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Biological basis for the management of 'luga negra' (*Sarcothalia crispata* Gigartinales, Rhodophyta) in southern Chile

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Abstract

The present paper describes growth dynamics in a natural bed of the resource 'luga negra' (*Sarcothalia crispata*) in Guapilinao, southern Chile (41°57' S, 73°31' W). This resource is currently harvested and exported as raw material for the production of carrageenan. Seasonal variation in biomass, frond size, density and phenology was determined by periodic sampling. Natural recruitment was evaluated on different substrata added to the field; at the same time, substrata were inoculated under greenhouse conditions. Results showed that 'luga negra' has seasonal growth: biomass increased from a minimum in spring to a maximum in mid to late summer. On the other hand, density was minimal in winter (200 ind. m⁻²) and increased to 2000 ind. m⁻² in late spring. Peak abundance of mature tetrasporic fronds occurred in late summer, whereas that of cystocarpic fronds occurred in winter. Recruitment began in summer and extended into winter. Survival on different substrata were compared. Gametophytes had better survival rates on clam shells and 5 mm rope while tetrasporophytes had the best survival rate on clam shells and secondarily on boulders.

Introduction

In Chile marine algae and their derivatives have economic and social importance. In 1993, they generated an income of US\$ 47 million and employed for over 8000 people. The resources *Sarcothalia*, *Gigartina* and *Mazzaella* have been exploited for more than three decades for the production of carrageenan. These algae have become particularly important over the last five years because of the increase in world consumption of carrageenan and due to the installation of processing plants in the country, producing 26 tons in 1989 (Avila & Seguel, 1993). In 1993, 7000 dry tons of carrageenophytes and 470 tons of carrageenan were exported with a value of US\$ 10 million.

Morphological variability and the different taxonomic criteria used to separate the species have generated some confusion in the identification of populations present on the Chilean coast (Kim, 1976; Etcheverry *et al.*, 1981; Guiry & Garbary, 1990; Ramírez & Santelices, 1991; Hommersand *et al.*, 1993). Out of the 12 species described for Chile by Ramírez & Santelices

(1991), only three are of economic importance: *Mazzaella laminarioides* (Bory) Fredericq ('luga cuchara' or 'yapín') occurs on intertidal shores from Valparaíso (33° S) to Tierra del Fuego (53° S); *Sarcothalia crispata* (Bory) Leister ('luga negra') is typically subtidal (down to 10 m) and is distributed from Valparaíso to the Strait of Magellan (53° S), and *Mazzaella membranacea* (J. Agardh) Fredericq ('luga') is found in the intertidal from Valparaíso to the Chacao Channel (41°50' S). Landings of the different species are concentrated in two Chilean regions (37° S and 42° S), contributing 36% and 54%, respectively.

As in other gigartinacean species, the life story of *S. crispata* is isomorphic and triphasic (Candia & Poblete, 1981; Candia, 1983). Environmental factors such as light, temperature and water movement may determine the predominance of one phase. Nonetheless, other studies have shown that the relative abundance of the phases can be correlated to differential recruitment, to perennation of holdfasts (May, 1986) and to substratum dynamics (Poblete *et al.*, 1985; Hannach & Waaland, 1986).

Ecological studies indicate that the abundance of *Sarcothalia* populations is mostly regulated by two mechanisms: holdfast regeneration capacity and settlement of spores (Santelices, 1989). According to Santelices, there is coincidence between the time of maximum biomass and that of higher abundance of reproductive blades, so that intensive exploitation could decrease reproductive potential. On the other hand, although there are reports of regeneration of *M. laminarioides* from holdfasts (Santelices & Norambuena, 1987), as for *S. crispata*, this type of response has been described only in beds where the substratum exhibits seasonal sand invasion (Poblete *et al.*, 1985; Poblete & Lafón, 1987).

Some studies have shown seasonal variations in biomass and phenological changes in central Chilean populations (33°35' S) and in Bahía Concepción (36°42'; Hannach & Santelices, 1985; Poblete *et al.*, 1985). These studies have shown biomass increases in spring-summer, when maturation of the reproductive structures occurs, and decreases in autumn-winter.

