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Spatial distribution pattern analysis of subtidal macroalgae assemblages by a non-destructive rapid assessment method

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ABSTRACT

The extensive field work carried out over the last century has allowed the worldwide description of general distribution patterns and specific composition of rocky intertidal communities. However, the information concerning subtidal communities on hard substrates is more recent and scarce due to the difficulties associated with working in such environments. In this work, a non-destructive method is applied to the study and mapping of subtidal rocky bottom macroalgae assemblages on the coast of Cantabria (N Spain) which is quick, easy and economical. *Gelidium corneum* and *Cystoseira baccata* were the dominant species, however, the composition and coverage of macroalgae assemblages varied significantly at different locations and depth ranges. The high presence of *Laminaria ochroleuca* and *Saccorhiza polyschides*, characteristic of colder waters, shows the transitional character of this coastal area. The results obtained throughout this study have been very useful to the application of the European Water Framework Directive (WFD 2000/60/EC) and could be of great interest for the future conservation and management of these ecosystems (e.g. Habitats Directive 92/43/EEC).

1. Introduction

Coastal reefs, defined as "Submarine, or exposed at low tide, rocky substrates and biogenic concretions, which arise from the sea floor in the sublittoral zone but may extend into the littoral zone where there is an uninterrupted zonation of plant and animal communities" (European Commission, 2003), are one of the natural habitat types of community interest at the European level. Their conservation has promoted their designation as Special Areas of Conservation (92/43/EEC Habitats Directive, code 1170), but according to Annex III of the Commission Decision 2004/813/EC, they are amongst the list of habitats which require further clarification in order to complete the list of sites of community importance for the Atlantic biogeographical region. The intertidal and shallow subtidal rocky bottoms (<30 m) comprise a continuous and heterogeneous mosaic of environments (platforms, blocks, pools, ridges, crevices, overhangs) that are colonized by assemblages of the most competitive species of flora and fauna in response to a likely combination of physical (tide, temperature, wave exposure, light, substrate), chemical (salinity, nutrients) and biological factors (competence, predation). Macroalgae, as sessile organisms, respond directly to the abiotic and biotic aquatic environment (Murray and Littler, 1978), therefore becoming sensitive indicators of water quality changes (Fairweather, 1990).

Due to all these reasons, macroalgae and angiosperms, together with phytoplankton and benthic invertebrates, are the biological quality elements which must be evaluated when assessing the ecological status of coastal water bodies, as stated by the European Water Framework Directive. Nevertheless, before macroalgae based environmental quality assessments or management plans are carried out in a specific zone, knowledge of the structure, composition, natural variability and distribution patterns of the usual assemblages occurring in that zone are essential to obtain adequate results. The existing biogeographical differences on macroalgae communities along the Spanish coast of the Gulf of Biscay are well known, first mentioned by Sauvageau (1897), and the causes explained by Fischer-Piette (1955). Consequently, for the development of any work related to the subtidal rocky bottoms of the Cantabrian coast, appropriate cartographies of the most important macroalgae species in the region must be elaborated and their general variability and distribution patterns all along the coast studied.

As stated by Diaz et al. (2004), broad-scale mapping studies of reef communities, together with information on the biological and environmental tolerances of different species and assemblages, constitute an important management tool necessary for the ecological assessment of the sustainability of these habitats. In this sense, the biomass cartography, including localization and quantification, and the understanding of its evolution over time (Santelices, 1989), is the most extended assessment method, being more applied than a basic scientific research.

Different techniques have been used for the cartography of marine benthic vegetal resources, most of them directed towards the evaluation of standing stocks of commercial species (Juanes and Sosa, 1998). The techniques based on sampling representative surfaces were the first ones used for the assessment of seaweed resources (Baardseth,

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1970; Chapman, 1950; Grenager and Baardseth, 1966; MacFarlane, 1952; Marshall et al., 1949). Later, Mann (1972) proposed the "transect method", whose most important contribution consisted of a more complete statistical analysis and the development of a precise error calculating system. This method, or variations of it, have often been used in some of the most recent cartographic studies developed on the northern coast of Spain for both intertidal (Anadón, 1983; Anadón and Fernández, 1988; Anadón and Niell, 1981) and subtidal (Borja, 1987, 1988; Juanes and Gutiérrez, 1992) zones. Other extensive carthographic studies have also been carried out focusing on individual species of particular ecological interest, such as *Caulerpa taxifolia* (Vaugelas et al., 1999) or the marine phanerogam *Posidonia oceanica* (Piazzi et al., 2000). More recently, major interests in macroalgae communities have focused on the study of their responses to anthropogenic pressures (Díez et al., 1999; Echavarri et al., 2007; Gorostiaga and Díez, 1996; Juanes and Canteras, 1995) or to environmental factors (Borja et al., 2004; Díez et al., 2003; Gorostiaga et al., 1998).

Due to the difficulties and elevated costs associated with working in sublittoral rocky zones, works related to macroalgae communities have often been limited to the intertidal fringe. However, according to the Habitats Directive (92/43/EEC), coastal reefs, including both intertidal and subtidal environments, constitute an ecological unit, whose conservation management must be carried out from an integrated point of view. Trying to reduce these costs, several authors have underlined the need to develop methodologies which, without losing their scientific rigor, are economically reasonable and easy to apply in order to carry out extensive management or monitoring works (Borja, 2005; Panayotidis et al., 2004). In this sense, the use of non-destructive sampling methods, included among the recommendations of the *International Council for the Exploration of the Sea* (ICES, 2001), supposes the absence of laboratory work, simplifying data processing and notably reducing the total monitoring costs (Ballesteros et al., 2007; DEFRA, 2004; García-Castrillo et al., 2000a). Another interesting aspect to take into account is the taxonomic level required in the works. Since the taxonomic sufficiency concept was introduced by Ellis (1985), many studies have demonstrated that, in some cases, identification of organisms to higher taxonomic levels such as family or order, is enough to discriminate the different macrobenthic communities, especially between disturbed and non-disturbed areas (Díez et al., 2010; Ferraro and Cole, 1990; Puente and Juanes, 2008; Somerfield and Clarke, 1995; Warwick, 1988a, 1988b).

