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Observations on the Biology and Ecology of Selected Macroalgae from the Littoral of São Miguel (Azores)

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The dominant benthic algal species from two sites, located on opposite coasts of the island of São Miguel, Azores (São Roque in the south and São Vicente on the north coast) were studied over a two-year period (September 1993–September 1995). From both sites monthly collections were made in the intertidal zone and in the adjacent subtidal zone down to a depth of 15 m. The algae occur under different ecological conditions, a few species being restricted to the intertidal zone (*Fucus spiralis*, *Gelidium microdon*, *Jania crassa*, *Caulacanthus ustulatus* and *Chondria coerulescens*), while others (*Codium elisabethae*, *Zonaria tournefortii*, *Jania verrucosa* and *Sphaerococcus coronopifolius*) were exclusively present subtidally. Other species were present at both levels. Differences were observed between the two sites. A few species (*Chaetomorpha linum*, *Corallina elongata* and *Caulacanthus ustulatus*) were more abundant at São Roque, their presence on the north being only sporadic or occasional. On the other hand, *Fucus spiralis*, *Gelidium microdon*, *Sphaerococcus coronopifolius* and *Centroceras clavulatum* were statistically more abundant at São Vicente. Seasonal changes were seen in the growth and/or reproduction of certain species, with many (*Ulva rigida*, *Bryopsis hypnoides*, *Stypocaulon scoparium*, *Dictyota dichotoma*, *Padina pavonica*, *Colpomenia sinuosa*, *Gelidium microdon*, *Asparagopsis armata*, *Chondracanthus acicularis* and *Plocamium cartilagineum*) having larger plants and/or higher values of biomass in spring and/or summer. With the exception of *Dictyota dichotoma* that was statistically more abundant in the second sampling year, no differences were observed on the species abundance between the two years. Reproductive phenology varied according to species, with many (*Fucus spiralis*, *Ulva rigida*, *Gelidium microdon*, *Jania rubens*, *Sphaerococcus coronopifolius*, *Caulacanthus ustulatus*, and *Plocamium cartilagineum*) having prolonged fertile periods. Some species were more seasonal in their reproduction, being fertile only over two seasons: *Codium elisabethae* and the tetrasporophyte of *Asparagopsis armata* in autumn and winter; *Cystoseira abies-marina* and *Pterocladiella capillacea* in summer and autumn; the gametophyte of *Asparagopsis armata* in winter and early spring. A few had a more restricted fertile period: *Chaetomorpha linum* and *Jania verrucosa* in summer; *Chondracanthus acicularis* in autumn.

Introduction

The Azorean algal flora was poorly known until very recently. The published information (Neto 1994, 1997) was mostly the result of expeditions by visiting scientists restricted to short periods of time, and mainly focused on the intertidal region. The published floristic studies revealed a mixed flora with a strong component of cold water species together with a few tropical and subtropical elements (Neto 1997). Recent ecological studies (Neto *et al.* 2000) revealed the ecological importance of some algal species on the Azorean intertidal and shallow subtidal communities. The present paper is the result of two years of investigation and includes information about thirty of the more abundant species in the littoral communities of the island of São Miguel. It is the first long-term study of the biology and ecology of littoral algae from the Azores.

Material and Methods

The archipelago of the Azores comprises nine volcanic islands and several small islets organized into three separate groups (eastern, central and western), and is located between the coordinates 37° to 40°N and 25° to 31°W (Fig. 1). The islands are surrounded

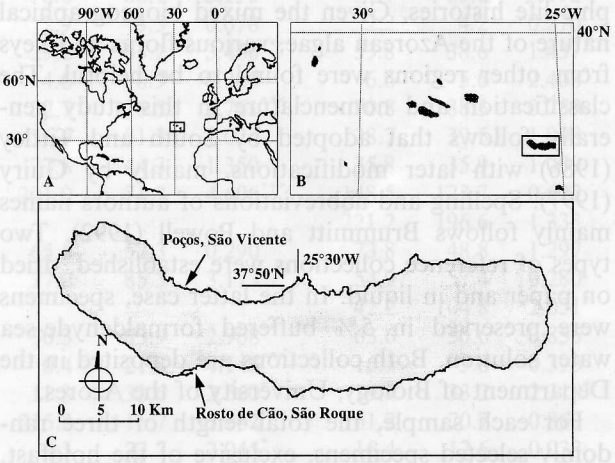

Fig. 1. Location of the Archipelago of the Azores in the Atlantic (A); position of the island of São Miguel in the Archipelago (B); location of the study sites in the island of São Miguel (C).

by very deep water, a depth of 1000 m occurring within a mile or two off shore. The island of São Miguel, of approximately 750 km^2, is the largest of the archipelago. The coastline is mostly of difficult access by land and subject to swell and surge most of the year.

Research was undertaken between September 1993 and September 1995 in two sites selected on the open coast of São Miguel (Fig. 1), one on the south coast (Rosto Cão, São Roque) and the other on the north coast (Poços, São Vicente). Both sites were located within bays enclosing relatively shallow waters, permitting easy access for shore work and for diving, and are opposite to each other on the island.

The field methodology involved monthly collecting at both intertidal and subtidal levels. Collections were done by carefully scrapping with a chisel all the attached algae inside pre-determined areas (100 cm^2 for the intertidal and 2500 cm^2 for the subtidal, Neto 1997) into labelled cloth bags. At the intertidal, the collections were made in the eulittoral zone and six random replicates were taken on each occasion. At the subtidal, the collections were made between 5 and 15 m depth and nine replicates were collected at random on each sampling occasion. The location of each quadrat was determined by reading from a table of random numbers the azimuth and the distance (up to 1 m for the intertidal, up to 10 m for the subtidal).

In the laboratory, the algae were sorted into species. Whenever possible the material was checked the same day, otherwise the samples were kept in the refrigerator overnight. Samples that could not be examined alive were preserved in 5% buffered formaldehyde-sea water solution (Nezelof *et al.* 1972). Identification of species was based on morphological and anatomical characters and reproductive structures. This is usually a difficult task, as many algal species are known to be polymorphic, exhibiting variable phenotypes according to their environmental conditions. Furthermore, many species have heteromorphic life histories. Given the mixed biogeographical nature of the Azorean algae, various floras and keys from other regions were found to be helpful. The classification and nomenclature in this study generally follows that adopted by South and Tittley (1986) with later modifications, mainly by Guiry (1997). Spelling and abbreviations of authors names mainly follows Brummitt and Powell (1992). Two types of reference collections were established, dried on paper and in liquid. In the latter case, specimens were preserved in 5% buffered formaldehyde-sea water solution. Both collections are deposited in the Department of Biology, University of the Azores.

For each sample, the total length of three randomly selected specimens, exclusive of the holdfast, was recorded. For specimens with a different morphology (e. g. *Codium elisabethae*), the maximum diameter was recorded. Plants were dried in an oven at 70°C, until constant weight was attained. The dry weight (henceforth considered a synonym of biomass) of each species was then determined on an electronic top-pan balance. For the purposes of further analysis, the average biomass over all quadrats at each sampling level was used.

