

# Seasonal variations in growth and reproduction of *Sargassum orotavicum* (Fucales, Phaeophyceae) from the Canary Islands

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## Abstract

Phenology and spatial-temporal variation patterns during an annual cycle of *Sargassum orotavicum* from the Canary Islands have been studied for the first time. Data on morphological variation of general habit, stipes, primary and secondary branches, primary and secondary blades, vesicles and receptacles are presented. *Sargassum orotavicum* is a pseudoperennial species showing a significant seasonality in most parameters that have been studied. This species has four phases within the year: (1) regeneration, from perennial stipes and holdfasts in late autumn; (2) growth, with the beginning of the development of thallus structures that renew every year, in winter; (3) reproductive, with a vegetative climax prior to the reproductive, in spring; and (4) senescence and degeneration, with detachment of thallus structures that renew yearly, in summer. Biomass of branches, blades, vesicles and receptacles showed a significant seasonal variation, with maximum values in spring and minimum in late summer and autumn. This warm-temperate species exhibited a phenological behaviour intermediate between tropical and cold-temperate species of *Sargassum*. Analysis of within- and between-individual stability of eleven continuous traits indicated that the highest variation occurred temporally.

**Keywords:** biomass; Canary Islands; phenology; *Sargassum orotavicum*; trait stability.

## Introduction

Most of the species of *Sargassum* C. Agardh exhibit a great variability in their morphological characters throughout the year (DeWreede 1976, Ang and Trono 1987, Kilar 1992, Kilar et al. 1992a,b). Knowledge of temporal variations in vegetative and reproductive morphology of specimens is necessary in most *Sargassum* species for correct identification, with concomitant simplification of the taxonomy of the genus (Kilar et al. 1992b).

Studies on the phenology of *Sargassum* have concentrated mainly on tropical and subtropical species (De-

Wreede 1976, McCourt 1984, Hurtado and Ragaza 1999), in which seasonal cycles in growth, abundance and reproduction occur (De Ruyter Van Steveninck and Breeman 1987). In particular, the phenological behaviour of some western Atlantic tropical species is well known, i.e., for *Sargassum mathiesonii* Kilar from the Gulf of Mexico (Kilar 1992), *S. polyceratium* Montagne from the Caribbean Sea (De Ruyter Van Steveninck and Breeman 1987, Kilar and Hanisak 1988), *S. pteropleuron* Grunow from Florida (Prince and O'Neal 1979) and *S. cymosum* C. Agardh from Brazil (Paula and Oliveira 1980). From the eastern Atlantic coasts, only the temperate invasive *Sargassum muticum* (Yendo) Fensholt has been the subject of studies on temporal variations in morphology (Fletcher and Fletcher 1975, Paula and Eston 1987, Arenas and Fernández 1998, Wernberg et al. 2001). Seasonal changes in features of branches, blades, vesicles and receptacles have not been considered for other temperate species of the genus although, for some species, the months in which they were fertile have been documented (Gómez-Garreta 2001).

The phenology of *Sargassum orotavicum* Díaz-Villa, Afonso-Carrillo et Sansón, a species recently described from the Canary Islands, is presently unreported. The morphology of this species has been documented and the arguments that segregate it from *Sargassum vulgare* C. Agardh have been discussed in a previous paper (Díaz-Villa et al. 2004). The aim of this study was to analyse the patterns of spatial-temporal variation of specimens during an annual cycle. This kind of study was recommended by Kilar et al. (1992b) as decisive for simplifying taxonomy of this genus. The present work represents the beginning of phenological analysis of *Sargassum* species present in the Canary Islands.

## Materials and methods

The study site is located in Puerto de la Cruz on the north slope of Tenerife (28° 24' N, 16° 34' W). Sampling was conducted in tide pools in the lower eulittoral zone exposed to wave activity, where *Sargassum orotavicum* formed dense populations accompanied by *Pterocladia capillacea* (Gmelin) Santelices et Hommersand, *Cystoseira compressa* (Esper) Gerloff et Nizamuddin, *Ulva rigida* C. Agardh and other species.

Between 10 and 15 complete thalli were randomly collected in each month from October 2001 to September 2002. They were placed in plastic bags and carried to the laboratory, where they were preserved in 4–10% formalin in seawater.

For each individual, number, length and diameter of stipes and primary branches as well as numbers of

blades, branched blades and vesicles were noted. Individual length was estimated as the highest value of the sum of a primary branch and its stipe. Length and width of the largest blade of each primary branch were measured and length-width ratios were calculated. In December 2001, March, June and September 2002, one additional specimen was dissected into primary and secondary blades (blades on primary or secondary branches, respectively). Length, width and morphological features of all these blades were noted, and their length-width ratios were calculated. For each specimen collected during these months, the numbers of cryptostomata were counted in two blades (one from the basal and the other from the mid portion of a branch) and the major and minor diameters of the three largest cryptostomata were measured with an ocular micrometer to calculate their area.

For all the primary branches, numbers of vesicles, length and diameter of the largest vesicle, as well as the lengths of their stalks were measured. The distance from the base of a primary branch where vesicles began to appear was recorded. Frequencies of different morphologies of vesicles were quantified. Number of primary branches bearing receptacles, length, diameter, and number of lateral branches and spines at receptacles were noted. For the study of gametangia, transverse sections of receptacles were made, and their distribution and stage of development were reported.

Dry weight of holdfasts, stipes, branches, blades, vesicles and receptacles of all specimens collected were determined after 24 h oven-drying (100°C).

Data obtained were analysed using parametric statistical methods, following Sokal and Rohlf (1981). Data were tested for homogeneity of variances using Bartlett's test and transformed to satisfy homoscedasticity when necessary. One-way analysis of variance, with equal and unequal sample sizes, were used to detect temporal variation between months. The factor "time" allowed comparisons of the variables included in Table 1 throughout the sampling period (number of factor levels and degrees of freedom are shown in Table 1). Student-Newman Keuls (SNK) or Scheffé multiple range tests were used to segregate group means. Following Kilar (1992), annual coefficients of variation ( $CV \times 100$ ), a size-independent estimation of variation, were calculated averaging monthly CVs to distinguish temporally stable from temporally variable characters. Variability between individuals (V), a spatial estimator, was calculated using one-way nested ANOVAs to partition variation between and within the individuals [ $V = 100 \times S^2_A / (S^2 + S^2_A)$ , where:  $S^2_A$  = added variance component among groups;  $S^2$  = variance within groups]. Characters with the lowest combined estimations of CV and V were taken as the most stable, as determined from their Euclidean distances (Ed) from origin (Kilar et al. 1992a).

Some selected individuals from different months have been deposited in TFC (Departamento de Biología Vegetal, Botánica, Universidad de La Laguna, Canary Islands), with the numbers TFC Phyc 11675, 11676, 11677, 11678, 11679, 11680, 11681, 11682, 11683, 11684, 11685. Herbarium abbreviations follow Holmgren et al. (1990).