Considering all these aspects, visual sampling techniques, based on in situ estimations of coverage or frequency counts, using only easily recognizable conspicuous species, appear to be an effective strategy for the rapid assessment of subtidal macroalgae assemblages in order to carry out extensive management or monitoring works (Díez et al., 2010; Parravicini et al., 2010; Puente and Juanes, 2008). According to these guidelines, a low cost and easily applicable methodology is proposed for the study and mapping of subtidal rocky bottom macroalgae assemblages. In this methodology, the use of a non-destructive visual sampling method and a selection of the most conspicuous macroalgae species are combined in order to achieve two main objectives; 1) to analyze the general structure and main distribution patterns of subtidal macroalgae communities in the coastal area of Cantabria and 2) to elaborate basic distribution maps of some of the most important macroalgae species in the region.

2. Material and methods

The sampling procedure used in this work for the study of subtidal rocky bottom macroalgae was based on the general method applied by Mann (1972), incorporating continuous and non-destructive assessment practices proposed by García-Castrillo et al. (2000a). A similar methodology was used by Dayton et al. (1992) in order to analyze long-term spatial and temporal patterns of disturbance and recovery in a kelp community in California. In the present work, 31 transects were systematically established along the 150 km shoreline of Cantabria (N Spain) in places with rocky bottoms and spaced about 2–3 km from each other (Fig. 1). The transects were covered by scuba divers during the year 2005, starting as close as possible to the seashore and extending up to a depth of approximately 20 m, although maximum depths of 25 m were reached in some transects.

Throughout each dive, the total coverage and the specific coverage of the most conspicuous macroscopically visible macroalgae species of the first vegetal cover were recorded in continuous segments of homogeneous characteristics. Each segment covered a 5 m wide area with a variable length depending on the change rate of macroalgae communities and geomorphology (between about 10 m in length in very variable situations, to over 100 m in very homogeneous situations). The beginning and end of each segment was determined using expert judgment based on visible changes of macroalgae assemblages or geomorphological characteristics. Total coverage of each segment was estimated considering all the characteristic macroalgae species colonizing any stable substrate at once, and not considering those surfaces which are inappropriate to be colonized by macroalgae, such as sedimentary substrates, stones or small blocks. For specific coverage estimations, a five level semiquantitative scale was used based on the Braun-Blanquet scale (Braun-Blanquet, 1932); <5% cover (1), 5–25% (2), 25–50% (3), 50–75% (4), and >75% (5). For statistical analyses, mean coverage values of each class were used (e.g. class 1 = 2.5%, class 2 = 15% etc.). Additionally, the type of substrate (rocky or sandy) and the morphology of the rocky substrate (cliffs, platforms, canyons, crevices, blocks or stones) were annotated at each segment, together with depth data and diving time. At the sea surface, using a pneumatic boat, the divers' position was determined following the air bubbles and annotated every 5 min by a GPS in order to locate approximately the information collected during the diving. All transects were filmed with a submarine camera to allow further analysis.

The collected information was standardized to the 0 tide level and homogenized to 7 depth classes (every 3 m), from 0 to 21 m. Information of segments covering two or more depth classes was duplicated and information of various segments corresponding to the same depth class was estimated following the Braun-Blanquet scale. Using this standardized information, an abundance data matrix was constructed, in which depth-classes of each transect were considered as individual stations (samples) and specific mean coverage values of each macroalgae species (variables) provided the abundance data. This data matrix constituted the starting point for the elaboration of basic distribution maps of the most conspicuous macroalgae species of the coast of Cantabria and also to carry out several statistical analyses explaining their general distribution patterns.

To create the cartographies, graphic schemes of interpolated abundance values were used, representing the spatial distribution of transects along the coast at the X axis (based on UTM coordinates) and the depth gradient at the Y axis. Surfer 8.0 was the software used for this task. The interpolation to create the coverage isolines was done using the "Kriging" method over the semiquantitative matrix raw data. To achieve a better adjustment of the representation to reality, seafloor spaces covered by a sedimentary substrate were included in the mapping with zero coverage of macroalgae. For a correct integration of this additional data, the information was introduced in the analysis before the interpolation process.

In order to analyze macroalgae distribution patterns in depth and along the coast, two factors were initially defined; a) depth classes and b) coastal zones. The first factor included the 7 depth ranges mentioned above, and the second factor considered 3 coastal regions along the study area (west zone; transects T01–T11, central zone; transects T12–T20 and east zone; transects T21–T31). The criterion used for the classification of the geographic zones was based on the coastal geomorphology and orientation. The eastern zone is characterized by the influence of Cabo Ajo (T20), a coastal cape where the

