

Contribution to the taxonomy and ecology of the Azorean benthic marine algae

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Algal zonation patterns were studied in two sites (Caloura, south coast and Ribeirinha, north coast) of the island of São Miguel, Azores. At each site two stations were studied and the transects revealed the occurrence of two distinct and well established algal zones. In the first zone, daily immersed and emersed by the tide, the algae were growing in a dense and short tangle forming a mat, referred to as algal turf. In the second zone, which was wet most of the time, the algae were larger and frondose. A list of the species of benthic marine algae occurring on the algal turf of each station is given. Of the total of 47 species found, eight are new for the Azores and another 13 species are recorded for the first time for São Miguel. *Gigartina acicularis* (Roth) Lamouroux and articulate coralline algae (*Corallina officinalis* Linnaeus and *Jania* spp.) were the more common species. Seasonal variation of the algal turf was studied and related to mean monthly values of air and sea water temperatures, insolation and hours of light. The zonation patterns and composition of algal species were compared with those from other open rocky shores.

KEY WORDS:—Azores – zonation – intertidal zone – algal turf – benthic marine algae.

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INTRODUCTION

The island of São Miguel is located in the Oriental Group of the Azores archipelago, at 37° 42' N/37° 55' N and 25° 08' W/25° 52' W, about 900 miles west of Lisbon. It is formed by volcanic rocks (basalt) and surrounded by very deep water. The coastline of São Miguel is *c.* 155 km long and is difficult to access from land. The dominant winds are from north and north-east and the tidal range is less than 2 m. For the island of São Miguel the maximum tidal difference recorded was 1.89 m, the mean values being 0.65 m in neap tides and 1.44 m in spring tides (Instituto Hidrográfico, 1981). The mean values of the air and sea water temperatures show a regular annual variation with maxima

(22°C and 21.5°C, respectively) in August and minima (14.2°C, 15.6°C) in February/March (Bettencourt, 1979).

Interest in the Azorean algae began in the latter half of the last century. The first studies were concerned with taxonomy (Seubert, 1844; Droüet, 1866; Agardh, 1870; Piccone, 1889; Trelease, 1897; Gain, 1914; Schmidt, 1929a, b). Schmidt (1931) presented a review of these studies together with research on algal associations in the Azorean waters.

More recently, as well as taxonomic studies (Palminha, 1957; Larkum, 1960; Fralick, Hehre & Mathieson 1985; Neto, 1989; Fralick & Hehre, 1990; Neto & Baldwin, 1990), which are currently being revised by the author, ecological studies, particularly related to zonation patterns, have been made. Research on the subject was begun by Pryor (1967) for the island of São Jorge (Central Group) and Ardré, Boudouresque & Cabioch (1973, 1974) for the Azores in general and continued by Castro & Viegas (1987) and Hawkins *et al.* (1990) for the island of São Miguel and Neto & Azevedo (1990) for the island of Flores (Occidental Group). However, these studies did not include research on seasonal variation.

All the authors mentioned above pointed out that there are different zones on the Azorean shores, but no attempt was made to correlate these zones with those of the 'Universal' Scheme of Zonation of Stephenson & Stephenson (1949, 1972). Hawkins *et al.* (1990) suggested the occurrence of three zones: one high on the shore populated by littorinids, another below, dominated by limpets, filter-feeding barnacles and *Gelidium microdon* Kuetz. and a third, low on the shore, dominated by what they called 'algal turf'. Studies on the intertidal zone of the islands of Flores (Neto & Azevedo, 1990) and Santa Maria (personal observations), revealed that this 'algal turf' could be divided in two distinct zones, with a different species-composition and morphology. Higher on the shore, the algae grew in a dense and short tangle forming a mat, which was almost impossible to separate into components. Further down the algae were frondose and larger. Thus it seemed appropriate to restrict the term 'algal turf' to the first zone. The second zone was named after the dominant species occurring there.

This study gives information on zonation patterns and species composition, weight and diversity of the algal turf zone on the rocky littoral of São Miguel island. Seasonal variation of these parameters is also analysed.

METHODS

Work was undertaken on two sites of the island of São Miguel (Fig. 1), one on the south coast (Caloura) and another one on the north coast (Ribeirinha), where wave action is higher. At each site, a relatively sheltered (S) and an exposed (E) station were chosen in order to evaluate the differences within sites. In this way, four stations with different degrees of exposure to wave action were studied. The abbreviations CS and CE are used to designate the stations in Caloura and RS and RE the stations in Ribeirinha. All the stations, steeply sloping and comprised of hard basaltic rock, were surrounded by shallow waters. The depth relative to the mean low water level at spring tides (LWST) varied from 1 m at CS to 5.5 m at RE, being *c.* 2 m at CE and RS.

