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Biological basis for the management of *Gigartina skottsbergii* (Gigartinales, Rhodophyta) in southern Chile

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Abstract

Environmental and biological parameters were analysed for populations of *Gigartina skottsbergii* (Setchell & Gardner) at Calbuco, Llanquihue Province (sheltered environment) and Ancud, Chiloe Province (exposed environment) in the south of Chile, with the aim of determining the biological basis useful in guiding management efforts for this species. In both populations, the biomass, density, recruitment, growth and survival showed maximum values in spring–summer. Most plants were sterile, and while cystocarps were present throughout the year, they were more abundant in autumn–winter. It was concluded that at Ancud, this species presents a synchronized and predictable population with high recruitment and low survival, while Calbuco showed low recruitment, higher survival and higher growth rates. Calbuco is, therefore, recommended as a growth (culture) area, and Ancud as an area for recruitment. As a management strategy, it is recommended that the harvest be mainly restricted to the end of spring (November–December), reducing towards the end of summer (February–March). Cutting should be selective and done by hand, removing fronds of at least 600 cm^2, corresponding to a frond length of a minimum of 25 cm.

Introduction

Gigartina skottsbergii is endemic to the extreme south of South America (Setchell & Gardner, 1936; Pujals, 1963; Kühnemann, 1972; Westermeier, 1981), and is of high commercial value for its biomass and carrageenan content. In 1989, carrageenophyte production reached 26 t, and within six years this figure had increased by over 4000% (Schnettler et al., 1996). About 80% of the national production originates in this region, and success achieved in its export has resulted in over-exploitation in some localities, producing the necessity to look for alternative areas for collection (Westermeier et al., 1995, 1996, 1997).

In the area of Ancud, this species dominates the subtidal zone, where it is found growing principally together with *Sarcothalia crispata*, *Macrocystis pyrifera* and calcareous algae (Zamorano & Westermeier, 1996). Most of the plants were found to be vegetative, with maximum production of biomass in September (spring) and March (Autumn). Piriz (1996) working in the Atlantic (Chubut, Argentina), recorded values similar to those reported for Chile by Zamorano & Westermeier (1996), although the periods of maximum biomass differed. In studies carried out by Westermeier et al. (1995, 1996, 1997) between 41° S and 53° S in areas where harvesting pressures were supposedly less, biomass values were obtained which were similar to those reported for the Ancud area. This implies that harvesting was either greater than previously supposed, or that the population was able to regulate its biomass. This factor, added to the dynamics of the phases (tetrasporophyte/cystocarpic balance) being different from that reported by Zamorano & Westermeier (1996) and Piriz (1996), makes it necessary to evaluate a series of factors in the population dynamics of this species with greater precision by analysing populations occurring in distinct environmental conditions within this geographic area.

In view of the above considerations, while previous studies were centred principally on phenology, production of biomass and chemical composition, the present study has as its objective the development of a basis for management of this species-resource.

For this, over 32 months period, we determined the dynamics of the phases of the life cycle, biomass, density, size structure, recruitment, demography and growth.

Materials and methods

Study area

The work was carried out on natural populations of *Gigartina skottsbergii* located near San Agustin in Calbuco (41° 43′ S; 73° 05′ W) and Ancud Bay (41° 51′ S; 73° 49′ W) of the X Region in Chile (Figure 1). The Calbuco bed has an average extent of 1 ha, at a depth of 15 ± 1 m, where the attachment substratum for the species consists of boulders of metamorphic origin. This bed is in a sheltered environment. In contrast, the bed at Ancud, being approximately 0.5 ha, is more exposed to waves and currents. It is located in a zone of broken coastline at a depth of 9 ± 1 m, upon large formations of metamorphic rock, known as 'slab rock formation' (Illies, 1970).

Methodology and experimental design

Research was carried out monthly between July 1995 and February 1998. Plants were collected by destructive sampling from five 1 m^2 quadrats for determination of biomass m^{-2}, density m^{-2}, length (cm) of fronds, size structure (see Table 1) and phenology. The phase of the life cycle was determined by the resorcinol method described by Garbary & De Wreede (1988). (This test was checked by using control plants whose reproductive phase was known.) After this determination, gametophytic plants were examined with a microscope and divided into fertile (cystocarpic) and vegetative types. Tetrasporic plants were not distinguished from sterile tetrasporophytes.

Recruitment was measured using artificial blocks cleared of plants and placed on the bottom.

