

Original article

# Macroalgal communities of intertidal rock pools in the northwest coast of Portugal

Rita Araújo<sup>*a*,\*</sup>, I. Sousa-Pinto<sup>*a*,*b*</sup>, I. Bárbara<sup>*c*</sup>, V. Quintino<sup>*d*</sup>

<sup>a</sup> CIIMAR, Centro Interdisciplinar de Investigação Marinha e Ambiental, 289, Rua dos Bragas, 4050-123 Porto, Portugal

<sup>b</sup> Departamento de Botânica, Faculdade de Ciências, Universidade do Porto, 1191, rua do Campo Alegre, 4150-181 Porto, Portugal

<sup>c</sup> Departamento de Bioloxia Animal, Bioloxia Vegetal e Ecoloxia. Campus da Zapateira, s/n. 15071A Coruña, Spain

<sup>d</sup> Departamento de Biologia, Universidade de Aveiro, CESAM—Centro de Estudos do Ambiente e Mar. Campus Universitário de Santiago. 3810-193 Aveiro, Portugal

#### ARTICLE INFO

Article history: Received 14 July 2005 Accepted 11 April 2006 Available online 12 June 2006

Keywords: Rock pools Macroalgae Environmental variables Intertidal NW Portugal

#### ABSTRACT

Macroalgal communities in littoral rock pools of the Northwest coast of Portugal were studied along 60 km of coastline. Thirty-eight pools were sampled twice between March and August 2003. Rhodophyta were the dominant algue group, whether the pools were located lower or upper on the shore, except in pools located between 2 and 3 meters where Rhodophyta share the dominance with Chlorophyta. Species richness increased from pools located at higher levels on the beach to the ones located lower on the shore. The macroalgal communities' species composition was the major source of variability between rock pools. Each pool presented a unique combination of species, forming particular communities. A reduced number of species with high percent cover are the main factor creating the differences between the pools. Also, clear differences could be found between the species compositions of macroalgal communities located in the pools and in the surrounding emergent substrata. The environmental variables considered in this study (tidal height, maximum pool depth, maximum pool width and maximum pool length), were poorly related to the communities' species composition. The results suggest that each pool is unique regarding its macroalgal community structure and that the environmental factors considered in this study were not of major importance in determining the variability between pools.

© 2006 Elsevier Masson SAS. All rights reserved.

# 1. Introduction

Rock pool systems, in spite of their ubiquity on rocky shores, have been the subject of few studies (Underwood and Skilleter, 1996; Van Tamelen, 1996, Thompson et al., 2002).

In these habitats, organisms experience unique living conditions. Rock pools remain submerged during the entire

tidal cycle, thus, they are not subjected to cyclic periods of emersion and desiccation. Also, the organisms living in pools suffer greater fluctuations of the physical environment than those found under constant submergence in the subtidal zone (Metaxas and Scheibling, 1993). Pools may suffer large fluctuation of pH, salinity and temperature, mainly when located at higher levels on the shore (Metaxas and Scheibling, 1993).

Studies on distribution patterns of organisms are scarce in rock pool systems. Several studies refer to a variation in the dominance of macroalgal assemblages, depending on tidal height (Femino and Mathieson, 1980; Wolfe and Harlin, abts reserved

<sup>\*</sup> Corresponding author: Tel.: +351 223 401 835; fax: +351 223 390 608.

E-mail address: ritaraujo@cimar.org (R. Araújo).

<sup>1146-609</sup>X/\$ - see front matter © 2006 Elsevier Masson SAS. All rights reserved. doi:10.1016/j.actao.2006.04.002

1988a; Kooistra et al., 1989). Important variability was also found by Metaxas et al., (1994) between macroalgal assemblages of pools sited at different tidal heights and within the same height at a distance of a few meters.

Rock pools are isolated habitats with well-defined boundaries (Metaxas and Scheibling, 1993). In these space-limited systems, a number of physical and biological factors interact to determine community structure. Physical features of pools (area and depth), tidal height and wave exposure have been considered important factors determining macroalgal abundance (Sze 1982, Wolfe and Harlin, 1988b; Metaxas et al., 1994). However, Underwood and Skilleter (1996) found that the diameter of the pool had no significant influence in the structure of assemblages of rock pools, in New South Wales. The importance of pool size is also referred by Femino and Mathieson (1980), who found that larger pools presented more stable physical conditions and contained a higher number of taxa. Besides physical features of the pool, biotic interactions can play an important role on the community species composition. The effects of grazing and competition have been documented in rock pools (Chapman, 1990; Benedetti-Cecchi and Cinelli, 1992, 1995, 1996; Van Tamelen, 1996). These biotic interactions are more pronounced in these habitats than in surrounding emergent substrata, due to space limitation and to more benign environmental conditions, mainly when pools are located at lower levels on the shore, allowing a wider variety of species (Femino and Mathieson, 1980).