At each station, a transect was made from a benchmark established above the

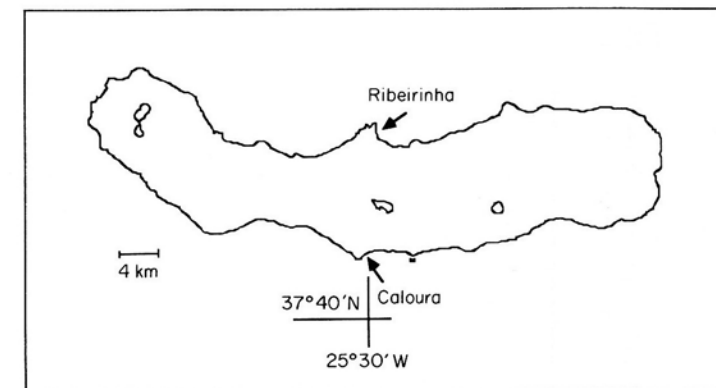


Figure 1. Position of the sampled sites, Caloura and Ribeirinha, on the island of São Miguel, Azores.

first point where living marine organisms occurred down to the bottom, in a continuous strip. Elevations along each transect were determined relative to low water, using two graduated poles, each one supporting a spirit level. Below low water, depth was measured relative to a known temporary intertidal benchmark of known elevation. All elevations were related to Chart Datum, Azores (CD), by using the level of the sea at the time of the predicted low water. Owing to the simplicity of the levelling equipment used, the presence of residual swell even on calm days and unpredictable tidal height, these elevations are only an approximate guide to the height or depth (± 0.1 m). A profile of each station was drawn and the vertical distribution of the main organisms recorded.

The algal turf zone of each site was sampled bimonthly for 1 year (from October 1988 to August 1989 at Caloura and from November 1988 to September 1989 at Ribeirinha). On each occasion three quadrats of 625 cm² were placed randomly in each station. Each sample consisted of the material obtained by scraping off the algal cover inside the quadrat with a chisel.

The algal species composition of each sample was determined and the importance of each species evaluated using a semi-quantitative scale (from Pérès & Picard, 1964). The wet and dry weight of each sample was also determined. Taxonomic authorities for the algal taxa present in the turf are given in Table 1. For the other taxa they are given at first mention in the text.

Data on the air and sea water temperature for that period were kindly made available by Instituto Nacional de Meteorologia e Geofísica (INMG). Other data sources are referred to in the text.

RESULTS

Zonation

On the sheltered station of Caloura (CS) four different zones were found (Fig. 2): high up the shore there was a zone with littorinids followed by one dominated by *Chthamalus stellatus* (Poli). The intertidal presented two very distinct bands of algae: the algal turf zone, followed by the upper fringe of the *Corallina officinalis*/*Pterocladia capillacea* zone, which continued subtidally.

TABLE 1. Specific composition of the algal turf at each station. The taxonomic authorities and the arrangement of families and orders follows South & Tittley (1986). Genera are listed alphabetically under each family, and species are listed alphabetically under each genus. AZ, new record for the Azores; SM, new record for São Miguel

Division	Order	Family	Taxa	CS	CE	RS	RE
Cyanophyta	Oscillatoriales	Oscillatoriaceae	<i>Lyngbya</i> sp.		*	*	*
			Number of species (Cyanophyta)	0	1	1	1
Chlorophyta	Ulvales	Ulveaceae	SM <i>Enteromorpha compressa</i> (Linnaeus) Greville			*	*
			<i>Enteromorpha linza</i> (Linnaeus) J. Agardh				*
			AZ <i>Enteromorpha ramulosa</i> (J. E. Smith) Hooker				*
			<i>Enteromorpha torta</i> (Mertens in Juerg.) Reinbold			*	
			<i>Ulva rigida</i> C. Agardh	*	*	*	*
	Cladophorales	Monostromataceae	SM <i>Blidingia minima</i> (Nacg. ex Kuetz.) Kylin				*
		Cladophoraceae	<i>Chaetomorpha aerea</i> (Dillwyn) Kuetz.	*	*	*	*
			SM <i>Chaetomorpha pachynema</i> Montagne			*	
			<i>Chaetomorpha</i> sp.	*	*	*	
			<i>Cladophora albida</i> (Hudson) Kuetz.	*	*	*	*
			SM <i>Cladophora coelothrix</i> Kuetz.	*			
			<i>Cladophora prolifera</i> (Roth) Kuetz.	*	*	*	
			<i>Rhizoclonium africanum</i> Kuetz.	*	*		
	Bryopsidales	Codiaceae	SM <i>Codium adhaerens</i> (Cabrera) C. Agardh			*	*
			Number of species (Chlorophyta)	7	6	9	8
Phaeophyta	Spacelariales	Stypocaulaceae	<i>Halopteris filicina</i> (Grat.) Kuetz.	*	*		
	Dictyosiphonales	Scytosiphonaceae	<i>Halopteris scoparia</i> (Linnaeus) Sauvageau	*		*	
	Fucales	Fucaceae	<i>Colpomenia sinuosa</i> (Roth) (Derbés et Solier	*			
			<i>Fucus spiralis</i> Linnaeus		*		
			Number of species (Phaeophyta)	3	2	1	0
Rhodophyta	Nemaliales	Gelidiaceae	<i>Gelidium latifolium</i> (Gréville) Bornet et Thuret	*		*	
			<i>Gelidium microdon</i> Kuetz.		*		*
			<i>Gelidium pusillum</i> (Stackhouse) Le Jolis	*	*	*	
	Palmariales	Palmaraceae	SM <i>Pterocladia capillacea</i> (S. Gmelin) Bornet et Thuret	*	*		
	Cryptonemiales	Peyssonneliaceae	<i>Palmaria palmata</i> (Linnaeus) O. Kuntze		*		
	Corallinales	Corallinaceae	<i>Peyssonnelia</i> sp.		*		
			<i>Corallina officinalis</i> Linnaeus	*	*		*
			SM <i>Jania adhaerens</i> Lamouroux	*			
			SM <i>Jania longifurca</i> Zanardini		*		
	Gigartinales	Phylloporaceae	AZ <i>Jania rubens</i> (Linnaeus) Lamouroux	*	*		*
		Gigartinaceae	<i>Phyllophora trailli</i> Holmes ex Baxters			*	
			<i>Gigartina acicularis</i> (Roth) Lamouroux	*	*	*	*
			<i>Gigartina pistillata</i> (S. Gmelin) Stackhouse	*			
			SM <i>Catenella caespitosa</i> (Withering) Linnaeus		*		
	Rhodymeniales	Caulacanthaceae	AZ <i>Rhodymenia holmesii</i> Ardissonne	*	*		
	Ceramiales	Ceramiceae	AZ <i>Callithamnion corymbosum</i> (Smith) Lyngbye	*	*	*	
			<i>Callithamnion hookeri</i> (Dillwyn) S. F. Gray	*		*	
			<i>Ceramium ciliatum</i> (Ellis) Ducluzeau	*	*		
			SM <i>Ceramium echinotum</i> J. Agardh	*			
			SM <i>Ceramium flabelligerum</i> J. Agardh	*	*	*	
			<i>Ceramium rubrum</i> (Hudson) Agardh			*	
		Rhodomelaceae	AZ <i>Chondria dasyphylla</i> (Woodward) C. Agardh	*			
			SM <i>Chondria tenuissima</i> (Gooden. & Woodw.) Agardh	*	*		
			<i>Laurencia pinnatifida</i> (Hudson) Lamouroux	*	*		*
			AZ <i>Polysiphonia atlantica</i> Kapraun et J. Norris		*		
			<i>Polysiphonia havanensis</i> Mont.		*		
			SM <i>Polysiphonia nigrescens</i> (Hudson) Gréville		*		
			AZ <i>Polysiphonia opaca</i> (C. Agardh) Mor. et De Not.			*	*
			AZ <i>Polysiphonia urceolata</i> (Lightfoot ex Dillwyn) Gréville			*	
			Number of species (Rhodophyta)	17	19	10	6
			Total number of species	27	28	21	15

