ORIGINAL ARTICLE

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Macroalgal species diversity and biomass of subtidal communities of São Miguel (Azores)

Abstract The benthic algal communities of two subtidal sites, located on opposite coasts of São Miguel Island (São Roque in the south and São Vicente on the north coast), were studied over a 2 year period (September 1993–September 1995). At both sites the sublittoral region was surveyed from low-tide level down to a depth of 15 m. Qualitative and quantitative changes are described. A depth-related gradient in species diversity and biomass was found at both localities. In general, red algae such as corallines and *Pterocladiella capillacea* predominated in the shallow sublittoral (5 m) while brown algae such as *Zonaria* and *Stypocaulon* were more abundant at 15 m. Multivariate analyses emphasized the existence at each study site of two communities (5 and 15 m depth), separated by a large transition zone. The 15 m community on the south coast site showed the largest number of species (52), whereas the lowest diversity (30 species) also occurred at this site in the 5 m community. A clear seasonal pattern of biomass change could be discerned only at São Vicente where the highest biomass was recorded in spring/summer. No major inter-annual variations could be detected, indicating relatively stable communities at least on a short-term basis.

Keywords Subtidal ecology · Rocky shores · Seasonality · Macroalgae · Azores

Introduction

Until recently the Azorean algal flora was poorly known, the published information (see revision in Neto 1994, 1997) being mostly the result of expeditions by visiting scientists and mainly focused on the intertidal region. There have been only few studies on the subtidal communities of the Azores (cf. Schmidt 1931; Neto and Tittley 1995; Tittley et al. 1998; Neto et al. 2000; Tittley and Neto 2000), all of them restricted to short periods of time. This is the first quantitative and long-term study of the Azorean subtidal algal communities.

The shallow rocky subtidal zone (0–30 m) has more seaweed species and greater macroalgal biomass than any other marine habitat (Foster et al. 1985). Nevertheless, until recently, subtidal algal communities have been relatively little studied (Anderson and Stegenga 1989) and quantitative approaches such as the present one are scarce. Little is known of the biotic associations and dynamics of these communities (John et al. 1977). Russell (1972) and Chapman (1973) have both suggested that it is necessary to use a quantitative and systematic approach in investigations of such communities if unifying concepts are to emerge. In the past, with only a few exceptions (e.g. Neushul 1967; Sanders 1968, 1969; Hughes and Thomas 1971; van den Hoek et al. 1975; Sears and Wilce 1975; Schiel and Foster 1986), investigations have been largely descriptive rather than quantitative and predictive. Worth mentioning are the studies on long-term changes in macroalgal communities of the Baltic-sea area (see revision in Middelboe and Sand-Jensen 2000). Although most of them were predominantly qualitative (e.g. Kukk and Martin 1992), some quantitative approaches were also developed (e.g. Lunälv et al. 1986; Breuer and Schramm 1988; Eriksson et al. 1988; Rönnberg and Mathiesen 1997; Johansson et al. 1998).

In general, stability was observed in littoral communities, although fluctuations and cyclic changes have been noted (John et al. 1977; Lewis 1977; Hartnoll and Hawkins 1985; Little and Kitching 1996). Changes along a depth gradient have been given in most descriptive studies of subtidal communities. John et al. (1977) concluded that these changes are related to factors such as light and water movement (wave-exposure) that are likely to be inversely related to increasing depth (Anderson and Stegenga 1989).

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Fig. 1 Location of the archipelago of the Azores on the North Atlantic (**A**); position of the island of São Miguel on the archipelago (**B**); location of the study sites on the island (**C**). Mean monthly values (±SD) of hours of sunshine (**D**, *top*) and surface seawater temperature (**D**, *bottom*) for the island of São Miguel (January 1993 to November 1995, data from INMG). The *dark line* (**D**, *bottom*) represents the day-length curve for the same period (data from OAL)
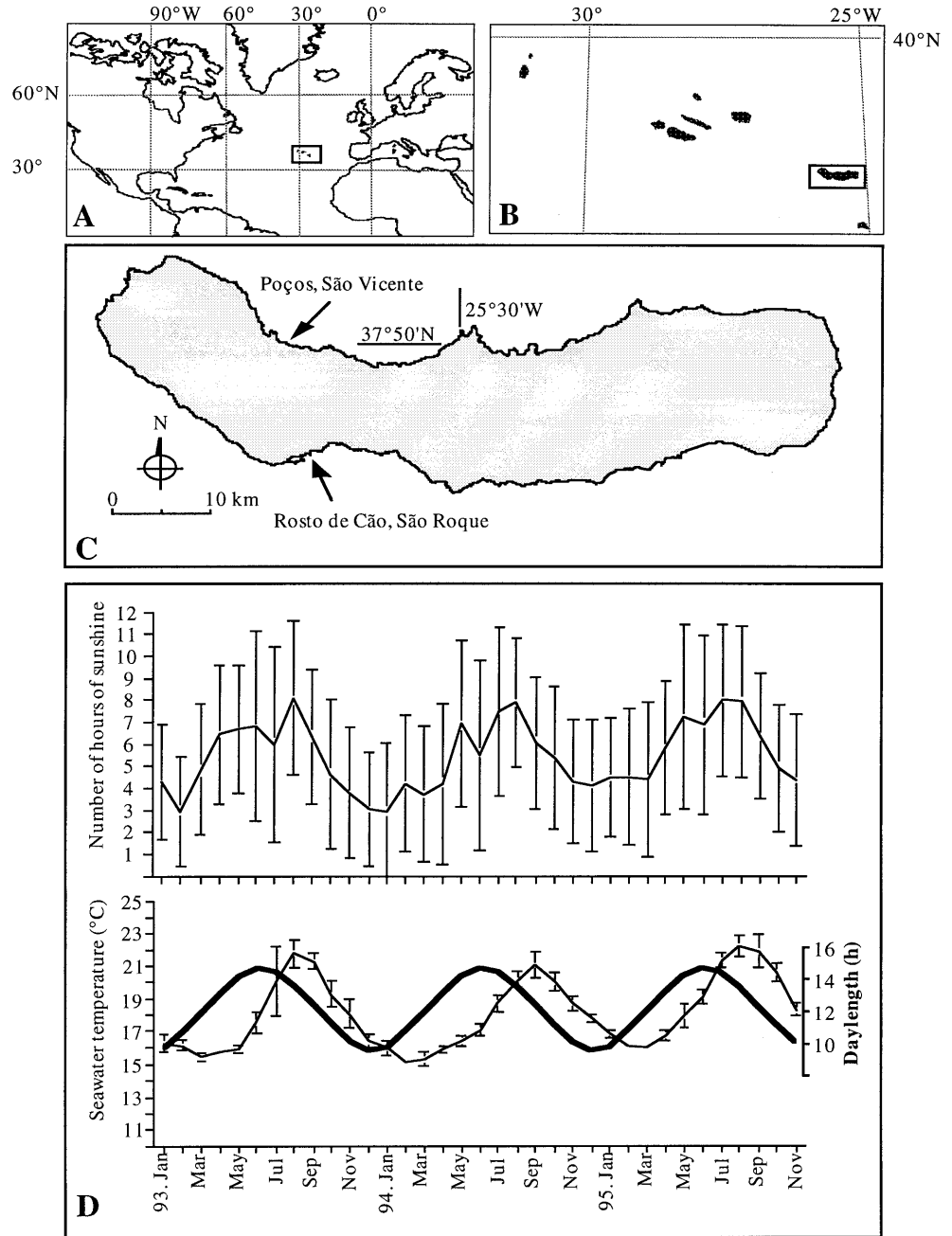
In the present study, the benthic algal vegetation of two bays of the littoral of São Miguel island is described and the effects of depth, geographic location (on the island) and time are analysed.