There are no data on the localization and productivity of *Sarcothalia* and *Mazzaella* beds, which are exploited seasonally from October to March–April, nor recommendations on the harvesting frequency or management plans in order to protect resource sustainability (Vásquez & Westermeier, 1993). Only single stock estimation has been done, such as those of Santelices & Lopehandía (1981) for the area of Quellón (43° S), where they reported wet biomass values of 23.1 kg m⁻² for the genus *Sarcothalia*. The purpose of this study was to establish biological bases for management of 'luga negra' (*S. crispata*) in the X Region, southern Chile. In this study we assessed recruitment and seasonal variations in abundance, as well as the size structure and phenology of a natural bed, in order to understand the population dynamics of this resource.

Materials and methods

A subtidal natural bed of *Sarcothalia crispata* was studied at Guapilinao (41°58' S) between August 1992 and June 1993. The absolute depth of the area studied was between 1 and 2 m, although diving was always done in 3 to 8 m depending on the level of the tide. The bottom was covered with boulders and sand. Rocky substrata were covered by calcareous crustose algae and leafy species like *Sarcothalia* and *Ulva*, the latter being present year round. Predominant macrofauna consisted of *Tegula atra* (Lesson), *Nassarius* sp.,

Crepidula sp., *Loxechinus albus* Molina, *Pseudoechinus* sp., and chitons. The area was limited on its upper and lower margins by sand banks. The bed contained a long strip of boulders parallel to the coastline, with irregular borders, and had a mean width of 30 m. For each sampling (every six to eight weeks), two transects were laid perpendicular to the bed, and five stations were located every five m along each transect and sampled using a 0.25 m² quadrat. Because of the gentle slope of the bottom and the homogeneity of the study site, analyses were done using each station as a replicate for that sampling date. In each quadrat, the entire harvestable biomass of *Sarcothalia* was collected as well as the substratum with recruits of 'luga'. In the laboratory, the maximum length, number, and biomass of the harvested blades of each reproductive phase were determined; juveniles (<1 cm) were counted directly on the collected boulders, using subsamples of 9.6 cm². Density was extrapolated to the substratum area to obtain the total value for the quadrat.

To evaluate natural recruitment, substrata were installed in four identical experimental series, on August and October 1992 and January and April 1993. For each series, two sites were selected. Two types of substrata were used: boulders previously stored in the laboratory, moved to the site from the upper intertidal, and boulders from the site itself. Substrata from the upper intertidal were labelled in the laboratory some days before placing them at the study sites. Substrata from the site itself were not marked but were positioned next to the intertidal boulders, forming pairs. Forty pairs were located at each site. In the last series concrete blocks and overturned boulders were added. During each sampling, five of each boulder type were collected from each site. This sampling was done without replacement. In the laboratory, the holdfast density on the upper surface of each boulder was evaluated under a binocular microscope. The total number of holdfasts was counted in five visual fields selected at random. All the values of holdfast density on the boulders were standardized to cm⁻². *Sarcothalia crispata* densities observed on different dates, sites and substratum types were compared in each series.

The quality of artificial and natural substrata as spore collectors was evaluated in greenhouse experiments. Cystocarpic and tetrasporic blades were collected at Bahía Pargua in February 1993, were taken to the greenhouse, washed with filtered sea water and used to inoculate boulders (natural substratum), clam shells and polypropylene filament ropes of 2 and 5 mm diameter. Seeding was done in aquaria of 60 × 44 × 18 cm,

