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Seasonal patterns of tidepool macroalgal assemblages in the North of Portugal. Consistence between species and functional group approaches

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ABSTRACT

Macroalgae are useful organisms to monitor the environmental quality and to detect impacts due to anthropogenic activities. However, it is very important to identify the scales of variation in natural assemblages, particularly for the detection of environmental impacts. Otherwise, changes due to anthropogenic impacts may be confused with differences due to natural temporal variability. Another important task is to determine the appropriate level of taxonomical effort needed to detect changes in the assemblage structure. Many taxonomical surrogates, at higher taxonomic levels than that of species, have been proposed but, the consistence in space and time of the results produced by surrogates with those obtained at specific level should be tested. The objectives of this study are to identify the seasonal patterns of tidepool macroalgal communities using objective procedures and to test the consistence between the patterns obtained considering data at the species level and functional groups. Results showed that the seasonal pattern obtained using functional groups and species was consistent. Tidepool macroalgal assemblages showed a seasonal pattern with significant differences between spring-summer and autumn-winter. This pattern can be explained by changes in environmental variables and the seasonal development of the dominating species. Ulva spp. and the non-indigenous species Grateloupia turuturu were the species responsible for this pattern due to their high seasonality in terms of biomass. Finally, the abundance and species diversity within the corticated functional group was proposed as indicator of environmental impacts due to its relatively constant abundance and its sensitivity to environmental impacts.

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1. Introduction

Benthic marine macroalgae are a conspicuous and diverse component of virtually all the coastal habitats where hard substrata is available. The polyphyletic nature of marine algae implies that these organisms embrace a much wider range of diversity than many higher plant or animal groups (Norton et al., 1996). Recent studies have linked the biodiversity with the ecosystem function, resilience and the services provided by aquatic ecosystems (Cardinale, 2011; Palumbi et al., 2009; Worm et al., 2006). However, pollution, habitat loss and introduction of alien species are considered as important threats that can impoverish macroalgal assemblages' diversity (Walter and Kendrick, 1998).

Marine biodiversity monitoring is a valuable tool for environmental conservation and management and has become a legal requirement in many regions like Europe (European Water Framework) or USA (National Environmental Policy Act). Due to their high diversity, sessile nature and wide distribution, macroalgae are considered as good

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descriptors of rocky shore communities and are widely utilised to characterise and monitor coastal systems (Leliaert et al., 2000; Lirman and Biber, 2000; Piazzi et al., 2002). Moreover, macroalgal assemblages have proven to be useful indicators of habitat modifications related to natural or human disturbance (Díez et al., 2009; Piazzi et al., 2001; Roberts et al., 1998).

Species richness, measured as the number of different species and their abundance, is the commonest descriptor of macroalgal assemblages (e.g. Araújo et al., 2006; Piazzi et al., 2002). However, enumerating all the macroalgal species for conservation monitoring programmes is time consuming, labour-intensive and requires a high level of expertise, because macroalgae present taxonomic problems due to their polyphyletic nature (Norton et al., 1996). In order to reduce the time and resources consumed in the taxonomical work several surrogates have been proposed. One of the commonest for macroalgae is the description of the assemblage using functional groups. According to Littler and Littler (1984), a functional group approach permits an evaluation of disturbance in the environment by the study of macroalgal morphological features. Although the loss of information when using this approach has been considered (Phillips et al., 1997), functional groups appear to be good descriptors of benthic communities in a number of ecological studies (Lirman and

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Biber, 2000; Steneck and Deither, 1994; Viejo, 1997). However, the use of surrogates implies certain assumptions. The main assumption to identify an appropriate surrogate is that the relationship between the surrogate and assemblage structure is consistent in space and time (Colwell and Coddington, 1994; Magierowski and Johnson, 2006). Previous works have already tested the spatial consistence of this relationship (e.g. Smale, 2010) but this topic has received less attention at temporal scale (Magierowski and Johnson, 2006).

Another problem in monitoring programmes is the complexity to precisely establish the limits for the natural variability and consequently, to discriminate anthropogenic disturbance effects from natural variability (Ferraro et al., 1991; Veiga et al., 2009). To deal with this problem, specific sampling designs and analytical procedures have been developed (Benedetti-Cecchi, 2001). Nevertheless, these designs preferably need information about the temporal and spatial patterns of the studied variables (Benedetti-Cecchi, 2001). Therefore, a previous understanding of the natural variability patterns of the assemblage both in time and space are an indispensable requisite to understand the natural or anthropogenic processes that shape assemblage structures (Underwood, 1981).

The macroalgal diversity of the north Portuguese coast has been largely studied and recently revised by Araújo et al. (2009). Therefore, the diverse tidepool macroalgal communities could be a valuable tool to monitoring coastal systems. In the north Portuguese coast Araújo et al. (2006) studied the macroalgal communities of tidepools finding more than 90 different taxa in this habitat but the temporal pattern of variability of these communities remains unexplored. The main aim of this study is to identify the seasonal patterns of tidepool macroalgal communities using objective procedures. Additionally, the consistence in the seasonal patterns obtained considering species and functional groups will be tested. To achieve these aims, the assemblage structure of tidepool macroalgae was examined seasonally to address the following hypotheses:

- 1. Tidepool macroalgal assemblages present significant seasonal changes in their structure.
- 2. The seasonal pattern of the macroalgal assemblages obtained by using species is consistent with that obtained using functional groups.

