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Ecology and dynamics of two intertidal algal communities on the littoral of the island of São Miguel (Azores)

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Abstract

The intertidal benthic algal communities of two sites located on opposite coasts of São Miguel Island (Azores), were studied over a 2-year period (September 1993–September 1995). At both sites (São Roque on the south coast and São Vicente on the north), the littoral region was surveyed from the upper intertidal down to the sublittoral fringe. The survey revealed five distinct zones, with a variable degree of overlapping. The two upper zones were characterized by animals (littorinids and barnacles, respectively). Lower down, algal communities formed three distinct zones: an upper *Fucus spiralis*/*Gelidium microdon* association, a more extensive turf zone, and a belt featuring erect or frondose algae. Upper in the eulittoral, the turf was mainly monospecific, and dominated by *Caulacanthus ustulatus.* The lower eulittoral turf was dominated by articulated coralline algae, the associated species differing between the two sites studied. Mainly erect algae (*Pterocladiella*, *Asparagopsis*, etc.) occurred furthest down the shore and extended into the nearby shallow sublittoral. Two intertidal communities were studied at each locality: the upper eulittoral (*Caulacanthus* turf in São Roque and the *Fucus spiralis*/*Gelidium microdon* association at São Vicente), and the lower eulittoral (the coralline turf). The lower littoral communities had a higher algal diversity. A general pattern was observed in the seasonal variation of biomass: the lower levels exhibited the higher values in late summer/early autumn, the period in which the upper levels had the lowest standing crops. Physical factors are proposed to account for this. No significant inter-annual variations could be detected, indicating relatively stable communities, at least on a short-term basis.

Introduction

A regular distribution of species and communities is particularly obvious on rocky shores, as has long been recognized by marine biologists. According to Stephenson & Stephenson (1949), the various physical and chemical gradients across the air/water interface may account for the distribution of communities into horizontal, apparently homogeneous fringes with sharp boundaries (zonation), although biotic factors, such as competition, are now also considered to be important (Chapman, 1973). Zonation patterns of the littoral region have been studied all over the world, with comparisons made between sheltered and exposed sites (e.g. Lewis, 1972), and between different types of substratum (e.g. Den Hartog, 1959).

Only a few studies have been done on the structure of the intertidal communities of the Azores. Neto (1991, 1992) studied the algal communities dominating the lower eulittoral zone and the sublittoral fringe of two places of the island of São Miguel. That study was done over a 1 year period and the effects of geographic location (on the island) and time were analysed. Neto & Tittley (1995) and Tittley et al. (1998), on the islands of Faial and Flores, respectively, studied the species associations and abundance of several intertidal communities, but only in one summer. On the other hand, there are several papers describing the zonation patterns in different areas of the Azores (Schmidt, 1931; Larkum, 1960; Pryor, 1967; Ardré et al., 1973; Castro & Viegas, 1987; Hawkins et al., 1990; Neto, 1992; Neto & Tittley, 1995; Tittley et al.,

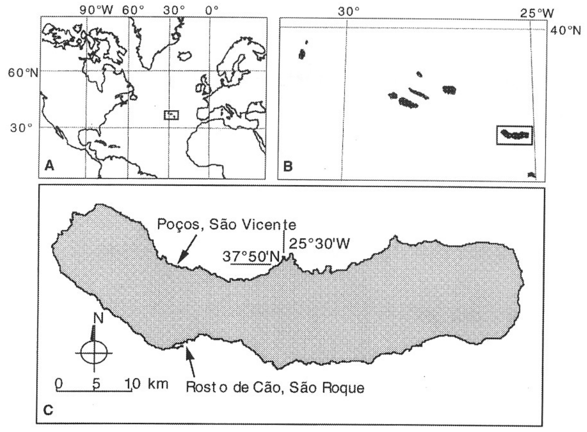

Figure 1. Location of the archipelago of the Azores on the North Atlantic (A); position of the island of São Miguel on the archipelago (B), and location of the study sites on the island of São Miguel (C).

1998). Three major zones were recognized: a splash and spray zone (littoral fringe) dominated by littorinids; a zone daily immersed and emmersed (eulittoral zone) dominated by barnacles and algal turf, and a lower zone (sublittoral fringe) dominated by subtidal algae (see Hawkins et al., 1990; Neto, 1992).

The present paper is a further contribution to the description of the structure of the intertidal communities of the Azores, focused on two sites of the island of São Miguel. It presents a new and detailed characterization of the zonation patterns on the island. For each site, the benthic algal vegetation of the upper and lower levels of the eulittoral zone is described and the effects of position on shore, geographic location (on the island) and time are analysed.

Description of sites studied

The archipelago of the Azores is located between the coordinates 37°–40° N and 25°–31° W (Figure 1) and it includes nine volcanic islands and several small islets, which are organized into three separate groups (eastern, central and western). All the islands are formed by volcanic rocks (mainly basalt) and surrounded by very deep water. A depth of 1000 m may occur within 2 or 3 kmeters off shore, mainly in zones with a steep slope. Most shores are subject to swell and surge. Few shores are sheltered, except for some bays and harbours. The island of São Miguel, with approximately 750 km^2, is the largest of the archipelago. The coastline is about 155 km in length and is mostly of difficult access by land.

The two studied sites are located on the open coast of São Miguel and are opposite to each other on the island (Figure 1): São Roque (on the south coast) and São Vicente (on the north coast). Both sites are within bays enclosing relatively shallow waters, permitting easy access for shore work and for diving. The studied areas are characterized by a compact bedrock of hard basaltic rock (steeply sloping in São Roque and gently sloping at São Vicente).