## Results

### Biometry

**Thallus, stipes and primary branches** Lengths of thalli showed a marked seasonality (Table 1). Maximum mean length of individuals of 36.6 cm was reached in late spring and minimum mean values of 3–4 cm were detected in late summer and during autumn (Figure 1). The longest specimen of 47.5 cm length was found in May. During spring, 75% of specimens (over percentile 25) were more than 15 cm long, while in late summer and autumn 75% of them (under percentile 75) measured less than 8 cm.

Neither length of stipes nor number of stipes per holdfast showed a seasonal variation (Table 1), with the mean value of these characters nearly constant through the study period. However, the length of the primary branches and number of primary branches per stipe showed significant seasonal differences (Table 1). Maximum mean number of primary branches per stipe was observed in June–July (6–7 branches), decreasing in August to the minimum mean values of 2–3 branches, remaining between 2 and 5 branches per stipe for the rest of the year.

Nearly all primary branches (under percentile 90) were less than 50 mm long in late summer and during autumn, whereas 20–25% of branches (over percentile 75) exceeded this size in spring (Figure 2). New primary branches (less than 25 mm long) were always present, constituting about 60% of branches in each month. However, fragments of detached branches (included in the same interval as new branches in Figure 2) were more frequent (10–30% of branches) in late summer and during autumn.

**Blades** Mean number of blades per primary branch showed a significant seasonal variation (Table 1), with maximal mean values (91–110 blades per branch) in spring, decreasing at the end of this season to reach the minimal mean values in late summer and early autumn, with scarcely 2–5 blades per branch. The highest number of 1836 blades was recorded in April (Figure 3).

Mean percentage of branched blades per individual varied seasonally (Table 1), with a mean maximum of 22.7% in August and a minimum of 1.6% in May. The thallus with the highest percentage of branched blades (60%) was collected in October. In late summer and autumn, half of the specimens studied (over percentile 50) had more than 15% of their blades branched, while in spring these blades occurred with a frequency of <10% in nearly all specimens (under percentile 90) (Figure 4).

Length, width and length-width ratios of blades showed a significant variation, not only among times of collection but also among positions of blades on the branches (Table 1).

Mean length and width of the primary blades were always higher than those of the secondary blades through the study period (Figure 5). Primary blades reached a maximum mean length of 4.2 cm in summer and a maximum mean width of 7.5 mm in winter. However, the minimum mean values in length (1.9 cm) and

**Table 1** *Sargassum orotavicum*: one-way analysis of variance table for effects of time on selected traits.

Traits	n	n.l.	F	p	SNK
Thallus length	122	12	F <sub>11,110</sub> =33.494	<0.001	a)10,9,8,11,12 b)12,1,7 c)1,7,2 d)3,4,6 e)5
Stipes per holdfast	122	12	F <sub>11,110</sub> =2.147	0.363	
Stipe length	281	12	F <sub>11,269</sub> =1.098	0.491	
Primary branch length	1282	12	F <sub>11,1270</sub> =14.321	<0.001	a)10,9,11,8,12,7,2,1 b)4,3,6 c)3,6,5
Primary branches per stipe	379	12	F <sub>11,367</sub> =4.554	<0.001	a)10,8,11,2,3,9,1,5,12,4 b)1,5,12,4,7,6
Blades per primary branch	1281	12	F <sub>11,1269</sub> =10.866	<0.001	a)10,9,8,11,7,12,1,2,6 b)4,5,3
% branched blades per specimen	122	12	F <sub>11,110</sub> =4.960	<0.001	a)5,4,6,2,1,3,7,12,11 b)3,7,12,11,9,10 c)12,11,9,10,8
Blade length	937	12	F <sub>11,925</sub> =4.960	<0.001	a)10 b)7,8,9,11,6,12,4,3,5 c)11,6,12,4,3,5,2,1
Blade width	937	12	F <sub>11,925</sub> =2.451	<0.001	a)10,7,8,9 b)7,8,9,11,6,12,4,3,5 c)11,6,12,4,3,5,2,1
Blade L/W ratio	937	12	F <sub>11,925</sub> =8.003	<0.001	a)10,7,8,9,11,6 b)7,8,9,11,6,12,4,3,5,2,1
Number of cryptostomata	79	4	F <sub>3,75</sub> =7.255	<0.001	a)6 b)12,9,3
Cryptostomatal area	231	4	F <sub>3,227</sub> =18.029	<0.001	a)3 b)12,9 c)6
Branches per receptacle	263	3	F <sub>2,260</sub> =2.354	0.097	
Spines per receptacle	287	3	F <sub>2,284</sub> =25.148	<0.001	a)6 b)5 c)4
Thallus biomass	118	12	F <sub>11,106</sub> =13.403	<0.001	a)9,10,8,11,12,7,1,2 b)1,2,3,6 c)2,3,6,4 d)5
Holdfast biomass	118	12	F <sub>11,106</sub> =1.306	0.231	
Stipe-branch biomass	118	12	F <sub>11,106</sub> =6.005	<0.001	a)9,12,8,10,11,1,7,3,2 b)1,7,3,2,5,6 c)3,2,5,6,4
Blade biomass	118	12	F <sub>11,106</sub> =8.478	<0.001	a)10,9,8,11,7,12,6,1 b)6,1,2,5 c)2,5,3,4
Vesicle biomass	118	12	F <sub>11,106</sub> =6.595	<0.001	a)8,9,10,11,12,1,7,2,6,4,3 b)5
Receptacle biomass	118	12	F <sub>11,106</sub> =28.726	<0.001	a)9,10,11,1,12,8,2,3,7,4 b)6 c)5

Groups depict months (1=January to 12=December) of similar value (SNK,  $p < 0.05$ ), n.l.=number of levels.

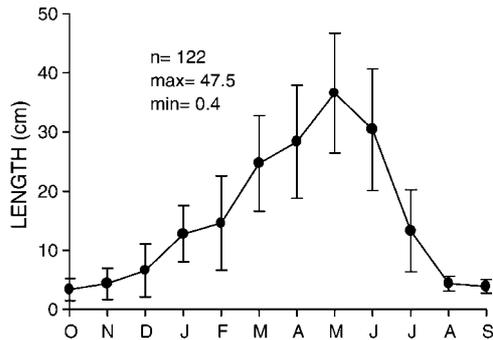
width (6.8 mm) were recorded in autumn. Secondary blades were not present in autumn; they reached their maximum mean width of 6.1 mm in winter and their maximum mean length of 2.8 cm in spring. Length-width ratios of primary and secondary blades displayed a similar pattern of variation through the study (Figure 5). In primary blades, the minimum mean ratio of 2.7 was observed in autumn and the maximum (5.6) in summer; in secondary blades, the minimum of 3.0 was detected in winter and the maximum of 5.7 in spring.