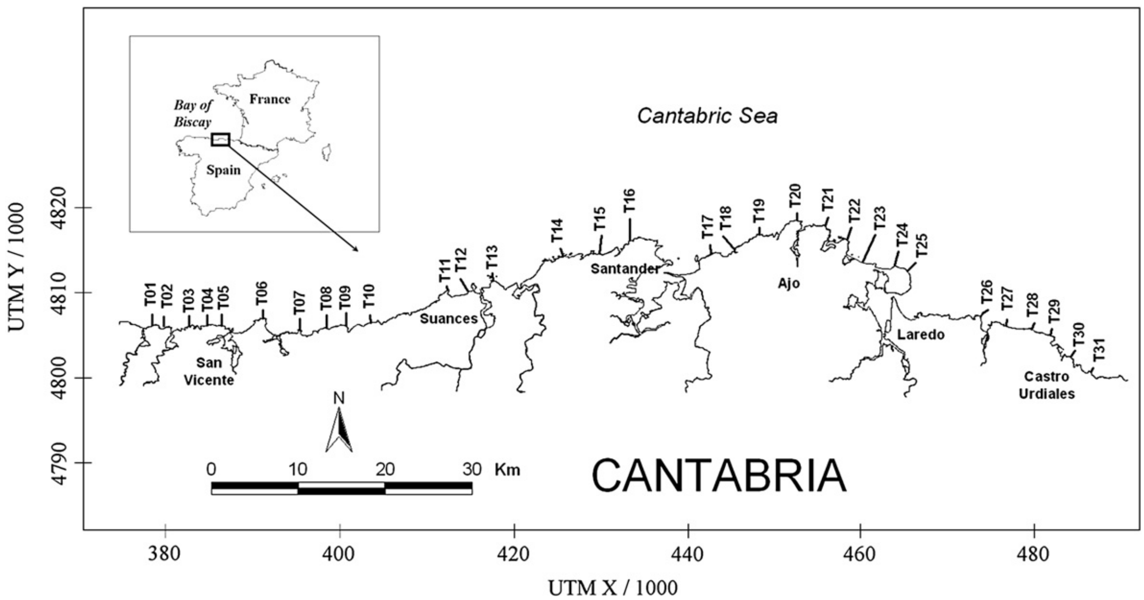

Fig. 1. Situation map and location of transects (UTM coordinates — zone 30).

general orientation of the coast changes from NW to NE, therefore changing the exposure towards the dominant coastal hydrodynamics, coming from the NW. The western and central zones are also separated by a smaller cape, Punta Ballota, and have a slightly different orientation (to the north and to the northwest respectively). The three predefined zones have similar coastal lengths and number of transects.

The following statistical analyses were then carried out using the Primer 5.0 software package (Clarke and Warwick, 1994). First of all, a similarity matrix was calculated based on Bray–Curtis similarity measure applied to square-root transformed data. In order to find significant differences between a) depth classes and b) coastal zones, a "Two-way crossed analysis of similarities (ANOSIM)" was applied considering these two factors. Then, the "SIMPER" tool was used to identify which species were driving the differences between depth groups. Using the information provided by the SIMPER analysis, the average coverage values of the most important species were graphically represented against the established depth classes. Finally, in order to detect other possible causes of similarities and interrelationships between stations, a Multi Dimensional Scaling ordination analysis (MDS) was performed.

3. Results

With the data collected from the 31 transects, an abundance data matrix was created made up of 27 rows, corresponding to the identified macroalgae species (Table 1) and 177 columns, corresponding to depth classes reached at each transect.

In Figs. 2 and 3 basic cartographies of the most important macroalgae species are shown. These graphic schemes represent the location of the transects using UTM coordinates (X axis) and depth classes on a graphic scale from 0 to 21 m (Y axis). As the Y axis is not represented in a true scale, these maps are not a real cartography, but a model of the distribution of the macroalgae species in depth. Consequently, the bathymetry of each zone must be considered for a correct interpretation of these maps.

As shown in the abundance distribution maps, *Gelidium corneum* and *Cystoseira baccata* are, due to their extensive distribution and high abundance, the dominant species in the coast of Cantabria. The first one is more abundant in shallower waters and tends to decrease with depth, while the second one remains more or less constant for the entire analyzed depth gradient. There is also a great abundance of *Laminaria ochroleuca* and *Saccorhiza polyschides*, which indicates the transitional character between cold and warm temperate coastal areas (Lüning, 1990). Most of the macroalgae species show clear distribution patterns with depth, showing different preferences for shallower (*Corallina* sp., *Codium tomentosum*) or deeper zones (*Spatoglossum solieri*, *Halidrys siliquosa*, *L. ochroleuca*).

The results of the two-way crossed ANOSIM, regarding tests for differences between depth groups, gave a global sample R statistic value of 0.216 with a significance level of $P = 0.001$, indicating the existence of significative although not very marked global differences among depth groups. In the case of tests for differences between zone groups, the global sample R statistic value was 0.141 with a significance level of $P = 0.001$, indicating also the existence of slight differences in this case. The pairwise tests between different depth and zone groups are summarized in Table 2. In order to avoid an excessive group fragmentation, a significance level of $P \leq 0.001$ has been considered to discriminate between different groups.

In the case of depth groups, significant differences ($P = 0.001$) with increasing R values can be observed when the distance between depth classes is increased. On the other hand, close depth classes show low R values and no significant differences ($P > 0.001$). As a result, two depth groups could be distinguished, the first one between

Table 1
List of conspicuous macroalgae species identified in this work (R: Red, B: Brown and G: Green species).

Asparagopsis armata (R)	*Dictyopteris membranacea* (B)	*Peyssonnelia atropurpurea* (R)
Calliblepharis ciliata (R)	*Dictyota dichotoma* (B)	*Phyllophora crispa* (R)
Carpomitra costata (B)	*Gelidium corneum* (R)	*Pterosiphonia complanata* (R)
Cladostephus spongiosus (B)	*Halidrys siliquosa* (B)	*Saccorhiza polyschides* (B)
Codium tomentosum (G)	*Halopitys incurvus* (R)	*Spatoglossum solieri* (B)
Corallina sp. (R)	*Halurus equisetifolius* (R)	*Sphaerococcus coronopifolius* (R)
Cutleria multifida (B)	*Heterosiphonia plumosa* (R)	*Stypocaulon scoparium* (B)
Cystoseira baccata (B)	*Kallymenia reniformis* (R)	*Taonia atomaria* (B)
Desmarestia ligulata (B)	*Laminaria ochroleuca* (B)	*Ulva* sp. (G)