2. Material and methods

2.1. Study area

This study was conducted on the NW coast of Portugal at two rocky shore sites, Foz do Douro (41°09'32.77"N and 08°41'11.33"W) and Aguda (41°02'43.22"N and 08°39'10.31"W). On both sites, the rocky shore is characterised by granitic substrate and high sediment input. The tidal regime is semidiurnal, with the largest spring tides of 3.5–4.0 m. This work was done on the mid-shore which is dominated by the mussel *Mytilus galloprovincialis* (Lamarck) and the barnacle *Chthamalus stellatus* (Poli) while seaweeds are mainly restricted to tidepools. The introduced seaweed species *Grateloupia turuturu* Yamada was recorded at both sites. The most common grazers on this tidal level are *Patella vulgata* Linnaeus and *Gibbula* spp.

Four meteorological seasons can be defined in the study area: summer with mean values of temperature about 19 °C and mean precipitation by month of 30 mm, autumn with mean values of temperatures around 11 °C and mean precipitation by month of 180 mm, winter with mean values of temperatures around 11 °C and mean precipitation by month of 168 mm and spring with mean values of temperatures around 15.5 °C and mean precipitation by month of 105 mm (http://www.meteo.pt/pt/oclima/climanormais/021). The light intensity and photoperiod also suffers gradual modifications along these seasons with a maximum of intensity and light period length in spring and summer (2 033.25 μ einsteins·m⁻²·s⁻¹±81.94 n–45 427) and

minimum values in autumn-winter (1 540.96 µeinsteins \cdot m⁻² \cdot s⁻¹ \pm 604.83 n = 52573). Moreover, sea water and hydrodynamic conditions of the study area suffer changes in temperature, nutrient content, wave height and storm frequency along the year. Sea water temperature reach the lowest value in winter, around 14 °C and the highest value is found in summer, around 18 °C. In the spring, temperature is around 15 °C and in autumn it is about 16 °C (Lemos and Pires, 2004). Concerning nutrients, the main change in their availability is closely related to upwelling events that increase the nutrient concentration. The upwelling regimen in the study area is more intense from April to September (Lemos and Pires, 2004). The mean wave height varies strongly with seasons. In the period spring-summer, typical wave heights are 1-3 m, with periods of 11-13 s. Whereas, during winter storms they often exceed 7 m, typically with periods of 13 s, but they can exceed 18 s (Dias et al., 2002). Most storms occur during winterautumn months (October-March) and on average the Portuguese coast is exposed to three storms a year (Dias et al., 2002).

2.2. Sampling design

Sampling was done between July 2009 and July 2010; both studied sites were visited during low tide at two different dates each season: summer (from July to September), autumn (from October to December), winter (from January to March) and spring (from April to June). On each sampling date, a total of 10 pools were randomly chosen at each site. In each pool, seaweed assemblage was sampled scrapping a randomly placed quadrate (30×30 cm). Seaweeds were collected in a labelled plastic bag and frozen $(-20 \degree C)$ until analysis. In the laboratory, all the samples were sorted, cleaned and macroalgae identified to the lowest possible taxonomic level (that of species in most of the cases). Then, each of the identified species was assigned to a functional group following Steneck and Deither (1994). Each species in any given sample was dried in an oven (50 °C) for 48 h and weighted on a scale plate (AND HF-2000G) to determine its dry weight. Finally, the abundance of each species and functional group was calculated as its dry weight biomass.

2.3. Data analysis

Multivariate study of assemblage was done using the statistical package PRIMER 6 with the PERMANOVA add-on. For each replicate (i.e., any tidepool), the values of biomass for each seaweed species were square-root transformed for the calculation of the Bray-Curtis similarity matrix. The assemblage structure and its seasonal pattern were examined, both at the species and functional group level, using permutational multivariate analysis of variance (PERMANOVA). The sampling design consisted in a three-way layout with Site (Si) with two levels: Foz vs. Aguda as random factor, Season (Se), with four levels: spring, summer, autumn and winter as fixed factor and Date (Da), with two levels as random factor nested within season. PERMANOVA analyses were done based on Bray-Curtis dissimilarities using permutation of residuals under a reduced model (999). Random factors that showed a negative value of its component of variation were pooled following Anderson et al. (2008) to increase the power of the test. When PERMANOVA showed significant differences (p<0.05), a pairwise comparison (999 permutations) was done to explore differences among all pairs of levels of the selected factor. When the number of unique permutations for a pairwise comparison was lower than 30, Monte Carlo P-values were considered (Anderson et al., 2008).

