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ORIGINAL ARTICLE

Macroalgal turfs in the Azores

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Abstract

Studies on macroalgal communities of the Azores report algal turfs as one of the most conspicuous ecological entities occurring on the rocky shores of these islands. The present study investigates the influence of shore height and substratum on turf composition. Data were analysed using the software PRIMER and results confirmed the previous distinction between calcareous, dominated by articulated coralline algae, and non-calcareous turfs, characterized mainly by small red algae. However, no differences in species composition were found in either type of turf occurring on different substrata or at different shore levels.

Problem

A suite of studies undertaken during the past 15 years has investigated the intertidal and subtidal algal communities of the Azores (Neto 1992, 2000, 2001; Neto & Tittley 1995; Tittley *et al.* 1998; Tittley & Neto 2000). Algal turfs are generally described as complex assemblages of macroalgae with compact growth, 5 cm in height and well developed entangled prostrate axes (Price & Scott 1992). Turfs are conspicuous features of warm temperate intertidal communities, and have been widely studied (Chapman 1955; Pryor 1967; Lawson & Norton 1971; Oliveira & Mayral 1976; Lawson & John 1977; Rogers & Salesky 1981; Stewart 1982; Neto & Tittley 1995; Morton *et al.* 1998). Some studies have classified communities systematically as biotopes based on broad ecological/taxonomic categories, such as green algae, calcareous and non-calcareous turfs and crusts (*e.g.* Neto & Tittley 1995; Tittley *et al.* 1998, Tittley & Neto 2000; Wallenstein & Neto 2006; Wallenstein *et al.* 2008). Turfs classified as calcareous or coralline occur with increasing abundance towards the low-shore and are usually not very conspicuous on less stable substrata such as cobbles, whereas turfs classified as non-calcareous are more evenly distributed across the intertidal with higher abundances at mid-shore (Neto & Tittley 1995; Wallenstein & Neto 2006; Wallenstein *et al.* 2008). Classification of turfs into these two broad categories has been based on the abundance of erect coralline algae (recognizable by the naked eye) and can thus be subjective and artificial. To evaluate whether such a classification is artificial we have tested differences between species composition in samples of turf provisionally identified *in situ* as calcareous (*i.e.* dominated by erect coralline algae) or non-calcareous turf.

Material and Methods

Data for analysis were gathered in the course of intertidal biotope surveys undertaken on three islands of the archipelago – São Miguel, Santa Maria and Graciosa (Fig. 1) in the summer periods of 2004, 2005 and 2006, respectively. As macroalgae communities are not evenly distrib-

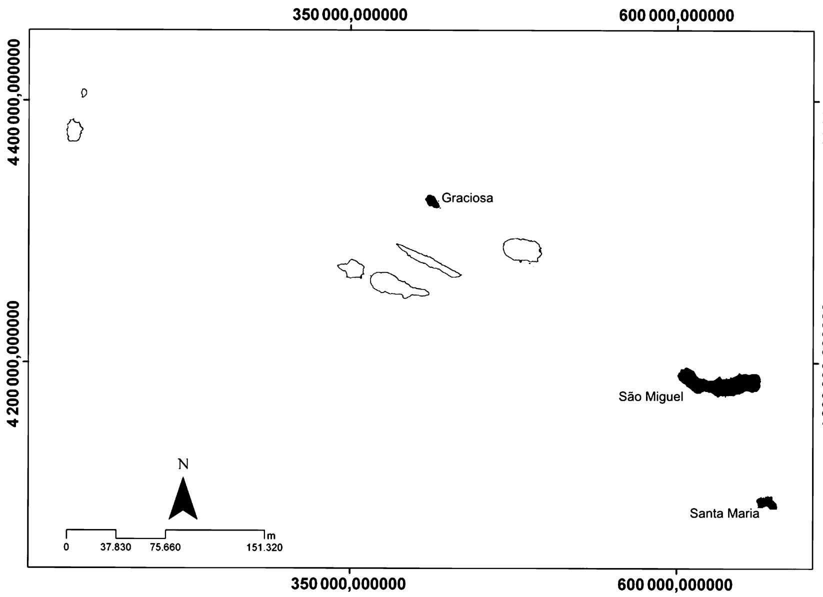

Fig. 1. Schematic representation of the Azores archipelago with the sampled islands in dark.

uted across the intertidal, both in terms of species composition and substratum coverage, they pose a difficulty in sampling designs that require the collection of an equal number of samples at differing 'substratum × shore level' combinations. Although the original aim was to acquire quantitative data for macroalgal communities at high-, mid- and low-shore, on three substrata (cobbles, boulders and bedrock), high-shore samples had to be excluded from the pool of data because there were several sites where calcareous turf was absent. At mid- and low-shore, whenever possible two 10 × 10 cm areas (minimal intertidal scraping area defined by Neto 1997) of each type of turf (calcareous and non-calcareous) were cleared (scraped with a chisel into a nylon mesh bag) from the upper facing surfaces of three different substrata and brought to the laboratory for examination. Additionally, owing to an irregular distribution of substrata along the shores of the surveyed islands, an uneven sampling design had to be adopted (Table 1).

