

Phytobenthic communities of intertidal rock pools in the eastern islands of Azores and their relation to position on shore and pool morphology

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Wallenstein, F.M., S.D. Peres, E.D. Xavier & A.I. Neto 2010. Phytobenthic communities of intertidal rock pools in the eastern islands of Azores and their relation to position on shore and pool morphology. *Arquipelago. Life and Marine Sciences* 27: 9-20.

This study aimed to characterize algal composition inside rock-pools from two islands of the Azores archipelago (São Miguel and Santa Maria) and relate it to shore height and pool morphology. Pools were categorized as upper, medium and lower intertidal according to the surrounding communities. Maximum depth and surface area were used to reflect morphology and qualitative sampling to evaluate algal species richness. PRIMER software assessed the similarity across islands, sites, shore heights and pool morphology. Eighty eight algal *taxa* were identified in pools from São Miguel and 52 from Santa Maria. Rhodophycean species dominated rock-pool flora on both islands. Differences were found across islands and sites. Higher species richness was observed at medium intertidal pools. Algae composition was not affected by shore height in pools from Santa Maria. São Miguel's medium and lower pools were grouped separately from upper ones. Pool morphology did not influence significantly the algae composition.

Key words: algae diversity, depth, shore height, spatial variability, surface area

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INTRODUCTION

Rock-pools are well defined bodies of water, influenced by sea and atmospheric conditions, that develop an obvious distinction in flora and fauna within restricted areas and for which one single classification system becomes difficult (Ganning 1971). Pool structure is determined by a complex set of biological and physical factors that interact to develop a patchy habitat (Benedetti-Cecchi & Cinelli 1996). The patchiness observed in intertidal pools is a result of small scale disturbances that affect communities

and is responsible for the variability observed among pools even on the same site (Dethier 1984; Metaxas & Scheibling 1993; Therriault & Kolasa 1999). Additionally, succession in recruitment and competition for space may contribute to increased variability of biotic communities in rock-pools (Astles 1993; Metaxas & Scheibling 1993; Araújo et al. 2006).

Physical harshness during low tide determines the distribution of intertidal algae (Ganning 1971; Underwood 1980; Huggett & Griffiths 1986; Metaxas & Scheibling 1993) and most physical-chemical conditions within individual pools relate

directly to their location on the shore relative to water level, weather conditions, tidal height and timing, and biological composition (Huggett & Griffiths 1986). The algal composition in rock-pools exhibits a marked gradient in many places, with green algae dominating pools that occur higher on the shore, whereas brown and red algae are dominant at lower shore levels, where common species from the adjacent subtidal communities occur (Metaxas & Scheibling 1993). A direct consequence of this is a decline in diversity with shore height (Femino & Mathieson 1980; Huggett & Griffiths 1986; Wolfe & Harlin 1988; Kooistra et al. 1989, Therriault & Kolasa 1999), although variations in species variability across shore levels may not be significant (Metaxas et al. 1994).

Martins et al. (2007) showed that depth is more important than area in explaining species diversity and community composition in both early successional and mature pools. Shallow pools and their biota experience more extreme variations in its physical and chemical conditions (Ganning 1971; Metaxas & Scheibling 1993); on the contrary, deeper pools are more stable and develop a thermal stratification, thus allowing the existence of more ecological niches (Martins et al. 2007). The lack of influence of area on the abundance of organisms in pools is in agreement with the work of Underwood & Skilleter (1996), who found little evidence that diameter (a surrogate for area) of rock-pools leads to significant differences in the abundance of most *taxa*.

The sole study on rock-pool macroalgae communities in the Azores was done by Neto & Baldwin (1990) on Flores Island. The present work aims to provide additional information on the algal flora of littoral rock-pools from the Azores, while analysing its spatial variability and relating it with shore height and pool morphology.

MATERIAL AND METHODS

THE AZORES ARCHIPELAGO

The Azores are centrally located in the North Atlantic (37°40' N, 25° 31' W, Fig. 1). The islands lack a continental shelf, thus presenting a res-

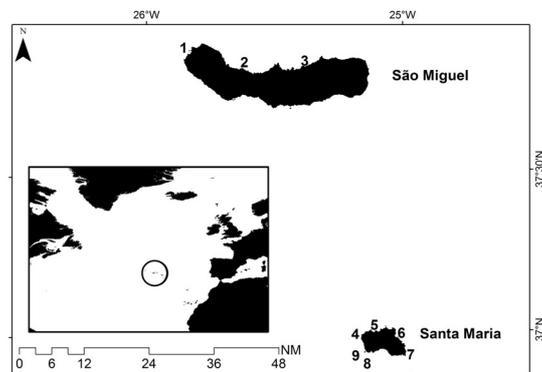


Fig. 1. Location of the Azores Archipelago and of the surveyed sites at the Island of São Miguel (1-3) and Santa Maria (4-9): 1) Mosteiros; 2) Fenais da Luz; 3) Maia; 4) Emissores; 5) Anjos; 6) São Lourenço; 7) Maia; 8) Ribeira Seca; 9) Ilhéu da Vila.

stricted coastal extension that reaches a depth of 1000 m only 200 m offshore (Morton et al. 1998), and are exposed to medium/high levels of wave action (Macedo 2002). Shore geomorphology alternates between high cliffs and rocky cobble/boulder beaches (Borges 2004). Tidal range is small (< 2 m, see Instituto Hidrográfico 1981), and therefore the extensive bedrock platforms that favour the occurrence of rock-pools are scarce and heterogeneous. Santa Maria has steeper and narrower shores than São Miguel and consequently a lower number of pools.