Centroids of the ten replicate samples, in each date and site, and the distances among them in Bray–Curtis space were calculated from the previously defined Bray–Curtis similarity matrix. Then, a nonmetric multidimensional scaling (nMDS) based on the centroids similarity matrix was done to visualise the multivariate assemblage structure and seasonal patterns. It must be noted that centroids in a

Species	Nover	nber	Decen	nber	Februa	ary	March	ı	April		May		June		Septe	mber	Functional groups
	A	F	A	F	A	F	A	F	A	F	A	F	A	F	A	F	
Anpheltiopsis sp.	+		+	+				+							+	+	Corticated macrophytes
Ahnfeltia plicata		+			+	+		+					+	+		+	Corticated macrophytes
Ceramium secundantum												+	+	+			Filamentous
Ceramium spp.						+		+	+	+		+	+	+	+	+	Filamentous
Chondracanthus acicularis	+	+	+			+			+	+			+	+	+	+	Corticated macrophytes
Chondria sp.		+						+									Corticated macrophytes
Chondrus crispus	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	Corticated macrophytes
Cladophora sp.								+									Filamentous
Condracanthus tedii	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	Corticated macrophytes
Corallina spp.	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	Articulated calcareous
Cryptopleura ramosa			+			+			+			+		+			Corticated foliose
Dictyota dichotoma		+		+	+	+	+					+		+		+	Corticated foliose
Fucus spiralis												+		+			Leathery macrophytes
Gastroclonium ovatum				+						+		+		+		+	Corticated macrophytes
Gelidium pulchellum	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	Corticated macrophytes
Gelidium sp.		+	+			+	+	+	+	+	+	+	+	+	+	+	Corticated macrophytes
Gracilaria sp.	+												+		+	+	Corticated macrophytes
Grateloupia minima							+		+		+		+	+			Corticated foliose
Grateloupia turuturu	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	Corticated foliose
Gigartina pistillata	+		+						+		+					+	Corticated macrophytes
Gymnogongrus crenulatus	+	+	+	+		+		+	+	+	+	+	+	+		+	Corticated macrophytes
Gymnogongrus griffithsiae	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	Corticated macrophytes
Lithoplyllum incrustans									+				+			+	Crustose
Lomentaria articulata		+									+	+		+		+	Corticated macrophytes
Lomentaria clavellosa	+	+							+								Corticated macrophytes
Mastocarpus stellatus		+	+	+							+	+		+		+	Corticated macrophytes
Osmundea pinnatifida		+	+	+	+	+	+	+	+	+		+	+	+	+	+	Corticated macrophytes
Polisiphonia spp.	+		+	+	+	+	+	+	+	+		+	+	+	+	+	Filamentous
Porphyra sp.										+		+		+			Foliose
Pterosiphonia complanata														+			Filamentous
Saccorhiza polyschides														+			Leathery macrophytes
Sargassum muticum			+				+					+					Leathery macrophytes
Ulva clathrata		+							+	+	+	+	+	+	+	+	Foliose
Ulva spp	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	Foliose

Table 1List of the species recorded in the study reported as present/absent on the two sites (A = Aguda, F = Foz) on different dates and the functional group to which were assigned.

Table 2

Details of the three-factor PERMANOVA test (with site as random factor with two levels, date as random factor nested in season with two levels and season as fixed factor with 4 levels) considering species as level of aggregation. df: degrees of freedom, SS: sum of squares, MS: mean squares.

Source of variation	df	SS	MS	Pseudo-F	P (perm)	Unique permutations
Si	1	19644	19644	4.4688	0.038	987
Se	3	66642	22214	3.1042	0.009	999
Dat(Se)	4	23401	5850.3	1.3309	0.268	999
Si X Se	3	8165.7	2721.9	0.61922	0.839	998
Si X Da (Se)	4	17583	4395.7	2.4887	0.001	997
Res	144	2.5435E5	1766.3			
Total	159	3.8978E5				

multivariate space is not the same as arithmetic mean of the original variables (Anderson et al., 2008).

Once a seasonal pattern was found, SIMPER analysis (Clarke, 1993) was used to identify the percentage of contribution of each species or functional group to the similarity and dissimilarity within and between groups identified from the PERMANOVA and nMDS analyses. Seasonal patterns of abundance of the main macroalgal species and functional groups were examined for each site using analysis of variance (ANOVA). Prior to the analysis, homogeneity of variance was checked using the Cochran's test. When necessary, data were transformed to meet the assumption of variance homogeneity. Whenever ANOVA showed significant differences (p < 0.05), a post hoc Student–Newman–Keuls (SNK) test was done for *a posteriori* comparisons. Whenever transformed biomass values did not attain the variance homogeneity, differences in the biomass of the main species or functional groups between seasons were analysed using PERMANOVA.