The island of São Miguel is located in the eastern group of the archipelago of the Azores between 37° and 40°N and between 25°and 31°W (Fig. 1). With an area of approximately 750 km², is the largest island of the archipelago. Like the others, it is formed of volcanic rocks (mainly basalt) and surrounded by very deep water (a depth of 1,000 m occurs a few kilometres offshore). The coastline is approximately 155 km in length and is generally of difficult access by land. In general the north coast is more exposed to the effects of wave action and swell (Instituto Hidrográfico 1981).

Methods

Two sites were selected on the open coast of São Miguel, one on the south coast (Rosto de Cão, São Roque) and another on the north coast (Poços, São Vicente). Both sites are located within bays enclosing relatively shallow waters, allowing easy access for diving, and are opposite to each other on the island (Fig. 1). The shallow subtidal zone of São Roque is characterized by a compact bedrock of hard basaltic rock, steeply sloping. At lower levels, patches of sand are overlain by large boulders and cobbles. At São Vicente the subtidal zone is a gently sloping bedrock, followed by

large cobble rocks, interspersed with many patches of sand. The algal communities of both sites are quite distinct and characterize both coasts of the island: the north with more luxuriant and frondose algae and the south coast where turf is the dominant form of algal growth.

The work was undertaken between September 1993 and September 1995. The field methodology involved monthly quantitative collections by scuba-diving. To investigate the possible effects of the depth gradient, three depth levels (5, 10 and 15 m below CD) were surveyed.

At each depth level, the sampling area covered approximately 1,000 m². Each collection consisted of three replicate samples of 50×50 cm each, collected at random. This sample size was determined for the studied communities by Neto (1997) using the species/area (Coppejans 1980; Vallmitjana 1987) and species biomass/area approaches (Bellan-Santini 1969; Sierra and Férnandez 1984). A sample consisted of the material obtained by carefully scraping with a chisel all the attached algae (excluding crusts) inside the quadrat into a labelled fine mesh bag. The location of each quadrat at each level was determined by successively reading from a table of random numbers two series of values, one for the azimuth and the other for the distance (up to 10 m). The azimuth was determined with an underwater compass and the distance with a measuring tape.

The algae were sorted into species and then weighed on an electronic top-pan balance, after the excess water had been removed by shaking the plants vigorously. The plants were then dried in an oven at 70°C until constant weight was attained to determine the dry weight for each species.

The classification and nomenclature in this study generally follows that adopted by South and Tittley (1986) with later modifications, mainly by Guiry (1997). Spellings and abbreviations of authors' names mainly follow Brummitt and Powell (1992). The recommendations of the ICBN (Greuter et al. 1994) were adopted.

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 and Coker 1996). The non-parametric Wilcoxon signed-rank test was used for comparisons following the methods of Snedecor and Cochran (1967) and Kent and Coker (1996). The usual level of significance of 5% was adopted. Floristic comparisons between the different sampling sites and levels were made by calculating their similarity. The Sørensen coefficient of similarity (S_S, also known as the Dice index), the Jaccard coefficient of similarity (S_J), and the dissimilarity coefficient of squared Euclidean distance (D_{ij}), were used (following the formulae in Kent and Coker 1996). The calculated similarity indexes were subjected, in most cases, to numerical multivariate analyses, as these are considered the best means of comparing samples in order to assess similarities and differences. Kent and Coker (1996) reviewed the use of such methods and their recommendations are followed here. The weighted-pairs method for cluster analyses with computer-assisted methods (NTSYS package; Rohlf 1994) was performed following Santelices and Abbott (1987), Ballesteros and Romero (1988), and Smith (1992). The different communities were classified using the two-way indicator species analyses (TWINSPAN) following Anderson and Stegenga (1989), and Kooistra et al. (1989).