Materials and methods

Work was undertaken in the period between September 1993 and September 1995. Both sites were surveyed monthly. Field methodology involved the assessment of the intertidal zonation patterns and qualitative and quantitative collections.

At each site, a permanent transect was laid down, perpendicular to the coast, from a benchmark established above the highest point where living littorinids occurred down to the low water level. Elevations along the transect were determined relative to a known intertidal benchmark of known elevation, following the spirit leveling method (Hawkins & Jones, 1992). All elevations were related to Chart Datum, Azores (CD), by using the level of the sea at the time of predicted low water. Considering the presence of residual swell even on calm days and the simplicity of the method used, the elevations are only approximate (± 0.1 m). Every zone distinguishable *in situ* was described, ranging from the lowest zone emerging during the deepest wave troughs up to the zone above which no macroscopic marine organisms were present. A profile of each station was drawn and the vertical distribution of the main organisms recorded along it. Motile animals were counted individually and the areal cover-abundance of barnacles and each algal species was estimated along the transect in a continuous belt, using a 0.25 m^2 quadrat marked with 36 dots, following the methods described by Hawkins & Jones (1992) and Meese & Tomich (1992).

For the qualitative collections, specimens were collected from the entire intertidal zone into labelled bags. The position and habitat of the species on the shore (substrate, tide pool, open rock, crevice) were noted. For the quantitative collections, samples of a pre-determined area (0.1 m^2, see Neto, 1997) were scraped with a chisel into labelled fine mesh bags. At each site, the collections were made from the upper and lower levels of the eulittoral zone. Three replicates were taken within each zone. Giving the narrowness of the zones surveyed, all replicates were made in horizontal row. The location of each quadrat was determined by successively reading from a table of random numbers the direction (E/W) and the distance (up to 1 m).

The algae from both qualitative and quantitative collections were sorted into species. The plants from quantitative collections were weighed on an electronic top-pan balance, after the excess water was removed by shaking them vigorously. The plants were dried in an oven at 70 °C until constant weight was attained to determine the dry weight of each species.

Diversity and species richness were assessed using the Shannon-Weaver diversity index (H'), probably the most widely used index that combines species richness with relative abundance. This index makes the assumption that individuals are randomly sampled from an 'infinitely large' population and also assumes that all the species from a community are included in the sample (Margaleff, 1957; Niell, 1974; Kent & Coker, 1996).

A numerical multivariate technique was used to compare the different sampling sites and levels over the two successive years. A cluster analyses (weighted-pairs method) of the dissimilarity coefficient of squared Euclidean distance was performed using the NTSYS package (Rohlf, 1994) and following the recommendations of Kent & Coker (1996). A similar technique was employed, in a similar context, by e.g. Santelices & Abbott (1987), Ballesteros & Romero (1988), and Smith (1992).

Meteorological information for the years 1993–5 was obtained from Instituto Nacional de Metereologia e Geofísica (INMG). The mean monthly values of the seawater temperature (Figure 2) were minimum in February/ March (15/16 °C) and maximum in August/September (22/23 °C). In the same period, the monthly mean hours of sunshine (Figure 2) were minimum (around 3 h/day) in winter (December–February) and maximum (around 8 h/day) in summer (July/August).

Results

Zonation

At both sites (Figures 3 and 4), five distinct zones were found, although a high degree of overlap was noted in some instances. High up in the shore there

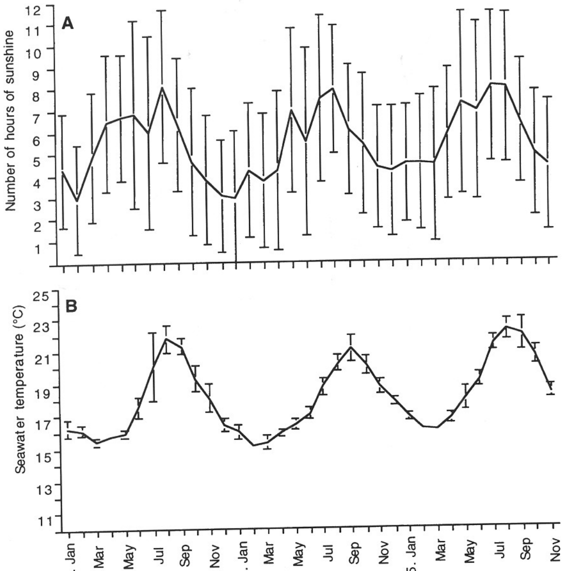

Figure 2. Mean monthly values (± standard deviation) of hours of sunshine (A) and surface seawater temperature (B) for the island of São Miguel in the period between January 1993 and November 1995.

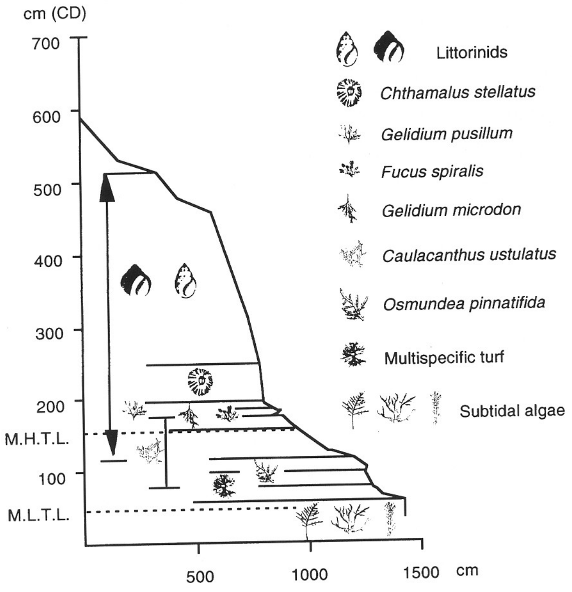

Figure 3. Schematic profile of the intertidal station of São Roque with the vertical distribution of the dominant organisms (MLTL – mean low tide level; MHTL – mean high tide level; CD – chart datum, Azores).