3. Results

A total of 34 macroalgal species were found and grouped on 7 functional groups (Table 1). Permutational multivariate analysis of variance (PERMANOVA) on observational data (biomass of each macroalgal species) detected a significant interaction between the factors site and date nested in season (Table 2). Moreover, significant differences were detected between different levels of the factor season (Table 2). Then, we did pair-wise comparisons for the factor of interest (here season) separately for each season level (Table 3). This analysis showed significant differences in the macroalgal assemblage structure between spring and autumn, spring and winter, summer and autumn and summer and winter (Table 3). However, significant differences were not detected in the assemblage structure between autumn and winter and between spring and summer (Table 3). Therefore, two main seasons were identified: one including spring and summer and a second one including autumn and winter (Table 3).

Permutational multivariate analysis of variance (PERMANOVA) considering biomass of each functional group, detected a significant interaction between the factors site and date nested in season

 Table 3

 Multivariate pair-wise comparison of assemblages, using species, at different seasons.

Groups	t	P(perm)	Unique permutations	P(MC)
Summer-autumn	2.5411	0.330	3	0.002
Summer-winter	2.5484	0.349	3	0.002
Summer-spring	0.78821	0.652	3	0.767
Autumn-winter	1.4726	0.347	3	0.076
Autumn-spring	2.0559	0.333	3	0.01
Winter-spring	1.916	0.337	3	0.012

Table 4

Details of the three-factor PERMANOVA test (with site as random factor with two levels, date as random factor nested in season with two levels and season as fixed factor with 4 levels) considering functional groups. df: degrees of freedom, SS: sum of squares, MS: mean squares.

Source of variation	df	SS	MS	Pseudo-F	P (perm)	Unique permutations
Si	1	9716.2	9716.2	4.8229	0.041	985
Se	3	61633	20544	5.1629	0.005	999
Da(Se)	4	13604	3401	1.6882	0.168	998
Si X Se	3	2905.2	968.38	0.48068	0.908	999
Si X Da(Se)	4	8058.4	2014.6	1.989	0.013	997
Res	144	1.4586E5	1012.9			
Total	159	2.4177E5				

(Table 4). Moreover, significant differences were detected between different levels of the factor season (Table 4). Pair-wise comparisons for the factor season pointed out the same results as for species level of aggregation (Table 5). Therefore, results considering either species or functional groups were similar.

The multidimensional scaling (nMDS) ordination obtained from the biomass of each macroalgal species identified two main groups of samples (Fig. 1A). One group consisted of samples collected in summer and spring and the second group was composed of samples collected in autumn and winter. However, one summer sample and one spring sample from Foz were placed between these two groups. The same pattern of grouping was found considering functional groups as level of aggregation (Fig. 1B).

Results of the SIMPER analysis considering species and functional groups are presented in Table 6, for the two groups of samples determined according to the PERMANOVA analysis. The main responsible species for the similarity within groups and the dissimilarity between groups were *Ulva* spp., *G. turuturu, Gelidium pulchellum* (Turner) Kützing and *Chondrus crispus* Stackhouse. The percentage contribution of these species to the total biomass of the assemblage was 42.61% for *Ulva* spp, 6.96% for *G. pulchellum*, 6.54% for *G. turuturu*, and 6.16% for *C. crispus*. The responsible functional groups for the similarity within groups and the dissimilarity between groups were foliose, corticated foliose and corticated macrophytes. The percentage contribution of these functional groups to the total biomass of the assemblage was 43.18% for the foliose, 29.24% for corticated macrophytes and 11.31% for corticated foliose.

The seasonal changes in the abundance of these species and functional groups were further studied at both localities. *Ulva* spp. ($F_{1,6} = 16.24$, p<0.05 at Aguda; $F_{1,6} = 4.01$, p<0.05 at Foz) and *G. turuturu* ($F_{1,6} = 12.24$, p<0.05 at Aguda; $F_{1,6} = 25.83$, p<0.05 at Foz) showed the same pattern as the whole assemblage with significantly higher abundances in summer and spring than in winter and autumn (Fig. 2). However, *G. pulchellum* ($F_{1,6} = 1.10$, p>0.05 at Aguda; $F_{1,6} = 2.24$, p>0.05 at Foz) and *C. crispus* ($F_{1,6} = 1.10$, p>0.05 at Aguda; $F_{1,6} = 2.24$, p>0.05 at Foz) and *C. crispus* ($F_{1,6} = 3.34$, p>0.05 at Aguda; $F_{1,6} = 0.13$, p>0.05 at Foz) did not show significant abundance differences among seasons (Fig. 2).

Concerning functional groups, corticated macroalgae ($F_{1,6} = 0.54$, p > 0.05 at Aguda; $F_{1,6} = 4.08$, p > 0.05 at Foz) did not show significant abundance differences between seasons (Fig. 3). However, foliose

Table 5

Multivariate pair-wise comparison of assemblages, using functional groups, at different seasons.