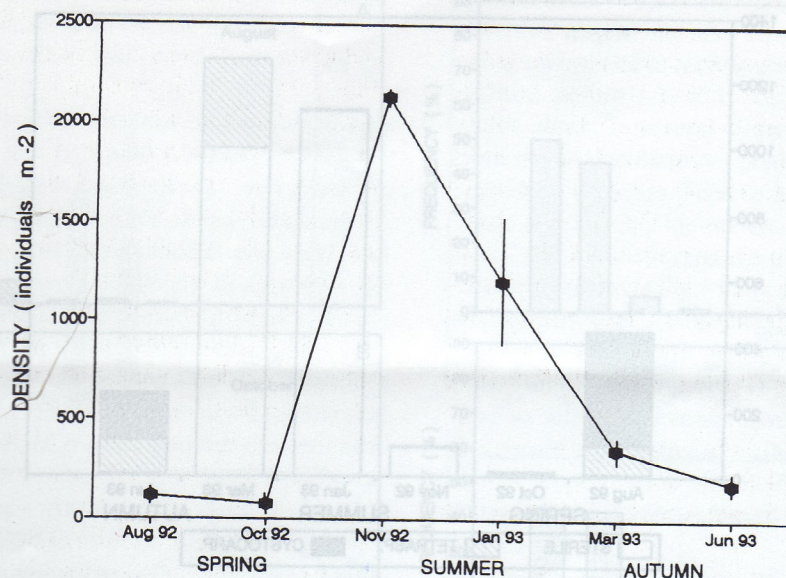


Figure 1. Average density ($\pm$ SE) of blades of *Sarcothalia crispata*, counting all blades in ten 0.25 m² quadrats in a natural bed in Guapilinao, Chiloé, southern Chile.

using one for each substratum type. Netting was used as support for reproductive blades, and the substratum was arranged beneath the blades on the bottom of the aquarium. The blades were allowed to release spores over 24 h and removed; the aquaria were maintained with regular sea water changes (every seven days) and four h of aeration daily. After four weeks the inoculated substrata were moved to culture tanks of 1 m³ capacity. To estimate spore availability for each substratum experiment, microscope slides were placed in the aquaria at the beginning of the experiments. To measure survival and density of the sporelings, six substrata were sampled from each aquaria. On each substratum 24 measurements were made after ten weeks in the greenhouse. Then substrata were transplanted to the natural environment, and ten weeks later they were sampled. Sporeling density data were standardized to ind. cm⁻². Survival was calculated as the difference between initial and final sporeling density and was expressed as survival percentage of the initial density.

Experiments were analyzed with ANOVAs (Sokal & Rohlf, 1981; Underwood, 1981) after testing for homoscedasticity (Cochran C tests, Underwood, 1981; Winer, 1982) and transforming data if required. Student-Newman-Keuls tests were used to disclose the means that caused significant p values (Underwood, 1981; Steel & Torrie, 1988).

Results

Figure 1 shows the variation in density of *Sarcothalia crispata* in the subtidal bed over the study period. Toward the end of winter and into early spring, blade density remained low (under 200 ind. m⁻²). Around mid-spring, density increased, reaching levels over 1000 ind. m⁻², then diminished gradually thereafter to less than 200 ind. m⁻² in June 1993. In winter, the biomass stayed low (Figure 2), with minimum values through most of the spring (less than 200 g m⁻²), then increased to values over 1000 g m⁻² during summer. In autumn, the biomass decreased to values under 320 g m⁻².

There was a shift in the occurrence of the recognizable reproductive phases. At the onset of this study, in August, the cystocarpic phase predominated both in density and biomass, whereas the tetrasporic phase was very scanty. Toward late spring and over the summer, sterile blades predominated. In late summer and early autumn (March), tetrasporic blades appeared as the dominant reproductive phase. In the early winter sampling (June), mature cystocarpic and tetrasporic blades were found, the former being more abundant.

Distribution by size frequency, considering all individuals, showed that the smaller size class (<1 cm) predominated throughout the sampling period (Figure 3). The maximum frequency of these small thal-

