2 slope3, -2 slope 2, +2 O	21.9%
Sciaphilic Algae	+7.2 slope4, +6.8 sedimentary, +5.9 slope5, +5.3 slope3, +5mineral, +4.8 plutonic, +3.6 slope2, +3.6 h minimum	18.4%
L. incrustans	-11.4 SST average, -7 plutonic, -3.5 h average, -3.5 h minimum, +2.4 Arti N	16.7%
Photophilic Algae	-21.7 h average, -17.8 plutonic, -13.7 h minimum, -9.7 slope3, -8.5 slope4, -6.1slope5, +6 Arti N, -3.6 slope2, -3.5 artificial, -3.06 sub5, -2.24 sub6, -2.4 sub9	9.7%
C. elongata	+17.4 h average, +13.8 plutonic, -13.7 Arti N, +11.97 h minimum, -9.4 sedimentary, +6.04 slope3, -5.15 artificial, +3.6 slope2, +2.6 slope4, -2.1 NO	9.2%
C. casespitosa	-3.7 plutonic, -3.6 SST average, -2.6 slope4, -2.09 slope3	8.8%

Table 4. Selected GLMs for infralittoral habitats. D^2 is the explained deviance of the models considering all significant variables. The z value is the Wald statistic for testing the null hypothesis that the corresponding regression coefficient is zero. The z value sign shows the relation (positive or negative) between the variable and habitat presence. Only z values with significant p values (Pr(>|z|)) were considered and presented in the table.