From a database containing the monthly biomass averages of each species at each site and level, comparisons were made between shore levels (intertidal versus subtidal), sites (north versus south) and sampling years (93/94 versus 94/95). Sequential, paired comparisons, were done, using the Mann-Whitney signed rank test (following Snedecor and Cochran 1967). This non-parametric technique was chosen to circumvent the non-normality of the data. All observations in both groups to be compared (e. g. all the monthly biomass averages of the intertidal versus those of the subtidal) are put in a single array, tagged so that their original group can be distinguished, and sorted. Ranks are then assigned to the combined array. The smaller sum of ranks and the number of observations in each group are then used to calculate the approximate normal deviate Z, from which the significance probability is obtained. To minimize the probability of a Type I error, given that nearly 90 tests were performed, a significance level of 0.1% was chosen.

Meteorological information was obtained for the years 1993–1995 from the Instituto Nacional de Metereologia e Geofísica (INMG). The daily mean hours of sunshine are minimum in December and maximum in June/July (Bettencourt 1979). In the period from 1993 to 1995 the minimum values (3 hours) occurred in winter (December to February)

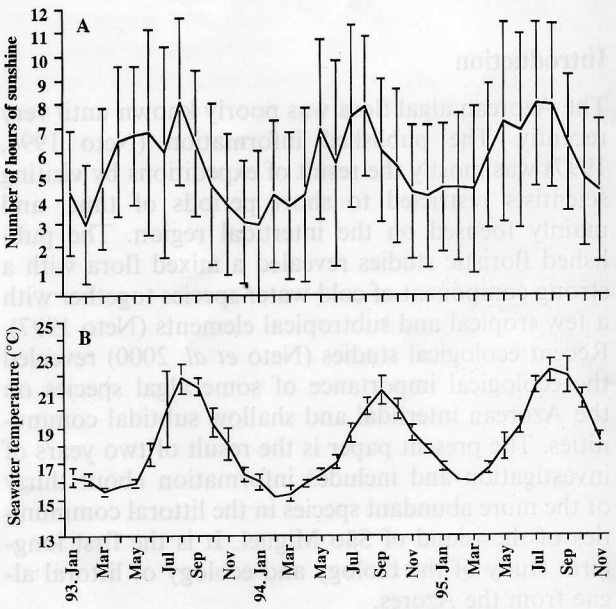

Fig. 2. Mean monthly values (± standard deviation) of hours of sunshine in São Miguel (A) and mean monthly number (± standard deviation) of the surface seawater temperature (B) for the period between January 1993 and November 1995.

and the maximum (8 hours) in summer (July/August, see Fig. 2). The mean monthly values of the seawater temperature were minimum (15/16°C) in February/March and maximum (22/23°C) in August/September (Fig. 2).

Results

The thirty more abundant species of benthic marine algae (5 Chlorophyceae, 8 Phaeophyceae and 17 Rhodophyceae) occurring at the locations surveyed were studied. Observations on the biology (data on the seasonality and reproduction) of each species are given. Comments on seasonality and reproduction in other locations in the Atlantic Ocean, based on the available literature, are also included.

Chlorophyceae

Ulva rigida C. Agardh

Ulva rigida was frequent in the intertidal and subtidal levels at both sites, although more significantly abundant intertidally (Table I). The length of the plants varied between 1.5 and 18 cm, the larger plants being present in summer and the smaller ones in autumn/winter on both coasts. Reproductive plants were found throughout the year in the intertidal, while at the subtidal level they were found only in May and October at São Roque, and in May, June and August at São Vicente.

Remarks: Recently reported in the Netherlands (Koeman and van den Hoek 1980), this species is distributed generally in the North Atlantic Ocean, probably more commonly than indicated by the records (Gayral 1966, Irvine 1982, Tittley *et al.* 1985 a, b, Wynne 1985, Anadón and Fernández 1986, Boudouresque *et al.* 1992, Cabioc'h *et al.* 1992). In the British Isles, plants are common during the summer months and may be present all year round. Reproductive plants have been found in summer, but details of reproductive seasonality are not known (Burrows 1991). Further south, this species has also been recorded throughout the year in Morocco (Gayral 1958), Madeira (Levring 1974), the Canaries (Børgesen 1925) and in Tropical West Africa (Lawson and John 1982).

Table I. Average algal biomass (per species, g/m^2) at each shore level, site and sampling year. Significance levels of comparisons are also given (Z-values from a Mann-Whitney signed rank test, with probability levels 5, 1 and 0.1% indicated respectively by *, **, and ***). See text for further details.

	Shore level			Sites			Year		
	Intertd.	Subtd.	Z	South	North	Z	93/94	94/95	Z
Ulva rigida	25.0	4.1	**5.640*****	13.6	15.9	0.987	9.6	20.1	1.938
Chaetomorpha linum	18.9	1.0	**5.475*****	25.3	6.8	**4.130*****	18.7	7.3	0.365
Cladophora prolifera	14.0	0.7	**3.420*****	0.4	7.5	2.009*	7.3	2.9	1.529
Bryopsis hypnoides	2.5	0.4	0.956	2.0	0.9	1.400	1.6	1.3	0.900
Codium elisabethae	Subtidal only			7.3	5.0	1.418	6.0	6.2	0.101
Halopteris filicina	0.5	1.9	1.671	1.3	1.1	0.234	0.7	1.7	1.014
Stypocaulon scoparia	32.7	72.3	**6.693*****	32.7	35.5	1.460	38.2	30.0	0.588
Dictyota dichotoma	1.3	16.9	**6.719*****	8.1	10.0	0.660	8.0	10.1	**4.066*****
Padina pavonica	1.4	1.1	0.620	0.5	1.5	1.150	0.9	1.5	0.070
Zonaria tournefortii	Subtidal only			6.6	66.1	**5.170*****	37.1	35.6	0.192
Colpomenia sinuosa	3.8	2.6	0.332	2.9	3.5	0.078	2.2	4.2	0.270
Fucus spiralis	Intertidal only			29.2	63.2	**3.450*****	53.8	38.6	1.437
Cystoseira abies-marina	10.7	3.9	0.874	4.6	6.9	0.200	6.6	5.6	2.408*
Gelidium microdon	Intertidal only			32.7	126.5	**3.761*****	70.8	88.3	0.759
Pterocladiella capillacea	32.1	36.1	0.933	36.9	31.3	1.024	28.7	39.5	1.908
Asparagopsis armata	24.3	47.4	1.820	27.8	44.3	1.350	35.8	35.9	1.099
Corallina elongata	179.1	93.2	1.395	201.0	71.3	**4.606*****	148.5	123.7	0.627
Jania crassa	Intertidal south only						221.2	196.6	1.333
Jania longifurca	88.5	34.2	0.686	65.5	57.3	0.290	73.8	48.8	1.297
Jania rubens	102.5	9.8	**6.719*****	27.0	85.3	3.173**	54.9	57.4	0.280
Jania verrucosa	Subtidal south only						42.2	104.8	2.051*
Chondracanthus acicularis	100.5	13.7	**6.062*****	30.3	83.9	2.968**	63.6	50.6	0.855
Sphaerococcus coronopifolius	Subtidal only			0.4	21.8	**4.145*****	16.3	5.8	0.393
Hypnea musciformis	8.9	35.0	1.574	11.8	33.6	2.560*	19.4	33.2	2.318*
Caulacanthus ustulatus	Intertidal only			215.2	16.7	**5.262*****	161.2	70.7	0.869
Plocamium cartilagineum	0.9	28.2	**6.456*****	6.3	22.7	2.045*	16.4	12.6	0.033
Centroceras clavulatum	34.1	2.0	**3.325*****	4.9	31.1	**3.624*****	11.5	24.6	1.492
Chondria coerulescens	Intertidal only			22.2	3.1	2.278*	5.2	20.1	2.095*
Osmundea pinnatifida	44.5	0.5	**7.018*****	27.6	17.5	0.673	25.9	19.2	0.361
Symphyocladia marchantioides	13.0	34.2	**3.709*****	13.3	34.0	2.903**	19.2	28.0	2.493*