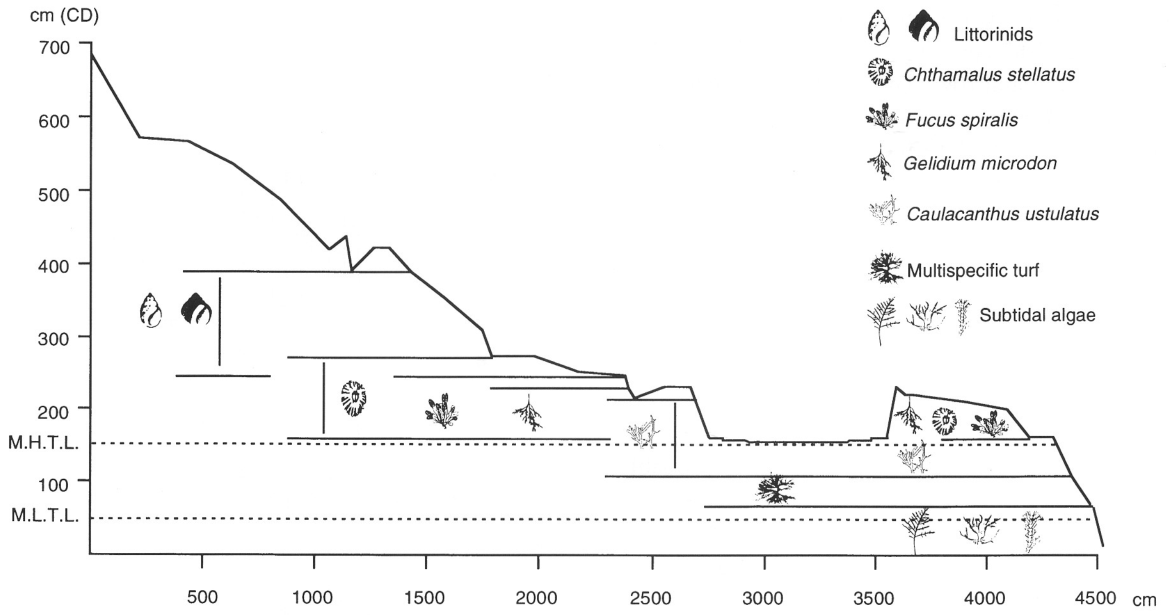

Figure 4. Schematic profile of the intertidal station of São Vicente with the vertical distribution of the dominant organisms. Abbreviations as in Figure 3.

was a splash and spray zone with littorinids (*Littorina striata* King and *Melaraphe neritoides* (L.)), followed by one dominated by barnacles (*Chthamalus stellatus* (Poli)). The algal populations formed three distinct zones: below (on the south coast) or overlapping the lower fringe (in the north coast) of the barnacles there was a distinct zone of *Fucus spiralis* Linné and *Gelidium microdon* Kützing, followed by a turf zone. This in turn was comprised of two fairly distinct belts, the upper one an almost monospecific turf of *Caulacanthus ustulatus* (Turner) Kützing, the lower comprising a multispecific turf dominated by coralline algae in the south and by *Centroceras clavulatum* (C. Agardh) Montagne in the north. The lowest algal zone, which continued subtidally, was dominated by frondose algae, mainly articulated corallines, *Asparagopsis armata* Harvey and *Pterocladiella capillacea* (S. G. Gmelin) Santelices et Hommersand.

The major differences between the two coasts were the upper limit of the littorinids, which was higher at São Roque, and the physiognomy of the *Fucus spiralis/Gelidium microdon* zone, which was patchy at São Roque but continuous at São Vicente. At São Roque (Figure 3) the *Caulacanthus* turf formed a distinct and well established belt, whereas the *Fucus spiralis/Gelidium microdon* association was restricted to the transition between the barnacles and the *Caulacanthus*. A narrow band of *Gelidium pusillum* (Stackhouse) Le Jolis was present for most of the year below the barnacles zone, overlapping the *Fucus spiralis/Gelidium microdon* zone. A very different situation was observed on the north coast (Figure 4) with the association *Fucus spiralis/Gelidium microdon* dominating the upper eulittoral. A few limpets (*Patella* spp.) were seen at both sites. All zones were present throughout the year and, although some annual fluctuations were detected in their upper and lower limits, most species showed a well established vertical position on the shore.

Community structure and floristic analyses

Fifty four species were collected (9 Chlorophyta, 6 Phaeophyta, 39 Rhodophyta), the lower levels having a much higher number of species (Table 1).