The large variability between rocky pool assemblages and the complexity of the interactions between physical and biological factors, have contributed to the lack of knowledge that exists relative to the surrounding rocky shore communities (Underwood and Skilleter, 1996; Van Tamelen, 1996).

On the Portuguese coast, macroalgal communities from rock pools remain unstudied. In this study we characterize the macroalgal community composition and variability on rock pools in a total 60 km stretch of the northwest coast of Portugal. The importance of physical features of the habitat in determining macroalgal communities composition in these habitats is also investigated.

## 2. Material and methods

#### 2.1. Study area and sampling

Sea surface temperature on the western Portuguese coast varies between 11 and during the year. The west coast is exposed to the prevailing northwest oceanic swell which can reach values over 5 m in winter. The tidal regime in the Portuguese coast is semi-diurnal, with an extreme tidal range of spring tides approximately of 3.5–4 m. On the northwest coast, rocky shores are typically granite.

At each of the 11 sites studied, located from Moledo (41° 50'35''; 8°52'18'') to Apúlia (41°29'14''; 8°46'58'') (Fig. 1), one transect (approximately 5 m wide) was randomly placed from the lower to the upper shore. The study sites were chosen according to the presence of extensive rocky shore sys-

tems and were restricted to open bedrock. In each transect permanent rock pools containing algal communities, located under the transect line, were selected. In average, three pools were sampled per transect. A total of 38 pools, distributed along 60 km of coast were studied in the first sampling period (Spring) whilst 36 of these pools were sampled in the second sampling period (Summer). For each pool sampled, tidal height, maximum depth, maximum width and maximum length of the pool were recorded. Pools ranged in tidal height from 0.2 to 3.3 m, in depth from 0.1 to 1.3 m, in width from 0.4 to 9.6 m and in length from 1.0 to 26.1 m. According to their tidal height, pools were placed in four groups: A: < 1 m, B: 1–2 m, C: 2–3 m and D: > 3 m.

Each pool was sampled twice during the study period, once in Spring (March–May 2003) and once in Summer (June–August 2003). The largest pools were sampled with  $50 \times 50$  cm quadrats, while  $30 \times 30$  cm quadrats were used to study the smaller ones. The quadrats were divided into sub-quadrats of  $1.0 \times 10$  cm and placed randomly within the pool. The percent cover was assessed using non-destructive methods by counting the number of sub-quadrats occupied by each species (Dethier et al., 1993). Nevertheless, whenever necessary, sampling was stratified in different layers, and the upper visible layer of macroalgae was distinguished from the substrate cover. Four replicates were taken in each pool and each sampling period. Sampling was done by a single observer.

The specimens were collected and identified in laboratory, except when accurate identification was possible in the field. All the macroalgae were identified to species level, except for the genus *Ulva*.

Sampling of emergent substrate was done according to the methodology described in Araújo et al. (2005).

#### 2.2. Data analysis

The species richness was calculated for each rock pool and at each sampling period.

With the objective of assessing the existence of zonation patterns of species distribution along tidal height, macroalgae were grouped according to their phylum and to their morpho-functional group (Littler and Littler, 1983).

Multivariate analysis was used to estimate the spatial variability in macroalgal assemblages of rock pools and to search for significant factors of the variability encountered. Data analysis was performed with non-parametric multivariate techniques using the PRIMER software (Clarke and Gorley, 2001). A triangular matrix of similarity between samples was constructed using the Bray-Curtis similarity with log(x + 1)data transformation. Non-metric multidimensional scaling (NMDS) was used to produce two-dimensional ordination plots. One-way ANOSIM (Clarke and Warwick, 2001) was used to test the null hypothesis of no significant differences between: 1) sampling periods; 2) the pools and 3) transects. When conducting this test, the R-statistic is obtained, the value of which lies in the range (-1, 1). Values of R = 1 are only obtained when all replicates within groups are more similar to each other than any replicates from different groups, whereas a value of R = -1 can only be obtained when the





Bray-Curtis similarities within the replicates of the groups are all lower than any of the similarities between replicates from different groups. Negative values of R are uncommon and may result from an erroneous allocation of the replicates. Under the null hypothesis of no significant differences between the groups, the R value will be close to zero. This value becomes closer to 1 as the similarity within the replicates of the groups become larger than the similarities between replicates from different groups (Clarke and Warwick, 2001).

To test the null hypothesis 1, samples were grouped into a sampling period factor and the comparison was made between each pool within the same transect. This test also included the comparison of the whole transect, sampled in the two periods. In all these tests, only the global *R* value for each analysis will be presented, given the very large number of possible pairwise comparisons. To test for the null hypothesis 2, a pool factor was established, with four replicates per pool. The analysis was conducted for all the pools. This test was conducted with the data collected on the first sampling occasion. To test the null hypothesis 3, the test was conducted over a transect factor, comparing different transects along the study area. All sampling units taken per transect were regarded as replicates of the same sample. This test was conducted with the data collected on the second sampling period.