Number of primary blades per individual increased from autumn to spring, decreasing in summer, whereas secondary blade numbers increased from winter to sum-

mer (Figure 6). In spring-summer, the number of secondary blades surpassed considerably that of primary blades (more than 90% of blades were secondary).

As observed in Table 2, the morphological characteristics of blades, such as branching, presence of spines on blade stalk as well as sinuous margin, were always present in a higher proportion in primary than in secondary blades.

Both the number and the area of cryptostomata showed a seasonal variation (Table 1, Figure 7). Minimum mean number of cryptostomata (about 17 on one side) was observed in summer, agreeing with their maximum mean area of 6444  $\mu\text{m}^2$ . In contrast, in spring, mean



**Figure 1** *Sargassum orotavicum*: temporal variation in mean length of individuals (cm) ( $\pm$ standard deviation) from October 2001 to September 2002.

n=sample size, max=maximum value, min=minimum value.

number of cryptostomata per blade surface was maximal (up to 43) whereas their mean area was at a minimum ( $2960 \mu\text{m}^2$ ).

**Vesicles** Number of individuals with vesicles increased from January to March, when all specimens bore vesicles. The numbers decreased during summer (Figure 8). Vesicles were present on 15–30% of the primary branches on each stipe. In winter, the mean number of vesicles per primary branch was clearly low, reaching a maximum mean value of 45 vesicles in spring. The highest number of 128 vesicles per primary branch was found in May on a 45.7 cm long primary branch. Usually, vesicles were arrayed over the first 10–20 cm above the bases of primary branches.

Six types of vesicles were recognised (Figure 9). The most frequent were a-type and b-type (with unbranched stalk and mucicous or mucronate vesicles, respectively), constituting 94% of all vesicles studied (Table 3). C-type vesicles (with unbranched stalk and vesicle apiculate with a leaf-like blade) represented 4% of the total and were present only from February to May. Finally, the remaining types (with branched stalk) were uncommon (less than 2%) and occurred irregularly.

**Receptacles** In late spring, all specimens collected were fertile; the first specimens with receptacles were detected in winter, when 10% of individuals were fertile. The receptacles were present in 20–30% of primary branches of almost all stipes (Figure 10).

First receptacles were detected in December–January (Figure 11), attaining 4 mm length and less than 1 mm in diameter. In these months, only some conceptacles were formed, principally towards the base of receptacles. During February and March, the length of the receptacles remained unchanged, although the diameter increased slightly to 1–1.5 mm. Commonly, female conceptacles were formed in the lower half of the receptacle, displaying an easily recognisable mucilaginous hyaline plug closing the ostiole (with eggs retained inside). Male conceptacles were also formed at the basal portion of the receptacle. In April, conceptacles did not possess mucilaginous plugs, and egg liberation began. Both eggs and zygotes in the first stages of development were retained in mucilage around receptacles. Receptacles were up

to 17 mm long and 2 mm in diameter in June. Empty antheridia were also detected in male conceptacles. In July, receptacles deteriorated morphologically. Receptacles were damaged and had empty conceptacles in the mid-basal portion. Conceptacles with eggs occurred only in the apical portions of less damaged receptacles.

When receptacles were mature, the number of spines varied temporally (Table 1), decreasing from maximum mean values of 5–6 spines per receptacle in April to minimum of 1–2 spines in June. In contrast, the number of branches per receptacle (4 branches on average) was a nearly stable parameter (Table 1).

## Biomass

Mean biomass per thallus showed a seasonal variation (Table 1), with minimal mean values in autumn and late summer [0.2–0.8 g dry weight (DW)], and maximum mean value of 7 g DW in spring (Figure 12).

Holdfast mean biomass did not vary seasonally (Table 1), remaining around 0.035–0.125 g DW. However, the mean biomass of stipes-branches displayed a temporal fluctuation (Table 1), mainly due to variation in branch biomass, with maximal values in spring.

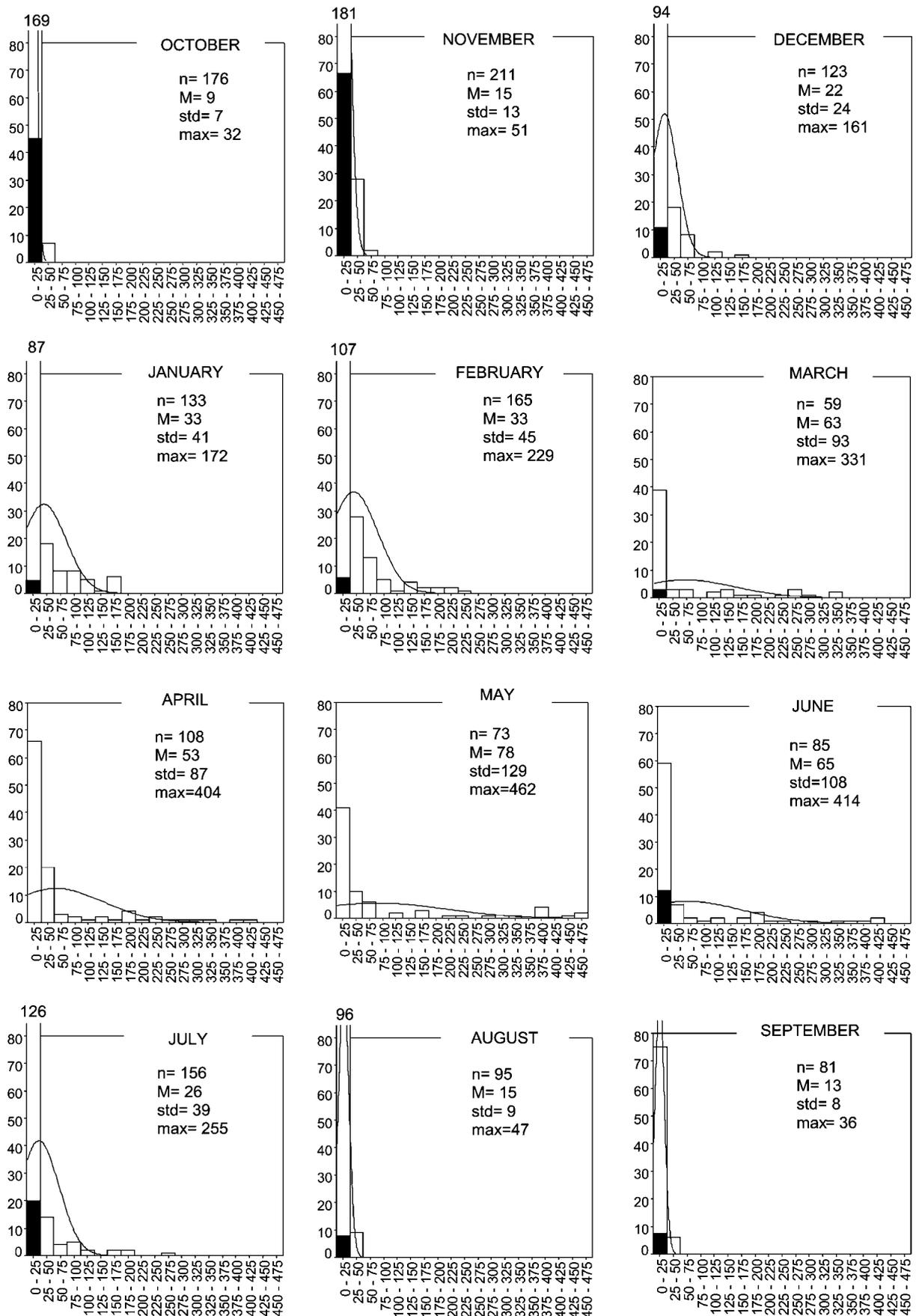
Mean biomass of blades, vesicles and receptacles per individual also varied through time (Table 1). Blades showed a maximum mean biomass of 2.65 g DW per individual in spring and minimal mean values of 0.07–0.13 g DW per individual in autumn and late summer (Figure 13). In autumn, all blade biomass was represented by primary blades, and in winter, the contribution of primary blades was over 75%. These percentages were reversed in spring–summer, when secondary blades were responsible for 80–95% of blade biomass. The mean biomass of vesicles was always low, with a high value of 0.20 g DW per individual in May. Although receptacles were present from December to August, their biomass was only important from April to June, increasing 4.5 times from April to May when the maximum mean value of 3.87 g DW per individual was recorded (Figure 13).