STRUCTURE OF INTERTIDAL COMMUNITIES

Intertidal communities in the Azores are organized into three major zones: (i) an uppermost zone (spray and splash) with littorinids [*Littorina striata* King, *Melharaphe neritoides* (L.)]; followed by (ii) a barnacle zone [*Chthamalus stellatus* (Poli)]; and (iii) an algae dominated zone (Neto 1992, 2000; Wallenstein & Neto 2006). The algae dominated zone can be further subdivided into three main bands: (a) an upper band of *Ulva* spp. that overlaps with the lower limit of the *C. stellatus* zone (Neto 1992) at about 1.5m ($\pm 0,6m$) above low water level, followed by (b) an algae turf dominated zone at about 1m ($\pm 0,5m$) above low water level, with occasional occurrence of frondose algae, namely *Fucus spiralis* Linné and *Gelidium microdon* Kützting (Neto 1992; Wallenstein & Neto 2006), and (c) a frondose algae dominated zone located

in the lower limit of the intertidal zone at about 0,7m ($\pm 0,3$ m) above low water level, establishing the transition to the subtidal (Neto 1992, 2000; Wallenstein & Neto 2006), co-dominated by a variable set of species.

FIELD WORK

Surveys took place at six sites on Santa Maria during June and July 2005 and at three sites on São Miguel during August through September of the same year (Fig. 1), chosen directionally. Surveyed sites present a variable number of intertidal rock-pools of different shape and depth occurring at different shore heights. Rock-pools are not a common habitat in the Azores thus imposing uneven sampling designs - on Santa Maria four pools were surveyed at each site, while on São Miguel four pools were surveyed at Maia, 14 at Fenais da Luz and 44 at Mosteiros. Based on the adjacent exposed bedrock algae community distribution, pools were categorized as: upper shore pools (U) when located where green algae dominate; mid shore pools (M) when located where turfs dominate; and low shore pools (L) when located where frondose algae dominate. Measures of depth and maximum and minimum diameter of all pools were recorded. Surface area of each rock-pool was calculated based on its maximum and minimum diameter adjusting it to the nearest circular shape. Pools were numbered and a sample of all species present inside each was collected. Identification to species level was made *in situ* whenever possible, otherwise taken to the laboratory for diagnosis. Species were grouped into the classes Rhodophyceae, Phaeophyceae and Chlorophyceae for data treatment and analysis. Species nomenclature follows Guiry [cited 2007].

DATA ANALYSIS

Species-accumulation plots were built for (i) the total number of species, for (ii) the number of species occurring inside rock-pools at just one island (hereafter referred to as exclusive species) and for (iii) the number of species inside rock-pools at each shore level, to assess whether a reliable number of pools were sampled. Presence/absence data was analysed using the software PRIMER 6.1.5 (Clarke & Warwick

2001). Species richness was assessed by the total number of species for each island and shore height. ANOSIM (non parametric analysis of similarity) and MDS (non metric multi-dimensional scaling) analysis were based on the Bray Curtis similarity matrix. ANOSIM tested differences between islands, locations, and shore height, while MDS analysis was used to identify rock-pool grouping patterns according to pool depth and surface area, since proper replication for these two factors was not possible. The SIMPER routine was based on the presence/absence data matrix and used to identify species that contributed most for the differences between the relevant factors identified with the ANOSIM procedures.

RESULTS

On Santa Maria 10 pools were categorized as L, seven as M and seven as U and on São Miguel eight pools were categorized as L, 38 as M and 16 as U.

A total of 104 algae *taxa* were identified, of which 52 recorded in Santa Maria, and 88 in São Miguel (Table 1 in Appendix): 26 Chlorophyceae, 23 Phaeophyceae and 55 Rhodophyceae. A total of 16 *taxa* were exclusively found inside rock-pools from Santa Maria and 52 exclusively inside rock-pools from São Miguel. Rhodophyceae species were dominant inside rock-pools from both islands, followed by Phaeophyceae on Santa Maria and Chlorophyceae on São Miguel (Fig. 2a). Additionally, Rhodophyceae species dominate low and mid shore rock-pools both in São Miguel and Santa Maria, while a large number of upper shore rock-pools were dominated by Phaeophyceae species in Santa Maria and by Chlorophyceae species in São Miguel (Fig. 2b, c).

Cumulative species plots for Santa Maria (Fig. 3a) show that the total number of species does not stabilize with increasing area, although the number of exclusive species does tend to stabilize around 10 when more than 10 pools have been sampled. At São Miguel (Fig. 3b) both the total and the exclusive number of species tend to stabilize at 80 and 50 species respectively,