Chaetomorpha linum (O. F. Müller) Kützing

Significantly more abundant at the intertidal level of São Roque (Table I), this species was present throughout the sampling period at all levels. The length of the plants sampled ranged from 2.5 to 10 cm. Fertile plants were only found from June to September 1995 at São Roque, indicating that reproduction takes place in summer.

Remarks: Attached and unattached plants are abundant in spring and summer, but occur at any time of the year in the British Isles (Burrows 1991) and along the northeastern coast of North America (Taylor 1957). Gametes have been recorded in attached plants, mainly from April to August, and zoospores mainly from August until November (Price 1967), but fertile plants can be found all year round (Knight and Parke 1931). Common in spring in the Aegean Sea (Athanasiadis 1987). Collected from November to July at Cadiz, Spain (Seoane-Camba 1965) and between autumn and spring from mainland Portugal (Ardré 1970). Plants of this species were collected in Madeira all year round (Levring 1974).

Cladophora prolifera (Roth) Kützing

Significantly more abundant in the intertidal and at São Vicente than at São Roque (Table I), this species was present throughout the sampling period in the intertidal. It occurred occasionally at the subtidal level of both sites. The mean biomass varied between 5 and 50 g/m^2 and the length of the plants observed was between 1.5 and 6 cm. Reproductive plants were found in July and October 1994, and between February and April 1995, indicating that reproduction takes place throughout the year.

Remarks: This species is probably present throughout the year in the British Isles but most of the records refer to the summer months (Burrows 1991). Also it is more abundant in the summer in the Gulf of Gascogne (Hamel 1924). It was collected in March and from July to December at Cadiz, Spain (Seoane-Camba 1965) and throughout the year from mainland Portugal (Ardré 1970), Madeira (Levring 1974) and Canaries (Børgesen 1925). Production of swarmers has not been reported for the British Isles (Burrows 1991). Van den Hoek (1963) found biflagellate swarmers on a few occasions in plants from France and Spain, and he reported that they germinate directly to form new plants. Funk (1955) found young plants in August and September at Naples.

Bryopsis hypnoides J. V. Lamouroux

This species was present at all levels sampled. Never abundant, it was more common at the southern intertidal site, where plants were present for much of the sampling period, the biomass being greatest in November 1994 and February 1995. Plant lengths varied between 3 and 7.5 cm, the larger plants being collected in spring. Elsewhere, only a few, smaller plants were collected, which resulted in lower values for biomass and size. At São Roque fertile plants were found throughout the year in the intertidal, and in April and February in the subtidal; at São Vicente only one fertile plant was seen in January 1995, from the intertidal level.

Remarks: Present most of the year in the British Isles, but most conspicuous in the spring, sexual plants were observed between May and September (Burrows 1991). Also noted as common along the northeastern coasts of North America (Taylor 1957), this species was collected between April and June from mainland Portugal (Ardré 1970).

Codium elisabethae O. C. Schmidt

This species was equally common at both localities (Table I) but was restricted to the sublittoral and often in clusters. It was collected throughout the sampling period. At both study sites plants were similar in size, up to 8 cm in diameter. Fertile plants were found in October, December and February, indicating that reproduction of this species takes place in autumn/winter.

Phaeophyceae

Halopteris filicina (Grateloup) Kützing

Present at all levels sampled, this species was never abundant, its mean monthly biomass never exceeding 17 g/m^2. The length of plants did not vary much at São Roque (4 to 7.5 cm). At São Vicente, plants were generally larger (5 to 11.5 cm). Most plants were sporophytes, with unilocular sporangia.

Remarks: This species is generally distributed in the Atlantic Ocean, probably more commonly than indicated by the records (Børgesen, 1926, Seoane-Camba 1965, Gayral, 1958, 1966, Ardré 1970, Levring 1974, Afonso-Carrillo and Sansón, 1999). It was collected in all seasons from mainland Portugal (Ardré 1970).

Stypocaulon scoparium (Linné) Kützing

Present at both levels, this species was clearly more abundant in the subtidal (Table I). At this level, it was collected throughout the sampling period, its mean biomass being higher in the spring and summer months (Fig. 3). As with *Halopteris*, plants at São Vicente were larger (up to 11 cm) than at São Roque (usually less than 5 cm). Intertidal plants with unilocular sporangia were collected between April and December at São Roque, and from December to February at São Vicente. In the subtidal, unilocular sporangia were seen from January to August at São Roque, and in October at São Vicente.

Remarks: It was present all year round in the Aegean Sea (Athanasiadis 1987), Spain (Seoane-Camba 1965, Anadón and Fernández 1986), mainland Portugal (Ardré 1970), Madeira (Levring 1974) and Canar-

ies (Børgesen 1926). Reproductive plants with unilocular sporangia were found in November in the Aegean Sea (Athanasiadis 1987), in February from mainland Portugal (Ardré 1970) and in January on the Canaries (Børgesen 1926).

Dictyota dichotoma (Hudson) Lamarck

This species was present on both sites, being significantly more abundant at the subtidal level (Table I). In the intertidal, it was more common at São Vicente, where plants were collected for most of the year, the largest plants (nearly 8 cm in length) occurring in late spring and summer. In the subtidal *Dictyota* was collected throughout the sampling period on both coasts, the higher biomass values occurring in late spring to early summer (Fig. 4). Only sporophyte plants were collected at São Roque in the intertidal (March and June 1995), whereas at São Vicente both generations were present. Here, diploid plants were collected between December and July. Female gametophytes, with sori of oogonia, occurred in March and one male plant, with antheridial sori, was collected in November 1994. Both generations were collected subtidally at the two sites. In São Roque, sporophytes were found for much of the year (October to July). Female gametophytes were found in November, February, March and August, while only one male plant was collected, in June 1995. At São Vicente sporophyte plants were also found, from October to July. Female thalli were present in August and December but no male plants were found at all.