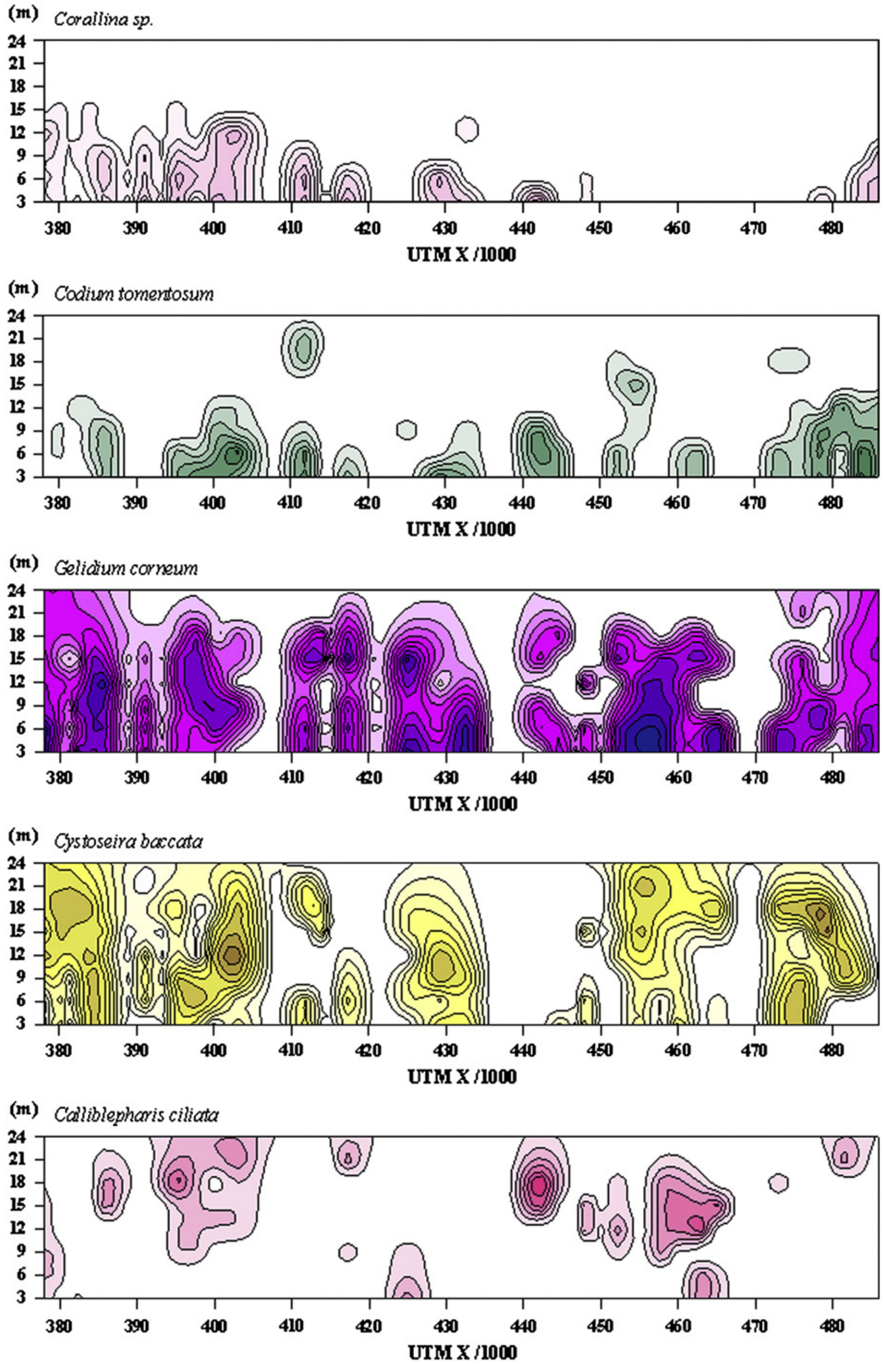

Fig. 2. Interpolated graphic representations of *Corallina* sp., *C. tomentosum*, *G. corneum*, *C. baccata* and *C. ciliata* distributions respectively. Isolines represent increments of 0.5 units according to the described semiquantitative scale and darker colors correspond to higher abundances.

3 and 12 m (Group A) and the second between 15 and 21 m (Group C), with a transition zone between 12 and 18 m (Group B). Regarding geographic zones, pairwise tests show significant differences between zone 1 and zones 2 and 3 ($P = 0.001$), but do not show significant differences between zones 2 and 3 ($P = 0.002$). Nevertheless, R values are very low in all cases, indicating that the differences among geographic groups are not very clear.

The results of the SIMPER analysis based on the depth factor are shown in Table 3 with a cut-off percentage of 90% of the cumulated similarity. *G. corneum*, *C. baccata*, *S. polyschides*, *C. tomentosum*, *L. ochroleuca*, *S. solieri*, *Corallina* sp. and *H. siliquosa* are the macroalgae that contribute most to the discrimination of the different depth classes. In Fig. 4, the average abundance distribution curves of these species are represented along the 0–21 m depth gradient.

The great abundances and lower variability of *G. corneum* and *C. baccata* confirm the observations made from Figs. 2 and 3, demonstrating that they constitute the dominant macroalgae species in most depth classes of the coast of Cantabria. These two species show a reversal of their relative importance after 18 m depth. *G. corneum* is the most important specie at a depth between 3 and 15 m (always measured with respect to the 0 tide level), also being very important up to a depth of 21 m, and decreasing significantly after 18 m. It has an overall coverage of 34.7% and shows its highest value at a depth of 6 m, with an average coverage of 54.7%.