To investigate the relationships between the pool communities and environmental variables the BIO–ENV and the RE-LATE routines were used (Clarke and Gorley, 2001). Finally, the SIMPER routine (Clarke and Gorley, 2001) was used to find the species with higher contribution to the differences found between each pair of pools.

# 3. Results

In the 38 pools analyzed, a total of 99 taxa were identified.

The largest number of pools was found between 1 and 3 m. Pools were sparse in the highest levels (> 3 m).

The dominance of macroalgal phyla varied slightly with tidal height. Rhodophyta was the dominant group at all levels, but the absolute number of species decreased from lower to higher levels. The number of Chlorophyta and Heterokontophyta slightly increased along the same tidal height gradient up to 3 m (Fig. 2a). In the pools located higher on the shore (> 3 m), a decrease in the total number of species for all the groups of algae was observed (Fig. 2a). The differences between the three groups of algae are not so pronounced if their mean percent cover is considered. With the exception of the pools located higher on the shore, mean values of cover of Rhodophyta are very close to those of other groups (Fig. 2b). Brown algae show their highest mean percent cover between 1-2 m and highest number of species between 2-3 m (Fig. 2b). In pools located above 3 m the dominance of red algae is clear.

All the morpho-functional groups of macroalgae were present at all heights on the shore (Fig. 3). Mid-zone pools (1–3 m) showed high similarity in terms of number of species and percent cover (Fig. 3). The most important differences were found in lower shore and upper shore pools (<1 m and > 3 m, respectively) (Fig. 3).

In pools below 3 m, the number of species was dominated by filamentous and coarsely-branched algae. Above 3 m, the dominance of the pools was shared between sheets and filamentous algae (Fig. 3a). The highest number of sheets, filamentous, coarsely branched and thick leathery species was found in the pools located below 1 m. When considering mean percent cover, the thick leathery group dominates below 1 m, sheets are the dominant group between 2 and 3 m while between 1 and 2 m, all the morpho-functional groups have similar mean percent cover. Above 3 m, the crustose group clearly dominates the pools due to the high abundance of Lithophyllum incrustans (Fig. 3b).

A decrease in species richness mean values from lower to higher tidal heights was observed (Fig. 4). The mean values of species richness were slightly higher in spring than in summer. Monospecific pools were found between 2 and 3 m and were exclusively composed of green algae.

Along each transect, some species were recorded both in the rock pools and the emergent rocky shore and others were exclusively recorded in one of these two habitats. Considering the results obtained in all the transects, which Table 1 presents, for a selected number of species, the distribution of their relative abundance between the two habitats and shows that some species appear in one environment but not in the other and that the species common to both environments occur at very different abundances in the two habitats. The species composition in rock pools and in low littoral zones (< 50 cm above chart datum) is in fact distinct as shown in Fig. 5. A clear division can be established between the assemblages of these two environments, with a minor overlap. It could be expected that communities overlapping would correspond to lower-shore pools, but no clear correspondence with tidal height could be established (Fig. 5).

The differences among pools are the most important source of variation in the studied area, noticed from the highest R value obtained in the one-way ANOSIM test (Table 2). Each pool is a particular entity and all the pools analyzed were differently from each other. Differences between transects, in spite of significant, were less important than the ones attributable to pool composition (Table 2). No signif-



Fig. 2 – Total number of species of each macroalgal phylum (a) and their respective mean percent cover (± S.E.) (b) in pools at different heights on the shore (< 1 m; 1–2 m; 2–3 m; > 3 m), in the first sampling period. C – Chlorophyta; H – Heterokontophyta; R – Rhodophyta.



Fig. 3 – Total number of species of each macroalgal morpho-functional group (a) and their respective mean percent cover (± S.E.) (b) in pools at different tidal heights (< 1 m; 1–2 m; 2–3 m; > 3 m), in the first sampling period. SH: Sheet group; FI: Filamentous group; CB: Coarsely branched group; TL: Thick leathery group; JC: Jointed calcareous group; CR: Crustose group.



Fig. 4 – Mean values (± S.E.) of Species Richness for the macroalgal communities in rock pools located at the four tidal heights studied (< 1 m; 1–2 m; 2–3 m; > 3 m), in spring (SP) and summer (SU).

icant differences were identified in composition of rock pool assemblages between the two sampling periods (Table 2). The most obvious difference found between the two sampling periods was a shift in the dominant organisms of some pools either due to the increase of the percent cover of ephemerals like *Ulva* sp. or to changes in the abundance of species with different development phases along the year like *Sargassum muticum* or *Sacchorhiza polyschides* (Table 3).

The results of SIMPER analysis show that the Average Dissimilarity between each pair of pools ranged from 25% to 100% but the majority of the values (74%) were above 80%. Only a small percentage of the species present in the pools was needed in order to reach 90% of the average dissimilarity between each pair of pools. In 10 randomly chosen pairwise comparisons between pools, a mean value of 39% of the total number of species present in the pools was needed to reach 90% of the average dissimilarity. The reason is that in general, these species present high percent cover in a reduced number of pools and do not occur in the others (Fig. 6 and Table 3).