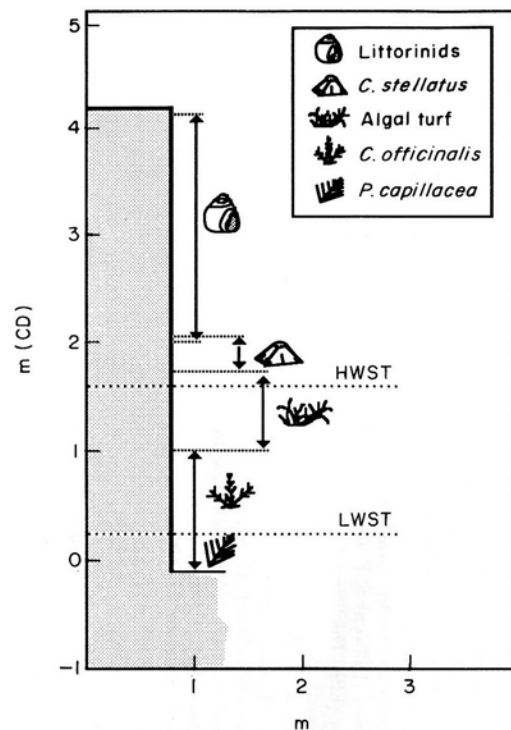


Figure 2. Caloura sheltered station—transect profile and distribution of the dominant organisms. Numbers on the vertical axis indicate metres above or below Chart Datum (CD), Azores, and on the horizontal axis distance from the established benchmark. HWST, mean high water level at spring tides; LWST, mean low water level at spring tides.

On the exposed station of Caloura (CE) (Fig. 3) the zonation was quite similar to that of the sheltered station. However, there was some overlap between the algal turf and the lower limit of the *C. stellatus* zone. Moreover, there was a band of *Codium adhaerens* between the *C. officinalis*/*P. capillacea* zone and the bottom.

Algal zonation on the sheltered station of Ribeirinha (RS) was different from that seen on Caloura (Fig 4). Overlapping the lower limit of the *C. stellatus* zone, there was a band of *Enteromorpha* spp. The algal turf extended over the intertidal zone. Below it has a frondose algal zone dominated by *C. officinalis* and *Halopteris* spp. A band of hole-boring sea urchins (*Paracentrotus lividus* (Lamarck)) covered part of these two zones. A band of *C. adhaerens* was also present on the upper fringe of the *C. officinalis*/*Halopteris* spp. zone.