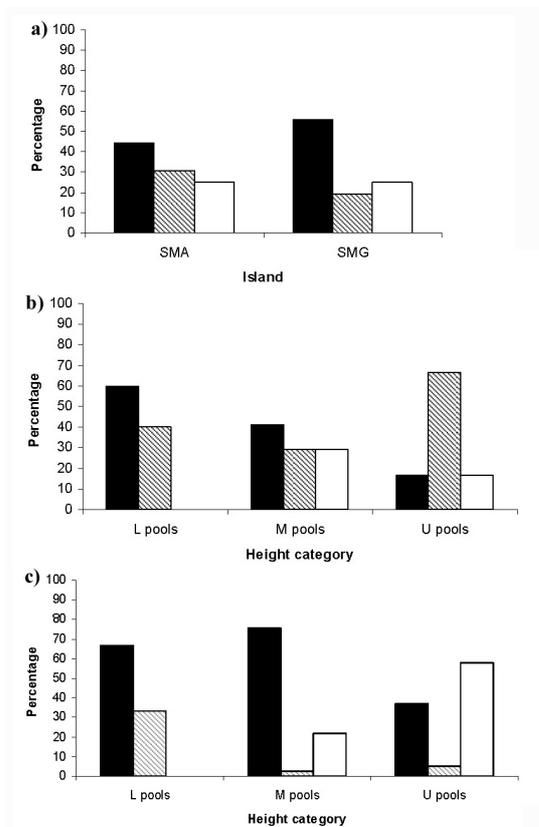


Fig. 2. Relative proportion (%) of major groups of algae on rock-pools from Santa Maria (SMA) and São Miguel (SMG): (a) all shore levels considered; (b) at different shore heights in Santa Maria; (c) at different shore heights in São Miguel. (L – lower shore; M – mid-shore; U – upper shore; black bars – Rhodophyceae; dashed bars – Phaeophyceae; white bars – Chlorophyceae).

when over 50 pools have been sampled. Considering rock-pools from separate shore height categories on both islands, total number of species does not tend to stabilize (Figs. 3a, b).

Mid shore rock-pools presented species richness (translated by the total number of species) than upper shore rock-pools on both islands (Table 2). The ANOSIM tests (Table 3) showed that rock-pools from São Miguel and Santa Maria differ significantly. Rock-pools on the latter island showed higher significant differences across survey sites but lower differences across shore levels than those on São Miguel. However, on São Miguel low shore (L)

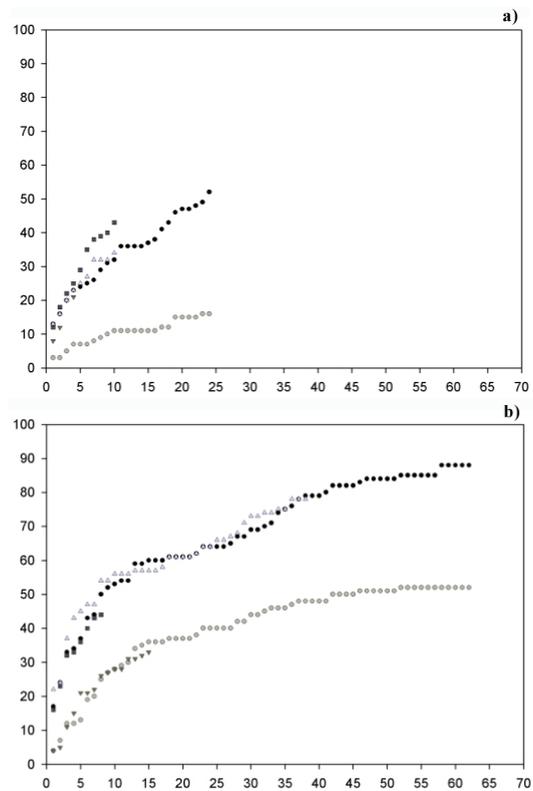


Fig. 3. Cumulative number of species (y-axis) relative to the number of rock-pools sampled (x-axis): (a) for Santa Maria; (b) for São Miguel (black circles – total n° of species; inverted white triangle – n° of exclusive species; black squares – total n° of species at upper shore levels; white diamonds – total n° of species at mid shore levels; black triangles – total n° of species at low shore levels).

and mid shore (M) rock-pools are not significantly different, but do differ significantly from upper shore rock-pools (U), a pattern clearly observed at Mosteiros, where most pools from São Miguel were sampled and replication was highest. Consistent with the ANOSIM results, the average similarity results given by the SIMPER routine (Table 4) evidences a higher similarity between rock-pools within Santa Maria than within São Miguel.

Species with a cumulative contribution of at least 70% were selected as relevant for the separation of rock-pools from both islands (Table 4). According to this criterion, *Pterocladia capillacea* is the only species in common between both islands. Rock-pools on São Miguel are

Table 2. Total number of species (S) for different shore heights (U – upper-shore; M – mid-shore; L- low-shore) in Santa Maria and São Miguel.

Island	Shore level	S
Santa Maria	L	12
	M	13
	U	10
São Miguel	L	13
	M	14
	U	7

Table 3. One-way ANOSIM results (global and pairwise comparison between levels of each factor) for each of the factors considered (999 random permutations from a large number possible; *significance <5%).

Tests	R-Value	Significance (%)
Factor “island”		
Global	0.605	0.1*
Factor “survey site”		
Global Santa Maria	0.581	0.1*
Global São Miguel	0.306	0.1*
Factor “shore height”		
Global Santa Maria	0.123	5.5
Global São Miguel	0.333	0.1*
Pairwise Tests S. Miguel		
M, L	0.048	29.2
M, U	0.453	0.1*
L, U	0.32	0.1*
Global Mosteiros	0.439	0.1*
Pairwise Tests Mosteiros		
L, M	-0.008	47.6
M, U	0.761	0.1*
L, U	0.691	0.4*

characterized by a lower number of contributing species (4 as opposed to 7 in rock-pools from Santa Maria; see Table 4). *Sargassum cymosum* and *Cladophora prolifera* are the most representative species in rock-pools from Santa Maria, whereas *Pterocliadiella capillacea* and *Ulva rigida* are the most representative species from this habitat on São Miguel. On this island the SIMPER routine evidenced that M and L pools are more similar when compared to U pools (M>L>>U, Table 5, next page). *Pterocliadiella capillacea* is the species contributing to the similarity between rock-pools across the whole intertidal, although with varying average abun-

Table 4. Species that contribute most for the similarity of rock-pools within Santa Maria and São Miguel. their respective average abundances (Ab) and percentage contribution (%Con) for similarity from SIMPER routine applied to the factor “island”.