Table 1 – Relative abundance of the species common to intertidal pools and emergent rocky shore (contribution > 30% of the percent cover in one of the two environments) and of the exclusive species to each habitat (contribution > 3%)

Species	Pools	Emergent						
1		rocky shore						
Sargassum muticum	98.8	1.2						
Ahnfeltia plicata	98.1	1.9						
Monostroma obscurum	94.7	5.3						
Lithophyllum incrustans	80.5	19.5						
Leptosiphonia schousboei	77.4	22.6						
Chaetomorpha linum	69.6	30.4						
Bifurcaria bifurcata	69.1	30.9						
Laminaria ochroleuca	54.7	45.3						
Fucus vesiculosus	0.4	99.6						
Lomentaria articulata	0.4	99.6						
Pterosinhonia complanata	0.4	99.6						
Fucus serratus	0.5	99.5						
Ophidocladus simpliciusculus	0.8	99.2						
Ascophyllum nodosum	0.9	99.1						
Giaartina pistillata	0.9	99.1						
Sacchorhiza polyschides	1.7	98.3						
Gelidium corneum	2.0	98.0						
Osmundea ninnatifida	2.0	97.6						
Mastocarnus stellatus	25	97.5						
Dictvota dichotoma	2.8	97.2						
Pterocladiella capillaceae	3.6	96.4						
Porphyra umbilicalis	60	94.0						
Hildenbrandia rubra	6.5	93.5						
"Petrocelis cruenta" [stage]	6.6	93.4						
Chondracanthus acicularis	6.6	93.4						
Cystoseira baccata	87	91.3						
Blidinaia minima	9.1	90.9						
Rhodothamniella floridula	13.6	86.4						
Chondrus crispus	14.2	85.8						
Chondracanthus teedei	14.8	85.2						
Strehlocladia collabens	21.5	78.5						
Ulua sp	42.7	57 3						
Corallina elonaata	45.8	54.2						
Corallina officinalis	100	0						
Gratelounia filicina	100	0						
Callithamniom aranulatum	0	100						
Catenella caesnitosa	0	100						
Cystoseira tamariscifolia	0	100						
Dumontia contorta	0	100						
Fucus spiralis	0	100						
Haliptilon sayamatum	0	100						
Himanthalia elonaate	0	100						
Laminaria hyperborean	0	100						
Peluetia canaliculata	0	100						
Pornhyra dioica	0	100						
Pornhyra linearis	0	100						
i orphyra intearis	0	100						

The environmental variables measured in this study were poorly related with the biological data (Table 4). The first best correlation in the BIOENV analysis was established with maximum length of the pool and the second was with the combination between length and height above chart datum, but the values were very low (below 0.05). All the correlations established with other environmental factors or combination of factors were negative.

#### 4. Discussion

The species richness in the intertidal pools within the study area was generally in agreement with the results described in other studies, increasing as the pool tidal height decreases (Wolfe and Harlin, 1988b; Kooistra et al., 1989; Metaxas et al., 1994). The harsh environmental conditions in the pools located higher on the shore may limit the number of species able to colonize those levels (Metaxas et al., 1994). Pools located lower on the shore present a more stable environment (Femino and Mathieson, 1980), allowing the occurrence of a wider variety of organisms.

In this study the global zonation patterns of macroalgal phyla (Rhodophyta, Chlorophyta and Heterokontophyta) show some differences from those mentioned elsewhere. Previous studies suggest that the pools located lower on the shore are dominated by red and brown algae and those located higher on the shore by monospecific communities of green algae (Femino and Mathieson, 1980; Wolfe and Harlin, 1988a; Kooistra et al., 1989). In this study, the low shore pools were clearly dominated by red algae, for both the mean percent cover or the number of species. In spite of decreasing abundance from the lower to the higher tidal height pools, red algae were the dominant group at all levels studied, except for pools located between 2-3 m, where they share the dominance with green algae. The higher level pools (> 3 m) show the highest mean percent cover of Rhodophyta, dominated by Lithophyllum incrustans. On the intertidal rocky shore, this species is characteristic of low and mid-shore levels and in higher levels appeared only in the pools, which is in agreement with the results from Galicia (Bárbara et al., 1995). Crusts predominate in areas of high disturbance or high stress (Dethier, 1994). Coralline crusts can survive in pools where erect algae and encrusting colonial animals are virtually absent (Kooistra et al., 1989). This dominance can be achieved by greater stress tolerance or by inhibiting settlement of epiphytes (Kooistra et al., 1989).

Considering the distribution of morpho-functional groups along tidal height, some differences were found from previous works. Percent cover of latter successional forms, such as thick leathery and crustose macroalgae, was not higher in mid pools as was reported in the study by Metaxas et al., (1994). The highest percent cover of crustose forms was found above 3 m due to the dominance of Lithophyllum incrustans.