At São Roque, the two eulittoral algal communities studied were dominated, respectively, by the *Caulacanthus* turf (upper in the shore) and the erect Corallinaceae turf (at the lower level). The former was mainly monospecific with *Caulacanthus* accounting for 66% of the total mean biomass (Figure 5). The Corallinaceae turf was dominated by *Corallina elongata* J. Ellis et Solander and *Jania crassa* J. V. Lamouroux (both species responsible for over 60% of the total mean biomass), but comprised a few accompanying species: *Osmundea pinnatifida* (Hudson) Stackhouse,

Table 1. List of species and stages and their mean dry weight (g/m^2) at each intertidal level. SH: Upper eulittoral of São Roque; SL: Lower eulittoral of São Roque; NH: Upper eulittoral of São Vicente; NL: Lower eulittoral of São Vicente

		São Roque	(S)	São Vicente	(N)
	Abbrev.	SH	SL	NH	NL
Chlorophyta					
Bryopsis hypnoides	bryhyp		0.540		0.387
Chaetomorpha crassa	chacra		0.001		
Chaetomorpha linum	chalin	9.473	0.498	0.441	1.189
Cladophora coelothrix	clacoe				0.449
Cladophora prolifera	clapro				0.234
Codium adhaerens	codadh				1.277
Enteromorpha intestinalis	entint			0.213	
Enteromorpha muscoides	entmus				0.025
Ulva rigida	ulvrig	0.576	1.617	0.445	1.945
No of Chlorophyta	9	2	4	3	7
Phaeophyta					
Colpomenia sinuosa	colsin		0.049		0.974
Cystoseira abies-marina	cysabi				2.085
Dictyota dichotoma	dicdic		0.118		0.126
Fucus spiralis	fucspi	3.038		19.604	
Hydroclathrus clathratus	hydcla				0.180
Stypocaulon scoparium	stysco		0.196	5.016	
No of Phaeophyta	6	1	3	1	5
Rhodophyta					
Asparagopsis armata	asparm		7.757		0.697
Botryocladia botryoides	botbot		0.519		
Callithamnion granulatum	calgra		0.017		0.039
Callithamnion tetragonum	caltet		0.001		
Caulacanthus ustulatus	cauust	56.379	5.151	2.565	0.101
Centroceras clavulatum	cencla		0.252		26.876
Ceramium botryocarpum	cerbot		0.068		
Ceramium ciliatum	cercil				10.701
Ceramium deslongchampii	cerdes		1.504		
Ceramium diaphanum	cerdia		0.005		0.405
Ceramium nodulosum	cernod				0.081
Ceramium strictum	cerstr	1.064			
Chondracanthus acicularis	choaci		7.509		11.002
Chondria coerulescens	chocoe		1.034		0.419
Chondria dasyphylla	chodas		0.039		0.121
Corallina elongata	corelo	1.617	71.862		22.205
Cryptopleura ramosa	cryram		0.009		0.255
Falkenbergia rufolanosa stadium	falruf		0.003		
Gastroclonium ovatum	gasova		0.249		
Gastroclonium reflexum	gasref		1.005		0.046
Gelidium latifolium	gellat		0.085		
Gelidium microdon	gelmic	5.495		52.001	
Gelidium pusillum	gelpus	0.530	0.279	0.352	1.580
Gymnogongrus crenulatus	gymcre	0.825			
Gymnogongrus griffithsiae	gymgri	0.151	0.360	0.120	0.525

Continued on p. 140

Table 1. Continued

		São Roque	(S)	São Vicente	(N)
	Abbrev.	SH	SL	NH	NL
Hypnea musciformis	hymus				1.251
Jania crassa	jancra		33.827		
Jania longifurca	janlon				10.881
Jania rubens	janrub		4.426		23.879
Laurencia viridis	lauvir		0.091		9.407
Lomentaria articulata	lomart		0.501		
Nytophyllum punctatum	nytpun		0.161		0.161
Osmundea pinnatifida	osmpin	4.803	5.365		8.740
Plocamium cartilagineum	plocar		0.051		0.177
Polysiphonia denudata	polden				0.845
Pterocladiella capillacea	ptecap		16.592		1.922
Pterothamnion crispum	ptecri		0.012		0.083
Rodhymenia holmesii	rhohol		0.133		0.074
Symphyocladia marchantioides	symmar	3.121		1.673	
No of Rhodophyta	39	8	31	4	27
Total number of species	54	11	38	8	39

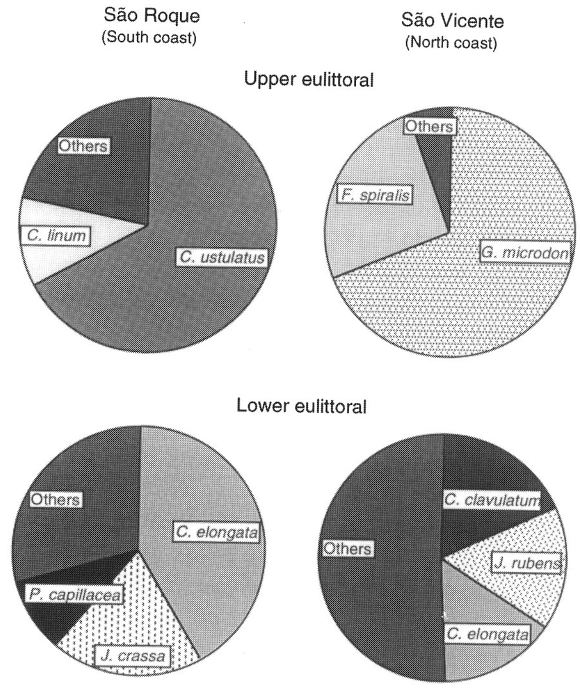

Figure 5. Relative mean biomass of the algal species at each intertidal level and site.

Chaetomorpha linum (O. F. Müller) Kützing, *Gastroclonium reflexum* (Chauvin) Kützing, *Chondria* spp. and *Ceramium ciliatum* (J. Ellis) Ducluzeau.