Turf constituents were identified with the help of a microscope and species abundances recorded using a semi-quantitative DAFOR scale (Dominant; Abundant; Frequent; Occasional; Rare). To test for differences between types of turfs (calcareous *versus* non-calcareous), substrata (cobbles *versus* boulders *versus* bedrock) and shore levels (low-shore *versus* mid-shore), PERMANOVA analyses were run on species richness (as presence/absence data) and species relative abundance data with the software PRIMER (Anderson *et al.* 2008). PERMANOVA combines the best of traditional test-statistics (ANOVA designs) and flexible multivariate nonparametric methods, and can thus be based on symmetric dissimilarity or distance measures (or their ranks) providing probability values (P; significant if <0.05; not significant if ≥0.05) using appropriate permutation methods. The greater the number of possible permutations, the stronger the result of the tests. The island where samples were collected was set as a random factor, as there was no hypothesis regarding differences between islands. Furthermore, SIMPER analysis on relative abundance data was used to identify the species responsible for the differences found between both types of turf.

Table 1. Number of samples collected according to the surveyed islands, turf types, substrata and shore level.

	Graciosa	Santa Maria	São Miguel	Total
Turf type				
Calcareous	32	27	39	98
Non-calcareous	34	47	48	129
Substrata				
Cobbles	22 (3 sites)	14 (4 sites)	28 (5 sites)	64 (12 sites)
Boulders	20 (3 sites)	19 (3 sites)	22 (4 sites)	61 (10 sites)
Bedrock	24 (3 sites)	41 (9 sites)	37 (6 sites)	102 (18 sites)
Shore level				
Low	32	40	40	112
Mid	34	34	47	115
Total	66 (9 sites)	74 (16 sites)	87 (15 sites)	227 (40 sites)

Results

Species present

The turf samples contained 139 species of algae from 24 orders; the Ceramiales contained 60 species, the Gigartinales 11 species, and the Corallinales 9 species. These

Table 2. PERMANOVA analysis of differences in turfs according to substratum type (fixed factor with three levels: cobbles, boulders and bedrock) and to shore level (fixed factor with two levels: low-shore and mid-shore).

Source	df	PSpp. composition data/PA data	Permutations
All turfs			
Turf type	1	0.001/0.001[a]	999
Residual	225		
Total	226		
Calcareous turf			
Substratum	2	0.321/0.23	998
Shore level	1	0.278/0.468	998
Island	2	0.001/0.001[a]	998
Island × Substratum	4	0.001/0.001[a]	998
Island × Shore level	2	0.114/0.069	999
Substratum × Shore level	2	0.846/0.625	997
Island × Substratum × Shore level	4	0.01/0.001[a]	999
Residual	100		
Total	117		
Non-calcareous turf			
Substratum	2	0.393/0.289	998
Shore level	1	0.11/0.077	998
Island	2	0.001/0.001[a]	998
Island × Substratum	4	0.001/0.001[a]	998
Island × Shore level	2	0.006/0.037[a]	998
Substratum × Shore level	2	0.724/0.821	998
Island × Substratum × Shore level	4	0.001/0.001[a]	999
Residual	91		
Total	108		

[a]Significant test; df = degrees of freedom; P = probability value associated to the test; PA data = presence/absence data; Permutations = number of permutations on which the test was based.

three orders are all in the red algae (Rhodophyta). Other orders present had fewer species.

Numerical analysis

PERMANOVA tests on species composition and relative abundance upheld the basic separation into calcareous and non-calcareous turfs (Table 2).

When analysing data separately for each turf type there were no significant differences in turfs associated with substratum or shore level (Table 2).

Dissimilarity between calcareous and non-calcareous turfs is greater when comparing these using the relative abundance of its constituents (87.62) rather than using species richness (78.32). Differences between the two types of turf are mainly due to the co-dominant, erect calcareous species within one type of turf and *Gelidium* (dominant) and *Ceramium* spp. within the other (Table 3).