Remarks: This is a common species in Florida (Earle 1969), British Isles (Fritsch 1945), Aegean Sea (Athanasiadis 1987), Asturias, Spain (Anadón and Fernández 1986), mainland Portugal (Ardré 1970) and Madeira (Levring 1974), where it can be seen all year, although more abundant in summer. Sporophyte plants have been recorded throughout the year from Wales (Williams 1898), in April and July at Cadiz, Spain (Seoane-Camba 1965) and from March to October from mainland Portugal (Ardré 1970). Price and Tittley (1978) recorded sporophyte plants on the Island of Mull in August and September, and sexual plants in June.

Padina pavonica (Linné) Thivy

Only frequent in the intertidal at São Vicente, this species was also present in the subtidal level at both stations. In the intertidal, plants were collected throughout the sampling season, except for the period from October 1993 to February 1994. Small plants were present in late winter, their size increasing in spring and summer. Although frequent, this species was never abundant, its mean monthly biomass being less than 12 g/m^2. Subtidal specimens of *Padina* were restricted to summer (June–October) at both sites. The largest plants were about 6–7 cm in length from all locations. Only sporophytic plants were found. In the intertidal they were present throughout the year, while subtidally they were only seen in summer/earlier autumn (July–October).

Remarks: The genus *Padina*, although widespread in the Atlantic Ocean (Seoane-Camba 1965, Gayral 1966, Ardré 1970, Levring 1974), is particularly abundant in the Mediterranean Sea (Carter 1927, Gayral 1966, Athanasiadis 1987). Sporophyte plants of *P. pavonica* were collected in spring in the Aegean Sea (Athanasiadis 1987), in summer and autumn on mainland Portugal (Ardré 1970) and all year round on Madeira (Levring 1974).

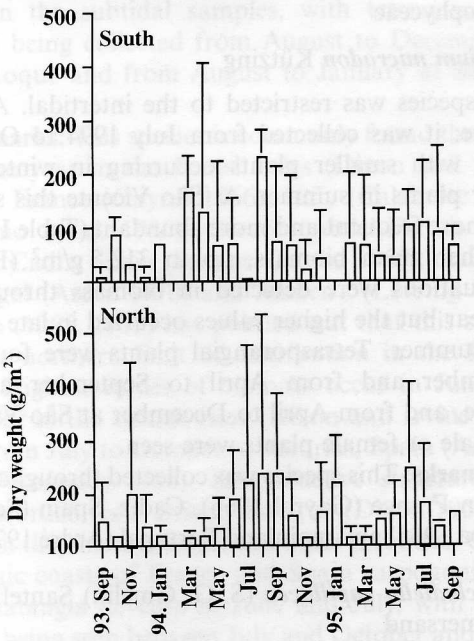

Fig. 3. Monthly biomass (mean + standard deviation) of *Stypocaulon scoparium* at the subtidal level of both sites.

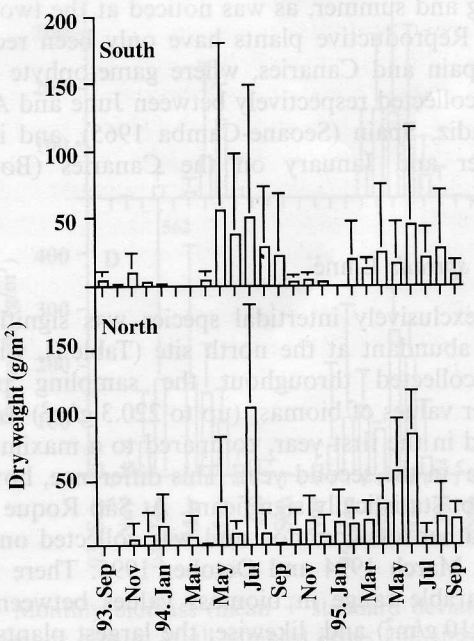

Fig. 4. Monthly biomass (mean + standard deviation) of *Dictyota dichotoma* at the subtidal level of both sites.

Zonaria tournefortii (J. V. Lamouroux) Montagne

Restricted to the sublittoral, this species was significantly more abundant in the north (Table I), where it was one of the dominant species. The plants were also larger at São Vicente, usually over 10 cm in length. Most plants displayed sori of unilocular sporangia with paraphyses, representing the sporophyte generation. Gametophyte plants, all female, were only found at São Vicente in December, February, April, May and August.

Remarks: This species was collected on Madeira throughout the year (Levring 1974). On the Canaries plants of this species were only found in January (Børgesen 1926).

Colpomenia sinuosa (Mertens *ex* Roth) Derbès *et* Solier

This species was present in the intertidal and sublittoral at both localities. Collected from April to October at São Roque and throughout the year at São Vicente, it was never abundant. On both coasts the larger plants (nearly 7 cm broad) were found in spring and summer. Most of the material collected was reproductive, forming sori of biseriate plurilocular sporangia, intermingled with unicellular paraphyses.

Remarks: This species is widely distributed in warmer seas (Lawson and John 1982). Although the species was collected only in spring and summer in the Gulf of Mexico (Earle 1969), it was collected throughout the year in the Aegean Sea (Athanasiadis 1987), Cadiz, Spain (Seoane-Camba 1965), mainland Portugal (Ardré 1970) and Morocco (Gayral 1958). In all these places, the larger plants and the correspondingly higher values of biomass were found in spring and summer, as was noticed at the two study sites. Reproductive plants have only been recorded for Spain and Canaries, where gametophyte plants were collected respectively between June and August at Cadiz, Spain (Seoane-Camba 1965), and in December and January on the Canaries (Børgesen 1926).

Fucus spiralis Linné

This exclusively intertidal species was significantly more abundant at the north site (Table I), where it was collected throughout the sampling period. Higher values of biomass (up to 220.3 g/m^2) were recorded in the first year, compared to a maximum of 50 g/m^2 in the second year. This difference, however, was not statistically significant. At São Roque *Fucus* was rather less common and was collected only between March 1994 and October 1995. There was a comparable range in biomass values between sites (21–210 g/m^2) and, likewise, the largest plants were similar in length, c. 9 cm. All the plants examined possessed hermaphrodite conceptacles.

Remarks: This species was collected in all seasons at Cadiz, Spain (Seoane-Camba 1965), mainland Portugal (Ardré 1970), Morocco (Gayral 1958) and the Canaries (Børgesen, 1926). It is present in many other places in the North Atlantic Ocean but no information has been found on its seasonality. Conceptacles were observed in summer in Canada (Robertson 1987) and on the northeastern coasts of America (Niemeck and Mathieson 1976, Mathieson and Guo 1992), between March and November on the Isle of Man (Knight and Parke 1931), in spring in France (Gayral 1966), from spring to early autumn on mainland Portugal (Ardré 1970) and in winter in Morocco (Gayral 1958). São Miguel seems to be the only place where conceptacles have been seen throughout the year. It is worth noting that European plants are bigger than those from this study, e. g. up to 30 cm in Norway (Rueness 1977) and to 40–50 cm on Helgoland (Kornmann and Sahling 1977).