Concerning the number of species, lower pools presented the highest number of filamentous and coarsely-branched algae. However, mid shore pools were also dominated by these two groups of species. In higher pools, sheet and filamentous group represent the highest number of species. However, these two groups of algae are also among the four groups with higher percent cover in low level pools. This is in accordance with the studies of Femino and Mathieson (1980) and Wolfe and Harlin (1988b) that found that some genera of sheet and filamentous algae were more abundant in lower pool and others in higher pools.

In general, the pools surveyed in this study contain specific groups of species and communities that do not occur on the surrounding emergent substrate, which is in agreement with Femino and Mathieson (1980). These authors distinguished four groups of algae based on their occurrence in pools and in the surrounding rocky shore: sublittoral species that, at the littoral zone, only appear in pools, sublittoral and littoral species which appear in both environments, exclusively sublittoral and littoral species and species exclusive



Fig. 5 – Two-dimensional MDS ordination representing replicates of communities for low shore assemblages (< 50 cm above chart datum) in emergent shore (R = black triangles) and for pools sited at different tidal heights (grey symbols).

Table 2 – One-way ANOSIM. Values of global test statistics
(R) and associated probability (p). The factors tested were
pools, transects and sampling period. Only the null
hypothesis of no differences between sampling occasions
is accepted. n.s.: non-significant

Source of variation	Global R	Р
Pools	0.975	0.001
Transects	0.301	0.001
Sampling period	0.006	0.309 n.s.

of pools. This selection of habitat is related to the tolerance of species to emersion/desiccation: some of these species do not survive continuous submergence in pools and others are not tolerant to desiccation (Femino and Mathieson, 1980).

Differences in species composition of pools' macroalgal assemblages were the major source of variability in the coastal area under study. Significant differences were found between communities among all pools. However, a small percentage of the species were responsible for these differences. These species presented high percent cover and appeared in a small number of pools. Even the pools dominated by the same species showed significant differences among themselves due to the fact that dominance was shared with different macroalgae in each pool.

Few quantitatively replicated studies have been done on the spatial variability of macroalgal communities in pools along a large sampling area. Metaxas et al. (1994) found great variability between macroalgal communities in pools located at the same height on the shore, in Nova Scotia, Canada. The authors suggested that variability in recruitment and/or differences in physical features of the pools might be responsi-

ble for the variability in percent cover of macroalgae among pools. Great variability between macroalgal communities in pools was also found in the present study. However, the relationship between the environmental factors investigated in this study and the macroalgae species composition was very weak. The only individual factor which showed positive correlation with macroalgal assemblages was the maximum length of the pool. Studies on the influence of the size of the pools upon macroalgal communities are scarce. In this study, the diameter of the pools was not measured. However, it was expected that maximum length, width and depth of the pool showed a similar correlation with macroalgal communities as would the diameter of the pool. Underwood and Skilleter (1996), found that the diameter of the pool had no influence on the species composition of tidepools in New South Wales. Femino and Mathieson (1980) stated that in larger pools temperature changes were not so pronounced and less evaporation occurred. They found the largest number of taxa in the lower shore larger pools and suggested that the physical configuration of the pool was an important factor. Wolfe and Harlin (1988b), found a positive relation between species diversity and pool height on the shore, volume and surface area in Rhode Island. We have no consistent explanation for the fact that length of the pool showed higher correlation with species composition than did the width. Nevertheless, the correlation was very weak and we concluded that in this study, the size of the pool was not important in determining variability in the composition of the pool communities.

Tidal height plays a determinant role in emergent rocky shore assemblages. However, in rock pools this factor does Table 3 – Species composition and their respective cover percentage in the pools sampled in spring (a) and in summer (b). For each sampling occasion, the table includes the subset of species which gather more than 10% of the total cover percentage in at least one of the pools. The dominant species in each pool and for each sampling occasion is marked in grey. The pools are numbered and arranged from 1 to 36 according to increasing tidal height