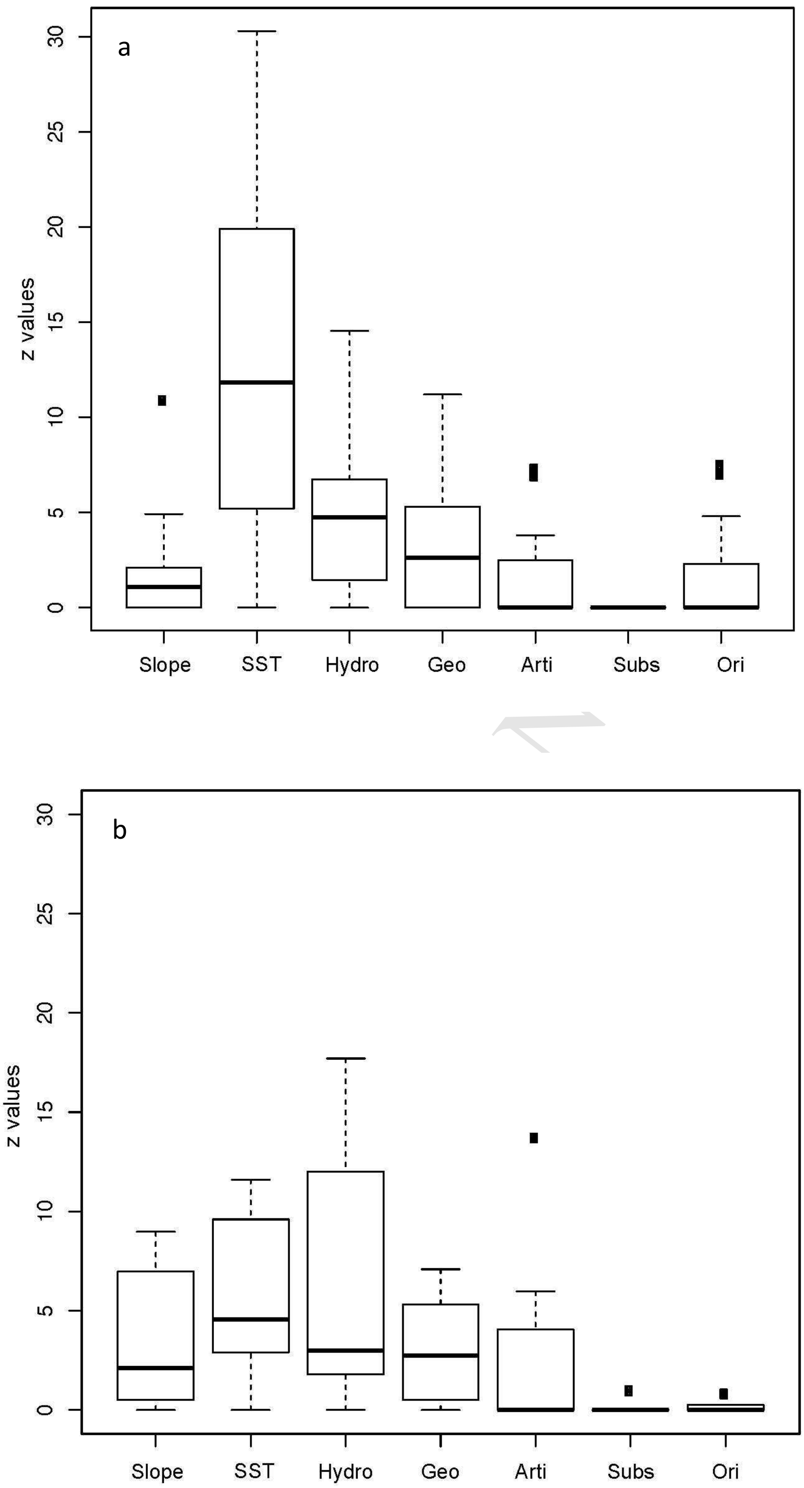

Figure 3. Boxplots of significant GLMs z values for a) mediolittoral zone models, b) upper infralittoral zone models. The mean and the percentiles (5% and 95%) of z values are shown. See Table 2 for codes explanation.