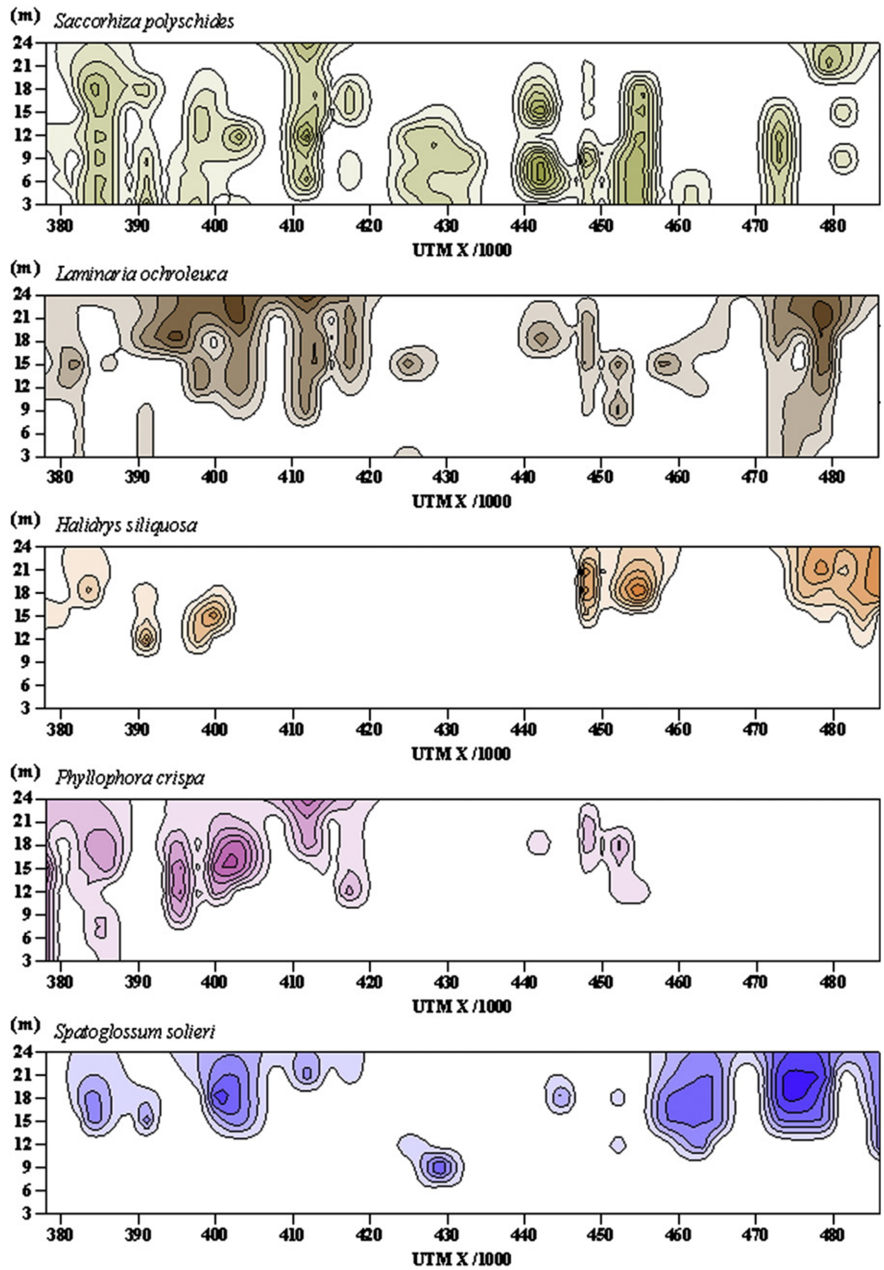

Fig. 3. Interpolated graphic representations of *S. polyschides*, *L. ochroleuca*, *H. siliquosa*, *P. crispa* and *S. solieri* distributions respectively. Isolines represent increments of 0.5 units according to the described semiquantitative scale and darker colors correspond to higher abundances.

From this depth on it decreases progressively up to 21 m, where its coverage presents an average value of 5%. In the case of *C. baccata*, the distribution is more homogeneous in depth, with an overall coverage of 23.4% and a variation range between 18% and 29.8%. Other than that which occurs with *G. corneum*, the distribution of *C. baccata* does not seem to be as conditioned by depth. Its highest values have been recorded at 9 and 18 m, while the lowest ones are found at 3 and 21 m. *S. polyschides* and *L. ochroleuca* are the next species in abundance, with overall coverage values of 8.6% and 4.9% respectively. These two species show an inverse distribution pattern in depth, with *S. polyschides* being more abundant in shallow waters, with a maximum at 9 m, while *L. ochroleuca* reaches its highest values in the deepest zones (21 m). *C. tomentosum* and *Corallina* sp., with *Cladostephus spongiosus* and *Halopitys incurvus* in a second plane, represent the characteristic macroalgae species of shallower zones, practically disappearing after 15 m depth. On the other hand, *S. solieri*, *H. siliquosa*, *Phyllophora crispa* and *Calliblepharis ciliata* represent the characteristic macroalgae species of deeper zones, though the last two suffer a significant decrease at a depth of 21 m. *Peyssonnelia atropurpurea* and *Sphaerococcus coronopifolius* (also decreasing at 21 m) and *Carpomitra costata* and *Dictyopteris membranacea*, constitute other representative species of the deepest zones.

The depth groups with the most homogeneous stations regarding the composition of macroalgae are those of 6 and 9 m, with an average similarity of 51% and 47.4% respectively, followed by the groups of 3 and 15 m. On the other hand, the most heterogeneous groups are those of 12 and 21 m, with average similarities of 30.4% and 27.2% respectively. The cause of this heterogeneity has to do with the change of communities that occurs around these depths, where characteristic species of different depth zones coexist. In the case of the 12 m class depth, the species of shallow zones (*Corallina* sp., *C. tomentosum*, *C. spongiosus*, *H. incurvus* and *S. polyschides*) are gradually substituted by species of intermediate-deep zones (*L. ochroleuca*, *C. ciliata*, *P. crispa*, *S. solieri*, *H. siliquosa*, *P. atropurpurea*

Table 2
Two-way crossed ANOSIM pairwise tests between depth and zone groups. A, B and C: depth class groups.