a)																		
· ·	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Ahnfeltia plicata		36.00		1.24														
Bifurcaria bifurcate					1.52					4.24			3.52	27.00	21.00			0.24
Blidingia minima								24.00										
Ceramium botryocarpum				1.00	0.24		3.00		2.52				0.24	3.76	2.52	0.24	2.52	0.24
Ceramium secundatum		11.44	1.00	2.52	0.76					0.24						1.31		
Chaetomorpha linum		0.24							0.24		1.00	60.00						0.24
Chondrus crispus						10.00				2.52				4.00	5.52	1.24		
Corallina elongate	2.52		13.00	0.52	43.00	25.00	4 60		04.00	34.00	0.24		2.76	0.52	6.00	7 50	1.24	1.52
Corallina officinalis							1.68		24.00							1.52		
Genalaria aracilis					1 24						0.24					0.24		
Gratelounia filicina			0.52		1.27				0.52		10.24					0.24		
Laminaria ochroleuca			0.52			72.25			0.52	36.00	10.21		9.00					
Leptosiphonia				1.24	0.24		0.32								0.24		54.00	0.24
schousboei																		
Lithophyllum incrustans		1.24	9.24	2.00	0.24		97.00		4.00		3.00			2.00		4.00	1.52	
Mastocarpus stellatus			1.24	0.24											6.00			
Rhodothamniella		3.52		23.00														
floriaula	02.00				1 04				27.00	20.00			00.00	<b>C2 00</b>		0.00	1 50	40.00
Surgassum muticum	83.00	0.24	1 24		2.00				27.00	20.00			90.00	0.24	052	8.00	2.00	46.00
Illua sn	8 00	5.52	8 24	2 00	35.00	2 00	19.00	27.00	3 28	0.76	55 24	7 24	4 52	4 52	13.04	24.00	0.24	9.00
Monostroma obscurum	0.00	5.52	0.21	2.00	55.00	2.00	15.00	27100	5.20	0.24	55.21	,	1.52	0.24	10.01	0.24	0.21	5.00
a)																		
	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Ahnfeltia plicata	9.00																	
Bifurcaria bifurcate			2.52	21.00	54.00	12.00				19.00								
Bilaingia minima	4 5 2	2.76	1 01		1 5 0	10.04		2 00		0.24						1 24	0.76	10.00
hotryocarnum	4.52	2.70	4.24		1.52	12.24		5.00		0.24						4.24	2.70	19.00
Ceramium				1.52						7.24	7.24		0.56	0.24	2.76			
secundatum																		
Chaetomorpha linum																0.24		
Chondrus crispus	8.24	0.24		0.24	13.52	0.76		9.00		3.00	0.76				0.24	4.52	0.76	2.00
Corallina elongate	2.00		11.00	17.00	1.24			3.24	18.00	5.00	7.00		17.00	0.24		20.00	1.76	34.00
Corallina officinalis		11.00				1.24												
Gelidium spinosum				0.52										2.24				
Gracilaria gracilis	2 5 0			0.24				0.70						12.52	3.58			
Laminaria ochrolauca	3.52				052			3.76										
Lentosinhonia		0.52	3 5 2		1.52			0.24	3 5 2		0 24		3 24			0.24	1 52	
schousboei		0.52	5.52		1.52			0.21	5.52		0.21		5.21			0.21	1.52	
Lithophyllum		2.00	6.00	1.00	0.52	6.76		50.00		2.52	11.00	1	12.00	2.24			82.00	56.00
incrustans																		
Mastocarpus stellatus									0.24	2.00	0.24							
Rhodothamniella												28.00						
Saraassum muticum	2.24		1 76	0.24	2 76	27.00		2.00	052	14.00				28.00		22.24		
Strehlocladia collahens	1 52	3 24	1.70	0.24	5.70	27.00		2.00	0.52	14.00				38.00		22.24		
Ulva sp.	11.52	1.76	10.00	16.00	2.28	17.52	69.00	0.70	11.76	8.00		58.24	3.52	17.00	67.00	14.24	4.00	7.00
Monostroma obscurum								0.24		0.52	5.00							
b)																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Ahnfeltia plicata		29.00		1.00														
Bifurcaria bifurcata			0.24		20.00			04.00		7.00				24.00	14.00			0.24
Bilaingia minima	1.00	1 00	2 5 2	1 24	1 5 0			31.00	7.00	0.76				0 5 2	2 5 2	12.00	7.00	
botryocarnum	1.00	1.00	5.52	4.24	1.52				7.00	0.70				0.52	2.52	12.00	7.00	
Chaetomorpha linum											46.00	6.52						
Chondracanthus	10.00				0.24											5.24		
acicularis																		
Chondrus crispus	3.52					21.00				2.00	2.00			1.24			,	
																	(con	tinued

b)