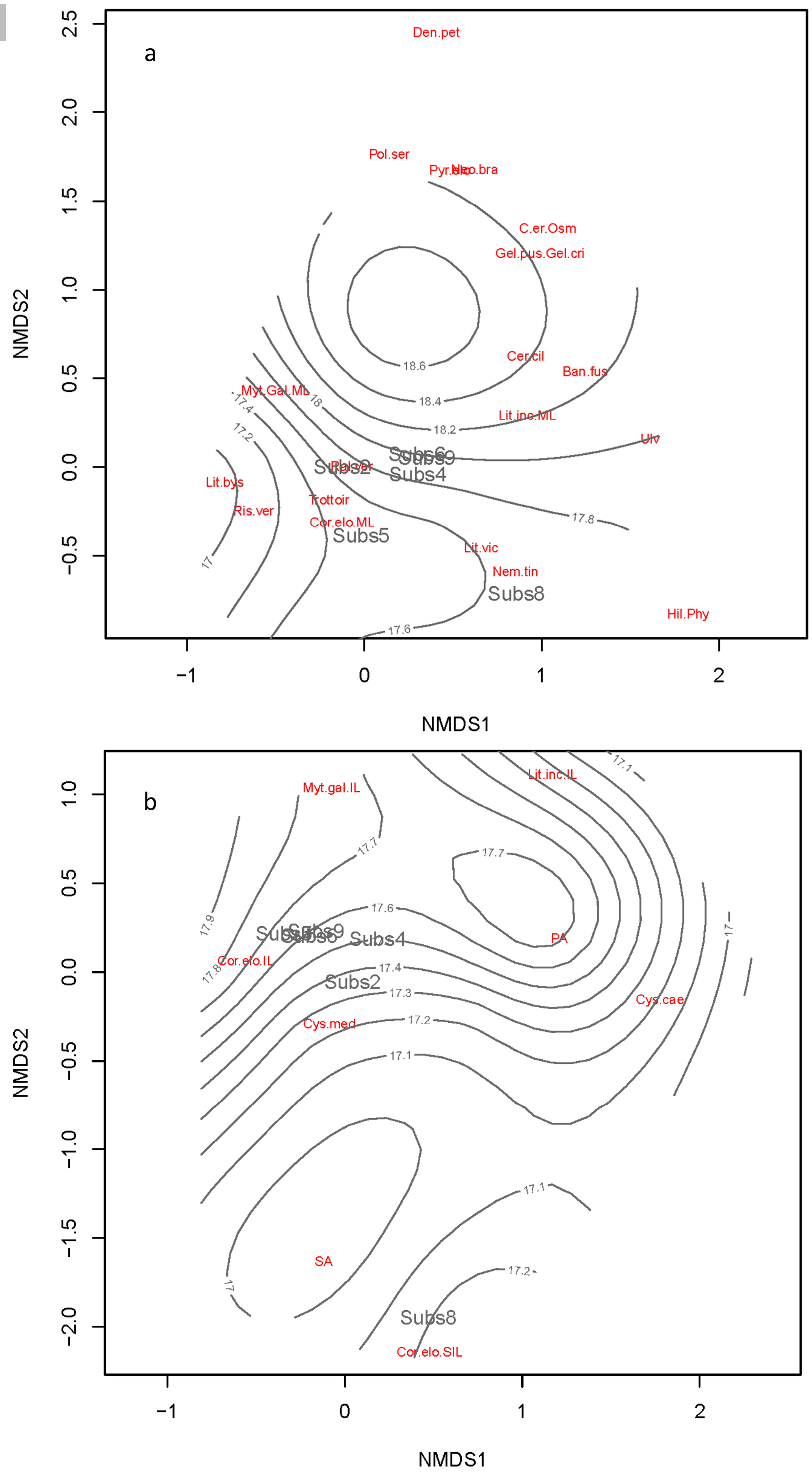

Figure 4. a) nMDS of the mediolittoral habitats. b) nMDS of the upper infralittoral habitats. SST mean (isothermal lines) and substrate type are fitted in both plots. See table 1 and 2 for abbreviations. Each habitat is represented by its centroid. The analysis has been performed with a database of 1000 points (see text).