Meteorological information for the years 1993–1995 was obtained from Instituto Nacional de Metereologia e Geofísica (INMG) and Observatório Astronómico de Lisboa (OAL). The mean monthly values of the seawater temperature (Fig. 1) were minimum in February and March (15/16°C) and maximum in August and September (22/23°C). In the same period the monthly mean hours of sunshine (Fig. 1) were a minimum of 3 h/day in winter (December to February) and a maximum of 8 h/day in summer (July/August), while the mean monthly values of daylength (Fig. 1) were minimum (10 h) in December and January and maximum (15 h) in June.

Results

Community structure and floristic analyses

Subtidal communities from both São Roque and São Vicente, and at the three depth levels on each coast, varied both in species composition and dominance. In total, 71 species (10 Chlorophyta, 15 Phaeophyta, 46 Rhodophyta) were recorded (Table 1). The 15 m level at São Roque possessed the highest number of species (52), the lowest number (30) being present in the 5 m level at the same site. At São Vicente, no major differences were observed in the number of species amongst the three depth levels.

Differences in species composition and abundance were more marked at São Roque. Here, the 5 m level was dominated by erect coralline algae (*Corallina elongata* and *Jania* spp.) which continued down to the 10 m level where they were also dominant species, together with *Stypocaulon scoparium* (Fig. 2A). At 15 m depth, the coralline algae lost their importance and the brown algae *S. scoparium* and *Dictyota dichotoma* were the dominant species. Other noteworthy species were *Pterocladiella capillacea* at 5 m depth, *Symphyocladia marchantioides* at 10 and 15 m depths, and *Asparagopsis armata* at all depth levels. In São Vicente, dominance was shared by a larger number of species (Fig. 2A). At 5 m, although *S. scoparium* was the most abundant species (15%), *A. armata*, *Hypnea musciformis* and *P. capillacea* were only slightly less abundant. At 10 m depth, *H. musciformis* became the dominant species, followed by *A. armata*, *S. marchantioides*, *Sphaerococcus coronopifolius* and *Zonaria tournefortii*. This latter species increased its abundance with depth to be the dominant species at the 15 m depth community and was responsible for 29% of the total mean biomass. Other noteworthy species included *S. marchantioides* and *S. scoparium*.

A depth-related gradient was observed in the community composition of both sites (Fig. 2B). This gradient was more distinct at São Roque where the erect coralline algae, dominant at 5 and 10 m, were rare at 15 m depth. On the other hand, *S. scoparium*, a species with low biomass at 5 m, became more abundant with depth to be the dominant species at 15 m. In São Vicente, a more gradual transition was observed between the two shallower levels with *S. scoparium* and *P. capillacea* losing their importance with depth, while *H. musciformis* and *S. marchantioides* gradually became more abundant. *Asparagopsis armata* was the second most important species at both levels, while *Zonaria*, absent at 5 m, became increasingly abundant with depth and was the dominant species at 15 m, followed by *Symphyocladia* and *Stypocaulon*. *Sphaerococcus* was most abundant at 10 m. On both coasts there was a clear dominance of the red algae at the shallower levels, while the brown algae dominated the 15 m depth levels.

A cluster analyses, based on the Euclidean distance between the various depth levels of both coasts, separated the 5 m level at São Roque from all the other levels

Table 1 List of species and stages and their mean dry weight (g/m^2) at each subtidal level. *5mS* São Roque 5 m; *10mS* São Roque 10 m; *15mS* São Roque 15 m; *5mN* São Vicente 5 m; *10mN* São Vicente 10 m; *15mN* São Vicente 15 m