Depth groups	R statistic	Significance level (P)
3, 6	−0.059	0.959 (A)
3, 9	0.045	0.133 (A)
3, 12	0.117	0.01 (A)
3, 15	0.271	0.001*
3, 18	0.428	0.001*
3, 21	0.718	0.001*
6, 9	−0.033	0.802 (A)
6, 12	0.111	0.005 (A)
6, 15	0.268	0.001*
6, 18	0.466	0.001*
6, 21	0.832	0.001*
9, 12	−0.018	0.641 (A)
9, 15	0.166	0.001*
9, 18	0.347	0.001*
9, 21	0.751	0.001*
12, 15	0.029	0.229 (B)
12, 18	0.111	0.015 (B)
12, 21	0.399	0.001*
15, 18	−0.009	0.542 (C)
15, 21	0.284	0.002 (C)
18, 21	−0.009	0.514 (C)
Zone groups	**R statistic**	**Significance level (P)**
1, 2	0.167	0.001*
1, 3	0.134	0.001*
2, 3	0.143	0.002

* Significant differences at $P \leq 0.001$.

and *S. coronopifolius*), while in the case of 21 m some of these species tend to disappear, with only those of the deepest zones (*L. ochroleuca*, *S. solieri*, *H. siliquosa*, *C. costata* and *D. membranacea*) remaining. The general coverage at this depth is more reduced than at shallower zones, however, the characteristic macroalgae richness is moderately higher, probably because the lower coverage of the dominant species allows the development of a higher variety of secondary species.

The ordination analysis carried out by Multi Dimensional Scaling (MDS), even with a moderately high stress (0.23), shows some distribution pattern in depth but no clear pattern along the coast (Fig. 5). When depth classes are represented (Fig. 5a), a tendency to arrange the stations following a depth gradient can be easily appreciated. The stations corresponding to the shallowest depth classes (3–12 m) are situated in the upper left side of the figure, grouped approximately into the zone marked with the word “A”. Next to them, the stations of intermediate (12–15 m, zone B) and deeper depths (15–21 m, zone C) are situated successively on the lower right side of the figure. On the other hand, when zone groups are represented (Fig. 5b), the ordination shows a homogeneous distribution of the stations corresponding to the 3 coastal zones.

As a result of all the analysis performed up to this moment, two broad subtidal fringes could be established from the point of view of the macroalgae communities living on them. The first one, corresponding to the shallower zone (3 to 15 m depth approximately), would be characterized by *G. corneum* and *C. baccata* as dominant species, with *Corallina* sp., *C. tomentosum* and *S. polyschides* as the main accompanying species. The second fringe, corresponding to the deepest zone, extends from approximately 15 to 25 m in depth, and would be characterized by a progressive substitution of *G. corneum* by *C. baccata* and by the progressive appearance of *C. ciliata*, *P. crispa*, *L. ochroleuca*, *S. solieri* and *H. siliquosa* as the main accompanying species.

4. Discussion

The proposed methodology has allowed us to carry out a preliminary analysis of the distribution patterns of the subtidal macroalgae assemblages present at a regional scale, in a fast, easy and economical way, improving the existing knowledge about these communities on

Table 3
Main macroalgae species at 3 m depth intervals. ASG: Average Similarity of the Depth Class Group, Simil/SD: Similarity divided by standard deviation, Contrib.%: Percentage of contribution to the similarity of the group, Cumul.%: Cumulated similarity percentage.

Depth class group	Macroalgae specie	Average coverage (%)	Average similarity	Simil/SD	Contrib.%	Cumul.%
3 m (ASG: 45.43)	*G. corneum*	49.82	27.64	1.38	60.83	60.83
	C. baccata	19.29	6.8	0.6	14.96	75.8
	C. tomentosum	15	5.64	0.68	12.41	88.21
	Corallina sp.	12.95	3.37	0.5	7.41	95.62
6 m (ASG: 51.04)	*G. corneum*	54.73	35.13	2.28	68.82	68.82
	C. baccata	21.25	7.22	0.65	14.15	82.97
	C. tomentosum	13.39	3.59	0.57	7.03	90
	S. polyschides	10	2.46	0.6	4.83	94.83
9 m (ASG: 47.42)	*G. corneum*	44.35	28.13	1.5	59.32	59.32
	C. baccata	27.78	12.16	0.94	25.64	84.97
	S. polyschides	12.59	3.47	0.56	7.32	92.29
12 m (ASG: 30.42)	*G. corneum*	30.48	14.91	0.93	49.01	49.01
	C. baccata	25.1	10.1	0.82	33.19	82.2
	S. polyschides	10.19	2.1	0.41	6.9	89.1
	L. ochroleuca	3.27	1.04	0.41	3.42	92.52
15 m (ASG: 39.47)	*G. corneum*	39.07	22.33	1.18	56.59	56.59
	C. baccata	22.87	8.23	0.75	20.85	77.44
	S. solieri	5.74	1.99	0.39	5.04	82.48
	S. polyschides	8.43	1.93	0.42	4.89	87.37
	L. ochroleuca	6.85	1.92	0.48	4.86	92.23
18 m (ASG: 31.93)	*C. baccata*	29.81	12.38	0.78	38.77	38.77
	G. corneum	19.23	8.02	0.65	25.12	63.89
	L. ochroleuca	8.65	2.87	0.59	8.98	72.86
	S. solieri	9.23	2.56	0.47	8.03	80.89
	S. polyschides	6.73	1.48	0.37	4.64	85.53
	H. siliquosa	9.42	1.47	0.31	4.6	90.13
21 m (ASG: 27.18)	*C. baccata*	18.04	9.24	0.72	33.98	33.98
	L. ochroleuca	13.21	7.02	0.95	25.83	59.81
	S. solieri	13.57	5.95	0.63	21.89	81.7
	H. siliquosa	12.14	2.01	0.35	7.39	89.09
	G. corneum	5	0.53	0.21	1.97	91.05

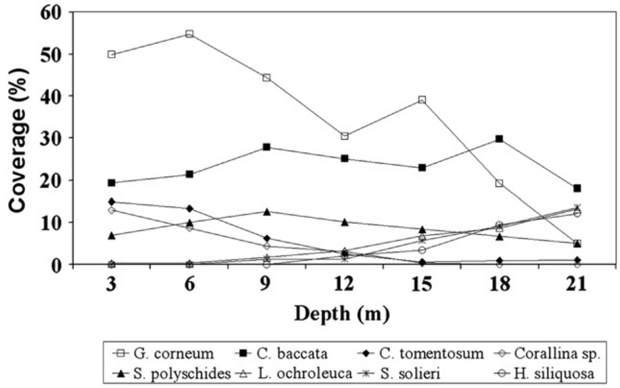

Fig. 4. Distribution curves of key macroalgae species along the depth gradient.

the coast of Cantabria (García-Castrillo et al., 2000a, 2000b; Juanes and Gutiérrez, 1992; Puente, 2000) and constituting a good reference point for future change monitoring.