	Santa Maria		São Miguel	
	Ab	%Con	Ab	%Con
Av. similarity:	42.79		29.51	
<i>Pterocliadiella capillacea</i>	0.63	7.1	0.75	21.35
<i>Cladophora prolifera</i>	0.92	16.9		
<i>Sargassum cymosum</i>	0.83	14.56		
<i>Stypocaulon scoparium</i>	0.75	11.3		
<i>Padina pavonica</i>	0.63	7.58		
<i>Cystoseira abies-marina</i>	0.58	6.41		
<i>Chondria dasyphylla</i>	0.5	5.08		
<i>Ulva rigida</i>			0.75	19.46
<i>Corallina elongata</i>			0.58	12.77
<i>Ulva intestinalis</i>			0.42	10.55

dance values. In Mosteiros there is no species that contributes to the similarity between rock-pools on all shore height categories and there is a large number of species shared by L and M pools (frondose and turf forming), while U pools are characterized by a lower number of species, usually green and filamentous algae (*Ulva* spp. and *Aglaothamnion* sp.). Additionally, mid-shore rock-pools present a higher average similarity than both upper-shore pools and lower-shore ones (Table 6, next section).

Surface area and maximum depth do not seem to influence algal community composition in rock-pools from Santa Maria and São Miguel, as shown by the nmMDS (Fig. 4, next section).

DISCUSSION

The higher number of *taxa* in rock-pools from São Miguel is likely to reflect the higher number of pools sampled there, mainly due to the contribution of the survey site Mosteiros. The qualitative inventory of algae inside intertidal rock-pools on São Miguel was achieved when about 50 pools were sampled. In the survey conducted on Santa Maria, where only 24 pools were considered, the total number of species never stabilised, suggesting that the minimum number of pools required for qualitative

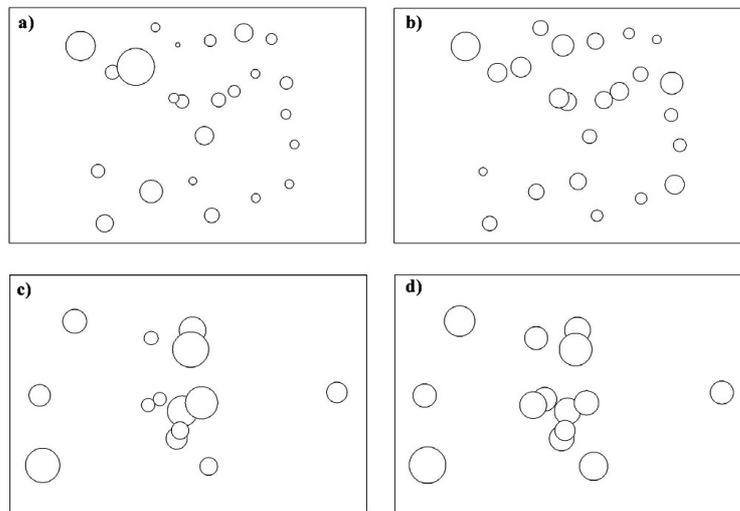


Fig. 4. nmMDS plots for Santa Maria (stress 0,11): (a) bubble size according to surface area (m²); (b) bubble size according to maximum depth (m); and São Miguel (stress 0,22): (c) bubble size according to surface area (m²); (d) bubble size according to maximum depth (m).

Table 5. Species that contribute most for the similarity of rock-pools within shore levels on São Miguel, their respective average abundances (Ab) and percentage contribution (%Con) for similarity from SIMPER routine applied to the factor “shore height” (L – lower intertidal pools; M – medium intertidal pools; U – upper intertidal pools).

Av. similarity:	L		M		U	
	Ab	%Con	Ab	%Con	Ab	%Con
Species contributing for three shore height categories						
<i>P. capillacea</i>	0.5	5.14	0.61	7.91	0.38	5.95
Species contributing for only two shore height categories						
<i>C. prolifera</i>	0.75	12.9	0.68	10.25		
<i>S. cymosum</i>	0.75	12.79	0.53	5.59		
<i>C. elongata</i>	0.63	9.18	0.84	15.67		
<i>U. clathrata</i>	0.5	5.14	0.39	3.21		
<i>C. pellucida</i>	0.5	4.87	0.45	3.96		
<i>U. rigida</i>	0.5	5.74			0.5	11.64
Species contributing for only one shore height category						
<i>S. scoparium</i>	0.75	12.99				
<i>C. clavulatum</i>			0.58	6.27		
<i>A. fragilissima</i>			0.45	4.2		
<i>Ulva</i> sp.			0.45	3.79		
<i>Herposiphonia</i> sp.			0.45	3.61		
<i>Cystoseira</i> sp.			0.39	3.28		
<i>U. compressa</i>					0.75	39.08
<i>Aglaothamnion</i> sp.					0.44	8.44

assessments was not achieved at Santa Maria due to the low occurrence of such habitats and suggesting also that for the azorean rock-pools this number is 50. Nevertheless, the total number of exclusive species stabilized at about 10 in Santa Maria and 50 in São Miguel. This suggests lower variability of algae communities inside rock-pools at Santa Maria.