Demography and growth were evaluated using non-destructive sampling following the methods of Bhattacharya (1985). Four size classes were determined, using the blade surface as the discriminating factor (Table 1). Forty plants were marked in each class, using plastic labels attached to boulders; these were followed over time, measuring blade area from drawings on acrylic sheets. Survival and mortality were determined and the relative percentage growth rate in area each month was calculated from: (final area – initial area)/initial area × 100.

Environmental factors measured included atmospheric temperature, solar radiation and precipitation. In the water column, we determined temperature, salinity, pH, CO_2, HCO_3, O_2, NO_3, NH_4 and PO_4. Data on current intensity was obtained from the Meteorological Division of he Chilean Navy.

Results

Phenology

In each of the 32 months at both sites most of the plants were sterile. Overall 15.1% of the plants were cystocarpic at Calbuco and 9.8% at Ancud. Reproduction was minimal in early summer, cystocarpic plants showing marked seasonality with a maximum in autumn/winter at both sites (Figure 2).

The tetrasporophytic phase was present throughout the year, with a slight maximum in spring/summer (Figure 2). The overall balance between the phases was strongly in favour of gametophytes with only 11.1% of the population being tetrasporophytes at Cabulco and 11.3% at Ancud.

Biomass, density and length

Overall, the biomass was similar at the two sites but it was more variable at Calbuco (Figure 3A). At both sites the variability obscured what might have been seasonality; if anything, the biomass was higher in spring or early summer. There was a drop in biomass after the first 12 months of study.

There was a lower density of fronds at Calbuco, with an average of 7.3 plants m^{-2}, without marked seasonality, whereas in Ancud Bay, the mean number of fronds was 26 m^{-2} (Figure 3B). Again, possible seasonality was masked by high variability. Concurrently, and similar to biomass values, after the first 12 months the number of fronds decreased considerably at the latter station.

Frond lengths of *G. skottsbergii* were consistently greater at Calbuco (Figure 3C). Here again variability masked possible seasonality.

Size structure

All size classes 1–10 were present in both populations. At Ancud there was a dominance of class 1 (30.7% overall) when compared with Calbuco, which,