As observed in Figure 14, the contribution of receptacles to the total biomass per thallus was approximately 60% in May–June while, in previous months (February–April), blades contributed 60–80%.

## Seasonal variation of specimens

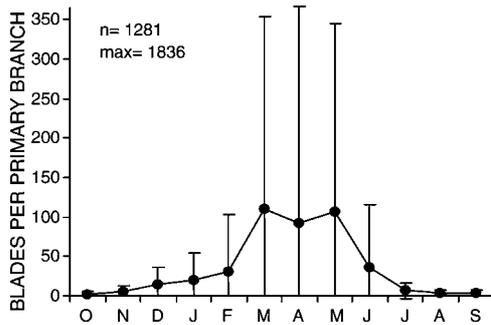
Specimens were pseudoperennial with marked variations in habit through the seasons (Figure 15). In autumn, specimens were small (Figure 15) and reduced to the holdfast, stipes and some very short primary branches, mainly smooth and with very few blades. Blades were primary, wide, frequently branched and sinuous. Individual biomass was very low and represented mainly by branches and blades in similar proportions.

In winter, old stipes began to regenerate. Primary branches grew in length, hence individual length increased (Figure 15). The first secondary branches appeared showing spines on their surfaces, whereas primary branches developed spines only on their mid-distal portions. Primary blades increased in number and the first secondary blades were formed. Percentage of

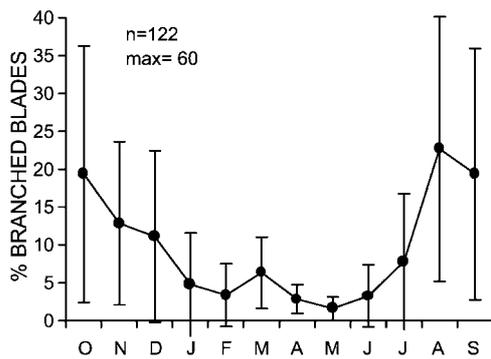


**Figure 2** *Sargassum rotavicum*: distribution of frequencies of the classes of primary branch length, and normal curves to which they adjust through the year.

First interval of frequencies includes fragments of detached primary branches (black) and new primary branches. Interval=25 mm, n=sample size, M=mean, std=standard deviation, max=maximum value.



**Figure 3** *Sargassum orotavicum*: annual variation in mean number of blades per primary branch ( $\pm$ standard deviation). n=sample size, max=maximum value.



**Figure 4** *Sargassum orotavicum*: annual variation in mean percentage of branched blades per individual ( $\pm$ standard deviation). n=sample size, max=maximum value.

branched blades decreased considerably during these months. Specimens with the first vesicles were detected, but they were present in a low proportion and only four of the six morphological types of vesicles recognised in this study were observed. Also, first receptacles in early stages of development were found. From December to February, mean biomass per individual doubled, blades were the main contributor to the total thallus biomass.

In spring, specimens were fully developed (Figure 15) (individuals reached their maximal length, secondary branch development and number of blades). Secondary blades were the most abundant. The detachment of primary blades began, and then the specimen morphology changed by displaying a higher number of narrow, flat and unbranched blades. In relation to the previous seasons, primary and secondary blades increased in length, while width remained nearly constant in primary blades and decreased in secondary blades. Length-width ratio increased from autumn to spring in both types of blades. Vesicles were very numerous, and all the morphological types were observed. Receptacles reached their maximum development, and liberation of eggs and sperms began. Thallus biomass increased, notably due to the marked increase in receptacle biomass (447% from April to May), in spite of the losses through blade detachment.

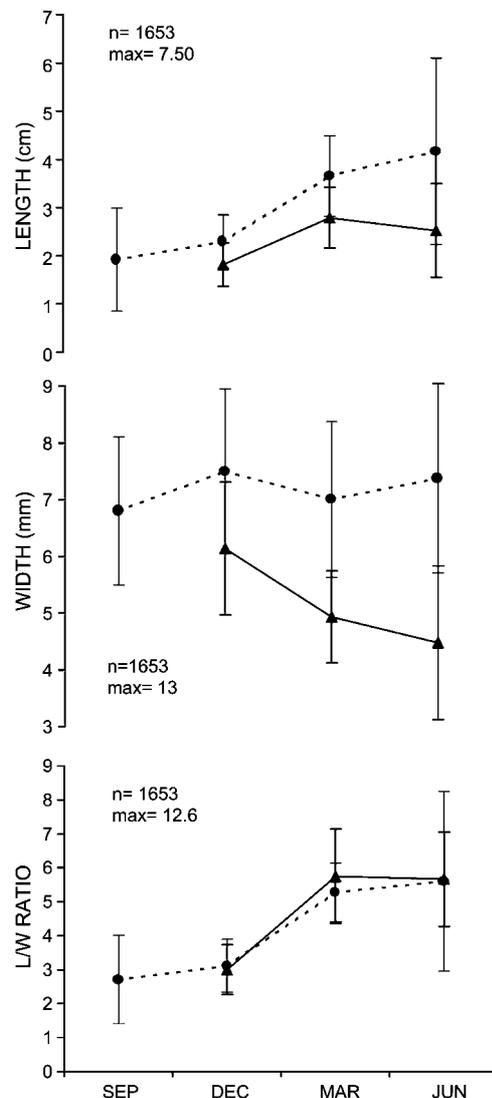
Finally, in summer, specimens appeared damaged (Figure 15), with few blades, no vesicles, incomplete receptacles, and an abundance of epiphytes. Spines on branches and receptacles were less frequent. Before the detachment of old branches at the end of summer, for-

mation of new branches occurred, increasing the mean number of primary branches per stipe. Blades were mostly secondary, decreasing in length and width in relation to spring blades. The length of the few primary blades that remained on the branches increased. Length-width ratios of blades were constant through spring and summer. The decrease in biomass during this period was due to the detachment of the longest branches. At the end of summer, branches and blades were again in the same proportion.