On the northwest coast of continental Portugal Rhodophyceae are dominant at all shore levels, except in pools located at 2m and 3m up on the shore where green algae dominate (Araújo et al. 2006). In other regions, however, the pattern is one of monospecific green algae communities in upper shore pools and dominance of red and brown algae in low shore rock-pools (Femino & Mathieson 1980; Wolfe & Harlin 1988; Kooistra et al. 1989). Although rock-pools on São Miguel did not exhibit monospecific communities, green algae are dominant in pools located higher on the shore, and red algae dominate the mid and low intertidal pools.

Table 6. Species that contribute most for the similarity of rock-pools within shore levels on Mosteiros, their respective average abundances (Ab) and percentage contribution (Cont.) for similarity from SIMPER routine applied to the factor “shore height” (L – lower intertidal pools; M – medium intertidal pools; U – upper intertidal pools).

Av. similarity:	L		M		U	
	Ab	%Cont	Ab	%Cont	Ab	%Cont
Species contributing for only two shore height categories						
<i>C. elongata</i>	0.8	14.63	0.83	12.11		
<i>C. prolifera</i>	0.8	13.57	0.83	12.88		
<i>S. scoparium</i>	0.8	13.29	0.55	4.36		
<i>C. pellucida</i>	0.8	13.01	0.59	5.92		
<i>Herposiphonia</i> sp.	0.6	7.29	0.59	5.4		
Species contributing for only one shore height category						
<i>U. clathrata</i>	0.6	6.78				
<i>C. clavulatum</i>			0.66	6.71		
<i>A. fragilissima</i>			0.59	6.29		
<i>S. cymosum</i>			0.55	5.14		
<i>Ulva</i> sp.			0.55	4.92		
<i>P. capillacea</i>			0.52	4.34		
<i>U. compressa</i>					1	68.98

The fact that surveyed bedrock shores in Santa Maria exhibit a steeper slope and smaller extension is the probable cause of having upper shore pools mostly dominated by frondose Phaeophyceae species. Surveyed pools were consequently closer together, thus causing smaller variation in physical-chemical conditions across pools at different shore heights. This might explain the absence of significant differences across shore height levels at Santa Maria. Additionally, the survey in this island occurred entirely during the summer period when desiccation and light temporarily eliminate the upper shore green algae communities that are more common in the winter period (Wallenstein et al. 2008). The range of physical-chemical conditions experienced inside pools is related to their position on the shore and thus community distribution patterns recognized on the exposed intertidal zone influences communities inside rock-pools (Huggett & Griffiths 1986).

Several studies report a diversity decrease inside rock-pools with shore height (e.g. Metaxas et al. 1994; Araújo et al. 2006). To clarify the relationship between algal diversity and shore

height, cumulative richness curves must be computed for each tidal level. This is not always possible or easy (Metaxas & Scheibling 1993) because of the greater replication needed at each shore level. This is the case on Azorean shores, where the number of natural pools is limited. Mosteiros is the only survey site where rock-pool replication for shore height was possible. At this site, mid-shore rock-pools exhibited the highest diversity and species richness, with the upper shore dominated by opportunistic Chlorophyceae species, with fast growing life strategies (Larsson et al. 1997; Björk et al. 2004). This is analogous to the situation described by Connell (1975): on a gradient of environmental stress diversity tends to be highest at intermediate shore levels, as sensitive species are less likely to survive under the harsh conditions of upper shore levels and out-compete the pioneer species on the lower shore, but both co-exist on the mid-shore. Differences reported in this study

between rock-pools from the two islands seem to reflect differences on bedrock communities evidenced by parallel biotope characterization studies conducted in Santa Maria and São Miguel (Wallenstein et al. 2008). This evidence is also supported by studies of Dethier (1981; 1984) and Astles (1993) that reveal a relation between differences in algae composition of rock-pools and that of adjacent bedrock, namely by facilitating recruitment (Metaxas & Scheibling 1993; Underwood & Skilleter 1996; Martins et al. 2007). Significant differences across sites on both islands are likely to be related to the variability of algal communities across Azorean shores associated to a highly variable morphology of bedrock platforms that may play a determinant role in influencing the tidal input and thus cause differences in the community composition of rock-pools (Metaxas et al. 1994). Variability of local intrinsic factors (e.g. wave action, temperatures, predation and herbivory) might be the main causes of variability in rock-pools (Dethier 1984; Astles 1993).

In the present study no significant relation was found between pool morphology (surface area

and depth) and the algae communities present. Martins et al. (2007) report a higher number of species in deeper pools (disregarding surface area) and link this observation to the higher number of niches in those pools. Pool morphology, however, affects the water volume inside it and the correspondent exposure to light and air, thus significantly affecting factors such as the water temperature (Femino & Mathieson 1980). Considering surface area and depth separately might neglect their joint effect on species diversity, since volume is related to both factors (Wolfe & Harlin 1988). A properly replicated set of rock-pools for all 'surface area x depth categories' combinations would be required, but this is virtually impossible to achieve in natural rock-pools on Azorean shores. The great variability encountered inside Azorean rock-pools is also reported elsewhere (e.g. Underwood & Skilleter 1996; Araújo et al. 2006; Martins et al. 2007). Pools at the same height and closer together may present different communities, and two pools at different height categories may be very similar, given the periodicity of tidal inputs (Metaxas & Scheibling 1993). Unique species assemblages inside each rock-pool make it difficult to establish an experimental design and a proper replication scheme that would suit the need to generalize about the factors that are known to affect physical-chemical and biotic conditions inside rock-pools.