In São Vicente, the upper eulittoral zone was dominated by the *Fucus spiralis*/*Gelidium microdon* association, the latter species being always dominant and responsible for 69% of the total mean biomass, while *F. spiralis* contributed only 26% (Figure 5). Lower in the shore, *Centroceras clavulatum* was the most abundant species (although only 19%) but, as a group, the erect coralline algae (here including *C. elongata*, *Jania rubens* (Linné) J.V. Lamouroux and *J. longifurca* Zanardini) were very important, providing nearly 40% of the total mean biomass. Other noteworthy species included *Ceramium ciliatum*, *Chondracanthus acicularis* (Roth) Fredericq and *Colpomenia sinuosa* (Mertens ex Roth) Derbès et Solier. The later species was found growing epiphytically on the coralline algae of the turf.

Changes over time

A seasonal pattern was observed in the mean monthly biomass values of the four intertidal algal communities (Figure 6). In São Roque, the pattern was more pronounced at the lower level (SL). Here, and in both years, the mean biomass was higher in Septem-

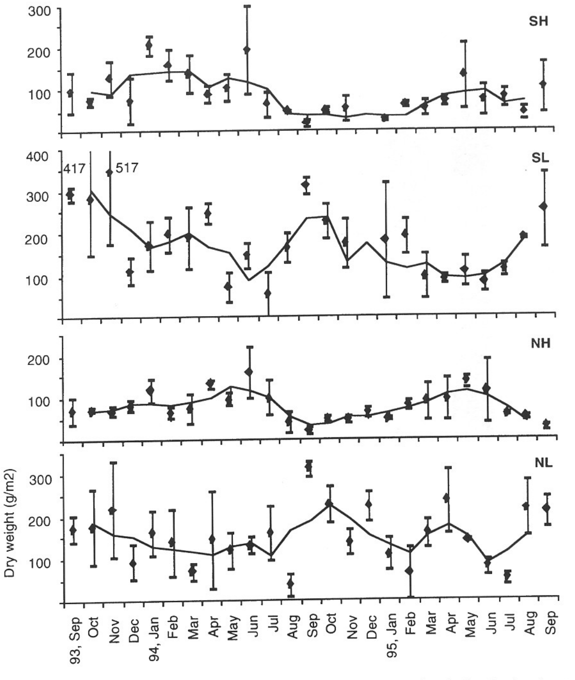

Figure 6. Monthly mean algal biomass (± standard deviation) at each intertidal level (the line indicates the moving average (3)); SH: Upper eulittoral of São Roque; SL: Lower eulittoral of São Roque; NH: Upper eulittoral of São Vicente; NL: Lower eulittoral of São Vicente.

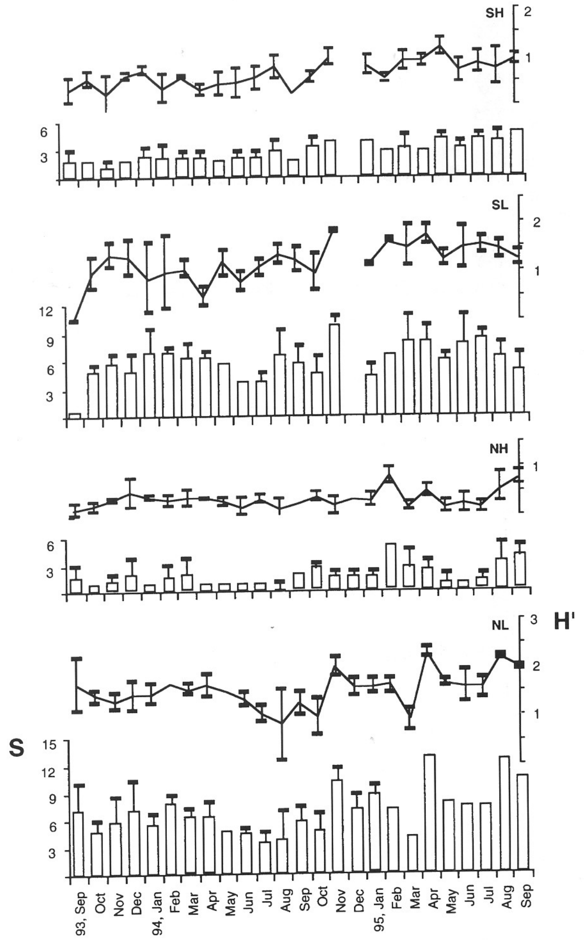

Figure 7. Monthly mean diversity at each intertidal level: number of species (S) + standard deviation; Shannon diversity index (H') ± standard deviation. Abbreviations as in Figure 6.

ber/October, decreasing towards the winter and spring, to be lower in late spring. This pattern basically followed the ones of *Corallina elongata* and *Jania crassa* which both showed large variations on their biomass over the sampling period, but were more abundant in autumn and had a low biomass in the late spring. In the upper intertidal (SH), the mean biomass was higher during the first sampling year, following the pattern of *Caulacanthus ustulatus*. It was higher in late autumn/winter, lower values of biomass occurring in August. In the second year, no clear pattern was apparent, although the higher values of biomass were observed in spring. In São Vicente, the upper level (NH) presented a clear pattern of seasonal changes in biomass, with the higher values occurring in spring and the lower ones being observed in late summer. A similar pattern was also observed for *Gelidium microdon*, the dominant species at this level. *Fucus*, the second most abundant seaweed in this community, was also important, being mainly responsible for the relatively high values of biomass observed in autumn/winter on the first year. In the lower intertidal (NL), large deviations were recorded but a pattern was nevertheless apparent: the biomass was higher in late summer/early autumn, and then decreased to a minimum in winter, increasing again towards spring and summer. The temporal variation in biomass of the three main species (*Centroceras clavulatum*, *Jania rubens*, *Corallina elongata*) coincided with the above described pattern.