Cystoseira abies-marina (S. G. Gmelin) C. Agardh

Present at all levels sampled, this was a common species at São Vicente, but only in tide pools, being collected over most of the sampling period. The length of plants varied between 3.5 and 39.5 cm and its mean biomass was likewise variable, ranging from 1.3 to 141.1 g/m^2. Subtidal plants were only collected in the summer and autumn. Hermaphrodite conceptacles were found in summer on subtidal plants and on one intertidal plant collected in December 1994.

Remarks: This species was collected at all seasons on Madeira (Levring 1974) and on the Canaries, where it is fertile in winter (Børgesen 1926). The Azores are the northern limit in distribution of this Macaronesian species.

Rhodophyceae

Gelidium microdon Kützing

This species was restricted to the intertidal. At São Roque, it was collected from July 1994 to October 1995, with smaller plants occurring in winter and larger plants in summer. At São Vicente this species was more frequent and more abundant (Table I), with a higher mean biomass, up to 312.5 g/m^2 (Fig. 5). Fluctuations were detected in biomass throughout the year but the higher values occurred in late spring and summer. Tetrasporangial plants were found in December and from April to September at São Roque, and from April to December at São Vicente. No male or female plants were seen.

Remarks: This species was collected throughout the year in France (Gayral 1966), Cadiz, Spain (Seoane-Camba 1965) and mainland Portugal (Ardré 1970).

Pterocladiella capillacea (S. G. Gmelin) Santelices *et* Hommersand

This species was collected throughout the sampling period at both levels. Intertidally, it was slightly more

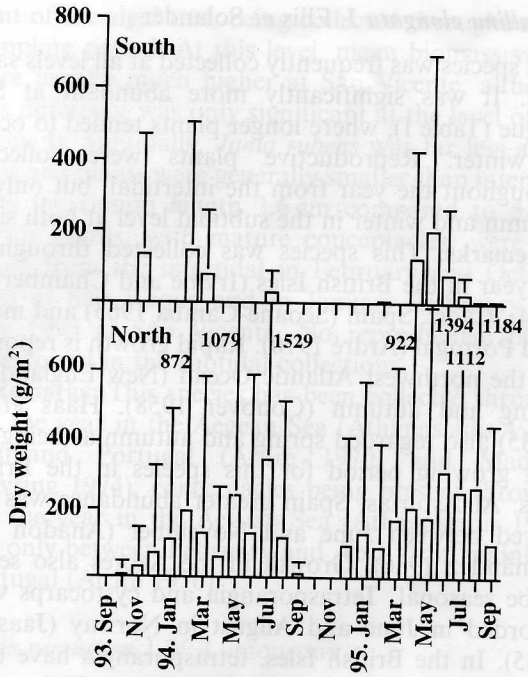

Fig. 5. Monthly biomass (mean + standard deviation) of *Gelidium microdon* at the intertidal level of both sites.

abundant at São Roque, although the largest plants were collected from São Vicente. Subtidal mean biomass values were similar at both places (maximum 112.7 g/m^2). The larger subtidal plants were also found at São Vicente (up to 17.2 cm, compared to a maximum of 9.6 cm at São Roque. Intertidal tetrasporangial plants were found in March 1994 and from August to October at São Roque and from October to December at São Vicente. Here only one female plant, with mature cystocarps, was collected (in April 1995). Only the sporophyte generation was present in the subtidal samples, with tetrasporangial plants being collected from August to December at São Roque and from August to January at São Vicente.

Remarks: This species is commonly found throughout the year in the British Isles (Dixon and Irvine 1977), France (Gayral 1966), Italy (Calabrese 1971, Tolomio *et al.* 1986), Greece (Abdel-Fattah *et al.* 1973), Cadiz, Spain (Seoane-Camba 1965), mainland Portugal (Ardré 1970) and Madeira (Levring 1974). Dixon (1965, 1973) has pointed out that this species has its northern limit of distribution in the British Isles. Highest values of biomass occur in June and October in the British Isles (Dixon and Irvine 1977) and from July to October at Asturias, Spain (Anadón and Fernández 1986). Reproductive structures are not recorded from British material (Dixon 1958), although they have been seen in other localities. On the Atlantic coasts of France and Spain carpogonia and spermatangia develop in June and July, with cystocarps being seen between July and October and tetrasporangia from June to October (Dixon and Irvine 1977).

Asparagopsis armata Harvey

Both phases of this species were present most of the sampling period in the intertidal and shallow subtidal on both coasts. In general, the biomass values were higher in spring and summer (Fig. 6), the seasons in which the larger plants were also found. In the subtidal, *Asparagopsis armata* was slightly more abundant in the north site, where it was present for a longer period. This difference however was not significant (Table I). The *Falkenbergia rufolanosa*-phase was present in the intertidal at São Roque from February to June and from January to May at São Vicente, its mean biomass never exceeding 11.2 g/m^2. Subtidally, this phase was collected between September and June

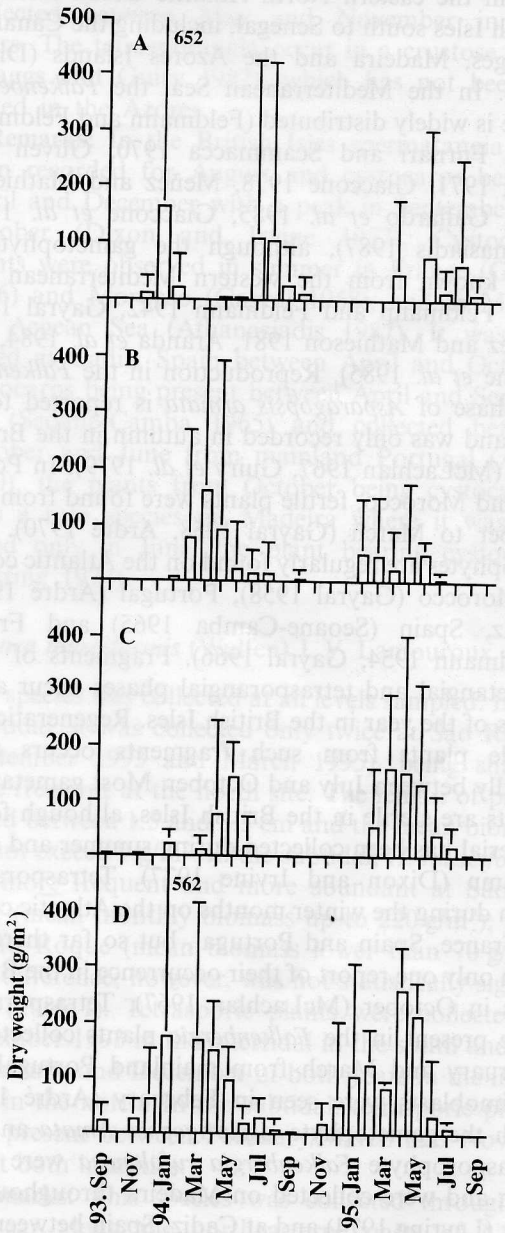

Fig. 6. Monthly biomass (mean + standard deviation) of *Asparagopsis armata* at all sampled levels and sites: intertidal south (A) and north (B), and subtidal south (C) and north (D).