0)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Corallina elongata	1.52		34.00	0.76	25.00	11.00	2.76		-	24.00		1.24	5.24	2.00	16.00	2.24	1.24	1.52
Corallina officinalis									22.00	)								
Gelidium spinosum																21.00		
Hildenbrandia rubra											3.52					0.24		
Laminaria ochroleuca						42.00				57.00			2.00					
Lithophyllum incrustans				0.52			76.00	)						0.24			2.24	3.00
Rhodothamniella		2.00		2.76	3.00													
floridula																		
Saccorhiza polyschides	21.00	)				7.24												7.00
Sargassum muticum	77.00	)			0.24				72.00	1.24			52.00	) 15.00		3.24		
Streblocladia collabens			2.00	5.00									0.24		0.96			
Ulva clathrata					0.52				0.52	0.76			2.24	0.76		38.00		
Ulva sp.	20.00	0.24	0.24	5.00	13.52	8.00		4.76	16.00	7.00	8.24	44.76	10.52	2 18.52	37.00	22.24	9.76	43.52
Monostroma obscurum														0.24				
b)																		
	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Ahnfeltia plicata	1.52																	
Bifurcaria bifurcata				43.00	75.00	13.00			3.00	29.00								
Blidingia minima								13.00										
Ceramium	0.52	9.00	2.76	0.76	4.24	2.00		0.24	1.52	0.52	1.24				0.52	0.24	0.52	
botryocarpum																		
Chaetomorpha linum																		
Chondracanthus			0.24	3.00		1.00			0.52	2.00	5.00					11.00		
acicularis																		
Chondrus crispus					2.52	1.00		5.00		5.00	1.00					1.00		1.52
Corallina elongata	0.52		12.00	12.00	1.24	6.00			21.00	3.24	18.00	)	21.00	0.24		50.00	4.24	23.00
Corallina officinalis		24.00																
Gelidium spinosum				0.24														
Hildenbrandia rubra					7.00			11.76						1.52	3.00	2.52		1.00
Laminaria ochroleuca										11.00								
Lithophyllum		1.52				13.24		51.00			6.00		8.00			2.00	65.00	64.00
incrustans																		
Rhodothamniella												12.00				6.00		
floridula																		
Sargassum muticum					5.52	40.00			0.52	34.00	0.24			81.00		4.24		
Saccorhiza polyschides					0.24													
Streblocladia collabens			0.24										5.52					
Ulva clathrata		3.24	2.54	52.00		2.52		0.52	0.76	7.00	1.76			55.00	45.00	1		
Ulva sp.	31.76	5 9.52	10.00	6.24	0.76	17.00	81.24	18.00	11.00	4.52	3.52	54.00	12.00	1.52	33.76		78.00	29.00
Monostroma obscurum																		

not assume the same importance because organisms do not experience the stress caused by desiccation during lower tide. Some works mention the importance of tidal height upon the composition of rock pool communities (Sze, 1982). In the present study, tidal height was not an important factor for community structure.

Metaxas et al. (1994) suggested that each pool has a unique combination of physical characteristics such as intertidal height, topography, depth, volume and wave exposure, which determines the different communities which develop there. However, the physical factors were not major determinants of community structure in the pools studied here. Macroalgal communities were different even in pools located at the same level, a few meters apart and of a similar size. Other factors should thus be important in determining the variability among pools. Recent works suggest that the history of colonization and season of disturbance may play a central role in structuring assemblages on rocky shores. Kaehler and Williams (1998) demonstrated that in emergent rocky shores in Hong Kong, the season when substrate became free for colonization was important in determining the composition of assemblages developing there. Airoldi (2000) found that different types of algae (crusts, turf and

erect algae) responded differently to time of disturbance due to variations in rates and type of recruitment (vegetative or sexual). On littoral rock pools on the west coast of Italy, it has been demonstrated that season of disturbance (clearing) of the substrate may alter the competitive relationships between species, depending on their time of recruitment and settlement and abundance of herbivores (Benedetti-Cecchi and Cinelli, 1996, Benedetti-Cecchi, 2000). Composition of early colonizer assemblages can suffer variability along the succession process in relation to competitive and grazing interactions. Thus, patches cleared at different times may suffer different sequences of colonization and support different assemblages of macroalgae in later stages of development. We suggest that in pools of the northwest coast of Portugal, physical features of the pools together with biological interactions may contribute to the development of particular macroalgal communities. However, other factors such as random factors and timing of colonization must be the most important agents in determining the composition of mature assemblages in rock pools when compared with physical characteristics of the habitat. This could explain the significant differences between pools of the same size and shape, located close to each other on the shore.



Fig. 6 – Two-dimensional MDS ordinations for all the pools sampled. Each plot represents the distributional pattern of a single species. The circle area is proportional to mean percent cover of species in each pool. The species represented were chosen using the BVSTEP procedure in PRIMER ( $P \ge 0.975$ ).

Table 4 – Correlation coefficients from BIO-ENV analyses, for comparisons between the macroalgal assemblages and environmental variables. Environmental variables considered for each pool were maximum length (Le), maximum width (Wi), maximum depth (De) and height above chart datum (He). None of the variables, single or in combination, was statistically significant. Using the RELATE routine, the value of P obtained was 0.228 for the best environmental variable (Le)

Variables	Correlation coefficients
Le	0.049
Le + He	0.028
Le + He + Wi	-0.002
Le + Wi	-0.004
Не	-0.005
De + Le + He	-0.037
De + Le + He + Wi	-0.043
De + Le + Wi	-0.045
De + Le	-0.055
He + Wi	-0.055
De + He	-0.073
Wi	-0.087
De + He + Wi	-0.100
De + Wi	-0.110
De	-0.112

## Acknowledgments

This work was developed under the project "Distribution, use and conservation of the botanical heritage of the Northern Coast of Portugal: a sustainable development approach for a (future) "Natura 2000" site" (PNAT/BIA/15204/99) funded by the Portuguese Foundation for Science and Technology (FCT). The first author was the recipient of a fellowship from this project. The authors acknowledge the help of Cristina Correia during the field work. We also thank the comments of two anonymous reviewers that greatly improved the manuscript.