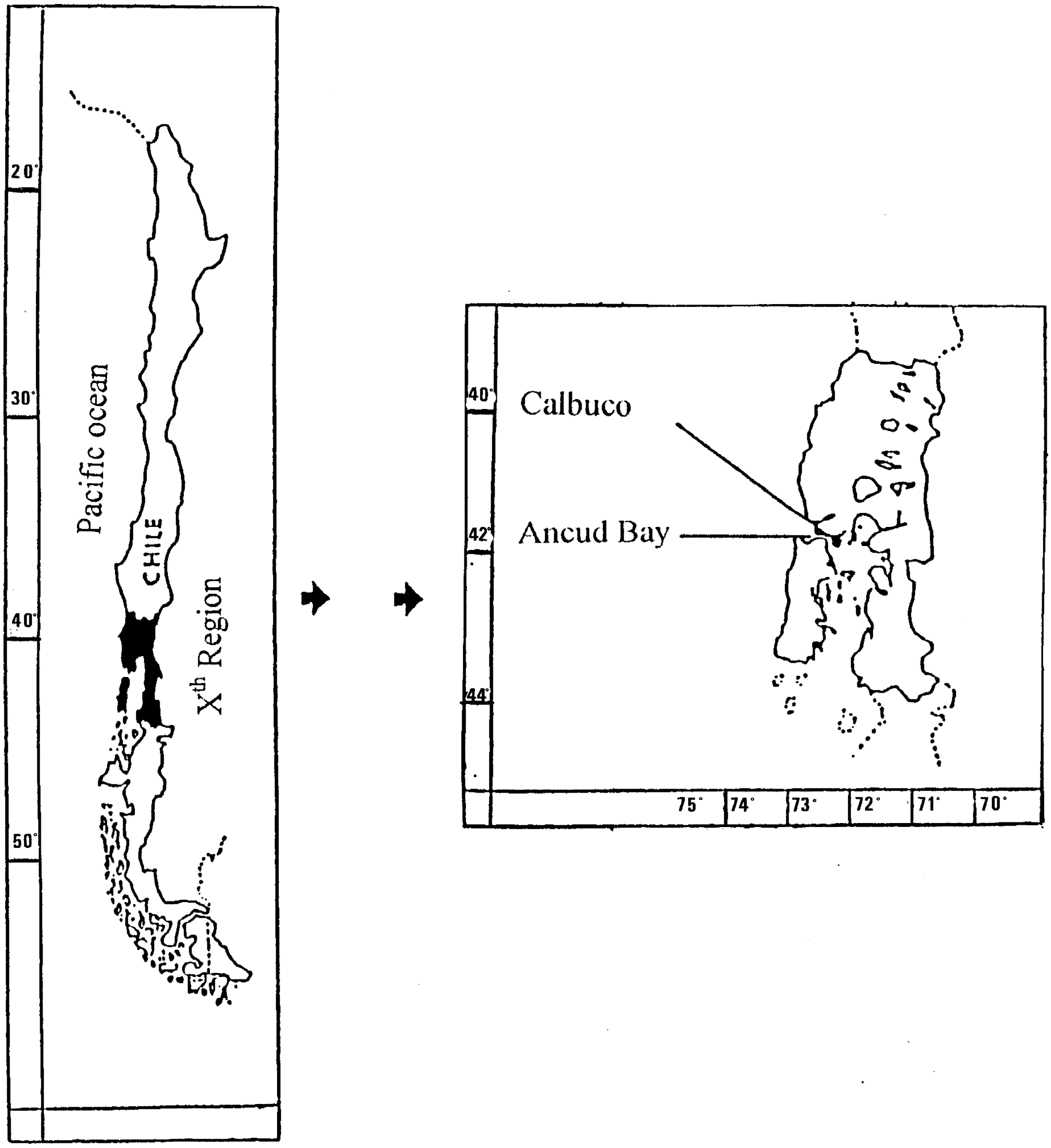


Figure 1. *Gigartina skottsbergii* study sites in Calbuco (Llanquihue) and Ancud Bay (Chiloe), in southern Chile.

although presenting an important proportion of this class (18.8%), showed a more homogeneous distribution of frequency among the different size classes (Figure 4A, B).

All classes I–VIII were present in the Calbuco population with class I (<1000 cm^{-2}) most abundant (62.9%) (Figure 4C, D). At Ancud, only the first six classes were present, with an average for class I of 93.3%.

Table 1. Definition of size classes used in the study on *G. skottsbergii*, based on thallus area

Size structure observations				Demography/growth observations	
Class	Area in cm^2	Class	Area in cm^2	Class	Area in cm^2
1	<100	I	<1000	A	<50
2	100–199	II	1000–1999	B	50–99
3	200–299	III	2000–2999	C	100–149
4	300–399	IV	3000–3999	D	>150
5	400–499	V	4000–4999		
6	500–599	VI	5000–5999		
7	600–699	VII	6000–6999		
8	700–799	VIII	7000–7999		
9	800–899				
10	900–999				

Recruitment, demography and growth

There were notable differences between populations in monthly recruitment; an average of 2.8 fronds m^{-2} was found at Calbuco, and 12.9 fronds m^{-2} at Ancud. Recruitment showed seasonality at both sites with clear maxima in the spring/summers of 1995/1996 and 96/97 (Figure 5).

G. skottsbergii showed seasonal behaviour, mortality being highest in the months of autumn/winter. Of 160 marked plants observed over a period of 28 months, about 20% of them survived at each site. The pattern was similar at the two sites; at the beginning of the second year of observation the survival curve changed from descending to stable (Figure 6). Overall mean mortality rates were 5% per month at Calbuco and 6% at Ancud, but there was no significant difference between the sites in the total number of plants 27 months later. By this time, however, at Calbuco there were significantly more original Class D plants than at Ancud Bay ($p < 0.025$, G-test of Independence) so large plant mortality had been greater at Ancud.

Growth showed seasonality, with an increase in rates in spring/summer at both sites (Figure 7). At Cabulco, the size groups remained discreet and their respective mean blade areas increased by 3 to 11-fold by the end of the year. In Ancud Bay, there was less growth in spring, more loss in autumn and little difference in the mean areas of the size classes after a year.

In both populations of *G. skottsbergii*, fronds with a blade area greater than 200 cm^{-2} were reproductive.