On the exposed station of Ribeirinha (RE) greater overlap occurred than on the sheltered station (Fig. 5). The band of *Enteromorpha* spp. was located higher up the shore, overlapping the transition between the littorinids and *C. stellatus*. Its lower limit corresponded to the upper limit of the algal turf zone, which started above the HWST line (mean high water level of spring tides) and overlapped most of the zone of *C. stellatus*. The algal turf zone was followed by the *C. officinalis*/*Halopteris* spp. zone, which dominated subtidally. A band of *Tenarea tortuosa* (Esper) Lemoine, seen only in this station, was centred on the

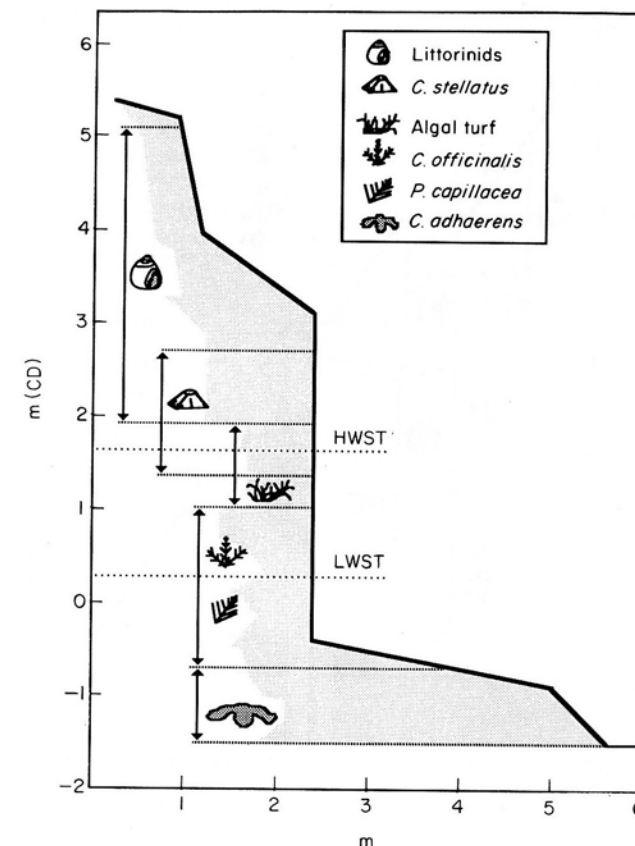


Figure 3. Caloura exposed station—transect profile and distribution of the dominant organisms. Details as in Fig. 2.

LWST line. The *P. lividus* zone of RE was narrower and located above the algal fronds.

The vertical distribution of the organisms at the four stations studied (Fig. 6), revealed that on both coasts the upper limit of the littorinids, *C. stellatus* and algal turf was higher at the exposed stations. This was also the case for *Enteromorpha* spp. at Ribeirinha. The station with the highest upper limits was CE followed, in decreasing order, by RE, CS and RS. In the exposed stations there was also greater overlap between the different zones.

Algal turf species composition

A high number of species was found on the algal turf (Table 1). Of these, 21 are recorded for the first time on São Miguel and of these eight are also new records for the Azores. The lowest number of species (15) was found at RE followed in increasing order, by RS (21), CS (27) and CE (28). In Caloura species of red algae were dominant (17 at CS and 19 at CE) followed by the green (seven at CS and six at CE) and brown algae (three at CS and two at CE). In Ribeirinha, the brown algae were reduced to a single species at RS and the

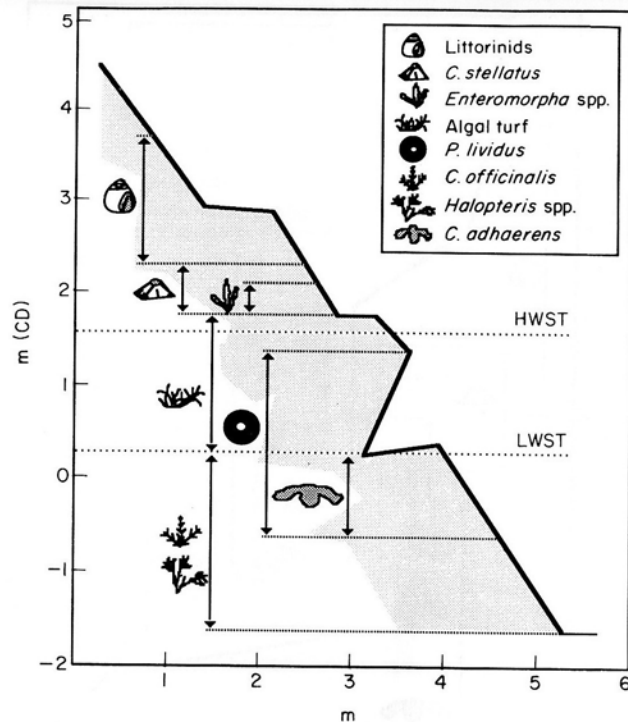


Figure 4. Ribeirinha sheltered station—transect profile and distribution of the dominant organisms. Details as in Fig. 2.

number of green algae species was almost equal or slightly larger than the number of the red algae species (9/10 at RS and 8/6 at RE). There were species common to both coasts (17) whereas others were only present in one of the sites (20 at Caloura and 11 at Ribeirinha). The presence of *Lyngbya* sp., the only cyanophyte present, on the turf of CE, RS and RE is noteworthy.