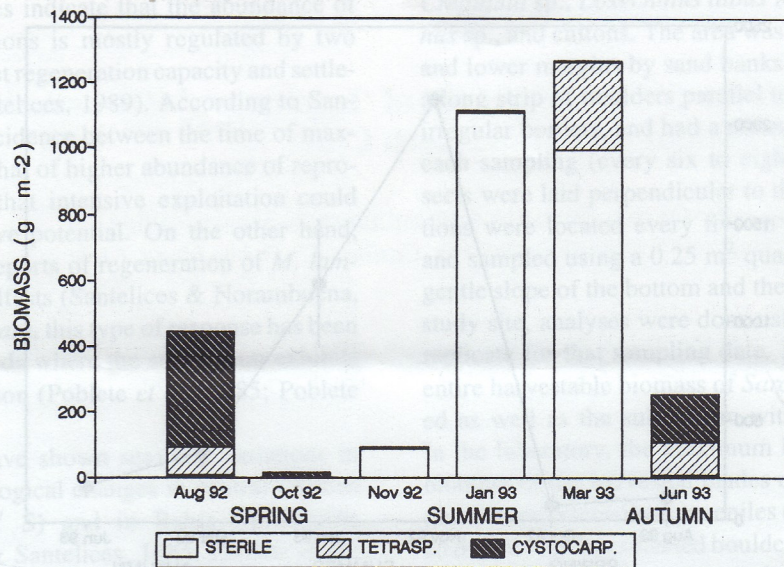


Figure 2. Average biomass (g wet wt) of *Sarcothalia crispata* weighing only blades >1 cm in length in ten 0.25 m^2 quadrats in a natural bed in Guapilinao, Chiloé, southern Chile. Mature blades were identified as tetrasporic or cystocarpic; otherwise they were classified as sterile.

li was recorded in October and November, when it reached 80% (Figures 3b & 3c). The next dominant category consisted of blades 1 to 10 cm tall, with maximum frequencies in January and March (Figures 3d & 3e). It is worth noting that within this category, the highest frequency corresponded to blades under 2 cm. Blades over 10 cm were recorded in mid-winter (August) 1992 (Figure 3a) and in January, March and June 1993 (Figures 3d, 3e & 3f), when blades up to 50 cm in length were found. However, the frequency of these combined size classes was never more than 10% of the total blades sampled.

Figure 4 illustrates the recruitment observed in the substratum introduction experiment. For each of the four experimental series the mean densities of *Sarcothalia* holdfasts occurring on the two types of boulders were plotted. Figure 4a shows the trend in recruitment for the first experiment, begun August 1992. Density of individuals on boulders from the high intertidal had a maximum of five ind. cm^{-2} in November. Differences in density between the two types of boulders were only marginal ($0.10 > p > 0.05$). Densities (close to two ind. cm^{-2}) detected on boulders from the site itself may correspond to individuals recruited before or during this experiment or to blades from old holdfasts. Nonetheless, differences in density recorded on different sampling dates are significant ($p < 0.001$). This dif-

ference is illustrated by densities in November, which were greater than those on any other sampling date.

In the second recruitment experiment (Figure 4b) mean density was less than 1 ind. cm^{-2} in all samples. No individuals were detected on boulders from the intertidal over the first five sampling periods, indicating that no recruitment had occurred since November. On boulders from the site itself, like in the first experiment, individuals were detected but their density decreased in April and July 1993. Although the difference between dates is at the threshold of significance ($p = 0.52$), the SNK test did not identify differences.

On the substrata installed in January 1993, very low densities (less than one ind. cm^{-2}) were recorded during the first two sampling periods (Figure 4c), and no significant differences were found between the types of substrata or between the sampling dates.

In the last experiment, sampled in July 1993 (Figure 4d), densities were high, indicating recruitment during that period. There were significant differences ($p < 0.05$) among the types of substrata. Boulders from the intertidal had mean densities of 9.8 ind. cm^{-2} , whereas boulders from the site reached mean densities of fewer than 1.2 ind. cm^{-2} . Concrete blocks, not tested in the other experiments, had the highest mean densities of this experiment, more than 14 ind. cm^{-2} , and the overturned boulders had intermediate values