(except for January) in the south, and from November to May at the north site. In the intertidal, female gametophytes were only found at São Vicente from December to May. Tetrasporangia were seen between January and March, again only at São Vicente. In the subtidal, carposporangial plants were present in April and May at São Roque and from January to June at São Vicente. Although looked for, no male plants were found. Tetrasporangia were observed in November and February, but again only at the north site.

Remarks: *Asparagopsis armata* was only introduced into the Atlantic and the Mediterranean early this century (Feldmann and Feldmann 1942, Guiry and Dawes 1992). The species is now widely distributed in the eastern North Atlantic Ocean from the British Isles south to Senegal, including the Canaries, Selvages, Madeira and the Azores Islands (Dixon 1964). In the Mediterranean Sea, the *Falkenbergia* phase is widely distributed (Feldmann and Feldmann 1942, Furnari and Scammacca 1970, Güven and Öztig 1971, Giaccone 1978, Meñez and Mathieson 1981, Gallardo *et al.* 1985, Giaccone *et al.* 1985, Athanasiadis 1987), although the gametophyte is only known from the western Mediterranean Sea (e. g. Feldmann and Feldmann 1942, Gayral 1958, Meñez and Mathieson 1981, Aranda *et al.* 1984, Giaccone *et al.* 1985). Reproduction in the *Falkenbergia*-phase of *Asparagopsis armata* is reported to be rare and was only recorded in autumn in the British Isles (McLachlan 1967, Guiry *et al.* 1979). In Portugal and Morocco, fertile plants were found from December to March (Gayral 1958, Ardré 1970). Gametophytes are regularly found on the Atlantic coasts of Morocco (Gayral 1958), Portugal (Ardré 1970), Cadiz, Spain (Seoane-Camba 1965) and France (Feldmann 1954, Gayral 1966). Fragments of both gametangial and tetrasporangial phases occur at all times of the year in the British Isles. Regeneration of whole plants from such fragments occurs most rapidly between July and October. Most gametangial plants are sterile in the British Isles, although fertile material has been collected during summer and early autumn (Dixon and Irvine 1977). Tetrasporangia form during the winter months on the Atlantic coasts of France, Spain and Portugal, but so far there has been only one report of their occurrence in the British Isles in October (McLachlan 1967). Tetrasporangia were present in the *Falkenbergia* plants collected in February and March from mainland Portugal and gonimoblasts were seen in February (Ardré 1970). Both the gametophyte *Asparagopsis armata* and the tetrasporophyte *Falkenbergia rufolanosa* were common and were collected on Madeira throughout the year (Levring 1974) and at Cadiz, Spain between November and August (Seoane-Camba 1965). In France, fertile plants of the *Falkenbergia*-stage were observed in November, December and September (Feldmann 1965).

Corallina elongata J. Ellis *et* Solander

This species was frequently collected at all levels sampled. It was significantly more abundant at São Roque (Table I), where longer plants tended to occur in winter. Reproductive plants were collected throughout the year from the intertidal, but only in autumn and winter in the subtidal level at both sites.

Remarks: This species was collected throughout the year in the British Isles (Irvine and Chamberlain 1994), Cadiz, Spain (Seoane-Camba 1965) and mainland Portugal (Ardré 1970). Rapid growth is reported for the northwest Atlantic Ocean (New England) in spring and autumn (Conover 1958). Haas *et al.* (1935) also regarded spring and autumn as being the best growing period for this species in the British Isles. At Asturias, Spain greater abundance was observed between June and November (Anadón and Fernández 1986). Growth in the Azores also seems to be seasonal. Tetrasporangia and cystocarps were recorded in June and August in Norway (Jaasund 1965). In the British Isles, tetrasporangia have been found throughout the growing season (Haas *et al.* 1935) but gametangial conceptacles are rare in Britain (Buffham 1888, Knight and Parke 1931, Blackler 1956) and surrounding areas (Suneson 1943, Hamel and Lemoine 1953). Athanasiadis (1987) reported tetrasporophytic plants in November and December for the Aegean Sea, while Ardré (1970) found conceptacles between February and July from mainland Portugal.

Jania crassa J. V. Lamouroux

This species was restricted to the intertidal south, where it was a major component of the algal turf, being collected for much of the sampling period. Its mean monthly biomass varied considerably, ranging from 0 to 1375.7 g/m^2. None of the observed plants was reproductive.

Jania longifurca Zanardini

This species was present at all levels sampled. In the intertidal it was more frequent at the north site, where plants were collected from October 1993 to December 1994 and in September 1995. It was a major contributor to the algal turf, with a mean monthly biomass up to 436.8 g/m^2. At the south intertidal site, populations were sporadic and variable. However, in the subtidal, small amounts of this species were consistently collected. No reproductive plants were observed at any level.

Remarks: Ardré (1970) found this species between October and June from mainland Portugal. Athanasiadis (1987) cited previous records of its occurrence in the eastern Mediterranean.

Jania rubens (Linné) J. V. Lamouroux

This species was significantly more abundant at the intertidal level (Table I), where it was a major compo-

nent of the algal turf, being collected throughout the sampling period. At this level, mean biomass values were usually much higher at São Vicente, although this difference was only significant at the level of 1% (Table I). Subtidally, *Jania rubens* was far less abundant and plants were generally smaller than intertidal ones (maximum length 3.6 cm compared to 5 cm). Fertile plants, with mature conceptacles, were collected from the intertidal in February and October 1995 at São Roque and in January, February and July 1995 at São Vicente. No reproductive plants were found in the subtidal collections.

Remarks: This species has been collected throughout the year in the Aegean Sea (Athanasiadis 1987), mainland Portugal (Ardré 1970) and Madeira (Levring 1974), conceptacles being present throughout the year in the Aegean Sea (Athanasiadis 1987) but only between February and April from mainland Portugal (Ardré 1970).

Jania verrucosa J. V. Lamouroux

This species was restricted to the subtidal communities of the south site, where it was collected throughout the sampling period, with a tendency for higher biomass in the second year. Plants were of a similar size to *Jania rubens*. No reproductive plants were found.