The European Water Framework Directive (WFD 2000/60/EEC) has motivated the rapid increase of methodologies that are easy to apply and have an effective cost–benefit relation. Macroalgae represent one of the biological elements to be evaluated for the assessment of the ecological status of the coastal water bodies. In this sense, some of the results and conclusions extracted from this work have been used for the development and adjustment of the CFR index (Juanes et al., 2008), an environmental quality assessment method based on coastal macroalgae communities. In addition to the WFD, the general knowledge about the distribution of macroalgae species obtained in this work could help to improve the description of EUNIS classification system of the European Environment Agency regarding marine habitats (A3 group: Infralittoral rock and other hard substrata), and can also be very useful for the implementation of the Habitats Directive (92/43/EEC), trying to provide answers to the Commission

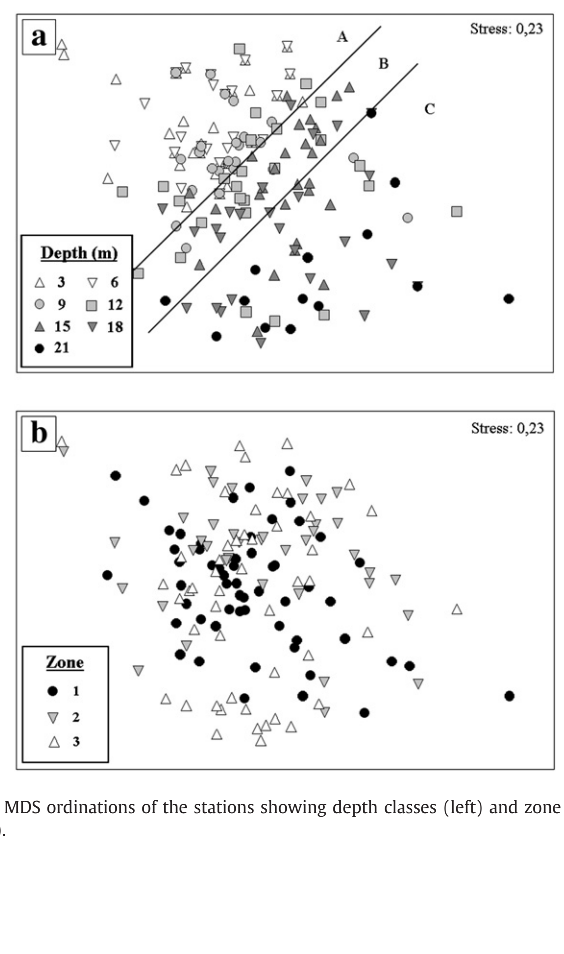

Fig. 5. MDS ordinations of the stations showing depth classes (left) and zone groups (right).

Decision 2004/813/EC, which requires further clarification regarding these habitats.

From the obtained results, it can be said that *G. corneum* and *C. baccata* are the dominant species in the subtidal areas of the Cantabrian Coast. The dominance of these species, instead of that of the Laminarians or Fucoids, characteristic of colder waters, is indicative of the southern character of the SE coasts of the Bay of Biscay, as described by Sauvageau (1897) and Fischer-Piette (1955). However, the relative abundance of *L. ochroleuca* and *S. polyschides* indicate that this character is not as marked as in the coastal waters of the Basque Country (inner part of the Bay of Biscay), where these species are not as abundant due to the warmer waters (Borja et al., 2004; Gorostiaga et al., 2004; Juanes and Sosa, 1998). The opposite occurs in the coastal waters of Asturias and Galicia (to the west of Cantabria), where colder waters produce a progressive increase of large brown algae to the west (Anadón, 1983; Anadón and Niell, 1981; Fernández, 1980; Pazó and Niell, 1977), producing a more northern appearance. The biogeographical distribution of these species experiences seasonal longitudinal (east–west) advances and retreats associated to climatic and oceanographic factors, as demonstrated by Borja and Gorostiaga (1990) for the Basque coast, so their monitoring could be a good indicator for the analysis of climate change effects.

The results obtained in this work suggest that biogeographic differences are not very marked along the Cantabrian coast, however, the ANOSIM results showed significant differences between the western side of Cantabria (zone 1) and the central and eastern zones of the region (zones 2 and 3 respectively). These slight differences are not appreciated in the MDS ordination, but could be associated with the longitudinal distribution of some species along the coast, such as *Corallina* sp., *P. crispa* and *L. ochroleuca* (more abundant on the western side), *C. spongiosus*, *D. membranacea* and *H. incurvus* (more abundant in the central zone) and *S. solieri*, *H. siliquosa* and *C. tomentosum* (more abundant on the eastern side). These results are somehow in agreement with the physical classification made by Ramos et al. (in press), who developed a methodology for the ecological typification of intertidal systems along the European NE Atlantic region, based on environmental variables such as temperature, wave height, radiation and tidal range. The results obtained in that study for the biotype A2, corresponding to the Iberian peninsula, established a biogeographic limit (A2b1–A2b2) between Cantabria and the Basque Country (N. Spain), about 100 km to the east of the limit obtained in this study. For a more detailed analysis of the changes detected in this work, a precise study of the environmental characteristics should be carried out at regional scale, not only spatially but also temporally. Regarding the application of European Directives, such as the Water Framework Directive, these biogeographical differences should be taken into account when the quality of biological communities are analyzed in different bioregions, otherwise, the application of the same assessment procedures, based on the existence of certain biological communities, to places with different species could produce confusing or inappropriate results (Guinda et al., 2008).