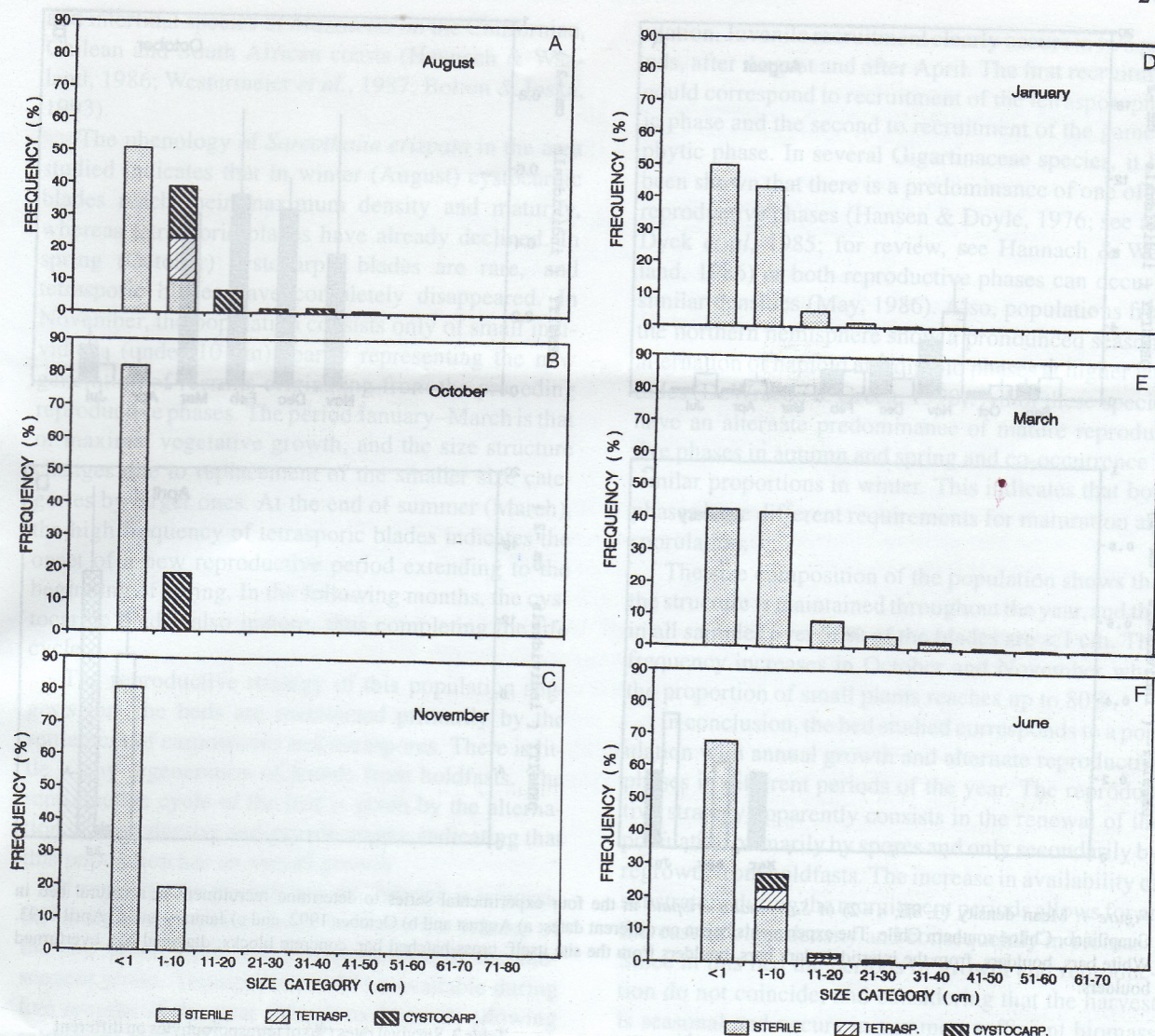


Figure 3. Length frequency distribution of blades of *Sarcothalia crispata* collected in ten 0.25 m² quadrats in a natural bed in Guapilinao, Chiloé, southern Chile on six sampling dates: a) August, b) October and c) November 1992, and d) January, e) March and f) June 1993. The first category includes only blades <1 cm in length. Mature fronds were identified as tetrasporic or cystocarpic; otherwise they were classified as sterile.

between those of the intertidal boulders and the *in situ* boulders (3.4 ind. cm⁻²).

The availability of spores in the experiment on quality of artificial substrata was over 400 spores cm⁻² on all substrata after two days of sporulation, and reached densities over 12 000 spores cm⁻²; however, this value showed considerable variability. Tables 1 & 2 show the comparison of survival rates of gametophytes and tetrasporophytes, respectively, grown in greenhouse and field conditions. On natural substrata, boulders and clam shells, final density of gametophytes was high (75

to 179 ind. cm⁻²) while final tetrasporophyte density ranged from 16 to 37 ind. cm⁻². Final density of gametophytes grown on ropes fluctuated between five and eight ind. cm⁻² while final density of tetrasporophytes was between two and six ind. cm⁻².