In general, for the upper eulittoral, the lower values of biomass were always present in the summer (August/September), on both coasts. The opposite was observed for the lower eulittoral, where the biomass was higher in late summer/early autumn.

As expected, considering that most species are pluriannuals or perennial, a relative stability was observed on the species composition of the studied communities. In fact, although annual variations were observed both on the number of species and diversity (Figure 7), no seasonal pattern was detected at any

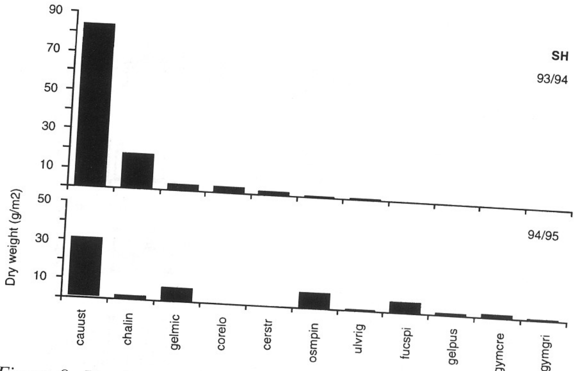

Figure 8. Yearly mean biomass of the main algal species collected on the upper eulittoral of São Roque (SH). For species abbreviations see Table 1.

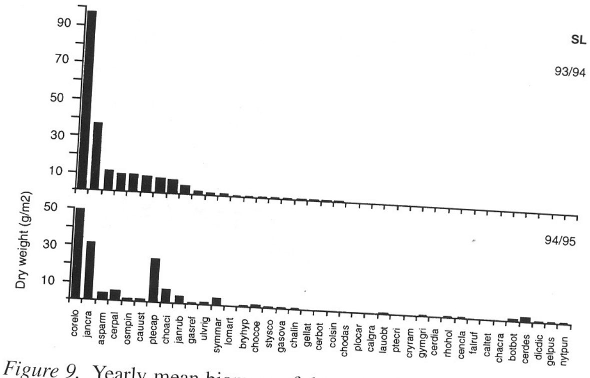

Figure 9. Yearly mean biomass of the main algal species collected on the lower eulittoral of São Roque (SL). For species abbreviations see Table 1.

level. The lower shore community at both localities contained generally more species throughout the year and a higher diversity.

With the exception of the north lower intertidal, no major differences were observed on the algal biomass of the dominant species between the two years (Figures 8–11). At São Roque, *Caulacanthus* was dominant on the upper level in both years (Figure 8), although more abundant on the first year, and responsible for the almost monospecific turf collected for most of the sampling period. At the low intertidal level (Figure 9), *Corallina elongata* and *Jania crassa* were the dominant species in both years, with the former being also much more abundant in the first year. During the second year, *Pterocladiella* became more abundant, being the third most abundant species, very similar to *J. crassa* in value. At São Vicente, *Gelidium microdon* was the dominant species of the upper level in both years (Figure 10), followed by *Fucus spiralis*. Differences were observed on their mean biomass between the 2 years, with the former remaining dominant dur-

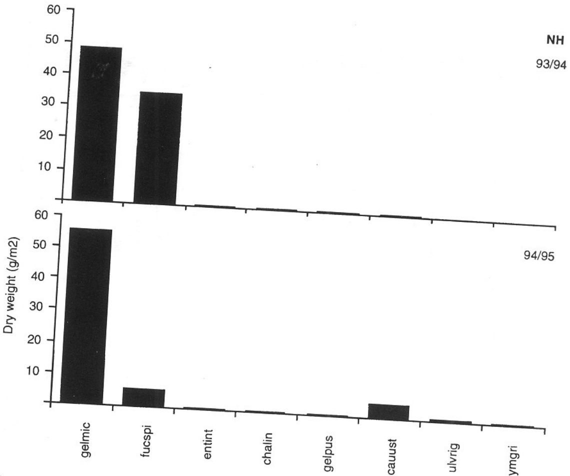

Figure 10. Yearly mean biomass of the main algal species collected on the upper eulittoral of São Vicente (NH). For species abbreviations see Table 1.

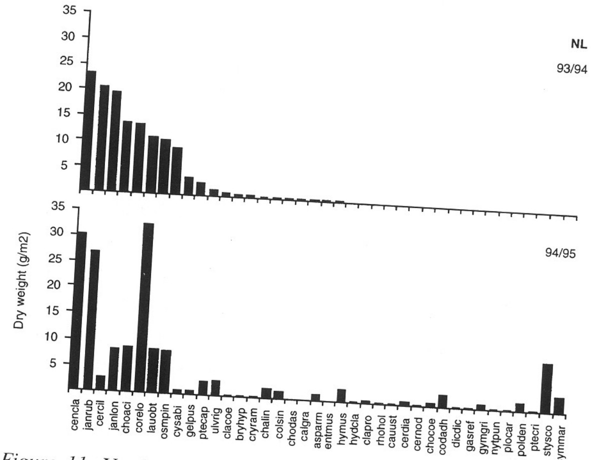

Figure 11. Yearly mean biomass of the main algal species collected on the lower eulittoral of São Vicente (NL). For species abbreviations see Table 1.