Source	t	P (perm)	Unique permutations	P(MC)
Summer-autumn	4.1923	0.335	3	0.003
Summer-winter	3.6223	0.332	3	0.001
Summer-spring	0.7605	0.643	3	0.728
Autumn-winter	1.4574	0.33	3	0.174
Autumn-spring	2.4665	0.314	3	0.015
Winter-spring	2.0938	0.346	3	0.029



Fig. 1. Non-metric multidimensional scaling ordinations on the basis of Bray–Curtis dissimilarity measure of centroids considering biomass data at levels of species (A) and functional groups (B). A: Aguda; F: Foz; Su: Summer; Au: Autumn; Wi: Winter; Sp: Spring. 1 and 2 indicated the two dates of sampling within each season. Full symbols correspond to Aguda and empty symbols correspond to Foz.

macroalgae ($F_{1,6} = 15.67$, p < 0.05 at Aguda; $F_{1,6} = 5.75$, p < 0.05 at Foz) and corticated foliose ($F_{1,6} = 14.41$, p < 0.05 at Aguda; $F_{1,6} = 19.49$, p < 0.05 at Foz) had significantly higher abundances in summer and spring than in winter and autumn at both studied localities (Fig. 3).

4. Discussion

Tidepool macroalgal assemblages at the studied sites showed a clear seasonal pattern with significant differences between the period spring-summer and the period autumn-winter. Therefore, the first hypothesis of our study was accepted. It is difficult to draw comparisons between our results and other studies because information about seasonal patterns of intertidal macroalgae is scarce. A similar work was done in the Gulf of Trieste by Rindi and Battelli (2005), who found variation in the intertidal macroalgal assemblage structure between the winter-spring and summer-autumn periods. As in the present study, Rindi and Battelli (2005) found a seasonal pattern with two different periods but, they did not propose any potential process to explain their results. Therefore, the present study provides new observational information on the seasonal patterns of tidepool macroalgae using objective procedures. Macroalgal assemblage showed significant differences between the period autumnwinter and spring-summer. This pattern fits well with the seasonal pattern of nutrient availability, wave height storm frequency and light intensity thus, these environmental conditions are potentially the major influence in shaping this assemblage. Several studies have shown that light is a major environmental factor controlling seasonal changes in primary productivity and thus biomass of intertidal macroalgae (Cheshire et al., 1996; Golléty et al., 2008). Higher light intensity in the study area was reported in the spring-summer period (see material and methods section). Upwelling events in this area occur from April to September providing nutrients which support the macroalgal growth (Lemos and Pires, 2004). On the other hand, the physical disturbance due to wave action during the spring-summer period is lower as that autumn–winter, when it may result in important losses of macroalgal biomass (Dethier, 1982). High values of air temperature or precipitation can increase the stress of macroalgal assemblages during low tide (Metaxas and Scheibling, 1993). However, this stress seems to be more important on emerged substrate than on tidepools because the latter remain submerged during low tide buffering the effect of these variables (Metaxas and Scheibling, 1993).

Although environmental variables could explain the seasonal pattern found in this study, biotic interactions such as those derived from grazing could play an important role in shaping macroalgal communities (Dethier, 1982; Underwood, 1981). The role of grazers could be especially relevant in tidepools where grazing intensity can be twice than in emerged substrata (Noël et al., 2009). The seasonal variability of recruitment, growth and reproduction of the species can also influence the assemblage seasonal patterns (Underwood, 1981). In this study, the SIMPER analysis showed that *Ulva* spp. and G. turuturu were the main species responsible for the similarity of samples from the two different periods. ANOVA analyses based on their abundance at the two studied sites showed that both species drove the seasonal pattern of the assemblage. Ulva spp. (mainly *U. lactuca* and *U. rigida* in the studied area) are present all year round but they usually reach their maximum abundance during the spring and summer (Burrows, 1991). Species of the genus Ulva have an opportunistic life strategy and as such they are able to reproduce by spores, zygotes, unfused gametes or by fragmentation (Burrows, 1991). These multiple modes of reproduction make Ulva species prone to rapid propagation and highly adaptable to the environment conditions. In Ulva lactuca, reproduction occurs all year round, in contrast with U. rigida, in which reproductive plants have been found

Table 6

SIMPER analysis results for within and between seasonal macroalgal assemblages as determined by PERMANOVA based on the biomass of species and functional groups. Percentage of similarity within each group and percentage of dissimilarity between groups are presented in bold. Taxa responsible for similarity or dissimilarity and their individual contribution are shown in italics.

Species	Contribution (%)	Cumulative (%)						
Summer-spring (average simil	arity 42.33%)							
Ulva spp.	43.11	43.11						
Grateloupia turuturu	29.93	73.04						
Gelidium pulchellum	9.76	82.80						
Autumn-winter (average simil	arity 31 14%)							
Grateloupia turuturu	41.83	41.83						
Gelidium pulchellum	18.30	60.12						
Ulva spp.	13.50	73.62						
Chondrus crispus	6.94	80.56						
Summer spring us autumn wi	ntor (avorago dissimilarity 72 '	25%)						
Ullya spp	24.81	2.3%)						
Cratelounia turuturu	9.40	24.01						
Celidium nulchellum	7.80	35.01						
Chondrus crisnus	7.80	42.03						
chonaras crispus	7.02	12.05						
Functional group	Contribution (%)	Cumulative (%)						
Summer-spring (average sim	ilarity 57.95%)							
Foliose	40.82	40.82						
Corticated foliose	26.07	66.89						
Corticated macrophytes	25.32	92.21						
Autumn-winter (average similarity 51 22%)								
Corticated macrophytes	52.47	52.47						
Corticated foliose	31.27	83.74						
Foliose	9.81	93.55						
Summer-spring vs autumn-wi	nter (average dissimilarity 58.	74%)						
Foliose.	38.44	38.44						
Corticated macrophytes	21.84	60.28						
Corticated foliose	14.43	74.71						