Chondracanthus acicularis (Roth) Fredericq

This species was collected at all levels sampled. It was significantly more abundant in the intertidal (Table I) where it very commonly formed a dense turf. At this level, it was collected throughout the sampling period at both places. It was more abundant at São Vicente (Table I), where the mean monthly biomass ranged between 24.1 and 434.3 g/m^2, while in the south it never reached 200 g/m^2. Thalli from São Vicente were also larger, nearly 6 cm in length, as compared to those from São Roque which were just over 4 cm, the largest plants being collected during the summer on both sites. In the subtidal, this species was less frequent and never abundant but the biomass and plant size were still greater for the São Vicente population. Only one cystocarpic plant was collected in the subtidal at São Roque in November 1994.

Remarks: This species has been collected throughout the year in the Aegean Sea (Athanasiadis 1987), Spain (Seoane-Camba 1965, Anadón and Fernández 1986, Fernández *et al.* 1987) and mainland Portugal (Ardré 1970). Little is known of its seasonal growth and reproduction in the British Isles (Dixon and Irvine 1977, Guiry 1984); cystocarps were only recorded in January and tetrasporangia in November (Guiry and Cunningham 1984). In France cystocarps were seen from November to February (Gayral 1966) and from August to March in Morocco (Gayral 1958). In Spain cystocarps were seen between December and February and tetrasporophytes between July and September (Seoane-Camba 1965, Anadón and Fernández 1986, Fernández *et al.* 1987). However, in mainland Portugal, only tetrasporangia were observed in October (Ardré 1970).

Sphaerococcus coronopifolius Stackhouse

This species was only found in the subtidal level. It was significantly more abundant at São Vicente (Table I), where it was collected throughout the sampling period. Its mean monthly biomass reached a maximum of 146.6 g/m^2, and the mean monthly length of the observed plants varied from 7.4 to 24.6 cm. It was more abundant in the first sampling year but this difference was not significant (Table I). No male plants were found but female plants were collected between May and November in both years. The tetrasporangia occur in a crustose phase (Maggs and Guiry 1982), which has not been detected in the Azores.

Remarks: In the British Isles spermatangia have been recorded for August and cystocarps between April and December with a peak in September and October (Dixon and Irvine 1977). Cystocarpic plants were observed in summer in France (Gayral 1966) and Morocco (Gayral 1958), and in May in the Aegean Sea (Athanasiadis 1987). It was collected at Cadiz, Spain between April and October, cystocarps being present between April and September (Seoane-Camba 1965) and collected between October and June from mainland Portugal (Ardré 1970), the plants from October being cystocarpic. It is a rare species on Madeira where it was collected only in June, the plant bearing cystocarps (Levring 1974).

Hypnea musciformis (Wulfen) J. V. Lamouroux

This species was collected at all levels sampled. In the intertidal, it was collected only twice at São Roque (September 1993 and March 1995), being slightly more frequent at the north site. The length of plants varied between 1.5 and 8.5 cm and the mean biomass did not exceed 9 g/m^2. In the subtidal, *H. musciformis* was more frequent and more abundant at São Vicente (mean monthly biomass up to 220 g/m^2), than at São Roque (mean biomass lower than 70 g/m^2). This difference, however, was not statistically significant (Table I). Tetrasporic plants were collected in September 1993 in the intertidal in the south and between June and December of both years in the intertidal in the north. In the subtidal, tetrasporic plants were present between February/March and November at both localities.

Remarks: This species was collected throughout the year along the northeastern coasts of North America (Taylor 1957), Brazil (Schenkman 1989), Aegean Sea (Athanasiadis 1987), Madeira (Levring 1974), Canaries (Børgesen 1929) and Ghana (Lawson 1957). It demonstrated a more seasonal occurrence

in other localities. At Cadiz, Spain it was found in February and from June to December (Seoane-Camba 1965); on mainland Portugal it was collected between February and August (Ardré 1970) and in Massachusetts and Florida was conspicuously seasonal in occurrence (Conover 1958, Benz *et al.* 1979). Not surprisingly, the abundance of this species also displayed annual fluctuations: at Asturias, Spain it was more abundant in July and August (Anadón and Fernández 1986); in Ghana, this species was more abundant between March and September, and less abundant from November to January (Lawson 1957); in São Paulo, Brazil, its biomass was lower when the sea temperature was maximal (26 and 29°C), the higher biomass values occurring when the temperature was lower (19 and 25°C). Growth was better in winter (July) and spring, when temperature was lower than 25°C (Schenkman 1989). Reproductive structures were found in summer on the northeastern coast of North America (Taylor 1957). No male plants were found in Brazil and cystocarpic specimens were rare, only being collected four times (October, November, May and July); on the other hand, fertile tetrasporophytes occurred throughout the year (Schenkman 1989). At Cadiz, Spain tetrasporangia were present in the plants collected in June and September (Seoane-Camba 1965) and in the Aegean Sea tetrasporophytes were present between November and August (Athanasiadis 1987). On the Canaries fertile plants were common throughout the year (Børgesen 1929).

Caulacanthus ustulatus (Turner) Kützing

Strictly intertidal, this species was present at both sites, but was significantly more abundant at São Roque (Table I). Here, plants were present throughout the sampling period being more abundant in the first year. Its mean monthly biomass reached a maximum of 543.9 g/m^2, although the plants were quite small (fronds up to 1.5 cm). At São Vicente, plants were only sporadically collected, as part of the algal turf, with a lower mean biomass (< 130 g/m^2). Tetrasporic plants were observed between November and June at São Roque and in November at São Vicente.

Remarks: This species has been collected at Cadiz, Spain at all seasons. Tetrasporangia have been seen most of the year (Seoane-Camba 1965). It is reported between October and June from mainland Portugal (Ardré 1970), where tetrasporangia were seen from February to August. It is common in the Aegean Sea where it was collected throughout the year, tetrasporophytes and plants with carposporophytes being present in the summer (Athanasiadis 1987). In other parts of the Mediterranean Sea, it is also a common species, growing in a dense and brownish turf form, plants never larger than 3 cm (Lebonché 1957). It is not common on Madeira, but it was collected there at all seasons (Levring 1974). Tetrasporangia were seen in spring in the western Mediterranean Sea (Feldmann 1938).

Plocamium cartilagineum (Linné) Dixon

This species was present at all levels sampled, although only abundant in the subtidal (Table I). In the intertidal, plants were occasionally found in lower pools. Subtidally, *Plocamium* was collected throughout the sampling period at both sites, being more abundant at São Vicente. The largest plants and the corresponding highest values of biomass occurred in spring at both sites (Fig. 7). Intertidal tetrasporic plants were collected in November 1994 and January 1995 at São Vicente. Subtidal tetrasporic plants were present at this site between November and May, and in December 1993 and from February to May at São Roque.

Remarks: Potentially perennial in the British Isles (Dixon and Irvine 1977), plants of this species were only occasionally collected in the Aegean Sea (Athanasiadis 1987) but were present throughout the year at Cadiz, Spain (Seoane-Camba 1965) and mainland Portugal (Ardré 1970). On the Isle of Man the largest plants were present in summer and autumn (Kain 1982), while at Cadiz, Spain they were seen earlier in the year (Seoane-Camba 1965). Fertile tetrasporophytes were present at all times of the year on the Isle of Man but there was a marked seasonality with a peak in fertility in the autumn and a distinct reduction in fertile plants in spring (Kain 1982). In France reproductive plants were observed in spring and winter (Gayral 1966), and in Morocco tetrasporophytes were observed between October and April (Gayral 1958). In mainland Portugal gonimoblasts were found in October, February and March, and tetrasporangia from February to August (Ardré 1970).