Discussion

The present study validates the empirical classification of two types of turf, calcareous, and non-calcareous, based on the presence of species of *Corallina*, *Jania* and *Haliptilon* that occur in such abundance that they are visually recognizable (*cf.* Neto & Tittley 1995). Although differences between the two types of turf are mainly due to the dominance of calcareous species within calcareous turfs, *Corallina elongata* can also be an important constituent of non-calcareous turfs; likewise, *Laurencia* spp. are a noticeable component of both communities. The few other major constituents of these two types of turf differ slightly, but there is a long list of minor constituents that are common to both (Table 3) and these are mainly filamentous red algae. The definition of both turfs in the present study is in accordance with the provisional biotope definition study of Tittley & Neto (2000). However, regarding non-calcareous turf in the present study we add *Gelidium microdon* to the species list defined as 'soft algal turf' by Tittley & Neto (2000). This is the main structuring species in our non-calcareous turf samples, which is certainly due to the fact that it occurs mainly in the mid-to-low eulittoral, which coincides with the distribution reported for the association of *Gelidium microdon* and *Fucus spiralis* by Tittley & Neto (2000). Approximately 30% of the total flora of the Azores was identified within the turfs sampled for the present study.

Highly mobile substrata tend to inhibit the attachment and growth of macroalgae and favour thin, turf-like growths that are resistant to abrasion, namely fast-growing, opportunistic algae (mainly green algae and filamentous red and brown algae) that comprise non-calcareous turfs. Our finding of the absence of substratum specificities in non-calcareous turfs with increasing substratum stability (cobbles to boulders to bedrock) was unexpected (Table 2). Increased stability was expected to allow the development of more mature communities, namely turfs with a greater number of species. However, unusual stability conditions in cobble beaches as a result of reduced wave action in the summer might have allowed non-calcareous turf communities on less stable substrata to develop towards those common on more stable substrata. Accordingly, sampling at other times of year might have detected changes in communities on different types of substrata.

Species composition of both types of turf does not vary significantly in the narrow mid- to low-shore range, probably because of the limited shore extension in the Azores. Steep shores and small tidal ranges provide very little space for macroalgae to attach. A turf-like life form may present an advantage in the competition for space and help resist the strong wave action prevalent on most

Table 3. Species that contribute to 90% of the differences between calcareous and non-calcareous turfs (SIMPER analysis) and their respective occurrence rate in all turf samples and abundance scores (DAFOR; in bold the most common category for each species).

Spp.	Contribution%	Occurrence	DAFOR categories
Calcareous turf			
Corallina elongata	56.73	0.73	**D**A
Haliptilon virgatum	9.63	0.32	**D**A
Jania spp.[a]	10.83	0.46	D**A**FO
Laurencia spp.[b]	7.37	0.51	A**F**O
Chondria spp.[c]	2.17	0.29	A**F**O
Gelidium spp.[d]		0.25	A**F**O
Stypocaulon scoparium		0.27	F**O**
Chondracanthus acicularis		0.25	F**O**
Ceramium spp.[e]	4.08	0.51	F**O**R
Chaetomorpha spp.[f]		0.26	**O**R
Other spp.(see below)		<0.25	**R**
Total	90.81		
Non-calcareous turf			
Gelidium spp.[d]	32.44	0.43	D**A**F
Corallina elongata	13.15	0.46	A**F**O
Laurencia spp.[b]	7.71	0.35	A**F**O
Ceramium spp.[e]	14.28	0.51	A**F**OR
Jania spp.[a]	2.66	0.26	**F**O
Ulva spp.[g]	2.48	0.28	**O**R
Chaetomorpha spp.[f]	3.22	0.35	**R**
Herposiphonia sp.	3.32		
Polysiphonia spp.[h]	2.68		
Gymnogongrus spp.[i]	2.52		
Ahnfeltia plicata	1.77		
Osmundea spp.[j]	1.57		
Centroceras clavulatum	1.53		
Caulacanthus ustulatus	1.4		
Other spp. (see below)		<0.25	R
Total	90.73		

[a]*Jania capillacea*, *Jania longifurca*, *Jania pumila*, *Jania rubens.*
[b]*Laurencia viridis*, *Laurencia* sp.
[c]*Chondria coerulescens*, *Chondria dasyphylla*, *Chondria capillaris.*
[d]*Gelidium microdon*, *Gelidium pusillum*, *Gelidium spinosum.*
[e]*Ceramium ciliatum*, *Ceramium circinatum*, *Ceramium diaphanum*, *Ceramium echionotum*, *Ceramium flaccidum*, *Ceramium virgatum.*
[f]*Chaetomorpha linum*, *Chaetomorpha pachynema.*
[g]*Ulva compressa*, *Ulva intestinalis*, *Ulva clathrata*, *Ulva rigida.*
[h]*Polysiphonia brodiei*, *Polysiphonia denudata*, *Polysiphonia elongata*, *Polysiphonia furcellata.*
[i]*Gymnogongrus griffithsiae*, *Gymnogongrus crenulatus.*
[j]*Osmundea hibrida*, *Osmundea pinnatifida.*