CONCLUSIONS

Natural rock-pools are highly variable in the Azores, as in most places in the world, due to a complex interaction of physical-chemical and biotic factors that are difficult to control and virtually impossible to replicate. The present study indicates that 50 is the minimum number of pools required for qualitative assessments of intertidal rock-pool algae community composition in the Azores. In general terms, shore height proved to be the main factor affecting rock-pool biodiversity and community composition.

Replication was found to be difficult for natural pools. Differences found between the two

islands are likely to be related to differences on adjacent bedrock communities. Differences across sites on both islands are likely to be related to the variability of algal communities across Azorean shores associated to a highly variable morphology of bedrock platforms.

ACKNOWLEDGEMENTS

The authors wish to thank Dr. José Azevedo for helping with valuable discussion and help with experimental design and field work. We also thank André Amaral, Catarina Santos, Eunice Nogueira, Joana Pombo, João Ferreira, Rodrigo Reis, Ruben Maciel and Tito Silva for helping with the field work. A special acknowledgment to Marlene Terra and Nuno Álvaro for helping in the field, laboratory and image processing. This work was developed under the project POCTIMGS/54319/2002 – Biotope – Classification, Mapping and Modelling of Azores Littoral Biotopes, and supported also by CIRC-Centro de Investigação de Recursos Naturais, Fundação para a Ciência e Tecnologia (Portugal).

REFERENCES

- Araújo R., I. Sousa-Pinto, I. Bárbara & V. Quintino 2006. Macroalgal communities of intertidal rock pools in the northwest coast of Portugal. *Acta Oecologica* 30: 192–202.
- Astles, K.L. 1993. Patterns of abundance and distribution of species in intertidal rock pools. *Journal of the Marine Biological Association of the United Kingdom* 73: 555–569.
- Benedetti-Cecchi, L. & F. Cinelli 1996. Patterns of disturbance and recovery in the littoral rock pools: non-hierarchical competition and spatial variability in secondary succession. *Marine Ecology Progress Series* 135:145–161.
- Björk, M., L. Axelsson & S. Beer 2004. Why is *Ulva intestinalis* the only macroalga inhabiting isolated rock pools along the Swedish Atlantic coast? *Marine Ecology Progress Series* 284:109–116.
- Borges, P.J.A. 2004. Ambientes litorais nos Grupos Central e Oriental do Arquipélago dos Açores - conteúdos e dinâmica de microescala. PhD Thesis, Azores University. [In Portuguese].
- Clarke, K.R. & R.M. Warwick 2001. *Change in marine communities: an approach to statistical analysis*