Environmental factors

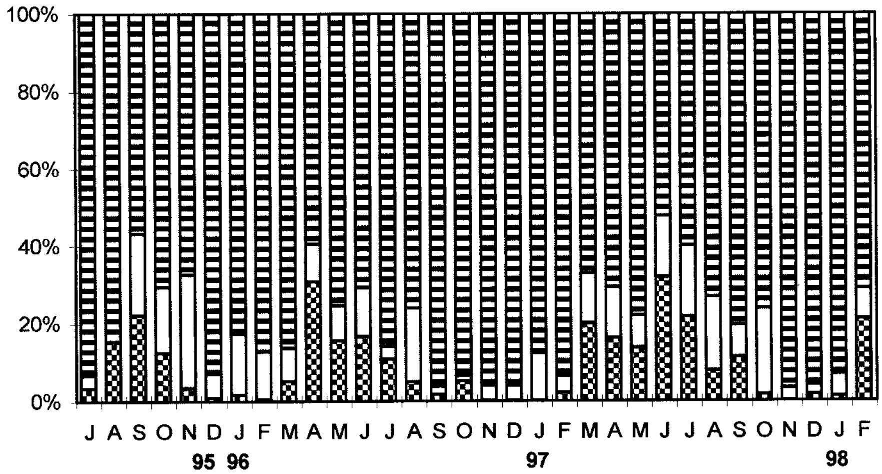
Atmospheric temperature, solar radiation, water temperature and salinity presented a clearly seasonal pattern, with values increasing during spring/summer and decreasing in autumn/winter (Figure 8). An inverse behaviour was reported for the parameters of precipitation, carbon dioxide, nitrate and phosphate, with highest values reached in autumn/winter, lowering in spring/summer. The pH, oxygen, bicarbonate and ammonium values showed no seasonal pattern.

Currents were under the primary influence of the semi-diurnal tidal oscillation. Current magnitude showed a bi-seasonal pattern. At Calbuco in summer (October–March), currents measured 2–16 cm s^{-1}; in winter (April–September) this value reached 10–45 cm s^{-1}. Corresponding values for Ancud, where prevailing winds from the fourth quadrant brought torrential rains, were 9–23 cm s^{-1} (summer) and 16–75 cm s^{-1} (winter).

Discussion

During 32 months of research, most of the plants were sterile. Cystocarpic plants were abundant in autumn/winter. Tetrasporophytes were always in a minority, with an overall level of 11%, but were slightly more common in spring/summer. Zamorano & Westermeier (1996) and Piriz (1996) found a similar pattern for cystocarpic plants, but not for tetrasporophytes. Westermeier (1995, 1996, 1997), studying populations of the XI Region (Melinka, 44° S), and the XII Region (Otway Sound 53 ° S), in spring/summer, found notable differences in these abundances: in the XII Region, 14% of the plants bore cystocarps at Charles Island, but 50% at Charles III Island and the proportions of tetrasporophytes were 26% and

Calbuco



Ancud Bay

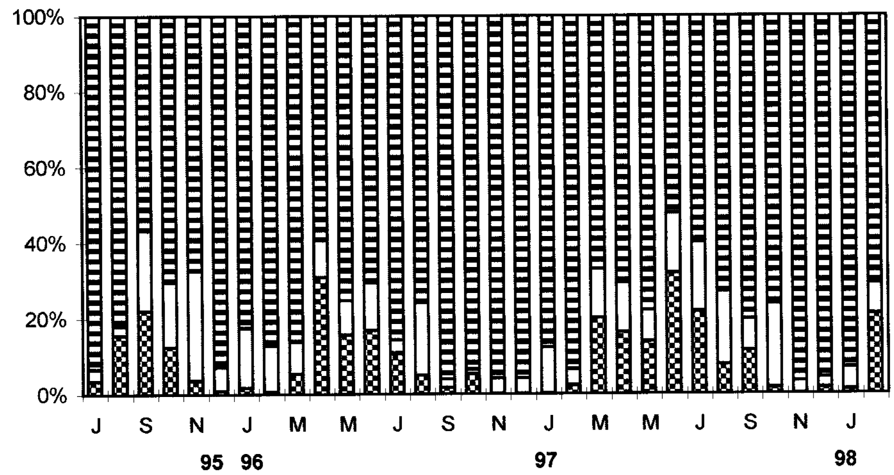


Figure 2. Percentages in relative frequency of the life history of *Gigartina skottsbergii* in the study areas. Horizontal bars, sterile gametophytes; white, tetrasporophytes; chequered, cystocarpic. Bars, SD.

33%, respectively. At some stations in the XI Region, although the differences were not marked as this, tetrasporophytes outnumbered cystocarpic plants. It is possible that differences in latitude, recruitment, harvesting pressure, and/or innate dynamics of the phases of the life cycle triggered these differences. We believe that *G. skottsbergii* is a long-lived species, having observed plants as old as 4 years, which implies that there may be cohorts maturing out of phase which could produce such changes. Variations in phase abundance have been described by Dyck et al. (1985) for *Mazzaella splendens* from British Columbia and by Westermeier et al. (1987) for *Iridaea laminaroides* in southern Chile.