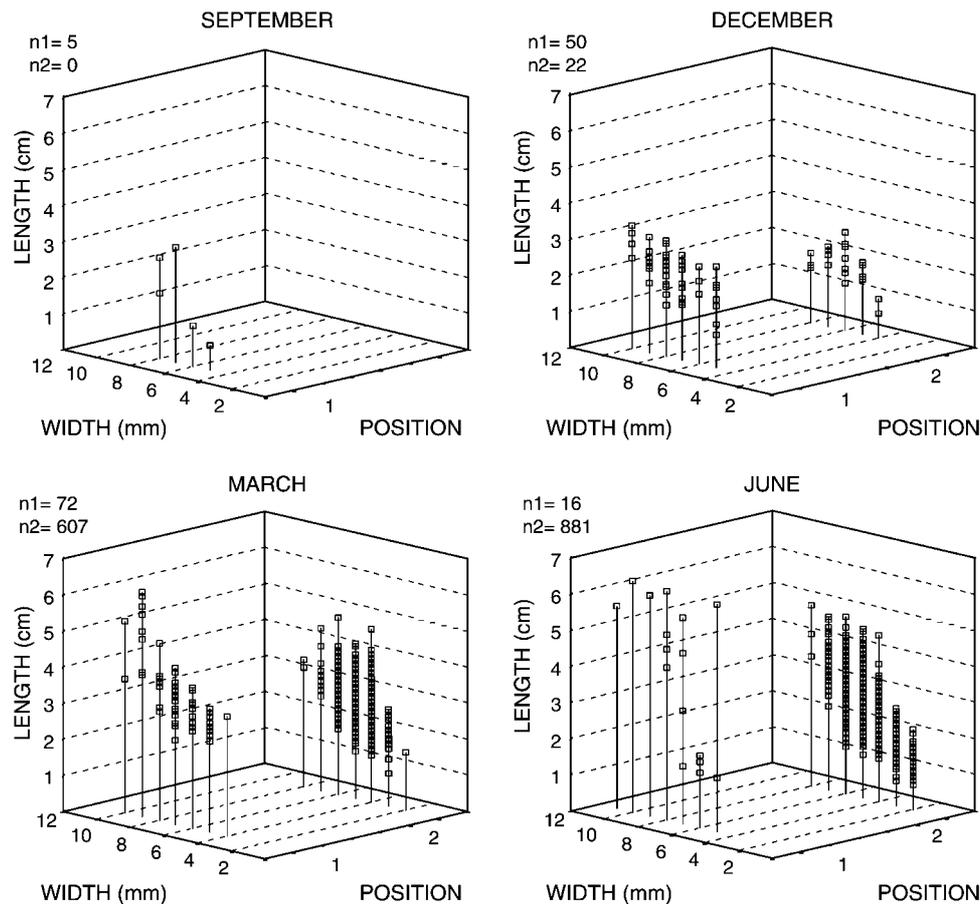
### Temporal and between-individual stability of continuous traits

Differences in the stability of continuous traits analysed temporally (CV) and between-individuals (V) in *Sargassum orotavicum* are shown in Figure 16.

Traits with the highest stability were vesicle-related: vesicle-stalk length (Ed=23), vesicle length (Ed=25) and vesicle diameter (Ed=28). Blade traits were less stable than those of vesicles, in decreasing order of stability



**Figure 5** *Sargassum orotavicum*: mean length (cm), width (mm) and length-width ratio ( $\pm$ standard deviation) of primary (●) and secondary (▲) blades through the year. n=sample size, max=maximum value.



**Figure 6** *Sargassum orotavicum*: length (cm) and width (mm) of blades according to their position on primary (1) or secondary (2) branches, in selected months. Each  $\square$  represents a blade, n1 and n2=number of primary blades and secondary blades measured.

were: blade width (Ed=28), cryptostomatal major (Ed=31) and minor (Ed=35) diameter, blade length-width ratio (Ed=46), blade length (Ed=50) and cryptostomatal area (Ed=52). Stipes showed traits with an intermediate stability, with an Ed of 27 for diameter and 42 for length. Finally, the least stable trait was the primary branch length (Ed=102) (Figure 16).

## Discussion

*Sargassum orotavicum* showed a marked seasonality in most of the characters studied. As in other species of *Sargassum*, it showed a phenological behaviour with four successive phases in the life history: regeneration,

growth, reproduction and senescence and degeneration (Hurtado and Ragaza 1999).

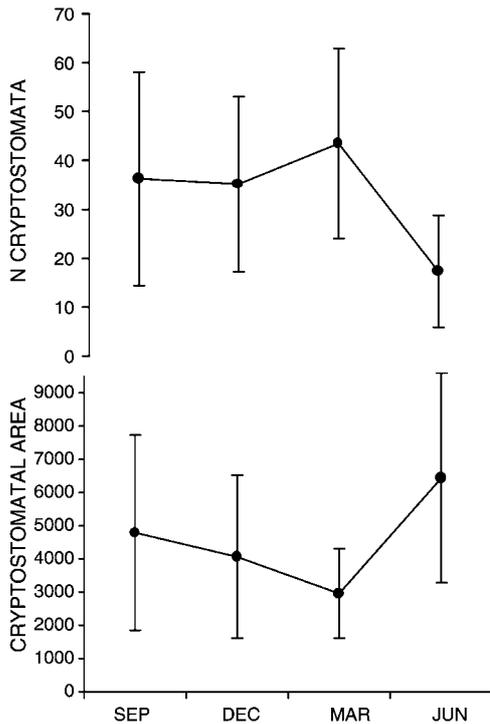
Regeneration from the perennial parts (holdfasts and stipes) began in late autumn. In winter, specimens doubled their biomass from one month to the next, and development of the structures that renew every year (branches, blades, vesicles and receptacles) began.