REFERENCES

- Airoldi, L., 2000. Responses of algae with different life histories to temporal and spatial variability of disturbance in subtidal reefs. Mar. Ecol. Prog. Ser. 195, 81–92.
- Araújo, R., Bárbara, I., Sousa-Pinto, I., Quintino, V., 2005. Spatial variability of intertidal rocky shore assemblages in the northwest coast of Portugal. Estuarine and Coastal Shelf Science 64, 658–670.
- Bárbara, I., Cremades, J., Pérez-Cirera, J.L., 1995. Zonación de la vegetación bentónica marina en la Ría de A Coruña ( N.O. de España). Nova Acta Científica Compostelana (Bioloxía) 5, 5–23.
- Benedetti-Cecchi, L., 2000. Priority effects, taxonomic resolution, and the prediction of variable patterns of colonization of algae in littoral rock pools. Oecologia 123, 265–274.
- Benedetti-Cecchi, L., Cinelli, F., 1992. Canopy removal experiments in Cystoseira-dominated rockpools from the Western coast of the Mediterranean (Ligurian Sea). J. Exp. Mar. Biol. Ecol. 155, 69–83.

- Benedetti-Cecchi, L., Cinelli, F., 1995. Habitat heterogeneity, sea urchin grazing and the distribution of algae in littoral rock pools on the west coast of Italy (western Mediterranean). Mar. Ecol. Prog. Ser. 126, 203–212.
- Benedetti-Cecchi, L., Cinelli, F., 1996. Patterns of disturbance and recovery in littoral rock pools: nonhierarchical competition and spatial variability in secondary succession. Mar. Ecol. Prog. Ser. 135, 145–161.
- Chapman, A.R.O., 1990. Effects of grazing, canopy cover and substratum type on the abundances of common species of seaweeds inhabiting littoral fringe tide pools. Bot. Mar. 33, 319–326.
- Clarke, K.R., Gorley, R.N., 2001. User manual/ Tutorial. PRI-MER-E Ltd.
- Clarke, K.R., Warwick, R.M., 2001. Change in marine communities: an approach to statistical analysis and Interpretation, PRIMER-E Ltd.
- Dethier, M.N., 1994. The ecology of intertidal algal crusts: variation within a functional group. J. Exp. Mar. Biol. Ecol. 177, 37–71.
- Dethier, M.N., Graham, E.S., Cohen, S., Tear, L.M., 1993. Visual versus random-point percent cover estimations: 'objective' is not always better. Mar. Ecol. Prog. Ser. 96, 93–100.
- Femino, R., Mathieson, A., 1980. Investigations of New England marine algae IV. The ecology and seasonal succession of tide pool algae at Bald Head Cliff, York, Maine. USA. Bot. Mar. 23, 319–332.
- Kaehler, S., Williams, G.A., 1998. Early development of algal assemblages under different regimes of physical and biotic factors on a seasonal tropical rocky shore. Mar. Ecol. Prog. Ser. 172, 61–71.
- Kooistra, W.H.C.F., Joosten, A.M.T., van den Hoek, C., 1989. Zonation patterns in intertidal pools and their possible causes: a multivariate approach. Bot. Mar. 32, 9–26.
- Littler, M.M., Littler, D.S., 1983. Evolutionary strategies in a tropical barrier reef system: functional-groups of marine macroalgae. Journal of Phycology 19, 229–237.
- Metaxas, A., Scheibling, R.E., 1993. Community structure and organization of tidepools. Mar. Ecol. Prog. Ser. 98, 187–198.
- Metaxas, A., Hunt, H.L., Scheibling, R.E., 1994. Spatial and temporal variability of macrobenthic communities in tidepools on a rocky shore in Nova Scotia, Canada. Mar. Ecol. Prog. Ser. 105, 89–103.
- Sze, P., 1982. Distribution of microalgae in tidepools on the New England coast (USA). Bot. Mar. 25, 269–276.
- Thompson, R.C., Crowe, T.P., Hawkins, S.J., 2002. Rocky intertidal communities: past environmental changes, present status and predictions for the next 25 years. Environmental Conservation 29 (2), 168–191.
- Underwood, A.J., Skilleter, G.A., 1996. Effects of patch-size on the structure of assemblages in rock pools. J. Exp. Mar. Biol. Ecol. 197, 63–90.
- Van Tamelen, P.G., 1996. Algal zonation in tidepools: experimental evaluation of the roles of physical disturbance, herbivory and competition. J. Exp. Mar. Biol. Ecol. 201, 197–231.
- Wolfe, J., Harlin, M., 1988a. Tidepools in Southern Rhode Island, U.S.A. I. Distribution and seasonality of macroalgae. Bot. Mar. 31, 525–536.
- Wolfe, J., Harlin, M., 1988b. Tidepools in Southern Rhode Island, U.S.A. II. Species diversity and similarity analysis of macroalgal communities. Bot. Mar. 31, 537–546.