		Abbre-viation	São Roque (S)			São Vicente (N)		
			5mS	10mS	15mS	5mN	10mN	15mN
Chlorophycota								
Anadyomene stellata	(Wulfen) C. Agardh	anaste						0.7
Bryopsis hypnoides	J.V. Lamouroux	bryhyp	0.0	0.0	1.0	0.3	0.0	0.0
Cladophora coelothrix	Kützing	clacoe		0.2	0.5	3.6	0.4	0.2
Cladophora laetevirens	(Dillwyn) Kützing	clalae	1.1	0.8	1.1	1.4	0.2	0.5
Cladophora prolifera	(Roth) Kützing	clapro	0.0	0.7	0.5	1.5	0.5	0.2
Codium adhaerens	C. Agardh	codadh	0.0	0.0				
Codium decorticatum	(Woodward) Howe	coddec		0.0	0.0			
Codium elisabethae	O.C. Schmidt	codeli	2.2	10.0	10.4	1.3	9.9	3.3
Ulva rigida	C. Agardh	ulvrig	4.1	2.3	1.6	7.6	3.4	0.9
Valonia utricularis	(Roth) C. Agardh	valutr	1.3	1.3	0.9	0.2	0.3	0.5
Number of Chlorophycota		**10**	**7**	**9**	**8**	**7**	**7**	**8**
Phaeophycota								
Carpomitra costata	(Stackhouse) Batters	carcos			0.2			
Cladostephus spongiosus	(Hudson) C. Agardh	claspo		0.0	0.7	0.3		
Colpomenia sinuosa	(Mertens ex Roth) Derbès et Solier	colsin	0.3	4.6	5.4	4.1	1.2	1.0
Cystoseira abies-marina	(S. G. Gmelin) C. Agardh	cysabi		3.3	6.2	2.7	2.9	3.9
Cystoseira foeniculacea	(Linné) Greville	cysfoe		0.2	0.2			
Dictyopteris polipodioides	(De Candole) J. V. Lamouroux	dicmem			0.1		0.8	
Dictyota dichotoma	(Hudson) J. V. Lamouroux	dicdic	0.8	20.6	25.7	17.6	17.2	21.6
Halopteris filicina	(Grateloup) Kützing	halfil		1.3	2.8	2.2	0.5	1.2
Hydroclathrus clathratus	(Bory ex C. Agardh) Howe	hydcla		0.0		0.0		
Padina pavonica	(Linné) Thivy	padpav		1.0	0.0	3.4	1.3	0.0
Sargassum vulgare	C. Agardh	sarvul		0.5	2.2			
Stypocaulon scoparium	(Linné) Kützing	stysco	6.3	49.0	83.5	109.0	37.2	44.5
Stypopodium zonale	(J. V. Lamouroux) Papenfuss	styzon		0.2				
Taonia atomaria	(Woodward) J. Agardh	taoato		0.6	1.3	0.2	7.4	5.7
Zonaria tournefortii	(J. V. Lamouroux) Montagne	zontou	3.1	14.8	2.5	13.0	45.6	139.5
Number of Phaeophycota		**15**	**4**	**13**	**13**	**10**	**9**	**8**
Rhodophycota								
Acrosorium venulosum	(Zanardini) Kylin	acrven	0.0		0.8			0.2
Aglaothamnion bipinnatum	(P. Crouan et H. Crouan) Feldmann-Mazoyer	aglbip		0.6	3.2			
Aglaothamnion hookeri	(Dillwyn) Maggs et Hommersand	aglhoo			0.1			
Anotrichium barbatum	(C. Agardh) Nägeli	anobar						0.2
Asparagopsis armata	Harvey	asparm	57.9	23.6	17.5	103.9	57.6	43.5
Bornetia secundiflora	(J. Agardh) Thuret	borsec			0.0			
Callithamnion corymbosum	(J. E. Smith) Lyngbye	calcor		0.7	2.6	0.5		0.1
Centroceras clavulatum	(C. Agardh) Montagne	cencla		0.9	0.3	8.0	1.1	0.8
Ceramium echionotum	J. Agardh	cerech	0.0			0.3		
Chondracanthus acicularis	(Roth) Fredericq	choaci	6.1	10.5	4.9	45.7	14.1	3.3
Chondracanthus teedii	(Roth) Kützing	chotee	0.0				1.2	
Corallina elongata	J. Ellis et Solander	corelo	384.2	91.8	4.7	70.2	25.1	8.6
Cryptopleura ramosa	(Hudson) Kylin ex L. Newton	cryram	1.5	2.5	1.6	2.1	1.4	2.5
Dasya hutchinsiae	Harvey	dashut		0.1	0.9	0.6	0.5	0.7
Erythrodermis traillii	(Holmes ex Batters) Guiry et Garbary	erytra			0.2			
Falkenbergia rufolanosa stadium	(Harvey) F. Schmitz	falruf		0.4	2.9			
Gastroclonium reflexum	(Meneghini ex Zanardini) Kützing	gasref	0.0	0.3	0.2	0.3	0.2	
Gelidium latifolium	(Greville) Bornet et Thuret	gellat	0.0		0.4			
Griffithsia corallinoides	(Linné) Batters	gricor			0.2			
Hypnea musciformis	(Wulfen) J.V. Lamouroux	hypmus	8.3	22.0	6.4	90.3	58.9	38.5
Hypoglossum hypoglossoides	(Stackhouse) Collins et Harvey	hyphyp		0.0	0.5	0.4		0.2
Jania adhaerens	J.V. Lamouroux	janadh		6.7				
Jania capillacea	Harvey	jancap					1.7	1.4

Table 1 (continued)

|	Abbreviation	São Roque (S)			São Vicente (N)		
		5mS	10mS	15mS	5mN	10mN	15mN
Jania longifurca	Zanardini	janlon	130.0	41.8	3.6	25.2	13.5	1.5
Jania rubens	(Linné) J.V. Lamouroux	janrub			4.0	40.1	6.0	5.7
Jania verrucosa	J.V. Lamouroux	janver	107.5	45.3				
Kallymenia reniformis	(Turner) J. Agardh	kalren				0.3		
Laurencia viridis	Gil-Rodríguez et Haroun	lauvir				0.5		
Osmundea pinnatifida	(Hudson) Stackhouse	osmpin		0.0	0.0	0.0	0.3	
Liagora viscida	(Forskål) C. Agardh	liavis		0.0				
Mastocarpus stellatus	(Stackhouse) Guiry	masste			0.0		0.3	
Nytophyllum punctatum	(Stackhouse) Greville	nytpun		0.7	1.0	0.6	0.0	
Peyssonelia squamaria	(Gmelin) Decaisne	peysqu	0.0			0.9	6.9	3.5
Phyllophora crispa	(Hudson) P. Dixon	phycri						
Plocamium cartilagineum	(Linné) Dixon	plocar	18.4	10.9	8.5	59.5	36.7	42.3
Polysiphonia atlantica	Kapraun et J. N. Norris	polatl						0.0
Polysiphonia foetidissima	Cocks ex Bornet	polfoe						0.4
Polysiphonia fucoides	(Hudson) Greville	polfuc		0.0	0.2			0.5
Pterocladiella capillacea	(Gmelin) Santelices et Hommersand	ptecap	70.0	8.8	10.0	81.5	29.0	23.8
Pterothamnion crispum	(Ducluzeau) Nägeli	ptecri	3.2	2.7	0.6	3.6	2.8	2.0
Pterothamnion plumula	(Ellis) Nägeli	pteplu	0.0	0.0				0.4
Rhodymenia holmesii	Ardissone	rhohol	1.1	5.2	5.0	5.1	1.5	0.2
Spermothamnion repens	(Dillwyn) Rosevinge	sperep			0.2			
Sphaerococcus coronopifolius	Stackhouse	sphcor			0.4	3.1	46.9	14.7
Sphondilothamnion multifidum	(Hudson) Nägeli	sphmul						0.0
Symphyocladia marchanthioides	(Harvey) Falkenberg	symmar	11.2	24.4	18.3	49.9	48.6	57.7
Number of Rhodophycota		**46**	**19**	**25**	**31**	**24**	**22**	**26**
Total number of species		**71**	**30**	**47**	**52**	**41**	**38**	**42**