On the other hand, the distribution of macroalgae species in depth follows a clear gradient, being able to distinguish two depth levels: a shallow level, which extends from 3 to 15 m approximately, and a deep level, extending from 15 to 25 m approximately. The shallow level would be characterized by the dominance of *G. corneum* and *C. baccata*, with *Corallina* sp., *C. tomentosum* and *S. polyschides* as the main accompanying species. The deeper level is characterized by the progressive substitution of *G. corneum* by *C. baccata*, and by the apparition of *C. ciliata*, *P. crispa*, *L. ochroleuca*, *S. solieri* and *H. siliquosa* as the main accompanying species. In this sense, the overlapping of different stations seen in Fig. 5 is normal, considering the high variability and patchiness characterizing the structure of rocky reefs (Creese and Kingsford, 1998).

Although the distribution patterns and variability of macroalgae communities analyzed in this study have been limited to their relation to depth gradient and spatial location at the macroscale level,

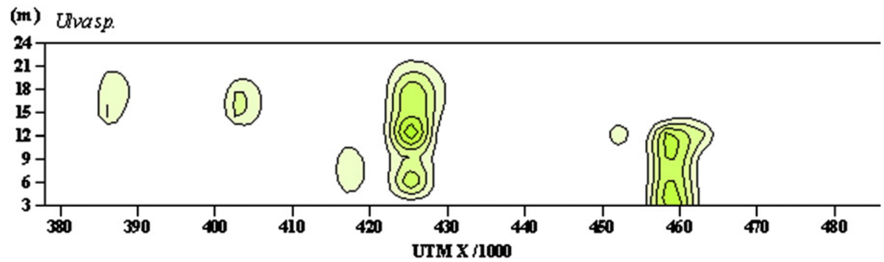

Fig. 6. Interpolated graphic representation of *Ulva* sp. Isolines represent increments of 0.5 units according to the described semiquantitative scale and darker colors correspond to higher abundances.

the effects of other environmental factors (e.g. hydrodynamics, temperature, water quality, substrate structure or presence of sediments) should be taken into account for a more detailed explanation of the variability observed in the distribution of macroalgae species (Lüning, 1990). As an example, several authors mention the high tolerance of *C. baccata* to sedimentation, against the preference of *G. corneum* and *L. ochroleuca* for exposed zones with little or no sedimentation (Díez et al., 2003; García-Castrillo et al., 2000a, 2000b; Puente, 2000). In accordance with these works in the present study it has been observed that *C. baccata* and *H. siliquosa* grow without problems in zones with high presence of sediments, while *G. corneum* prefers those with high hydrodynamics and low levels of sediments, such as the upper zones of big rocky blocks.

Water quality is another important aspect to be considered when analyzing macroalgae distribution patterns. Turbidity, abrasion, nutrient concentrations or presence of pollutants have a great influence in the occurrence of some species, whose existence will be determined by their individual tolerances to these variables. Since these factors are usually related to anthropogenic stressors, their study is crucial for the assessment of human impacts on the aquatic ecosystem. In this sense, *G. corneum* and *C. baccata* have been demonstrated to have low tolerances to pollution (Díez et al., 2003), hence, these two species are usually considered to be good quality indicators in most of the methodologies proposed to evaluate the ecological status of this biological element (Ballesteros et al., 2007; Juanes et al., 2008; Orfanidis et al., 2001; Wells et al., 2007). The high abundance and extensive distribution of these species on the coast of Cantabria give an idea of the general good water quality existing in the region. In some specific sites, such as Noja (T22), the disposal of nutrients coming from urban wastewater treatment plants produces elevated amounts of the opportunistic macroalgae *Ulva* sp. as an environmental response to that pollution (Fig. 6). However, the low discharge flow and the high hydrodynamics of the Cantabrian sea (Castanedo et al., 2006; Valencia et al., 2004) contribute to the fast dilution of the pollutants, also allowing the development of great amounts of *G. corneum* and *C. baccata* in the area. Sometimes, the adaptation and resistance of species to some anthropogenic pressures could show communities in an apparent good status, and, in other cases, natural variability could produce more alterations in communities than some anthropogenic pressures (e.g. Dayton et al., 1992; Tegner et al., 1995). This is why expert interpretation of the results should always complement the application of indices or other assessment procedures in the quality assessment process.

To better understand the structure, functioning and distribution patterns of these complex habitats, more efforts must be made. These should be carried out both in detail, through more specific studies of higher scientific rigor, and also more extensively, increasing the total surface covered and its spatial resolution. The main problem in carrying out extensive subtidal works, and one of the reasons for their scarce abundance, are the elevated costs associated with their implementation, especially when a high resolution is desired. In this sense, the combination of recently developed technologies, such as hydroacoustic techniques (e.g. multibeam, sidescan sonar), remote "viewing" methods (e.g. towed cameras, ROVs) and ecological models, constitute very promising methods for mapping extensive marine habitats and communities (e.g. Dolan et al., 2008; Galparsoro et al., 2009; Guinan et al., 2009a, 2009b; Mayer, 2006). These remote prospection and visualization techniques are usually used for the study of faunal communities at elevated depths, where direct sampling is difficult and expensive, however, they could also be very useful for the extensive study of vegetal communities at shallower coastal areas (e.g. Kutser et al., 2006; Pasqualini et al., 1998; Vahtmäe et al., 2006).

5. Conclusions

The methodology presented here, based on well established procedures and concepts (taxonomic sufficiency, continuous transects, non-destructive semiquantitative assessments) and totally extrapolable to other coastal regions, has allowed studying the general structure and main distribution patterns of subtidal macroalgae communities in Cantabria (Bay of Biscay), in a fast, easy and economical way, which is appropriate for extensive management activities. Additionally, it has been very useful for the creation of a basic cartography, using a graphic scheme, of the most important subtidal macroalgae species in the region. This information will be of great interest to assist in projects, conservation and management activities or monitoring works related to the subtidal environment of this coastal area. Possible applications of the obtained knowledge include the designation of marine protected areas, sustainable exploitation of marine resources, adaptation of marine engineering projects or the implementation of European Directives such as the Water Framework Directive or the Habitats Directive.

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