4. Discussion

Our study provides a general perspective on the relationship between the presence of littoral habitats and environmental factors and sheds some light on the importance of these variables as possible drivers for the distributions of both mediolittoral and infralittoral Mediterranean habitats on rocky shores. The abiotic factors analysed here have been generally disregarded in previous studies. Specifically, most research has focussed on the distribution of a single or a few habitats locally (Martin et al., 2014; Martínez et al., 2012; Bermejo et al., 2015). Our study is the first one examining the relationships between factors such as shore slope, orientation, geology, substrate type, wave exposure, seawater temperature, and coastal artificialization in shaping the distribution of a large number of habitats (19 from the mediolittoral zone and 10 from the infralittoral zone), at a very high resolution and at a regional scale. We found that the relative importance of the considered environmental variables differs among mediolittoral and upper infralittoral habitats. Despite their proximity to infralittoral habitats, mediolitoral habitats show strong dependence on limited, unpredictable water availability. However, different mediolittoral habitats rarely coexist at the same height at a same place. Abiotic factors related to seawater features (i.e seawater temperature) and coastal morphology may play important roles in determining the success of a particular habitat in a particular place (Feldmann, 1937; Ballesteros, 1992; Giaccone et al., 1993). Heterogeneity of coastal morphology (e.g. rock geology, slope, and orientation) may regulate the presence of specific mediolittoral habitats (e.g. *Rissoella verruculosa* vs. *Ralfsia verrucosa* or *Polysiphonia sertularioides*; *Lithophyllum byssoides* vs. "Trottoir" or *Neogoniolithon brassica-florida*). Although very limited periods of aerial exposure under prevailing conditions of calm waters and high atmospheric pressures occur (Rodríguez-Prieto and Polo, 1996), the upper infralittoral zone never faces the harsh conditions of the mediolittoral zone. It also shows lower habitat diversity in the first meter. In general, the main factors that affect the presence and distribution of uppermost infralittoral habitats (always or almost always submerged) are related to nutrient availability (Ballesteros, 1992; Arevalo et al., 2007; Ballesteros et al., 2007; Pinedo et al., 2013, 2015) or light intensity (Ballesteros, 1992; Rinné et al. 2011). Seawater temperature emerges as the main factor determining habitat distribution in the mediolittoral zone, followed by other factors such as hydrodynamism, geology and slope. On the contrary, the main factor driving habitat distribution in the upper infralittoral zone is hydrodynamism, followed by seawater temperature, slope and geology. Temperature has long been recognized as a key factor governing seaweed biogeography (e.g. Stephenson, 1944; Lewis, 1964; Lünning, 1984; Pakker et al., 1995; Anderson et al., 2012; Wernberg et al., 2013) and reproduction (Lüning, 1990; Ballesteros, 1991) and since it varies with latitude (Mieszkowska et al., 2006; Martínez et al. 2012), it is often responsible for the distribution of northern/southern geographic boundaries of seaweeds (Breeman, 1988). Some mediolittoral habitats show a strong relationship with the seawater mean temperature gradient (17º-18.6º) from northern to southern Catalan waters. In fact, some habitats, such as the "Trottoir", are circumscribed to the northernmost coast (i.e. coldest waters). Others are far more abundant in the north, such as the habitats dominated by *Rissoella verruculosa* or *Lithophyllum byssoides*. Other habitats, like the barrens of *Neogoniolithon brassica-florida*, are exclusively present in the south (i.e. warmer waters). Temperature variation in the study area is due to the effects of the warm-water Balearic current in the southern coast and the colder, deep-water generated current from the Lions Golf in the northern coast (Font et al., 1988). However, although quite reduced (less than two degrees ºC), temperature variation in the studied area is a relevant factor driving mediolittoral benthic habitat distributions. On the contrary, while water temperature plays an important role, upper infralittoral habitats do not show latitudinal differences in their distributions. For example, while *Sabellaria alveolata* reefs are only present in the southern coast, the rest of upper infralittoral habitats do not show any latitudinal difference at the geographical scale considered.

Hydrodynamism exerts direct and indirect effects on benthic organisms (Denny, 2006) and it plays a central role in coastal environments (Nishihara & Terada, 2010; Rattray et al., 2015). Hydrodynamism, namely wave exposure, is especially important in heterogeneous areas where it plays a key role in determining the distribution of macroalgae (Snikars et al., 2014). The role of wave exposure in shaping habitat distributions in the mediolittoral zone is crucial for reducing hydric stress due to prolonged emersion times (Chappuis et al., 2014). Increased water movement enhances nutrient availability to seaweeds (Ballesteros, 1989). Many macroalgae-dominated habitats (i.e. "Trottoir", *Lithophyllum byssoides, Rissoella verruculosa*, *Ralfsia verrucosa*) are best developed in high exposed areas. Nevertheless, very strong hydrodynamism can generate a mechanical stress which only a few, morphologically-adapted species, can withstand, causing breakage or even death in adult macrophytes (Viejo et al., 1995; Diez et al., 2003). In areas with high levels of erosion by sand scour, habitats are usually dominated by turf algae (such as *Polysiphonia sertularioides*, *Gelidium* spp.), which are well-known to be adapted to sand scour (Airoldi, 1998). Habitats dominated by Ulvales are mainly present in sheltered areas also subjected to sand scour. At the infralittoral zone, habitats dominated by either *Cystoseira mediterranea*, sciaphilic algae, *Corallina elongata* or