(Fig. 3A top). The second dichotomy separated the other shallow water level (5 m N). The third division grouped the deeper levels of each site separately. The TWINSPAN analyses of the same data (Fig. 3A bottom) produced different groupings: the first dichotomy separated the north from the south; the second dichotomy separated, in the north, the 5 m level from the deeper ones, and in the south, the 15 m level from the shallower ones. The presence/absence matrix of the same data was also analysed and this also produced different groupings. The cluster analyses using Sorensen's Index of Similarity (Fig. 3B top), also separated the 5 m S level from all the others in the first place, but included the 10 and 15 m levels of this coast in one group and all the north coast levels in another. The TWINSPAN analyses of the same data produced a similar grouping but at different levels (Fig. 3B bottom). The first dichotomy separated the two deeper levels of the south coast from all the others, and only the second dichotomy separated the 5 m S from the north levels.

Changes over time

No clear pattern was seen on the temporal changes in biomass of the south coast communities but a seasonal pattern was observed on the north coast (Fig. 4A). For the 5 and 10 m depth levels at São Roque, the mean biomass was lower during the first sampling year but the difference was not significant (Wilcoxon test: 13, 11 pairs, $P>0.05$; Wilcoxon test: 14, 11 pairs, $P>0.05$, respectively). At the 15 m depth the fluctuations in the total mean biomass were always less pronounced, and again no clear pattern was apparent. As expected, no correlation was seen among the algal biomass and the seawater temperature or the number hours of daylight ($r=0.01$ and 0.22, respectively, 21 degrees of freedom (df), $P>0.05$). In São Vicente a pattern was evident with maximum values of biomass occurring in spring (1994) or summer (1995) at the three depth levels and lower biomass occurring in late winter (5 and 10 m depth) or late autumn (15 m depth). The maxima and minima of algal biomass, daylength and seawater temperature generally coincided. The correlation between the mean algal biomass and those environmental variables was always positive, whether significant (number of hours of light, $r=0.55$, 21 df, $P<0.01$) or not (seawater temperature, $r=0.31$, 21 df, $P>0.05$). The seasonality observed at São Vicente is reinforced by the coincidence of seasonal growth patterns of the dominant species at each level. All of them exhibited higher values in spring (*A. armata*, *P. cartilagineum*, *S. marchantioides*), early summer (*S. scoparium*, *H. musciformis*, *S. coronopifolius*, *Z. tournefortii*) or late summer (*P. capillacea*).