Fig. 2. Abundance in terms of biomass of the most important species along the year at both studied sites.

during the summer although the seasonality of its reproduction is not well known (Burrows, 1991). Therefore, under favourable environmental conditions like upwelling events, Ulva spp. could quickly occupy the available space (Guimaraens and Coutinho, 2000). The seasonal development of the non-indigenous species G. turuturu is not so well known but, seasonal patterns similar to those described in the present study were found in the east coast of USA (Harlin and Villalard-Bohnsack, 2001) and in the French Brittany (Cabioch et al., 1997). Similarly to Ulva spp., G. turuturu presents different recruitment modes that enhance its ability to resist unfavourable conditions and help the spread of the species under the favourable environmental conditions usually found during spring and summer (Harlin and Villalard-Bohnsack, 2001). The important role of this non-indigenous species in shaping the seasonal pattern of tidepool macroalgal assemblages in the studied sites should be noticed. Since the first record of G. turuturu in the Portuguese coasts, this species has become locally very abundant and due to its dominance and seasonal development it could modify the assemblage structure and function. The ecological effects of the G. turuturu introduction have not been studied yet (Williams and Smith, 2007). Results of the present study did, however, show the importance of this non-indigenous species on tidepool macroalgal assemblages and thus future experimental work to establish the actual role of *G. turuturu* in shaping macroalgal assemblages is underway.

In addition to the two previous species, *C. crispus* and *G. pulchellum* also contributed to the similarity of the two seasonal periods. However, these two species did not show significant differences in their abundance between the spring–summer and autumn–winter periods, probably because they are perennial species contrary to *Ulva* spp. and *G. turuturu*. However, *G. pulchellum* did show higher abundances during the spring–summer period, with a maximum in June, at the two studied sites. It is very difficult to establish a relationship between the abundance pattern and the seasonal development of the *Gelidium* species. In this study, the most abundant species of the genus *Gelidium* was *G. pulchellum*. Some authors considered *G. pulchellum* as a synonym of *Gelidium pusillum*; Fredriksen et al. (1994), however, showed that *G. pulchellum* is a different species than *G. pusillum*. Anyway, both species show a similar life history (Fredriksen et al., 1994). Prathep et al.



Fig. 3. Abundance in terms of biomass of the most important functional groups along the year at both studied sites.

(2009) found that *G. pusillum* can occupy most of the available space because of its vegetative growth, densely clumped, and its ability to reproduce almost throughout the entire year. Similar traits can be responsible for the abundance of *G. pulchellum* in the studied sites along the year. The seasonal development of *C. crispus* is well known but in this study, showed different patterns of abundance at the two studied sites and, therefore, those can not be explained by its seasonal development.

The second hypothesis of this study may be accepted due to the consistence between the patterns found using the species and functional group approaches. Many other studies considering invertebrates or macroalgae found consistent results between different surrogates and species level at different spatial scales (e.g. Smale, 2010). Curiously, the consistence between surrogates and specific level within a temporal scale has received less attention (but see Magierowski and Johnson, 2006). Here we found a consistent pattern along time in concordance with the few studies that tested consistence between surrogates and specific level within a temporal scale using macroalgae (Phillips et al., 1997; Piazzi et al., 2002). Therefore, functional groups could be a valid surrogate to monitoring changes in tidepool macroalgal assemblages along time in the studied area. Particularly, the foliose macroalgae are considered as an opportunistic group that rapidly colonises free space and are thus, an indicator of disturbance (Littler and Littler, 1984). Here the foliose and corticated foliose functional groups showed significant seasonal changes in their abundance as has been reported by other authors (e.g. Viejo, 1997). However, surrogates intended to detect environmental disturbances should be relatively stable both in time and space (Barbour et al., 1992; Glasby and Underwood, 1998). Therefore, seasonal changes in the abundance of foliose and corticated foliose groups could make it difficult to relate their abundance with environmental impacts. However, the corticated macrophytes group was relatively constant in biomass at the studied sites. Steneck and Deither (1994) found that corticated macrophytes are abundant in environments with low disturbance. Moreover, in the studied sites, corticated macrophytes were mainly composed by species of Rhodophyta. Wells et al. (2007) found that Rhodophyta show a high diversity at pristine habitats and its diversity decreased in disturbed areas. Consequently, due to their relative constant abundance and the sensitivity of the species within the corticated functional group, the abundance and diversity of this group could be a proper indicator of environmental impacts.