- and interpretation (2nd edition). PRIMER-E. 144 pp.
- Connell, J.H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pp 460-490 in: Cody M.L. & J.M. Diamond (Eds). *Ecology and evolution of communities*. Belknap Press, Cambridge. 545 pp.
- Dethier, M.N. 1981. Heteromorphic algal life histories: the seasonal pattern and response to herbivory of the brown crust, *Ralfsia californica*. *Oecologia* 49: 333-339.
- Dethier, M.N. 1984. Disturbance and recovery in intertidal pools: maintenance of mosaic patterns. *Ecological Monographs* 54(1): 99-118.
- Femino, R. & A. Mathieson 1980. Investigations of New England marine algae IV. The ecology and seasonal succession of tide pool algae at Bald Head Cliff, York, Maine, USA. *Botanica Marina* 23: 319-332.
- Ganning, B. 1971. Studies on chemical, physical and biological conditions in Swedish rock-pool ecosystems. *Ophelia* 9: 51-105.
- Guiry, M.D. & Guiry, G.M. (Internet). AlgaeBase: world-wide electronic publication. *National University of Ireland, Galway*; (cited 15 June 2007). Available from: <http://www.algaebase.org/>
- Huggett, J. & C.L. Griffiths 1986. Some relationships between elevation, physico-chemical variables and biota of intertidal rock pools. *Marine Ecology Progress Series* 29: 189-197.
- Instituto Hidrográfico 1981. *Roteiro do Arquipélago dos Açores*. PUB. (N)-IH-128-SN. Instituto Hidrográfico, Lisboa.
- Kooistra, W.H.C.F., A.M.T. Joosten & C. van den Hoek 1989. Zonation patterns in intertidal pools and their possible causes: a multivariate approach. *Botanica Marina* 32: 9-26.
- Larsson, C., L. Axelsson, H. Ryberg & S. Beer 1997. Photosynthetic carbon utilization by *Enteromorpha intestinalis* (Chlorophyta) from a Swedish rock-pool. *European Journal of Phycology* 32: 49-54.
- Macedo, F.L.W.F.M. 2002. Biótopos do Intertidal rochoso da ilha de São Miguel, Açores. Marine Biology Final Dissertation Thesis. Azores University. [In Portuguese].
- Martins, G.M., S.J. Hawkins, R.C. Thompson & S.R. Jenkins 2007. Community structure and functioning in intertidal rock pools: effects of pool size and shore height at different successional stages. *Marine Ecology Progress Series* 329: 43-55.
- Metaxas, A. & R.E. Scheibling 1993. Community structure and organization of tidepools. *Marine Ecology Progress Series* 98: 187-198.
- Metataxas, A., H.L. Hunt, R.E. Scheibling 1994. Spatial and temporal variability of macrobenthic communities in tide pools on a rocky shore in Nova Scotia, Canada. *Marine Ecology Progress Series* 105: 89-103.
- Morton, B., J.C. Britton & A.M.F. Martins 1998. *Coastal Ecology of the Azores*. Sociedade Afonso Chaves. 249 pp.
- Neto, A.I. & H.P. Baldwin 1990. Algas marinhas das ilhas do Corvo e Flores. *Relatórios e comunicações do Departamento de Biologia* 18:19-25.
- Neto, A.I. 1992. Contribution to the taxonomy and ecology of Azorean benthic marine algae. *Biological Journal of the Linnean Society* 46: 163-176.
- Neto, A.I. 2000. Ecology and dynamics of two intertidal algal communities on the littoral of the island of São Miguel (Azores). *Hydrobiologia* 432: 135-147.
- Steneck, R.S. & M.N. Dethier 1994. A functional group approach to the structure of algal-dominated communities. *Oikos* 69: 76-498.
- Therriault, T.W. & J. Kolasa 1999. Physical determinants of richness, diversity, evenness and abundance in natural aquatic microcosms. *Hydrobiologia* 412: 123-130.
- Underwood, A.J. 1980. The effects of grazing by gastropods and physical factors on the upper limits of distribution of intertidal macroalgae. *Oecologia* 46: 201-213.
- Underwood, A.J. & G.A. Skilleter 1996. Effects of patch-size on the structure of assemblages in rock pools. *Journal of Experimental Marine Biology and Ecology* 197: 63-90.
- Wallenstein, F.F.M.M. & A.I. Neto 2006. Intertidal rocky shore biotopes of the Azores: a quantitative approach. *Helgolander Marine Research* 60: 196-206.
- Wallenstein, F.F.M.M., A.I. Neto, N.V. Álvaro & C.I. Santos 2008. Algae based biotopes of the Azores (Portugal): spatial and seasonal variation. *Aquatic Ecology* 42(4): 547-559.
- Wolfe, J. & M. Harlin 1988. Tidepools in Southern Rhode Island, U.S.A. II. Species diversity and similarity analysis of macroalgal communities. *Botanica Marina* 31: 537-546.

Accepted 14 June 2010.

APPENDIX

Table 1. List of *taxa* identified in the islands of Santa Maria and São Miguel, and corresponding authorities (1/3).

Class	Species	Santa Maria	São Miguel
Chlorophyceae	<i>Blidingia minima</i> (Nägeli ex Kützing) Kylin		X
	<i>Bryopsis cupressina</i> J.V. Lamouroux		X
	<i>Bryopsis hypnoides</i> J.V. Lamouroux	X	
	<i>Bryopsis plumosa</i> (Hudson) C. Agardh	X	X
	<i>Chaetomorpha aerea</i> (Dillwyn) Kützing	X	X
	<i>Chaetomorpha pachynema</i> (Montagne) Kützing		X
	<i>Cladophora albida</i> (Nees) Kützing	X	
	<i>Cladophora coelothrix</i> Kützing		X
	<i>Cladophora hutchinsiae</i> (Dillwyn) Kützing		X
	<i>Cladophora laetvirens</i> (Dillwyn) Kützing		X
	<i>Cladophora lehmanniana</i> (Lindenberg) Kützing		X
	<i>Cladophora liebetruthii</i> Grunow	X	
	<i>Cladophora pellucida</i> (Hudson) Kützing	X	X
	<i>Cladophora prolifera</i> (Roth) Kützing	X	X
	<i>Cladophora</i> sp.		X
	<i>Codium adhaerens</i> C. Agardh	X	X
	<i>Derbesia tenuissima</i> (Moris & De Notaris) P.L. Crouan & H.M. Crouan		X
	<i>Ulva clathrata</i> (Roth) C. Agardh	X	X
	<i>Ulva compressa</i> Linnaeus	X	X
	<i>Ulva intestinalis</i> Linnaeus	X	X
	<i>Ulva lingulata</i> A.P. de Candolle		X
	<i>Ulva prolifera</i> O.F. Müller		X
	<i>Ulva ralfsii</i> (Harvey) Le Jolis		X
<i>Ulva rigida</i> C. Agardh	X	X	
<i>Ulva</i> sp.		X	
<i>Valonia utricularis</i> (Roth) C. Agardh	X		
Phaeophyceae	<i>Bachelotia antillarum</i> (Grunow) Gerloff	X	
	<i>Cladostephus spongiosus</i> (Hudson) C. Agardh	X	
	<i>Colpomenia sinuosa</i> (Mertens ex Roth) Derbès & Solier	X	X
	<i>Cystoseira abies-marina</i> (S.G. Gmelin) C. Agardh	X	X
	<i>Cystoseira humilis</i> Schousboe ex Kützing	X	X
	<i>Cystoseira</i> sp.		X
	<i>Dictyota dichotoma</i> (Hudson) J.V. Lamouroux	X	X
	<i>Ectocarpus</i> sp.	X	
	<i>Feldmannia irregularis</i> (Kützing) G. Hamel		X
	<i>Fucus spiralis</i> Linnaeus		X
	<i>Halopteris filicina</i> (Grateloup) Kützing	X	X
	<i>Hincksia</i> sp.	X	
	<i>Sargassum cymosum</i> C. Agardh	X	X
	<i>Sargassum vulgare</i> C. Agardh	X	
	<i>Scytosiphon lomentaria</i> (Lyngbye) Link	X	X

Table 1. List of *taxa* identified in the islands of Santa Maria and São Miguel, and corresponding authorities (2/3).