The reproductive phase occurred in spring. In late spring, all specimens showed well developed receptacles releasing eggs and sperms ("climax" of the reproductive stage). Taylor (1960) suggested using specimens at the "climax" of the reproductive stage as typical specimens for species characterisation. But, the specimens examined here in this "climax" stage did not show the full range of vegetative variation in taxonomically important

**Table 2** *Sargassum orotavicum*: percentage of different features related to primary (B1) and secondary (B2) blades.

	September		December		March		June	
	B1 (n=5)	B2 (n=0)	B1 (n=50)	B2 (n=22)	B1 (n=72)	B2 (n=607)	B1 (n=16)	B2 (n=881)
Branched	60	–	20	0	11	2	25	2
Sinuous	40	–	80	50	94	6	69	25
Spinous blade stalk	60	–	70	54	85	44	56	45
Margin entire	60	–	46	18	0	14	31	42
Margin dentate	0	–	0	0	1	23	19	21
Margin serrate	40	–	54	82	99	63	50	37

n=sample size.



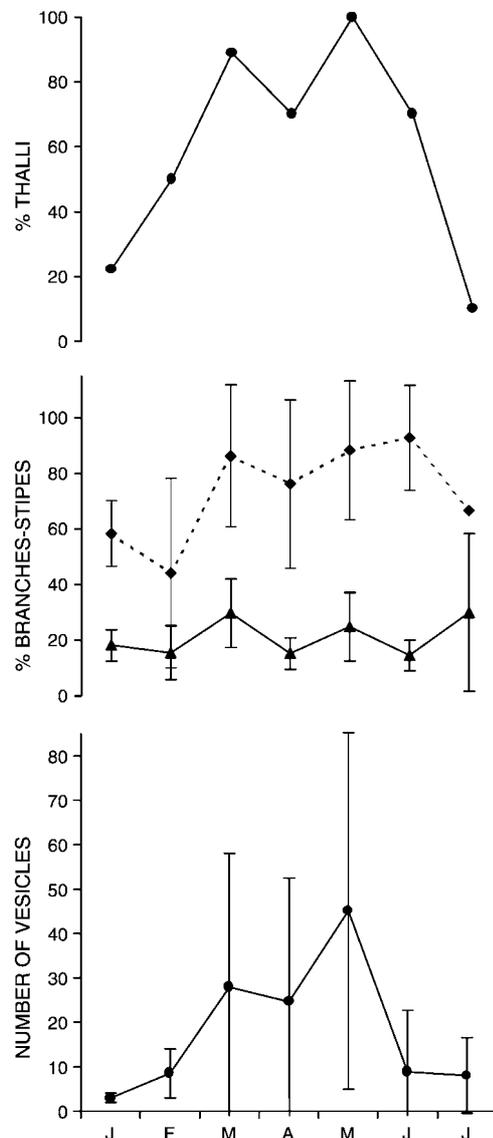
**Figure 7** *Sargassum orotavicum*: mean number of cryptostomata per blade (one side) and mean area of cryptostomata ( $\mu\text{m}^2$ ) ( $\pm$ standard deviation) in selected months. n=number/blade (one side).

features. Maximum development of vegetative features (“climax” of the vegetative stage) occurred before the reproductive “climax”. Elevated rates of growth before the reproductive phase have been reported for other species of *Sargassum* as well (DeWreede 1976, Prince and O’Neal 1979, Martin-Smith 1993). The reproductive phase also coincided with the period of maximum biomass, as seems to be characteristic of pseudoperennials (DeWreede 1976, Hurtado and Ragaza 1999).

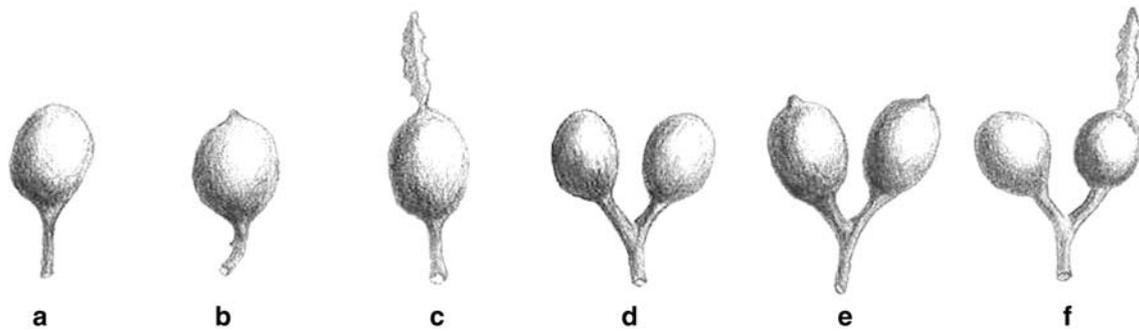
The senescence and degeneration phase began in summer, culminating with the detachment of the structures that renew every year. Although this massive loss has been documented in numerous species of *Sargassum* (DeWreede 1976, Prince and O’Neal 1979, Paula and Eston 1987, Kilar 1992, Hurtado and Ragaza 1999), it may occur at different periods throughout the year, depending on the geographic distribution of the species.

Seasonality in species of *Sargassum* has been correlated with the seawater temperatures by numerous authors (Fletcher and Fletcher 1975, DeWreede 1976, Prince and O’Neal 1979, Deysher 1984, McCourt 1984, De Ruyter Van Steveninck and Breeman 1987, Martin-Smith 1993, Hurtado and Ragaza 1999, Fernández 1999). It is assumed that the timing of the reproductive phase in *Sargassum* varies latitudinally in relation to the gradient of seawater temperature. This variation has been documented in the annual *Sargassum horneri* C. Agardh from Japan (Yoshida et al. 1998) and in the invasive pseudoperennial *Sargassum muticum* from the Pacific coast of North America (Norton and Deysher 1989, Espinoza 1990) and the west coast of Europe (Fletcher and Fletcher 1975, Arenas and Fernández 1998, Wernberg et al. 2001).

In species of *Sargassum* with tropical distribution, highest biomasses and their fertile period occur in winter (DeWreede 1976, Prince and O’Neal 1979, McCourt 1984, Hurtado and Ragaza 1999). In contrast, *Sargassum muticum* from the British Isles (Fletcher and Fletcher 1975) and Denmark (Wernberg et al. 2001) has been reported as fertile in summer, while on the north coast of Spain it has a spring-summer reproductive period (Arenas and Fernández 1998). This pattern of variation for the reproductive period has also been documented along the Pacific coasts of North America (Norton and Deysher 1989). Specimens of *Sargassum orotavicum* examined from the Canary Islands, at the southernmost limit of the warm temperate region, showed an intermediate phenological pattern with a reproductive phase during spring. McCourt (1984) found a similar behaviour in *Sargassum johnstonii* Setchell et Gardner and *S. herporhizum* Setchell et Gardner from the Gulf of California.



**Figure 8** *Sargassum orotavicum*: temporal variation in percentage of individuals, mean percentage ( $\pm$ standard deviation) of stipes ( $\blacklozenge$ ) and primary branches ( $\blacktriangle$ ) with vesicles, and mean number ( $\pm$ standard deviation) of vesicles per primary branch.