Mytilus galloprovincialis, require high water renewal (Bellan-Santini, 1965; Ballesteros, 1992) and reach their optimum development on exposed coasts (although *Mytilus galloprovincialis* can also grow in sheltered areas like bays or lagoons where it is cultivated). Other habitats show an opposite trend; this is the case of photophilic algal assemblages, *Sabellaria alveolata* reefs and infralittoral *Lithophyllum incrustans* barrens, which are far more frequent in sheltered areas. Slope and orientation are local factors also associated with seaweed distribution on the shore (see Diez et al., 2003). However, we found only a minor effect of rocky slope on the distribution of habitats both in the mediolittoral and in the upper infralittoral zone. Two exceptions are the "Trottoir", often accompanied by the habitat dominated by *Ralfsia verrucosa*, which are very characteristic of steep cliffs with reduced light levels (Boudouresque, 2004; Mannino, 2003). Rock steepness also benefits the presence of habitats formed by sciaphilic algae in the upper infralittoral zone. Although orientation has been documented to have an influence on terrestrial and rocky shore habitats and species (Boyce et al., 2005; Harley, 2008) we did not find any particular effect on the habitats studied here, both for the mediolittoral and the upper infralittoral zones. Another factor with a secondary but significant relation with habitat distribution in this study is geology, i.e. rock mineral content (Harris et al., 2013). Algae are unable to absorb nutrients or any other chemical component directly from the rocky substrate. However, Feldmann (1937) and Giaccone et al. (1993) have observed a close relationship between the presence of some seaweeds and rock types. For instance, "Trottoir" has already been reported to better develop over calcareous substrates (Mannino, 2003) and *Rissoella verruculosa* over granites or schists (Feldmann, 1937). Additionally, in the mediolittoral zone, we have observed widespread, massive presence of the habitat dominated by *Lithophyllum* cf. *vickersiae* on graywake rocks. Guidetti et al. (2004) report a preference of photophilic algae for granitic rocks and of sciaphilic algae for limestones, although we did not find this pattern in the upper infralittoral zone. Affinities between some habitats and the geology seem to be related with the texture and hardness of the different minerals, which has an effect on the recruitment and survival of certain algae (see Bourget et al., 1994). There is a clear difference between habitats usually growing over natural rock, and those present on man-made structures (e.g. harbour docks, breakwaters) (Connell & Glassby, 1999; Smith & Rule, 2002; Bulleri & Chapman, 2004; Ballesteros et al., 2007). Man-made structures usually do not harbour habitats with highly specific environmental requirements (e.g. *Lithophyllum byssoides*, *Rissoella verruculosa*, "Trottoir", *Neogoniolithon brassica-florida*, *Cystoseira mediterranea*), and are usually colonized by pioneering (Ulvales, *Polysiphonia sertularioides*, *Gelidium* spp., *Mytilus galloprovincialis*) or stress-resistant species (*Corallina elongata*).

Normally, artificial structures are abundant along coasts with high human pressures, where only tolerant habitats and species thrive (Ballesteros et al., 2007). Furthermore, pioneering species show a high propagule production and dispersal (Ceccherelli & Rossi, 1984; Bacchiocchi & Airoldi, 2003), thus allowing a more rapid colonization of new structures (Airoldi, 2000). Studying species-environment relationships is crucial to elucidate habitat pattern distributions. Littoral zones are ecologically important areas for a variety of reasons and detailed scientific information is needed to develop and implement appropriate measures of habitat protection and conservation. Knowledge on the biophysical components of these systems is still poor (see Rattray et al., 2015) and this study represents an important contribution towards a better understanding of the habitat-environment relationships. These relationships are at the core of predictive geographical modelling in ecology (Guisan & Zimmermann, 2000) and predictive species distribution models currently represent an essential tool for biodiversity conservation and management (Côté & Reynolds, 2002).

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Highlights

- We study habitat-environment relationships at a regional scale.
- We used high resolution datasets for 29 littoral habitats and 7 environmental factors.
- Water temperature is the main factor driving mediolittoral habitat distributions.
- Wave exposure is the main factor related to upper infralittoral habitat distributions.