The algal turf species composition at both stations of Caloura was similar (Fig. 7) in terms of *taxa*, but different in frequencies of occurrence. There were also some similarities between these two sites and RS (the dominance of *Gigartina acicularis* and the occurrence of *Ulva rigida*, *Gelidium pusillum* and *Ceramium flabelligerum*). RE had in common with all the stations the occurrence of *U. rigida* and *G. acicularis* and it shares with RS the presence of *Polysiphonia opaca* and with CS and CE the occurrence of *C. officinalis* and *Jania rubens*.

Algal turf dry weight

The seasonal mean dry weight patterns of the algal turf were similar for the four stations (Figs 8, 9): a minimum in winter and a peak in spring or beginning of summer. The higher values at RE are related to the dominance of articulate coralline algae.

Air and sea water temperatures were lowest between February and April (air) or May (sea water) and highest between July and September (Figs 10, 11). The number of hours of light was lowest in December and highest in June and July

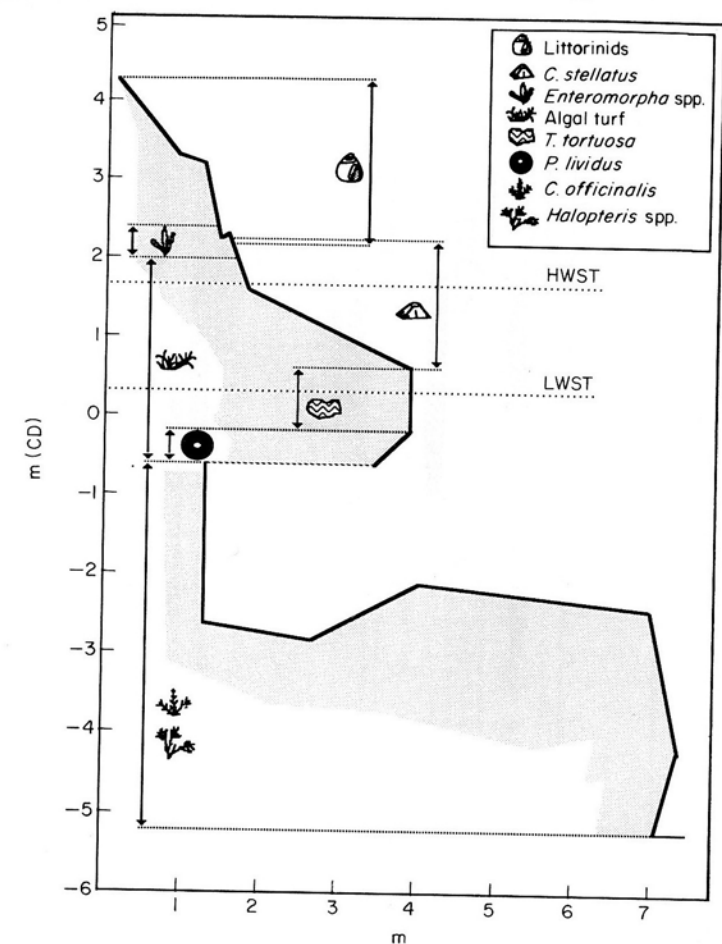


Figure 5. Ribeirinha exposed station—transect profile and distribution of the dominant organisms. Details as in Fig. 2.

(Fig. 12). The lowest values of insolation (non-clouded sunlight) occurred in January and the highest in August. Maximum insolation occurred when the hours of light were already decreasing and coincided with the maximum in temperature.

There was a correlation between algal dry weight and the number of hours of light. On the other hand rapid increase in algal dry weight corresponded to the time of the year when air and sea water temperatures were lowest. Decrease in the algal dry weight (between August and September) coincided with the maximum values of insolation and temperature.

DISCUSSION

Three main zones were found to occur on the shores of the island of São Miguel: a splash and spray zone dominated by littorinids; a zone daily immersed and emersed, dominated by filter-feeding barnacles and algal turf; and a zone

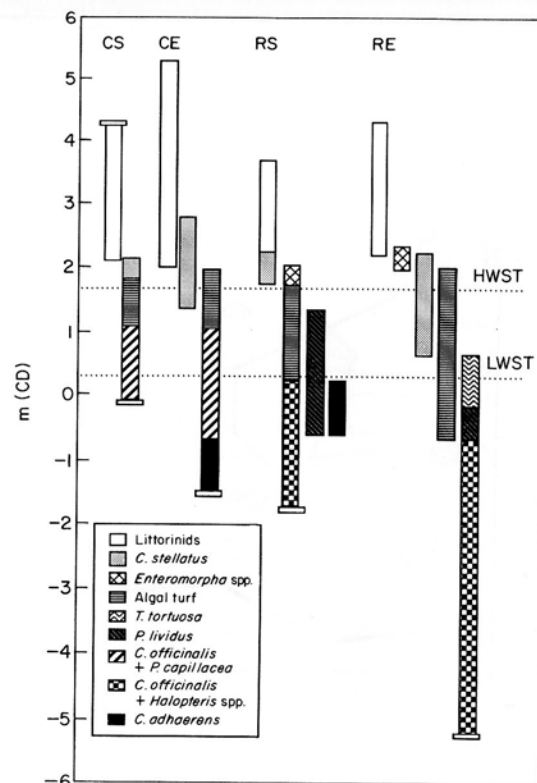


Figure 6. Vertical distribution of the dominant organisms at each transect. Details as in Fig. 2.