Other spp.: *Acrosorium venulosum*, *Aglaothamnion* sp., *Aglaozonia parvula*, *Ahnfeltia* sp., *Ahnfeltiopsis intermedia*, *Amphiroa* spp. (*Amphiroa beauvoisii*, *Amphiroa* sp.), *Anotrichium* spp. (*Anotrichium furcellatum*, *Anotrichium tenue*), *Antithamnion* sp., *Asparagopsis armata*, *Bachelotia antillarum*, *Boergeseniella* spp. (*Boergeseniella fruticulosa*, *Boergeseniella* sp.), *Bonnemaisonia asparagoides*, *Bryopsis* spp. (*Bryopsis cupressina*, *Bryopsis hypnoides*, *Bryopsis plumosa*), *Callithamnion* spp. (*Callithamnion corymbosum*, *Callithamnion tetragonum*, *Callithamnion* sp.), *Catenella caespitosa*, *Caulacanthus ustulatus*, *Centroceras clavulatum*, *Chondracanthus acicularis*, *Chondrophycus* sp., *Cladophora* spp. (*Cladophora albida*, *Cladophora coelothrix*, *Cladophora prolifera*, *Cladophora* sp.), *Cladophoropsis membranacea*, *Cladostephus spongiosus*, *Codium adhaerens*, *Compsothamnion decompositum*, *Cryptopleura ramosa*, *Cystoseira* spp. (*Cystoseira abies-marina*, *Cystoseira humilis*, *Cystoseira* sp.), *Dasya* spp. (*Dasya corymbifera*, *Dasya hutchinsiae*, *Dasya* sp.), *Dictyota* sp., *Diplothamnion* sp., *Dipterosiphonia* sp., *Drachiella minuta*, *Endarachne binghamiae*, *Erythrocystis montagnei*, *Falkenbergia rufolanosa*, *Fucus spiralis*, *Gastroclonium* spp. (*Gastroclonium ovatum*, *Gastroclonium reflexum*), *Gelidiella* sp., *Gelidiopsis* sp., *Gigartina pistillata*, *Grateloupia* spp. (*Grateloupia filicina*, *Grateloupia dichotoma*), *Griffithsia corallinoides*, *Halopteris filicina*, *Herposiphonia* sp., *Heterosiphonia crispella*, *Hypnea* spp. (*Hypnea arbuscula*, *Hypnea musciformis*), *Lomentaria articulata*, *Lophosiphonia* spp. (*Lophosiphonia obscura*, *Lophosiphonia reptabunda*), *Nemoderma tingitanum*, *Platysiphonia* sp., *Pleonosporium* sp., *Plocamium cartilagineum*, *Porphyra* sp., *Pterocladiella capillacea*, *Pterosiphonia* spp. (*Pterosiphonia pennata, Pterosiphonia* sp.), *Rhodymenia holmesii*, *Sargassum* spp. (*Sargassum cymosum*, *Sargassum vulgare*), *Sphacelaria* spp. (*Sphacelaria cirrosa*, *Sphacelaria plumula*), *Sphondylothamnion multifidum*, *Stylonema alsidii*, *Stypocaulon scoparium*, *Symphyocladia marchantioides*, *Valonia* spp. (*Valonia macrophysa*, *Valonia utricularis*).

shores of the Azores. Other advantages of the turf life form are the retention of water, the increased surface areas for attachment of admixed algae, increased resistance to herbivory, and increased ability in vegetative propagation (Price & Scott 1992).

No hypothesis was set regarding differences in turfs sampled on different islands. Sampling was done in different years on each island and differences in species composition might reflect variations in population dynamics of the turf constituents.

The turf life form may be an ecological response to severe environmental conditions, notably wave action. Although this life form is resistant to the prevailing harsh conditions, more delicate/fragile algae, such as the filamentous species of *Callithamnion* and *Dasya*, are able to survive as minor constituents within the turf community. Turfs are an important feature of the warm temperate shore communities that dominate intertidal communities in the Azores. They thus deserve special attention, not as major features of an ecosystem, but as a local ecosystem in their own right.

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