5. Conclusions

Tidepool macroalgal assemblages showed a seasonal pattern with significant differences in their structure between spring-summer and autumn-winter. The pattern obtained using species was consistent with that achieved by using a functional group approach. Therefore, the latter seem to be a reliable surrogate to explore temporal changes in macroalgal tidepool assemblages. Ulva spp. and the non-indigenous G. turuturu were the main species responsible for the assemblage seasonal pattern due to their significant changes in abundance along the year. Temporal changes in environmental variables and the seasonal development of the main species seem the responsible factors in shaping tidepool macroalgal communities. However, the role of other biological variables (e.g. grazing) on this seasonal pattern should be considered in future studies. Finally, the abundance and species diversity of the corticated macroalgae could be a reliable indicator of environmental impacts due to its constant abundance along the year and its sensitivity to environmental impacts.

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References

- Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E Ltd., Plymouth U.K.
- Araújo, R., Sousa-Pinto, I., Bárbara, I., Quintino, V., 2006. Macroalgal communities of intertidal rock pools in the northwest coast of Portugal. Acta Oecol. 30, 192–202.
- Araújo, R., Bárbara, I., Tibaldo, M., Berecibar, E., Diaz Tapia, P., Pereira, R., Santos, R., Sousa-Pinto, I., 2009. Checklist of benthic marine algae and cyanobacteria of northern Portugal. Bot. Mar. 52, 24–46.
- Barbour, M.T., Plafkin, J.L., Bradley, B.P., Graves, C.G., Wisseman, R.W., 1992. Evaluation of EPA's rapid bioassessment benthic methods: metric redundancy and variability among reference stream sites. Environ. Toxicol. Chem. 11, 437–449.
- Benedetti-Cecchi, L., 2001. Beyond BACI: Optimization of environmental sampling designs through monitoring and simulation. Ecol. Appl. 11, 783–799.
- Burrows, E.M., 1991. Seaweeds of the British Isles. : Chlorophyta, Volume 2. Natural History Museum, London.
- Cabioch, J., Castric-Fey, A., L'Hardy-Halos, M.T., Rio, A., 1997. Grateloupia doryphora et Grateloupia filicina var. luxurians (Rhodophyta, Halymeniaceae) sur les côtes de Bretagne. Cryptogamie Algol. 18, 117–137.
- Cardinale, B.J., 2011. Biodiversity improves water quality through niche partitioning. Nature 472, 86–91.
- Cheshire, A.C., Westphalen, G., Wenden, A., Scriven, L.J., Rowland, B.C., 1996. Photosynthesis and respiration of phaeophycean-dominated macroalgal communities in summer and winter. Aquat. Bot. 55, 159–170.
- Clarke, K.R., 1993. Non parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117–143.
- Colwell, R.K., Coddington, J.A., 1994. Estimating terrestrial biodiversity through extrapolation. Philos. Trans. R. Soc. B 345, 101–118.
- Dethier, M.N., 1982. Pattern and process in tidepool algae: factors influencing seasonality and distribution. Bot. Mar. 25, 55–66.
- Dias, J.M.A., Gonzalez, R., Garcia, C., Diaz-del Rio, V., 2002. Sediment distribution patterns on the Galicia-Minho continental shelf. Prog. Oceanogr. 52, 215–231.
- Díez, I., Santolaria, A., Secilla, A., Gorostiaga, J.M., 2009. Recovery stages over long-term monitoring of the intertidal vegetation in the Abra de Bilbao area and on the adjacent coast (N. Spain). Eur. J. Phycol. 4, 1–14.
- Ferraro, S.P., Swarts, R.C., Cole, F.A., Schults, D.W., 1991. Temporal changes in the benthos along a pollution gradient: discriminating the effects of natural phenomena from sewage-industrial wastewater effects. Estuarine Coastal Shelf Sci. 33, 383–407.
- Fredriksen, S., Guiry, M.D., Rueness, J., 1994. Morphological and biosystematic studies of *Gelidium pusillum* and *G. pulchellum* (Gelidiaceae, Rhodophyta) from Europe. Phycologia 33, 462–470.
- Glasby, T.M., Underwood, A.J., 1998. Determining positions for control locations in environmental studies of estuarine marinas. Mar. Ecol. Prog. Ser. 171, 1–14.
- Golléty, C., Migné, A., Davoult, D., 2008. Benthic metabolism on a sheltered rocky shore: role of the canopy in the carbon budget. J. Phycol. 44, 1146–1153.
- Guimaraens, M.A., Coutinho, R., 2000. Temporal and spatial variation of Ulva spp. and water properties in the Cabo Frio upwelling region of Brazil. Aquat. Bot. 66, 101–114.
- Harlin, M.M., Villalard-Bohnsack, M.V., 2001. Seasonal dynamics and recruitment strategies of the invasive seaweed Grateloupia doryphora (Halymeniaceae,

Rhodophyta) in Naragansett Bay and Rhode Island Sound, Rhode Island, USA. Phycologia 40, 468-474.