Discussion

The population studied had a markedly seasonal reproduction and growth cycle. Maximum densities

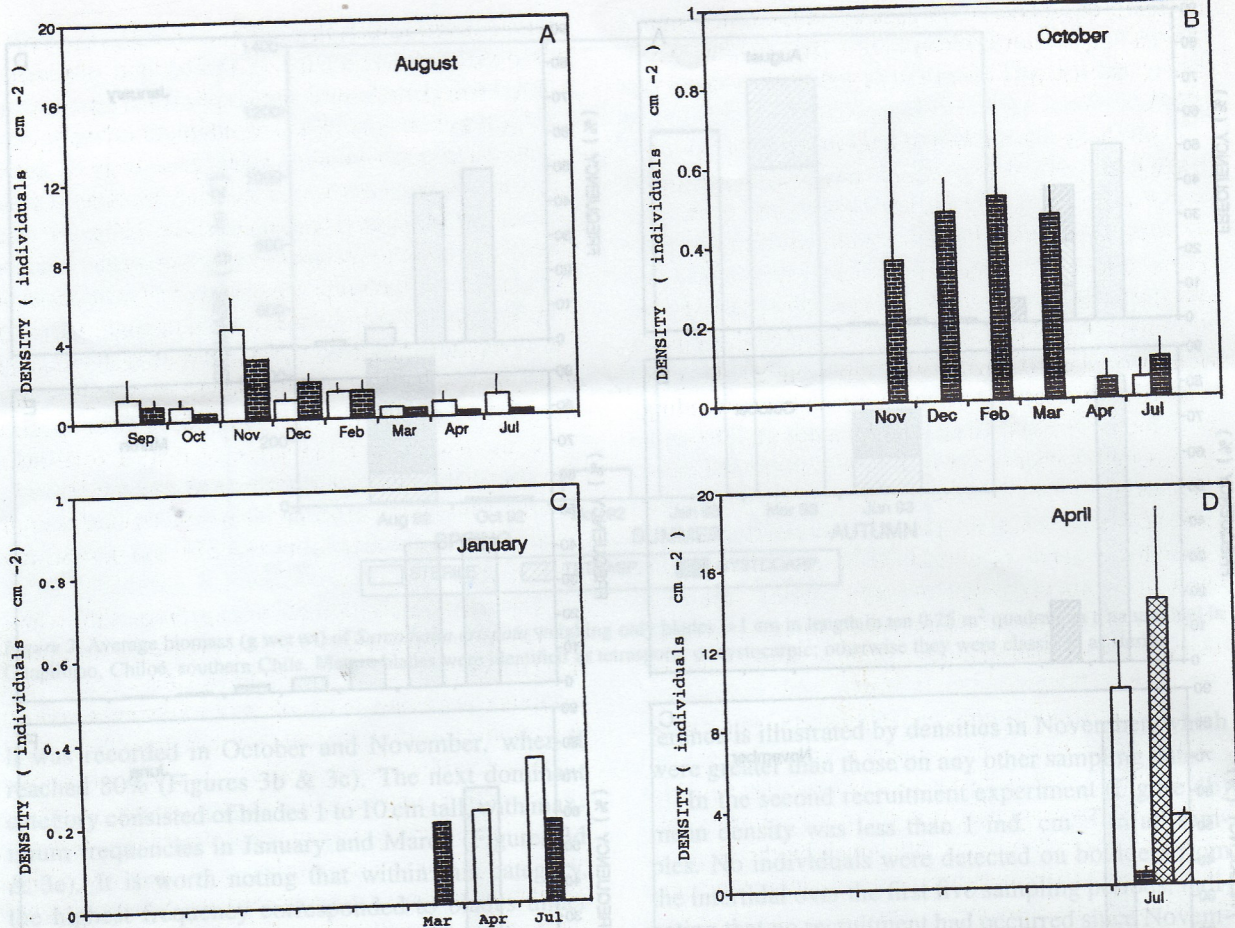


Figure 4. Mean density ($\pm$ SE, $n=2$) of *Sarcothalia crispata* in the four experimental series to determine recruitment in a natural bed in Guapilinao, Chiloé southern Chile. The experiments began on different dates: a) August and b) October 1992, and c) January and d) April 1993. White bars, boulders, from the intertidal; dark bars, boulders from the site itself; cross-hatched bar, concrete blocks; diagonal bar, overturned boulders.

Table 1. Survival rates (%) of gametophytes after cultivation for nine weeks in the greenhouse and after ten weeks in the field.