dominated by algal fronds. These zones were present through all the year and always showed some degree of overlap. In the zone daily immersed and emersed by the tide the organisms formed two distinct sub-zones. In the higher *C. stellatus* dominated and in the lower the algal turf was dominant. This situation

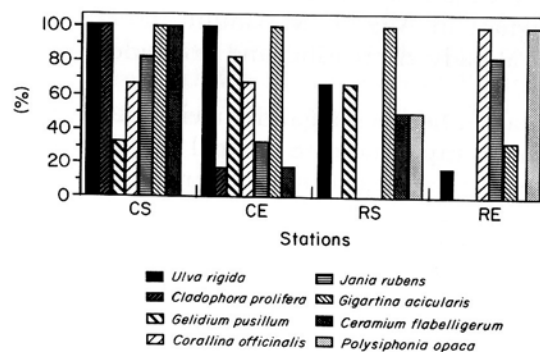


Figure 7. Absolute frequency of the principal components of the algal turf: CS and CE, respectively, sheltered and exposed stations of Caloura; RS and RE, respectively sheltered and exposed stations of Ribeirinha.

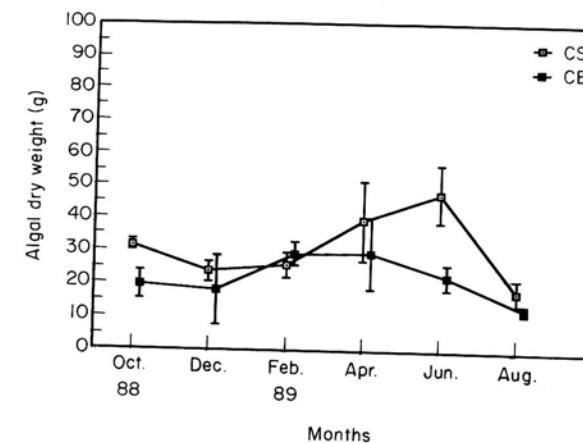


Figure 8. Bimonthly values of the algal turf mean dry weight (± 1 sd) at Caloura. Abbreviations as in Fig. 7.

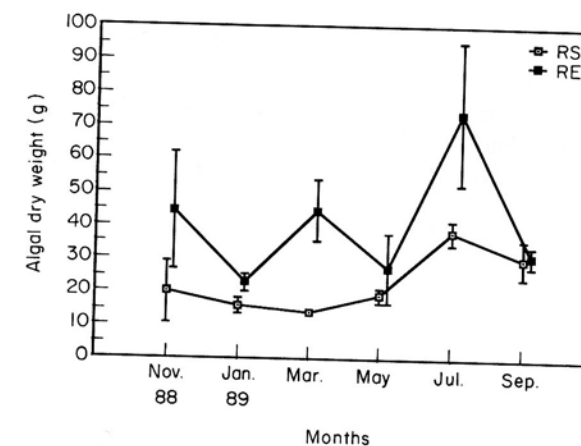


Figure 9. Bimonthly values of the algal turf mean dry weight (± 1 sd) at Ribeirinha. Abbreviations as in Fig. 7.

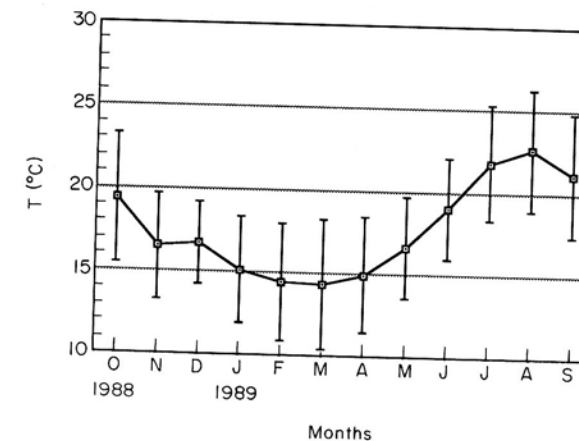


Figure 10. Mean monthly values (± 1 sd) or the air temperature in São Miguel (data from INMG).

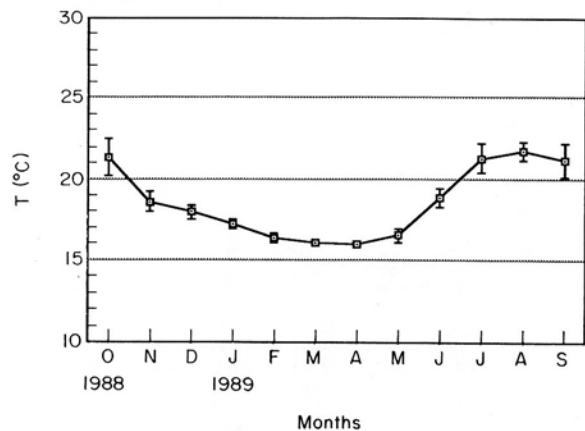


Figure 11. Mean monthly values (± 1 SD) of the sea water temperature in São Miguel (data from INMG).

according to Pérès (1967), is characteristic of places with small range tides (usually less than 1.5 m).