- Leliaert, F., Anderson, R.J., Bolton, J.J., Coppejans, E., 2000. Subtidal understorey alga community in kelp beds around the Cape Peninsula (Western Cape, South Africa). Bot. Mar. 43, 59–366.
- Lemos, R.T., Pires, H.O., 2004. The upwelling regime off the west Portuguese coast, 1941–2000. Int. J. Climatol. 24, 511–524.
- Lirman, D., Biber, P., 2000. Seasonal dynamics of macroalgal communities of the northern Florida Reef. Tract Bot. Mar. 43, 305–314.
- Littler, M.M., Littler, D.S., 1984. Relationship between macroalgal functional form groups and substrate stability in a subtropical rocky intertidal system. J. Exp. Mar. Biol. Ecol. 74, 13–34.
- Magierowski, R.H., Johnson, C.R., 2006. Robustness of surrogates of biodiversity in marine benthic communities. Ecol. Appl. 16, 2264–2275.
- Metaxas, A., Scheibling, R.E., 1993. Community structure and organization of tidepools. Mar. Ecol. Prog. Ser. 98, 187–198.
- Noël, L.M.L.J., Hawkins, S.T., Jenkins, S.R., Thomson, R.C., 2009. Grazing dynamics in intertidal rockpools: connectivity of microhabitats. J. Exp. Mar. Biol. Ecol. 370, 9–17.
- Norton, T.A., Melkonian, M., Andersen, R.A., 1996. Algal biodiversity. Phycologia 35, 308–326.
- Palumbi, S.R., Sandifer, P.A., Allan, J.D., Beck, M.W., Fautin, D.G., Fogarty, M.J., Halpern, B.S., Incze, L.S., Leong, J.A., Norse, E., Stachowicz, J.J., Wall, D.H., 2009. Managing for ocean biodiversity to sustain marine ecosystem services. Front. Ecol. Environ. 7, 204–211.
- Phillips, J.C., Kendrick, G.A., Lavery, P.S., 1997. A test of a functional group approach to detecting shifting macroalgal communities along a disturbance gradient. Mar. Ecol. Prog. Ser. 153, 125–138.
- Piazzi, L., Ceccherelli, G., Cinelli, F., 2001. Treat to macroalgal diversity: effects of the introduced green alga *Caulerpa racemosa* in the Mediterranean. Mar. Ecol. Prog. Ser. 210, 149–159.
- Piazzi, L., Pardi, G., Balata, D., Cecchi, E., Cinelli, F., 2002. Seasonal dynamics of a subtidal North-Western Mediterranean macroalga community in relation to depth and substrate inclination. Bot. Mar. 45, 243–252.
- Prathep, A., Lewmanomont, K., Buapet, P., 2009. Effects of wave exposure on population and reproductive phenology of an algal turf, *Gelidium pusillum* (Gelidiales, Rhodophyta), Songkhla Thailand. Aquat. Bot. 90, 179–183.
- Rindi, F., Battelli, C., 2005. Spatio-temporal variability of intertidal algal assemblages of the Slovenian coast (Gulf of Trieste, northern Adriatic Sea). Bot. Mar. 48, 96–105.
- Roberts, D.E., Smith, A., Ajani, P., Davis, A.R., 1998. Rapid changes in encrusting marine assemblages exposed to anthropogenic point-source pollution: a beyond BACI approach. Mar. Ecol. Prog. Ser. 163, 213–224.
- Smale, D.A., 2010. Monitoring marine macroalgae: the influence of spatial scale on the uselfulness of biodiversity surrogates. Divers. Distrib. 16, 985–995.
- Steneck, R.L., Deither, M.N., 1994. A functional group approach to the structure of algaldominated communities. Oikos 69, 476–498.
- Underwood, A.J., 1981. Structure of a rocky intertidal community in New South Wales: patterns of vertical distribution and seasonal changes. J. Exp. Mar. Biol. Ecol. 51, 57–85.
- Veiga, P., Rubal, M., Besteiro, C., 2009. Shallow sublittoral meiofauna communities and sediment polycyclic aromatic hydrocarbons (PAHs) content on the Galician coast
- (NW Spain) six months after the prestige oil spill. Mar. Pollut. Bull. 58, 581–588.Viejo, R.M., 1997. The effects of colonization by *Sargassum muticum* on tidepool macroalgal assemblages. J. Mar. Biol. Assoc. U. K. 77, 325–340.
- Walter, D.I., Kendrick, G.A., 1998. Threats to macroalgal diversity: marine habitat destruction and fragmentation, pollution and introduced species. Bot. Mar. 41, 105–112.
- Wells, E., Wilkinson, M., Wood, P., Scanlan, C., 2007. The use of macroalgal species richness and composition on intertidal rocky seashores in the assessment of ecological quality under the European Water Framework Directive. Mar. Pollut. Bull. 55, 151–161.
- Williams, S.L., Smith, J.E., 2007. A global review of the distribution, taxonomy and impacts of introduced seaweeds. Annu. Rev. Ecol. Evol. Syst. 38, 327–359.
- Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., Watson, R., 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314, 787–790.