Fig. 2 Relative mean biomass of the main algal species (**A**) and depth-related differences in species abundance based on average biomass (**B**). For species abbreviations see Table 1
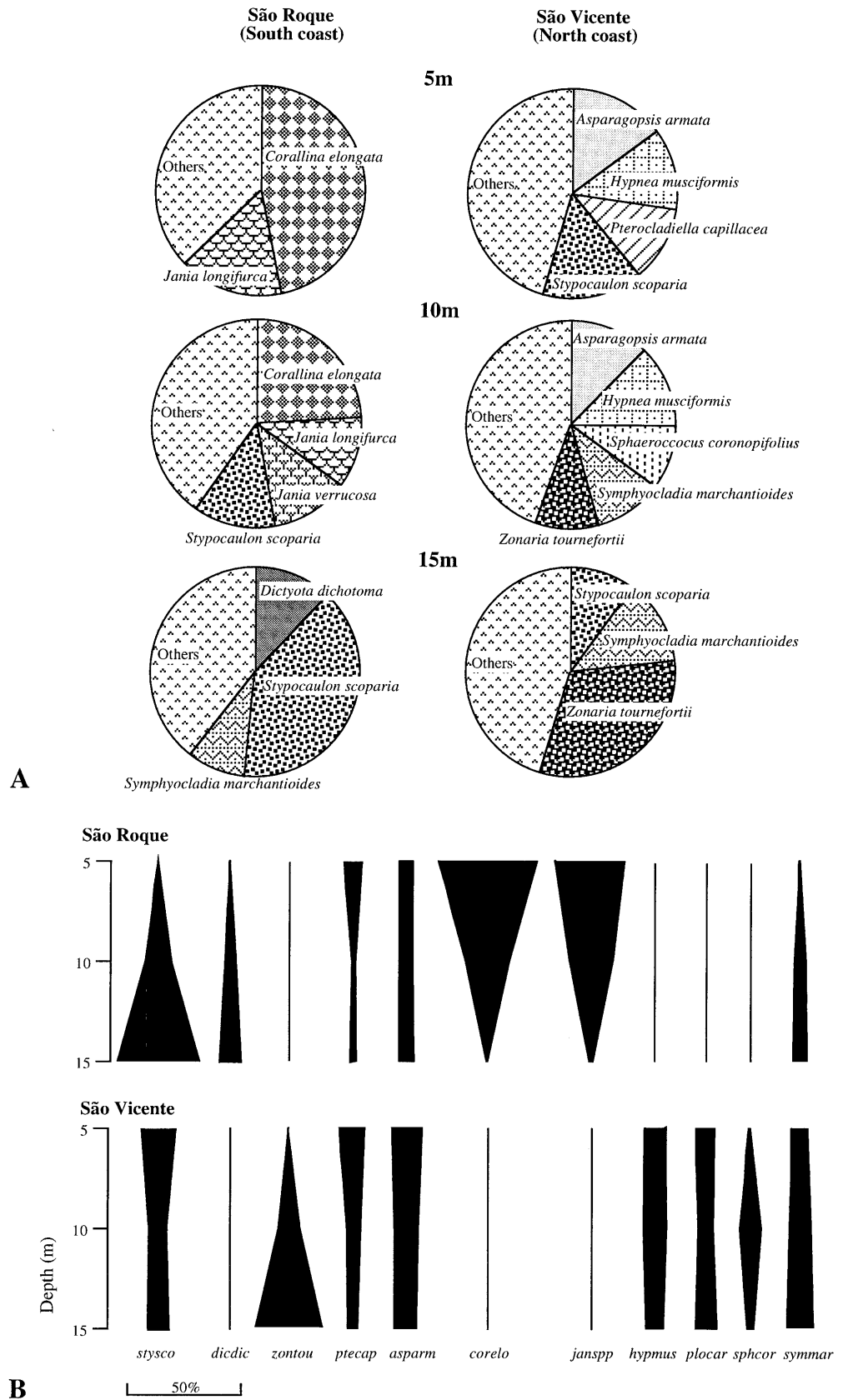
Fig. 3 Multivariate analyses of the species-abundance matrix (**A**): cluster analyses, based on the Euclidean distance (*top*); TWINSPAN (*bottom*). Multivariate analyses of the species presence/absence matrix (**B**): (*top*) cluster analyses, based on Sørensen's index of Similarity; (*bottom*) TWINSPAN. For site abbreviations see Table 1
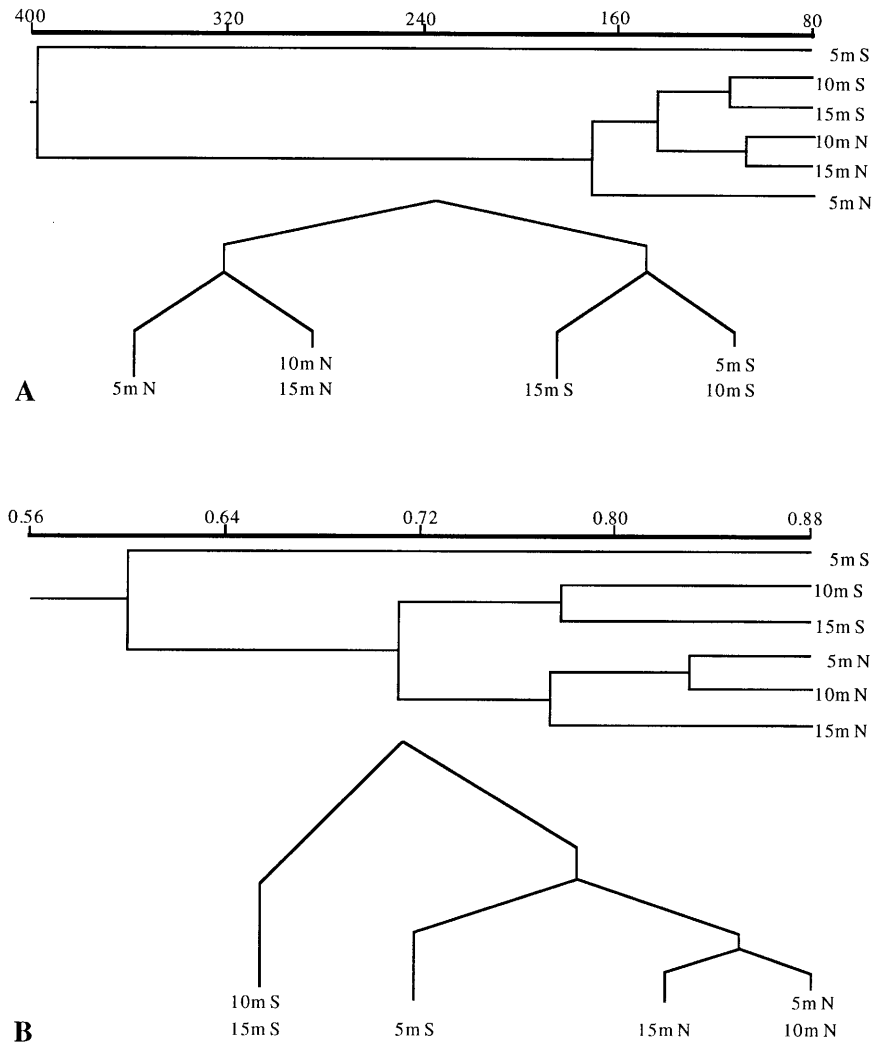
No pattern was found in the temporal variation of the mean diversity and mean number of species over the 2 year period at any of the studied communities (Fig. 4B). At São Roque there were large variations in these patterns throughout the year at all levels. The mean monthly number of species varied between 3 and 12 at 5 m, 9 and 17 at 10 m, and 4 and 18 at 15 m depth, the latter being the level with the highest diversity. In São Vicente the mean number of species was never less than 5 at any level. Large variations on both number of species and diversity occurred over the sampling period but no major differences were detected between the three depth levels.

Although differences existed in the algal biomass of the dominant/more important species between the two sampling years, the structure of the algal communities was similar (Table 2). At São Roque, the 5 m level was dominated by *Corallina elongata* in both years, although in the second year *Jania* spp., *Pterocladiella capillacea* and *Asparagopsis armata* became more important. At the 10 m depth, *Stypocaulon scoparium*, the dominant species in the first year, was replaced in the second year

by *C. elongata* (the second most important species in the first year) and *Jania* spp. At 15 m depth, *S. scoparium* was the dominant species for the whole sampling period, especially during the second year. Variations were observed in the biomass of other species between the two years: in general, the mean biomass of *D. dichotoma* and *P. cartilagineum* decreased in the second year, while that of *A. armata*, *C. elisabethae*, *H. musciformis* and *S. marchantioides* increased. In São Vicente differences were observed at 5 and 10 m in the biomass of the more important species between the two years. At 5 m depth, *Asparagopsis* was the dominant species in the first year, followed by *S. scoparium*, *Plocamium cartilagineum* and *Hypnea musciformis*, but in the second year *S. scoparium* and *H. musciformis* were co-dominant. At 10 m depth, dominance was distributed among more species, and the relative abundance of each changed in the second year. By contrast, at the 15 m depth, *Zonaria tournefortii* was the dominant species in both years, followed by *S. marchantioides*.