**Figure 9** *Sargassum orotavicum*: morphological types of vesicles.

(a) mucous with simple stalk; (b) mucronate with simple stalk; (c) with coronal blade and simple stalk; (d) mucous with branched stalk; (e) mucronate (at least one mucro) with branched stalk; (f)=with coronal blade (at least one) and branched stalk.

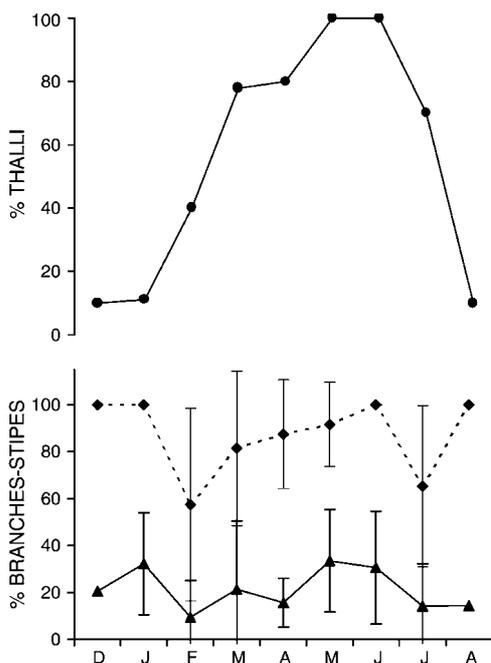
**Table 3** *Sargassum orotavicum*: percentages of different vesicles (as characterised in Figure 9) during the period that they were present (January 2002–July 2002).

Month	a	b	c	d	e	f	n
January	50.0	25.0		25.0			4
February	53.9	41.0	5.1				39
March	68.4	21.2	5.2	2.2	2.1	0.9	231
April	39.9	51.7	5.9	2.5			203
May	49.5	47.0	2.5	0.4	0.2	0.4	523
June	46.0	54.0					63
July	100.0						15
Annual	52.4	41.8	3.6	1.2	0.6	0.4	1078

n=number of vesicles present in all the individuals studied each month.

Phenological patterns seem to be regulated, at least partially, by optimum growth temperatures for zygotes, and there are marked variations in relation to the geographic distribution. DeWreede (1976) found that tropical *Sargassum obtusifolium* J. Agardh, *S. polyphyllum* J. Agardh and *S. oligocystum* Montagne had maximum

growth rates under 24°C, while in the cold temperate *Sargassum muticum*, the growth of zygotes was maximal at temperatures over 15°C (Norton 1977, Chapman 1995). Apparently, *Sargassum* species adjust their gamete release period to appropriate water temperatures. This period seems to occur in summer in cold temperate spe-

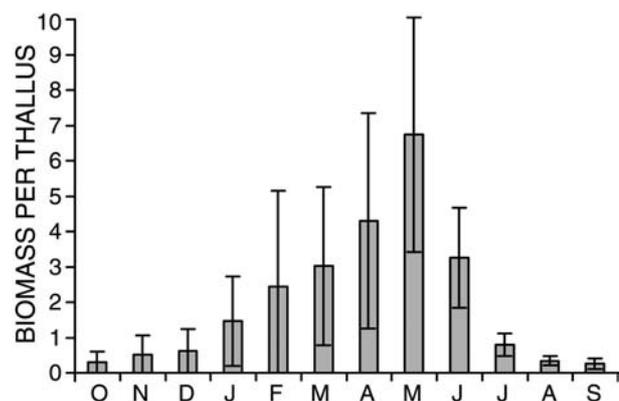


**Figure 10** *Sargassum orotavicum*: percentage of individuals, and mean percentage ( $\pm$ standard deviation) of stipes ( $\blacklozenge$ ) and primary branches ( $\blacktriangle$ ) with receptacles, through the period in which they were present.

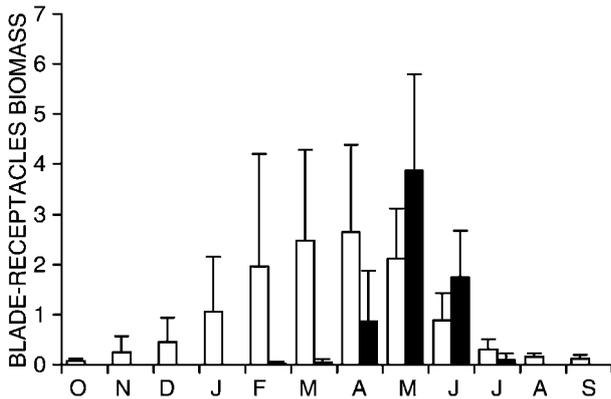
D	J	F	M	A	M	J	J	A
(4)	(3)	(3)	(3)	(10)	(14)	(17)		
INMATURE				MATURE			SENESCENT	

**Figure 11** *Sargassum orotavicum*: receptacle phenology through the period when present.

Numbers in brackets indicate the maximum length (mm) detected each month.



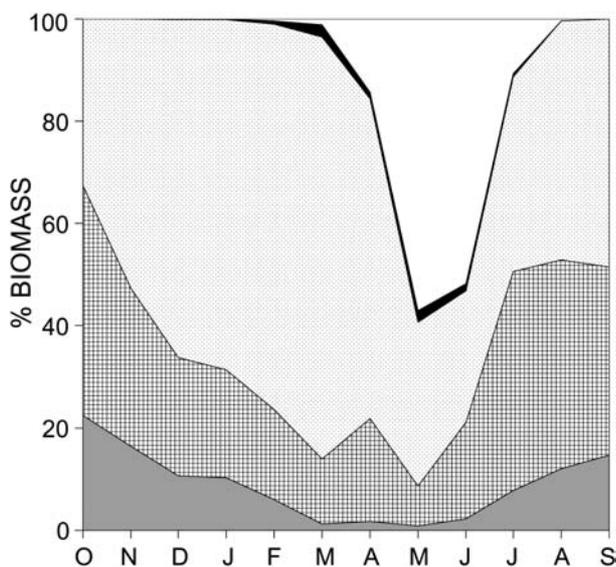
**Figure 12** *Sargassum orotavicum*: mean biomass (g DW) ( $\pm$ standard deviation) per individual through the year.



**Figure 13** *Sargassum orotavicum*: mean biomass (g DW) ( $\pm$ standard deviation) of blades (white) and receptacles (black) through time.

cies, in winter in tropical species, and in spring in subtropical taxa such as *Sargassum orotavicum*.