The zones encountered are basically the same as those in Flores (Neto & Azevedo, 1990), São Miguel (Hawkins *et al.*, 1990) and Santa Maria (personal observations). The zonation pattern found is different from the universal scheme defined by Stephenson & Stephenson (1972) but is very similar to the zonation found by Lawson & Norton (1971) in Tenerife, Canarias. It also resembles the Mediterranean (Feldmann, 1946; Pérès & Picard, 1964), especially in the narrow width of the zones.

Limpets (*Patella* spp.) were not present in the stations studied, a situation different from that reported by Hawkins *et al.* (1990). The absence of these grazers, probably due to overpredation by man, could explain the dominance of the algal turf seen on the intertidal zone. In fact, several studies (Southward, 1964; Southward & Southward, 1978; Underwood, 1980; Hawkins & Hartnoll,

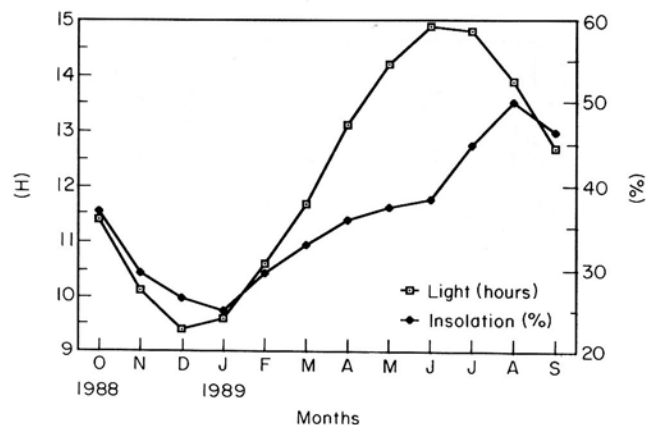


Figure 12. Mean monthly values of hours of light (h) and insolation (number of hours of bright sun/number of hours of light) in São Miguel (data from Bettencourt, 1979).

1983) have pointed out that grazers seem to be the main determinant of intertidal algal distribution.

The higher limit of the zones in the exposed stations agrees with the model of Lewis (1964) and can be attributed to the higher wave action at those stations. The amount of exposure affects the amount of spray and consequently the amount of desiccation experienced by plants up the coast. The greater the exposure, the greater the spray, which allows growth of algae further up the beach or wall. Similar results were found in S. Jorge (Pryor, 1967), Flores (Neto & Azevedo, 1990), São Miguel (Hawkins *et al.*, 1990) and Santa Maria (personal observations).

The higher number of species found on the south coast stations could be explained by the fact that, in open shores, the number of species usually increases in the more protected places (Lewis, 1964; Norton, 1985).

The relatively high number of new records found shows that further taxonomic studies of the benthic marine algae from the Azores are needed in order to establish the similarities between the algal flora of this archipelago and that of the surrounding shores.

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REFERENCES

- AGARDH, I. G., 1870. Om de under Korvetten Josephines expedition, sistliden sommar, insamlade Algerne, öfversigt of Kongl. Vetenskaps-Akademiens Forhanlingar, 4: 359–366.
- ARDRE, F., BOUDOURESQUE, C.-F. & CABIOCH, J., 1973. Note préliminaire sur la mission "Biaçores" du N. O. Jean Charcot (Algologie). *Bulletin de la Société Phycologique de France*, 18: 30–32.
- ARDRE, F., BOUDOURESQUE, C.-F. & CABIOCH, J., 1974. *Symphyocladia marchantioides* (Harvey) Falkenberg (Rhodomélacées, Ceramiales) aux Açores. *Bulletin de la Société Phycologique de France*, 19: 178–182.
- BETTENCOURT, M. L., 1979. O clima dos Açores como recurso natural especialmente em agricultura e indústria do turismo. *O clima de Portugal*, 18. Instituto Nacional de Meteorologia e Geofísica, Lisboa.
- CASTRO, M. L. & VIEGAS, M. C., 1987. Contribuição para o estudo da zona intertidal (substrato rochoso) da ilha de São Miguel-Açores. *Fácies de Corallina elongata* Ellis & Solander. Resultados preliminares. *Cuadernos Marisqueros*, 11: 59–69.
- DROUET, H., 1866. Catalogue de la flore des îles Açores précédé de l'itinéraire d'un voyage dans cet archipel. *Mémoires de la Société Académique de l'Aube*, 30: 81–233.
- FELDMANN, J., 1946. La flore marine des îles atlantides. *Mémoires de la Société de Biogéographie*, 28: 395–435.
- FRALICK R. A. & HEHRE, E. J., 1990. Observations on the marine algal flora of the Azores-II. An annotated check list of the Chlorophyta from the Azores. *Arquipélago, Série Ciências da Natureza*, 8: 11–17.
- FRALICK R. A., HEHRE, E. J. & MATHIESON, A. C., 1985. Observations of the marine algal flora of the Azores I: Notes on the epizoic algae occurring on the marine mollusks *Patella* spp. *Arquipélago, Série Ciências da Natureza*, 6: 39–43.
- GAIN, L., 1914. Algues provenant des campagnes de l'"Hirondelle II" (1911–1912). *Bulletin de l'Institut Océanographique*, 279: 1–23.
- HAWKINS, S. J. & HARTNOLL, R. G., 1983. Grazing of intertidal algae by marine invertebrates. *Oceanography and Marine Biology Annual Review*, 21: 195–282.
- HAWKINS, S. J., BURNAY, L. P., NETO, A. I., CUNHA, R. T. & MARTINS, A. F., 1990. A description of the zonation patterns of molluscs and other important biota on the south coast of São Miguel, Azores. In A. F. Martins (Ed.), *The Marine Fauna and Flora of the Azores*: 21–38. *Açoreana, Suplemento*.