Despite such temporal differences, a cluster analyses grouped together the two successive years of each level

Fig. 4 Monthly changes in algal biomass (mean ± SD, the *line* is the level 3 moving average, **A**) and diversity (number of species: S ± SD; Shannon diversity index: H' ± SD, **B**)
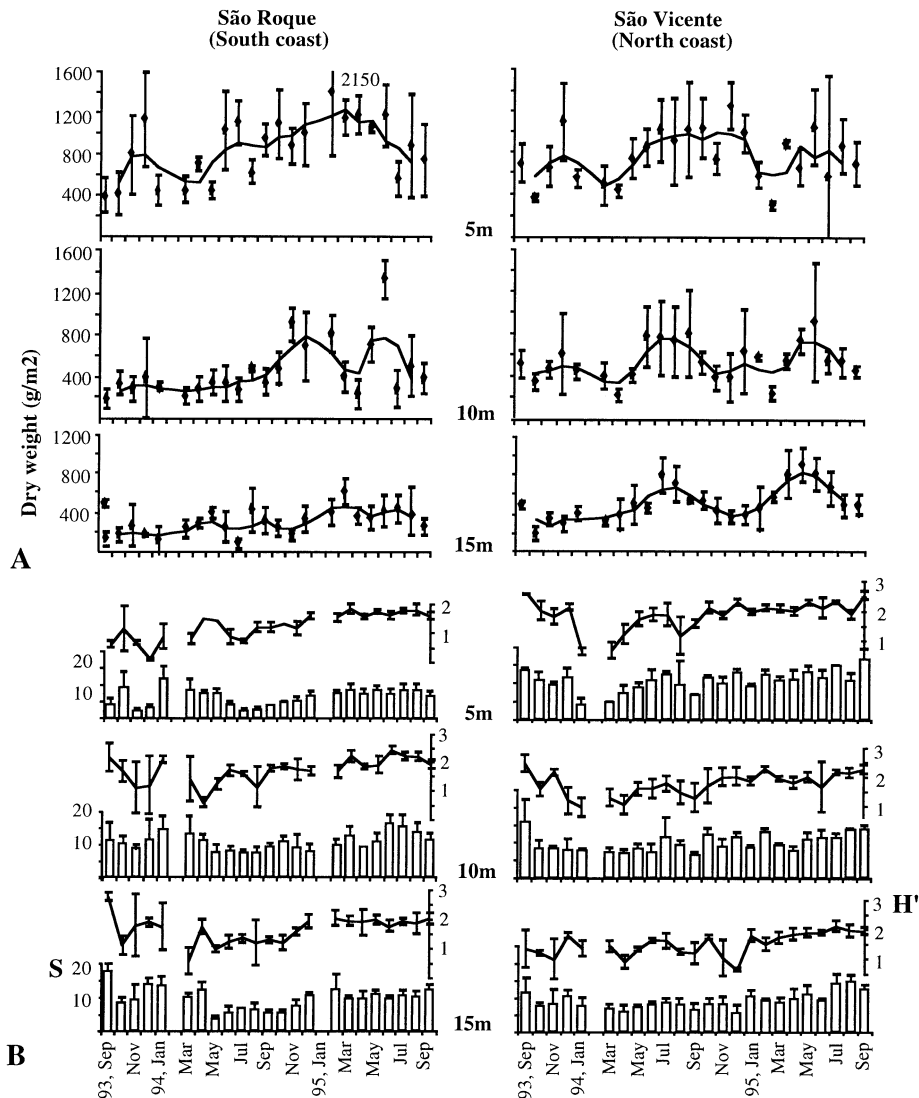

Table 2 Mean dry weight (g/m^2) of the dominant species at both years at all depth levels

	São Roque (S)						São Vicente (N)					
	5mS		10mS		15mS		5mN		10mN		15mN	
	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2
Asparagopsis armata	34.2	79.7	14.6	31.9	19.4	15.7	110.0	98.3	59.1	56.1	36.4	50.0
Codium elisabethae	0.8	3.5	9.8	10.3	4.4	15.9	0.0	2.6	12.1	8.0	2.7	3.8
Corallina elongata	403.7	366.2	60.0	121.2	3.8	5.5	59.8	79.7	21.9	28.1	8.0	9.2
Dictyota dichotoma	0.1	1.4	21.9	19.3	26.1	25.3	13.4	21.4	12.9	21.2	17.1	25.7
Hypnea musciformis	0.0	15.9	1.1	41.3	0.0	12.3	64.0	114.6	44.0	72.8	25.4	50.6
Jania spp.	165.9	303.6	28.0	154.7	5.8	9.3	32.9	95.1	11.8	30.0	3.2	13.4
Plocamium cartilagineum	23.6	13.6	6.4	15.0	8.7	8.4	78.2	42.1	42.7	31.1	51.7	33.7
Pterocladiella capillacea	15.3	120.6	3.8	13.5	8.3	11.6	61.7	99.9	21.2	36.2	14.9	32.0
Stypocaulon scoparia	2.4	9.9	78.8	21.5	65.8	100.0	98.6	118.6	26.7	46.9	32.1	56.0
Symphyocladia marchanthioides	0.9	20.7	14.9	33.2	6.5	29.3	43.6	55.7	49.1	48.2	53.9	61.2
Zonaria tournefortii	2.4	3.8	16.9	12.9	2.4	2.6	11.3	14.7	46.4	44.7	116.1	161.0