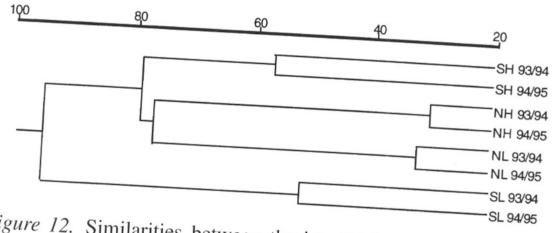

Figure 12. Similarities between the intertidal communities of the two successive years (cluster analyses based on the Euclidean distance). For abbreviations see Figure 6.

ing the second year, while the later decreased from the first to the second year. At the lower eulittoral (Figure 11), important differences were observed in the abundance of the dominant species between the 2 years. *Centroceras* and *Jania rubens* were very abundant in the turf in both years, being the dominant species on the first year and, respectively, the second and third more abundant species on the second year. *Ceramium ciliatum*, so important on the first year, was dramatically reduced on the second year, whereas *Corallina elongata*, not very important in the first year, become the dominant species in the second one. *Stypocaulon scoparium* (Linné) Kützing, not even present on the first year, showed a large increase of biomass on the second year. Despite these differences, a cluster analyses grouped together the two successive years of each level (Figure 12), thus indicating that differences between successive years in a given community are smaller than those between communities.

Discussion

Some of the intertidal zones present in this study are similar to those described by Conner et al. (1997) for Britain and Ireland and were provisionally identified as follows: (i) at upper eulittoral levels occurred the equivalent of the 'Barnacles & *Patella vulgata*' biotope (BP), although limpets are now rare on the shores of São Miguel; (ii) in shallow mid-littoral pools, 'coralline crusts & *Corallina*' (COR); iii) at lower eulittoral levels, the '*Corallina*' (RED.COR) and 'Red algal turf' (RED) biotopes were also common, together with COR. On the other hand, *Fucus spiralis*, although present, does not form such a distinct biotope (FSP) as is common on most shores in the North Atlantic. The sublittoral fringe at the study sites supports biotopes characterized by either *Corallina elongata*, *Pterocladiella capillacea*, *Asparagopsis armata*, *Centroceras clavulatum* and/or *Stypocaulon scoparium*, a very different situation from that occurring on northern Atlantic shores, where the large kelps are dominant. These large brown algae do not occur in the Azores intertidal.

The overall pattern of zonation found in the present study is quite different from that of Bermuda and other tropical areas within the Caribbean (see Van Loenhoud & Van de Sande, 1977; Thomas, 1985; Brattström, 1992), the Mediterranean (Pérès & Picard, 1964) and also from other areas of the North Atlantic (Stephenson & Stephenson, 1949, 1972; Southward, 1958; Pérès, 1967; Ardré, 1971; Lewis, 1972; Lubchenco, 1980; Mathieson et al., 1981; Norton, 1985, among many others). On the other hand, it is similar to the one occurring in Tenerife, also characterized by a littoral fringe dominated by littorinids, a eulittoral zone dominated by barnacles and two types of turf (the upper algal turf of *Caulacanthus ustulatus* and *Ulva* sp., and the lower turf of corallines), and a sublittoral fringe dominated by more frondose algae (see Lawson & Norton, 1971). The same general pattern was also found on the intertidal zone of Madeira Island (pers. obs.) and in other islands of the Azores (Larkum, 1960; Pryor, 1967; Neto & Tittley, 1995; Tittley et al., 1998).

This study adds a new algal zone (the *Fucus spiralis/Gelidium microdon* association) to the zonation pattern previously described for the littoral of São Miguel by Neto (1991, 1992). Recent personal observations showed that this zone is common in several other places on this island.

Elsewhere in the North Atlantic, *Fucus spiralis* is quite common higher up on the shore, where in sheltered and moderately exposed shores it can make a continuous and large belt (Lewis, 1972; Niemeck & Mathieson, 1976; Gayral & Cosson, 1986; Robertson, 1987; Hawkins & Jones, 1992). On exposed shores, if present, the plants are smaller and occupy only a small belt or are organized in patches (Gayral, 1966). In São Miguel, a different situation was observed, with larger patches of *Fucus* occurring in the more exposed north coast. A similar situation was observed by Lawson & Norton (1971) in Tenerife (Canary Islands), where *F. spiralis*, although restricted to small patches, was present on exposed rocks but it was absent on a sheltered zone of boulders nearby. *Gelidium microdon*, on the other hand, is quite common on the exposed Atlantic shores of France (Gayral, 1966), where it occurs in the lower eulittoral. In São Miguel, this species, when present, either forms a continuous belt (as in São Vicente) or small patches (as in São Roque) but always in the upper eulittoral, establishing the transition between the barnacles and the algal turf populations. This distinct habitat of *G. microdon* in São Miguel is probably related to the high interspecific competition for space known to occur in the Azorean shores (see Neto, 1997), associated to a good adaptation to widstand desiccation during the periods of emersion. Further surveys of the seashores around São Miguel Island and an evaluation of the main ecological parameters are needed to have a better understanding of the factors controlling the formation of this specific association.

The monospecific turf of *Caulacanthus ustulatus* has been also observed on the Atlantic coasts of France (Lebouché, 1957), and in the Canaries (Lawson & Norton, 1971). This species is adapted to withstand large emersion periods and tends to occur on exposed shores, where it extends up the shore to the upper intertidal (Lebouché, 1957). In Tenerife, it was mainly found below the barnacle zone, forming a distinct fringe (Lawson & Norton, 1971). Its lower limit is variable but *C. ustulatus* can be found within the lowest intertidal zone. In fact, although forming monospecific mats most of the time in France, *C. ustulatus* was also found associated with other species in the lower littoral zone (Lebouché, 1957). In the present study sites, these two situations were detected, mainly on the south coast**:** this species was present from the upper eulittoral (as a monospecific turf) down to the upper sublittoral fringe (as part of the multispecific coralline turf). It is a purely intertidal species, however (Lebouché, 1957), and this was confirmed in a parallel study (pers. obs.).