Since many of the morphological features of *Sargassum* vary significantly throughout the year, it is difficult to determine which should be used taxonomically. Usually, features for diagnosis are temporally and spatially variable. Nevertheless, the results obtained here showed that some characters, mainly those related to vesicles and blades, are quite stable. For analysing the variation of continuous traits in *Sargassum orotavicum*, coefficients of variation (CV) were used as a measure of temporal variability, while the variability between individuals (V) was used as a measure of spatial variation, as recommended by Kilar et al. (1992a). Similar variation patterns occur in *S. polyceratum* Montagne and *S. mathiesonii* Kilar, and the characteristics of the vesicles are most stable in the former species (Kilar et al. 1992b), and those related to vesicles and blades in the latter species (Kilar 1992).



**Figure 14** *Sargassum orotavicum*: mean percentage of the total biomass due to holdfasts (grey), stipes-branches (grid), blades (stippled), vesicles (black) and receptacles (white), through the year.

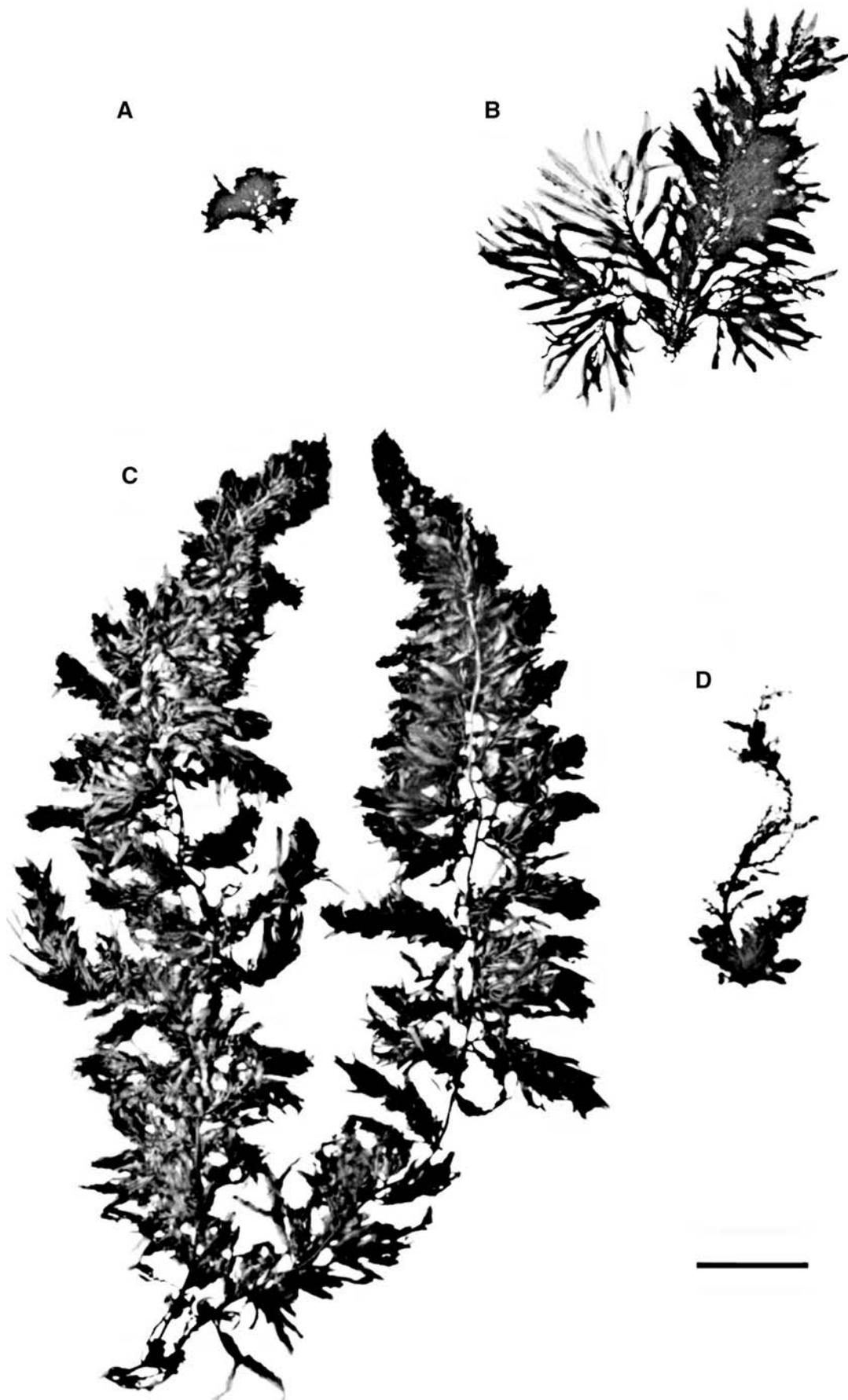
According to Kilar (1992), a trait with low values of CV and V is considered as stable, however, those traits with a high CV or low V are best for distinguishing species, as a single thallus contains the necessary information for its identification (Kilar et al. 1992a). *Sargassum orotavicum* showed greater values of CV than V for the twelve continuous traits studied, which means that the greatest component of variation was temporal, and the characters approached spatial stability. A detailed knowledge of the temporal-spatial variation of the continuous traits of the different species of *Sargassum* would simplify taxonomy, turning the variation patterns into useful taxonomic indicators, as pointed out by Kilar et al. (1992b).

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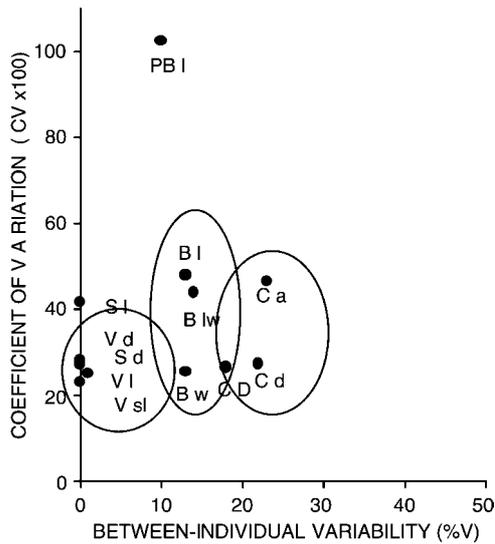
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**Figure 15** *Sargassum orotavicum*: seasonal variation in morphology. (A) Autumn-specimen (TFC Phyc 11676). (B) Winter-specimen (TFC Phyc 11678). (C) Spring-specimen (TFC Phyc 11681). (D) Summer-specimen (TFC Phyc 11683). Scale bar=5 cm.



**Figure 16** *Sargassum orotavicum*: coefficient of variation (CV $\times$ 100) vs. percentage between-individual variability (%V) for selected traits.

PBI: primary branch length, SI: stipe length, Sd: stipe diameter, VI: vesicle length, Vd: vesicle diameter, Vsl: vesicle-stalk length, BI: blade length, Bw: blade width, Blw: blade length-width ratio, CD: cryptostomatal major diameter, Cd: cryptostomatal minor diameter, Ca: cryptostomatal area.

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