Substrata	Greenhouse cultivation	Natural environment cultivation
Boulders	78.3	7.1
Clam shells (inside)	81.9	15.3
Clam shells (outside)	9.6	15.6
Rope (5 mm)	21.5	15.3
Rope (2 mm)	16.9	5.2

occurred in November (over 2000 ind. m^{-2}) and minimal in September (less than 200 ind. m^{-2}). The maximal biomass, 1200 g m^{-2} , occurred in late sum-

Table 2. Survival rates (%) of tetrasporophytes on different substrata after nine weeks in the greenhouse and after ten weeks in the field.

Substrata	Greenhouse cultivation	Natural environment cultivation
Boulders	76.9	15.4
Clam shells (inside)	59.1	9.4
Clam shells (outside)	6.1	62.7
Rope (5 mm)	33.1	7.3
Rope (2 mm)	16.5	3.7

mer (March) with predominance of non-reproductive plants. Biomass in summer was five-fold that in winter. This seasonal pattern is shared by other subtidal

and intertidal species of *Mazzaella* on the Californian, Chilean and South African coasts (Hannach & Waaland, 1986; Westermeier *et al.*, 1987; Bolton & Joska, 1993).

The phenology of *Sarcothalia crispata* in the area studied indicates that in winter (August) cystocarpic blades reach their maximum density and maturity, whereas tetrasporic blades have already declined. In spring (October) cystocarpic blades are rare, and tetrasporic blades have completely disappeared. In November, the population consists only of small individuals (under 10 cm), partly representing the new generation of recruits originating from the preceding reproductive phases. The period January–March is that of maximal vegetative growth, and the size structure changes due to replacement of the smaller size categories by larger ones. At the end of summer (March), the high frequency of tetrasporic blades indicates the onset of a new reproductive period extending to the beginning of spring. In the following months, the cystocarpic blades also mature, thus completing the life cycle.

The reproductive strategy of this population suggests that the beds are maintained primarily by the settlement of carpospores and tetraspores. There is little if any regeneration of fronds from holdfasts. The reproductive cycle of the bed is given by the alternation of reproductive and growth stages, indicating that this population has an annual growth.

If reproductive periods are considered, it is possible to identify a coincidence between the release of the two spore types and the appearance of the subsequent phase. Tetraspores would be available during five months of the year (March to August), allowing settlement and growth of the gametophytes. Apparently, such gametophytes stop growing over the winter until the following spring. In turn, carpospores are available over four months (June to October). Results of the natural recruitment experiments indicate that new substrata support significantly better recruitment than existing substrata, particularly when introduced in autumn and winter. This period coincides with the highest frequency of mature reproductive blades.

Among the important factors that have an influence on the abundance of this resource we must mention the availability of substrata. From our observations in the field, the periods of spore release coincide with the winter months, in which more substratum is free and available to be occupied. Our results on recruitment suggest that settlement of carpospores and tetraspores is important for the maintenance of the pop-

ulation. Juvenile recruitment clearly occurs in two periods, after August and after April. The first recruitment could correspond to recruitment of the tetrasporophytic phase and the second to recruitment of the gametophytic phase. In several Gigartinaceae species, it has been shown that there is a predominance of one of the reproductive phases (Hansen & Doyle, 1976; see also Dyck *et al.*, 1985; for review, see Hannach & Waaland, 1986) or both reproductive phases can occur at similar densities (May, 1986). Also, populations from the northern hemisphere show a pronounced seasonal alternation of haploid and diploid phases at higher latitudes (DeWreede & Green, 1990). All of these species have an alternate predominance of mature reproductive phases in autumn and spring and co-occurrence in similar proportions in winter. This indicates that both phases have different requirements for maturation and sporulation.

The size composition of the population shows that the structure is maintained throughout the year, and that in all samples over 50% of the blades are <1 cm. This frequency increases in October and November when the proportion of small plants reaches up to 80%.

In conclusion, the bed studied corresponds to a population with annual growth and alternate reproductive phases in different periods of the year. The reproductive strategy apparently consists in the renewal of the population primarily by spores and only secondarily by regrowth from holdfasts. The increase in availability of substratum during the recruitment periods allows for an increase in plant density and consequently in biomass. Since in this bed the periods of growth and reproduction do not coincide, and considering that the harvest is seasonal and occurs in summer, sufficient biomass must be left by the harvesters to insure reproduction of the population and preservation of the resource.

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