The *Corallina elongata* zone, found dominating the lower eulittoral zone, agrees with observations made elsewhere. This species also characterizes a very distinct community in the lower eulittoral and shallow subtidal levels of other geographic regions, e.g. the Spanish Atlantic coast (Sierra & Fernández, 1984), Mediterranean (Giaccone, 1970; Boudouresque, 1971; Verlaque & Tiné, 1979; Ballesteros, 1982, 1988; Ballesteros et al., 1984; Perera, 1986), the Canaries (Elejabeita et al., 1992; Pinedo et al., 1992; Reyes et al., 1994) and Madeira (Levring, 1974; Augier, 1985; Bianchi et al., in press; pers. obs.). This distribution is likely to be related to the survival strategies of this species. Its calcified thallus is particularly well adapted to environments with high wave action and abrasion (Vadas, 1977; Littler & Littler, 1980; Littler & Kauker, 1984; Ballesteros, 1988). These plants are also well able to resist grazing, and the compact mat formed retains water providing a suitable habitat including space for settlement and protection (Stewart, 1989). Many other species can grow as epiphytes and this ability seems to be very important on the Azorean littoral, which in most cases is very narrow in extent, thereby offering a reduced space for the settlement of propagules.

Only a few foliose and frondose algae were present in the intertidal, and only at the lower level. This is common on the Azorean shores, where the lower eulittoral zone is dominated by algal populations growing in a turf form. This type of growth seems to be a better adaptation both to the wave action in winter and desiccation in summer.

A certain degree of overlap between the different communities was observed at both study sites. This can be related to the small extent of the intertidal zone of the study sites, associated with the steep slope and the small tidal amplitudes that characterize Azorean shores. Additionally, this tidal regime, associated with the prevailing high wave action, causes short periods of emersion which allow the extension up the shore of species that usually occur further down.

At the study sites, there is at present low grazing activity. The sea-urchin *Paracentrotus lividus* Lamarck, although often occurring in large numbers in the algal turf zone, does not maintain bare areas, as seen in other places (see Lawrence, 1975; Hawkins & Hartnoll, 1983). These sea urchins are small and restricted to holes, and are only abundant where the rock is soft or if there are fissures and crevices. In hard rock with smooth surfaces, their presence is restricted to tide pools. They probably feed primarily on drift algae, which can be caught on their spines and transferred via pedicellaria to the mouth (Hawkins et al., 1990). Limpets (*Patella* spp.) used to be abundant at the eulittoral level of Azorean shores, but have recently been overexploited (Martins et al., 1987) in all the islands and, despite protective measures, do not seem to be able to recover to their original levels (Hawkins et al., 1990; pers. obs.). Overgrowth by the algal turf may be a delaying factor in the recovery of the limpet populations. Without the grazing activity of these organisms, the algal turf has developed dramatically and easily covered all the free space, leaving very few bare spaces. This dense algal cover may inhibit the colonization by sessile animals. This is probably also the reason why the barnacle *Chthamalus stellatus* did not extend to the lower eulittoral at the study sites. It may also help explain the difficulty in defining the boundary between the eulittoral and sublittoral fringe. This agrees with the observations of many researchers elsewhere (Dayton, 1971; Southward & Southward, 1978; Underwood, 1980; Underwood & Jernakoff, 1981; Hawkins & Hartnoll, 1983; Branch et al., 1992). The absence of herbivores would also allow subtidal algae to grow up into the lower intertidal (Southward & Southward, 1978). Experimental work in New South Wales (Australia) by Underwood (1980) revealed that the absence of herbivores in the eulittoral zone is followed by a rapid colonization by algae, extending upwards their normal limits of distribution. In these situations, the upper limit would be controlled by abiotic factors and the tolerance limits of each species, as discussed above.

The physiognomy of the two coasts was very similar, the major differences being more in terms of species dominance than composition. The same was observed on the western island of Flores (see Tittley et al., 1998), where the mid and lower eulittoral zones were covered by an algal turf, whose composition varied according to the location and vertical position on the shore. Upper littoral turfs were also dominated by *Caulacanthus*, as on São Miguel Island. Lower intertidal turfs were dominated by erect coralline algae and *Centroceras*, although *Laurencia* spp. were also important. An earlier expedition to Faial and Pico in July 1989 revealed similar communities (Tittley & Neto, 1994). Thus, it can be suggested that a basic pattern of littoral zonation and community organization probably occurs throughout the Azores archipelago, with local modifications.

The annual variation in total biomass followed, in general, the pattern of the dominant species of each community. At each level on the shore, these patterns presented concurrent periods of growth. At the upper eulittoral, the higher values of biomass were recorded in winter, when the wave action was higher and the air temperature and the number of hours of daylight were lower. The contrary was observed at the lower eulittoral, despite the known desiccation effect of high air temperature and number of hours of daylight caused in intertidal algae in the summer (cf. Lewis, 1972; Mishigeni, 1977). However, considering the small tide amplitude occurring on the Azorean shores and the narrow intertidal zone, the algal populations at this lower level are never exposed for long periods. Besides, the turf-growing form is also a good defense mechanism against desiccation (see Stewart, 1989). Without the problem of desiccation, the plants can grow when the light and temperature conditions are more favorable. Worth considering also the higher abrasive effect of wave action occurring in winter at the lower eulittoral, easily ripping plants from the rocks by erosion. On the other hand, in the upper eulittoral, plants are more exposed to the desiccation effect in the summer, and less exposed to the wave action in winter. This latter, causes higher humidity in the upper eulittoral, and is probably the responsible factor for the increase in biomass observed in that season, despite the shorter daylength and lower temperatures.

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