- INSTITUTO HIDROGRÁFICO, 1981. *Roteiro do Arquipélago dos Açores*, PUB. (N)-IH-128-SN. Lisboa: Instituto Hidrográfico.
- LARKUM, A. W., 1960. Botany (Algae). In Anon., *Azores Expedition 1959. Final Report*: 120-127. London: The Exploration Board, Imperial College of Science and Technology.
- LAWSON, G. W. & NORTON, T. A., 1971. Some observations on littoral and sublittoral zonation at Tenerife (Canary Isles). *Botanica Marina*, 14: 116-120.
- LEWIS, J. R., 1964. *The Ecology of Rocky Shores*. London: University Press.
- NETO, A. I., 1989. Algas marinhas do litoral da ilha Graciosa. *Graciosa/88 Relatório Preliminar, Relatórios e Comunicações do Departamento de Biologia da Universidade dos Açores*, 17: 61-65.
- NETO, A. I. & AZEVEDO, J. N., 1990. Contribuição para o estudo dos padrões de zonation litoral da ilha das Flores. *Relatórios e Comunicações do Departamento de Biologia da Universidade dos Açores*, 18: 89-102.
- NETO, A. I. & BALDWIN, H. P., 1990. Algas marinhas do litoral das ilhas do Corvo e Flores. *Relatórios e Comunicações do Departamento de Biologia da Universidade dos Açores*, 18: 103-111.
- NORTON, T. A., 1985. The zonation of seaweeds on rocky shores. In P. G. Moore & R. Seed (Eds), *The Ecology of Rocky Coasts*: 7-21. London: Hodder and Stoughton.
- PALMINHA, F., 1957. Sobre a existência de *Lithophyllum tortuosum* (Esper.) Foslie [= *Tenarea tortuosa* (Esper.) Lem.] nos Açores. *Boletim da Sociedade Portuguesa de Ciências Naturais*, 2ª Série, 22 (7): 61-67.
- PÉRÈS, J.-M., 1967. Les biocoenoses benthiques dans le système phytal. *Recueil des Travaux de la Station Marine d'Endoume*, 42 (58): 3-113.
- PÉRÈS, J.-M. & PICARD, J., 1964. Nouveau manuel de bionomie benthique de la mer méditerranéenne. *Extrait du Recueil des Travaux de la Station Marine d'Endoume*, 31 (47): 5-137.
- PICCONI, A., 1889. Alghe della Crociera del "Corsaro" alle Azzorre. *Nuovo Giornale Botanico Italiano*, 21: 171-214.
- PRYOR, J., 1967. Intertidal marine algae of São Jorge. In Anon., *Chelsea College Azores Expedition, Final Report*: 17-30. London: Chelsea College of Science and Technology.
- SCHMIDT, O. C., 1929a. Beiträge zur Kenntnis der Meeresalgen der Azoren I. *Hedwigia*, 69: 95-113.
- SCHMIDT, O. C., 1929b. Beiträge zur Kenntnis der Meeresalgen der Azoren II. *Hedwigia*, 69: 165-172.
- SCHMIDT, O. C., 1931. Die marine vegetation der Azoren in ihren Grundzügen dargestellt. *Bibliotheca Botanica*, 24 (102): ix + 116p., 10 Taf.
- SEUBERT, M., 1844. *Flora azorica*. Bonna: Adolphum Marcum.
- SOUTH, G. R. & TITTLE, I., 1986. *A Checklist and Distributional Index of the Benthic Marine Algae of the North Atlantic Ocean*. London: Huntsman Marine Laboratory and British Museum (Natural History).
- SOUTHWARD, A. J., 1964. Limpet grazing and the control of vegetation on rocky shores. In D. J. Crisp (Ed.), *Grazing in Terrestrial and Marine Environments*: 256-273. Oxford: Blackwell Scientific Publications.
- SOUTHWARD, A. J. & SOUTHWARD, E. C., 1978. Recolonization of rocky shores in Cornwall after use of toxic dispersants to clean up the Torrey Canyon spill. *Journal of the Fisheries Research Board of Canada*, 35: 682-706.
- STEPHENSON, T. A. & STEPHENSON, A., 1949. The universal features of zonation between tide-marks on rocky coasts. *Journal of Ecology*, 37: 289-305.
- STEPHENSON, T. A. & STEPHENSON, A., 1972. *Life Between Tidemarks on Rocky Shores*. London: Freeman.
- TRELEASE, W., 1897. Botanical observations on the Azores. *8th Annual Report of the Michigan Botanical Garden*: 77-220, pl: 12-16.
- 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.