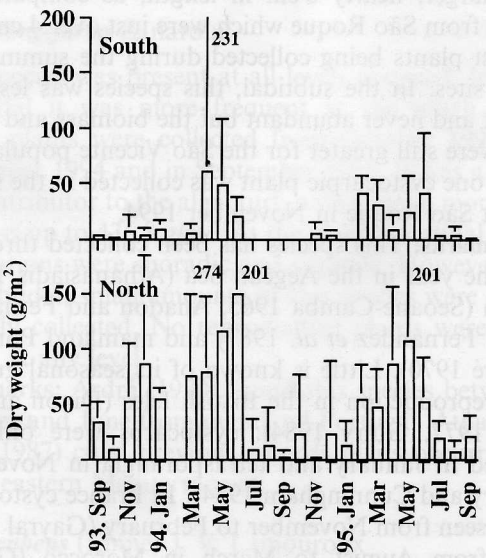

Fig. 7. Monthly biomass (mean + standard deviation) of *Plocamium cartilagineum* at the subtidal level of both sites.

toral. The other species studied were present at both the intertidal and subtidal levels, *Centroceras clavulatum* being strictly found in the algal turf. Three of the algae studied (*Chaetomorpha linum*, *Corallina elongata* and *Caulacanthus ustulatus*) were statistically more abundant at São Roque, their presence in the north being only sporadic or occasional. Among these, *Caulacanthus ustulatus* was particularly abundant in the intertidal algal turf, whereas *Corallina elongata* dominated the subtidal south populations. *Fucus spiralis*, *Gelidium microdon*, *Sphaerococcus coronopifolius* and *Centroceras clavulatum* were, on the other hand, statistically more abundant at São Vicente.

Although large variations were observed in the species abundance, size and reproduction over the sampling period, a seasonal pattern was detected in some species. Most showed a well-established seasonality in their growth, with larger plants and/or the higher values of biomass occurring respectively in spring (*Bryopsis hypnoides*, *Plocamium cartilagineum*), spring/summer (*Stypocaulon scoparium*, *Dictyota dichotoma*, *Padina pavonica*, *Colpomenia sinuosa*, *Gelidium microdon*, *Asparagopsis armata*) and summer (*Ulva rigida*, *Chondracanthus acicularis*). This seasonality is likely to be related to cyclic variations in environmental factors such as seawater temperature, daylength and wave action. Relationships between these environmental factors and the abundance and seasonality of seaweeds have been widely discussed and it has been reported that the maximum values of biomass and plant length are coincident with summer seawater temperature and longer day-lengths (Soeder and Stengel 1974, Guiry *et al.* 1987, Maggs and Guiry 1987, Kautsky and van der Maarel 1990). In the Azores, spring and summer are the seasons in which the seawater temperature and the number of hours of light are increasing or maximum while the wave action and the effect of the wind are lowest (Neto 1991).

With the exception of *Dictyota dichotoma,* which was statistically more abundant in the second sampling year, no differences were observed on the species abundance between the two years.

The reproductive phenology varied according to species. Some were fertile the entire year (e. g. *Ulva rigida*, and *Fucus spiralis*). Others had prolonged periods of fertility: *Plocamium cartilagineum* and *Caulacanthus ustulatus* (autumn to spring); *Gelidium microdon* and *Sphaerococcus coronopifolius* (spring to autumn); *Jania rubens* (summer to winter). A few species had a more restricted fertile period: *Chaetomorpha linum* and *Jania verrucosa* in summer; *Chondracanthus acicularis* in autumn; *Codium elisabethae* and the tetrasporophyte of *Asparagopsis armata* in autumn/winter; *Cystoseira abies-marina*, *Pterocladiella capillacea* and *Chondria coerulescens* in summer/autumn; *Asparagopsis armata* gametophyte in winter/spring. This reproductive seasonality can be related to several factors. Photoperiod appears to be the predominant property of light used as environmental signal in macroalgae (Dring 1984, 1988), as it is undoubtedly the most reliable trigger for gametogenesis in long-lived algae. The existence of a restricted 'reproductive window' is frequent in Rhodophytes (Maggs and Guiry 1987, Breeman and Guiry 1989) and light is considered the factor playing the major role in the induction of their reproduction (Dring 1984, 1988, Santelices 1990). Gametogenesis can be induced by both short-day and long-day conditions (Guiry and Cunningham 1984, Clayton *et al.* 1987, Wiencke and Clayton 1990, Dring 1984, Kain and Norton 1990). Temperature is also commonly thought to affect reproduction, although its direct role in the field is often unclear due to simultaneous (correlated) changes in other environmental factors that may be the true factor responsible for reproductive induction (e. g. nutrients levels, Deysher and Dean 1986 a, b, Kain 1989). Of the species studied here, detailed determination of the abiotic conditions affecting reproduction is known only for *Padina pavonica* and *Chondracanthus acicularis*. In the Mediterranean Sea, *Padina pavonica* is reported to have a temperature threshold above which gametophytes appear (see Ramón and Friedmann 1965 and Ramón 1969). This later author observed that up to a certain temperature the gametophytes were monoecious, but with a further increase in seawater temperature, they would become predominantly dioecious. The male gametophyte appeared first, while the female gametophyte was only detected during the period of relatively high summer temperatures (27–30 °C) on the Israeli coastal waters. The absence of gametophytes of *P. pavonica* at the study sites may indicate that the seawater temperature never reached the threshold necessary for their production. Guiry and Cunningham (1984) demonstrated that *Chondracanthus acicularis* shows a combination of photoperiod and temperature control of gamete formation. Gametogenesis is confined to a narrow temperature and photoperiod range (14 to 18 °C; night lengths $\geq$ 12 h), a combination of conditions that confines the formation of gametangia to the autumn in the British Isles. On the other hand, the formation of tetrasporangia does not seem to be limited by day length. In the present study, only one reproductive plant of *Chondracanthus acicularis* was found. It was a female gametophyte, and it was collected in autumn (November), when the environmental conditions are similar to the ones described by Guiry and Cunningham (1984). Surprisingly, no tetrasporophytic plants were seen but these sporangia are small and immersed in the thallus, and so could have been overlooked.

Although all plants from the present study were carefully observed, the sampling methodology was not designed to study the factors controlling reproduction. Detailed investigations of individual species accompanied by studies of the major environmental

factors known to affect algal growth and reproduction are now in progress and will help to understand whether reproduction occurs as a direct response to conditions that meet the physiological requirements for reproduction or whether environmental factors are used to coordinate the timing of reproduction so that other ecological benefits are obtained.

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