Fig. 5 Similarities between the subtidal communities of the two successive years (cluster analyses based on the Euclidean distance)
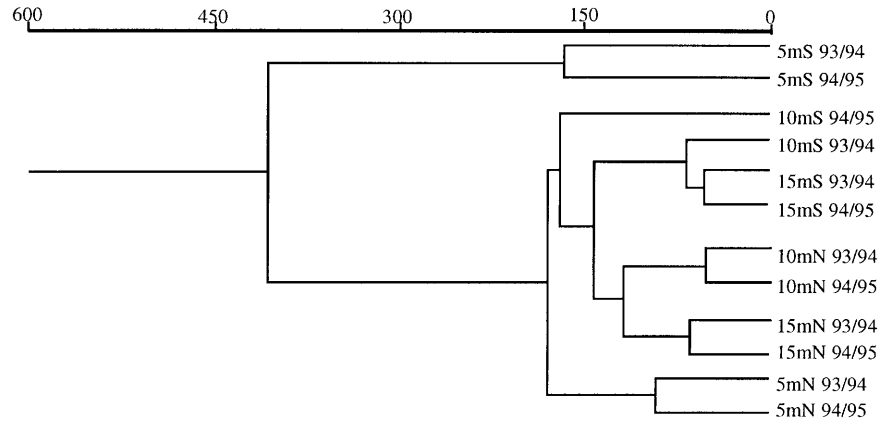
(with the exception of 10 m S, Fig. 5), thus indicating that temporal differences are smaller than those between depth levels.

Discussion

Qualitative and quantitative differences were found between the two localities on opposite coasts of the island and, within these, according to depth. The statistical analyses performed produced groupings that are based primarily on the geographic position (separating firstly the south site form the north), and secondarily on the depth levels occurring at each site. A depth gradient of species abundance and diversity was also observed on these analyses: some grouped the 5 and 10 m levels, others grouped the 10 and 15 m, but the 5 and 15 m levels were never grouped together. These results suggest the occurrence of four distinct communities: with a shallower (5 m) and a deeper water (15 m) community at each site. At both sites the transition between these communities is gradual both in species composition and abundance. The main effect of depth was the relative abundance of the different species rather than their presence or absence. Nevertheless some species were present only at the shallowest levels (e.g. articulated coralline algae) and others only at the deeper ones (e.g. *Zonaria tournefortii*). Such a change along a depth gradient has been reported in most descriptive studies of subtidal communities and John et al. (1977) suggested that it is related to factors such as light and water movement (wave-exposure) that are likely to be inversely related to increasing depth. The restriction to shallow water of certain species is probably related to changes in the quantity and quality of light, associated with increased depth (Anderson and Stegenga 1989). Conversely, the restriction to deeper water of many other species may be due either to intolerance to rough, turbulent water, or to an inability to compete with the abundant shallow-water plants and/ort to withstand high irradiation and UV.

The different distribution of red and brown algae observed in the present study is noteworthy, with the red algae dominating the shallower levels and the brown algae dominating the deeper levels on both coasts. Subtidal luxuriant communities of brown algae have been found elsewhere; *Z. tournefortii* is an abundant species in Mediterranean subtidal communities (Garcia Carrascosa 1987), where *Dictyopteris membranacea* is also dominant (Ballesteros et al. 1984; Boisset and Garcia Carrascosa 1987; Morri et al. 1988; Balduzzi et al. 1994). In the Azores, Neto and Tittley (1995) mention *Zonaria tournefortii* as being restricted to deep water (30 m) on the island of Faial. Further studies at São Vicente revealed the occurrence of this species down to at least 40 m (Neto et al. 2000).

The differences observed between north and south are likely to be related to the different physiognomy of the shores, and to the stronger influence of sand in the south. The extensive Corallinaceae-dominated turfs that in the present study dominated the 5 and 10 m communities at São Roque are also known to occur elsewhere in places where sand and wave action can have an abrasive effect, e.g. in France (Boudouresque 1971), in the Mediterranean (Giaccone 1970; Verlaque and Tine 1979; Ballesteros et al. 1984; Ballesteros 1988; Perera 1986), in the Canaries (Pinedo et al. 1992; Reyes et al. 1994) and in Madeira (Augier 1985). In the Azores, this type of turf has also been found dominating the lower eulittoral of exposed coasts in the islands of Faial (Neto and Tittley 1995), Flores (Tittley et al. 1998) and São Miguel (Neto 2000a). On the north coast, the absence of the abrasive effect of sand allows algae such *Zonaria* and *Stypocaulon* to establish relatively stable populations. Once established, they outcompete other species, such as *Corallina* spp., that have lower growth rates (Neto 2000b).

The annual variations observed in total mean biomass followed, in general, the pattern of the dominant species of each community. The decrease in biomass detected in the communities in the winter months is probably related to the high wave action that occurs then. Plants are ripped from the rocks by erosion and the combined accelerational and drag forces caused by wave action (Gaylord et al. 1994). On the other hand, it can also be a function of the autoecophysiology of the dominant species. As has been shown in many studies, perennial mac-

roalgae have a clear seasonality of growth and rest that is often triggered by the environmental factors photoperiod and temperature. This was observed for many Azorean algal species by Neto (2000b). The decrease in biomass in winter can thus be considered as a combined effect of the ecophysiology and of erosion.

As expected, considering the perennial nature of the dominant species, no major differences in species composition and abundance were observed over the 2 year investigation period. In fact, surveillance of rocky shores over several years elsewhere, especially in temperate regions of the North Atlantic, indicate general stability of littoral communities, although fluctuations and cyclic changes have been observed (Lewis 1977; Hartnoll and Hawkins 1985; Little and Kitching 1996). The same phenomenon has also been observed in Ghana by John et al. (1977). It is now important to continue this present study for a longer period so as to be able to evaluate long-term fluctuations. This should be complemented by monitoring the major environmental parameters. Global climate change and other related variations in environmental factors make it difficult to predict how the communities will be in 20 years time.

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