Phaeophyceae	<i>Sphacelaria cirrosa</i> (Roth) C. Agardh	X	X
	<i>Sphacelaria rigidula</i> Kützinger		X
	<i>Sphacelaria</i> sp.		X
	<i>Sphacelaria tribuloides</i> Meneghini		X
	<i>Stypocaulon scoparium</i> (Linnaeus) Kützinger	X	X
	<i>Zonaria tournefortii</i> (J. V. Lamouroux) Montagne		X
	<i>Acrochaetium crassipes</i> (Børgesen) Børgesen		X
<i>Acrosorium venulosum</i> (Zanardini) Kylin		X	
<i>Aglaothamnion</i> sp.	X	X	
<i>Amphiroa fragilissima</i> (Linnaeus) J.V. Lamouroux		X	
<i>Amphiroa rigida</i> J.V. Lamouroux		X	
<i>Anotrichium furcellatum</i> (J. Agardh) Baldock	X		
<i>Antithamnionella spirographidis</i> (Schiffner) E.M. Wollaston		X	
<i>Asparagopsis armata</i> Harvey		X	
<i>Boergeseniella fruticulosa</i> (Wulfen) Kylin	X		
<i>Botryocladia</i> sp.		X	
<i>Centroceras clavulatum</i> (C. Agardh) Montagne	X	X	
<i>Ceramium botryocarpum</i> A.W. Griffiths ex Harvey		X	
<i>Ceramium ciliatum</i> (J. Ellis) Ducluzeau		X	
<i>Ceramium codii</i> (H. Richards) Mazoyer		X	
<i>Ceramium diaphanum</i> (Lightfoot) Roth	X	X	
<i>Ceramium echionotum</i> J. Agardh		X	
<i>Ceramium rubrum</i> C. Agardh	X	X	
<i>Ceramium</i> sp.		X	
<i>Chondracanthus acicularis</i> (Roth) Frederiq	X	X	
<i>Chondria coerulescens</i> (J. Agardh) Falkenberg		X	
<i>Chondria dasyphylla</i> (Woodward) C. Agardh	X	X	
<i>Corallina elongata</i> J. Ellis & Solander	X	X	
<i>Dasya corymbifera</i> J. Agardh		X	
<i>Diplothamnion</i> sp.		X	
<i>Erythrocytis montagnei</i> (Derbès & Solier) P.C. Silva	X		
<i>Erythrotrichia carnea</i> (Dillwyn) J. Agardh		X	
<i>Falkenbergia rufolanosa</i> (Harvey) F. Schmitz	X	X	
<i>Gelidium arbusculum</i> Bory de Saint-Vincent ex Børgesen		X	
<i>Gelidium pusillum</i> (Stackhouse) Le Jolis	X		
<i>Grateloupia filicina</i> (J.V. Lamouroux) C. Agardh	X		
<i>Halarachnion ligulatum</i> (Woodward) Kützinger		X	
<i>Halitilton virgatum</i> (Zanardini) Garbary & H.W. Johansen	X		
<i>Herposiphonia</i> sp.A	X	X	
<i>Heterosiphonia</i> sp.B		X	
<i>Hypnea arbuscula</i> P. Dangeard		X	
<i>Hypnea musciformis</i> (Wulfen) J. V. Lamouroux	X	X	
<i>Jania adhaerens</i> J.V. Lamouroux		X	

Table 1. List of *taxa* identified in the islands of Santa Maria and São Miguel, and corresponding authorities (3/3).

Rhodophyceae	<i>Jania capillacea</i> Harvey		X
	<i>Jania pumila</i> J.V. Lamouroux		X
	<i>Jania rubens</i> (Linnaeus) J.V. Lamouroux	X	X
	<i>Laurencia minuta</i> H. Vandermeulen, D.J. Garbary & M.D. Guiry		X
	<i>Laurencia tenera</i> C.K. Tseng		X
	<i>Laurencia viridis</i> Gil-Rodríguez & Haroun	X	X
	<i>Lophocladia</i> sp. (Mertens ex C. Agardh) F. Schmitz		X
	<i>Monosporus pedicellatus</i> (J.E. Smith) Solier	X	X
	<i>Peyssonnelia rubra</i> (Greville) J. Agardh		X
	<i>Plocamium cartilagineum</i> (Linnaeus) P.S. Dixon		X
	<i>Polysiphonia denudata</i> (Dillwyn) Greville ex Harvey		X
	<i>Polysiphonia furcellata</i> (C. Agardh) Harvey		X
	<i>Polysiphonia</i> sp.	X	X
	<i>Porphyra</i> sp.		X
	<i>Pterocladia capillacea</i> (S.G. Gmelin) Santelices & Hommersand	X	X
	<i>Rhodymenia holmesii</i> Ardissonne		X
<i>Spyridia filamentosa</i> (Wulfen) Harvey	X	X	
<i>Symphocladia marchantioides</i> (Harvey) Falkenberg	X	X	