In comparing the life cycle phase between Ancud (exposed) with Calbuco (sheltered), we found no dif-

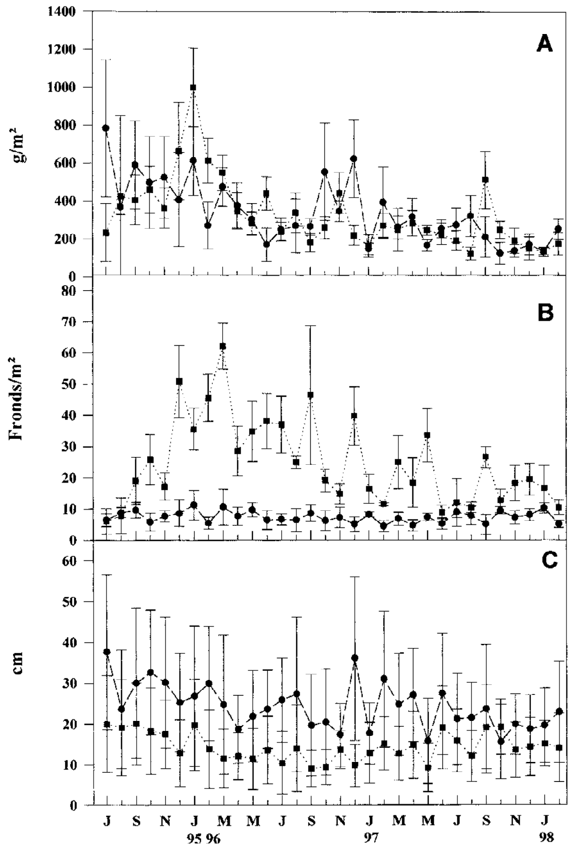


Figure 3. Monthly variation in (A) biomass, (B) density, and (C) thallus length of *Gigartina skottsbergii* in the study areas. —— ● ——, Calbuco; . . . ■ . . . , Ancud Bay.

ference in the proportion of tetrasporophytes in the populations. On the other hand, 11% signifies a considerable contribution by the diploid phase which until now had appeared to be of little importance. The dominance of gametophytes could be a response to the greater reproductive efficiency of the tetrasporophyte phase. In the laboratory, Westermeier & Sigel (1997) showed that tetraspores are superior in settlement, viability, germination and growth. Other studies point to the abundance of haploid plants as occurs with *Rhodoglossum affine* and *Gigartina* sp which may be the consequence of apomixis (Abbott, 1980). Our results suggest that this process is not involved in *G. skottsbergii*, and that this is likely a natural variation similar to that occurring in other Gigartinales in southern Chile (Westermeier et al., 1987; Westermeier et al., 1996). It is therefore necessary to concentrate on studying the gametophyte proportion (male and female plants) and with this clarify the phase balance.

In the study by Zamorano & Westermeier (1996), biomass was related to light and temperature; however, with more detailed sampling, no clear pattern emerges. This signifies that other biological and environmental factors (such as depth, exposure, substratum) also regulate timing and values. Size class distribution differed between sites. At Ancud, there was a gradient of abundance, with few large plants, while at Calbuco there was a more homogeneous distribution. Although overall mortality did not differ between sites, at Ancud the larger sized fronds showed greater mortality. Undoubtedly the greater movement of water and currents produce movement of boulders, and the large surface of the fronds incur greater abrasion, resulting in complete detachment, or partial destruction of fronds. Norall et al. (1981) reported this situation as 'storm pruning' in subtidal populations of *Phycodrys rubens* and *Callophyllis variegata* during winter. Bhattacharya (1985) observed a similar situation where the greater mortality of *Chondrus crispus* occurred in the larger size classes and those with major branching.

Nevertheless, recruitment at both stations showed some similarity in temporal variation, notably in the third year it was less, and occurred in mid-winter. This could have been due to a cohort temporally out of phase in germination and growth or the recruitment may have been produced by tetraspores liberated in winter of the same year which, due to some environmental factor were caused to recruit massively. Nevertheless, the plants are mature and viable at approximately 200 cm^2 which suggests that perhaps cohorts from the preceding year produced the recruitment, and that tetraspores need more time to germinate, recruiting later. This would suggest two periods of recruitment, one by way of carpospores in winter (with plants in summer), and another by way of tetraspores in summer (with plants in winter). This is consistent when it is considered that the carpospores are viable in the laboratory only in winter (Westermeier & Sigel, 1997).

This also suggests that the tetraspores are better adapted for growth in winter and carpospores to spring/summer, thus tetrasporophytic (2N) plants would be more abundant in summer, while gametophytes (N) would be present in winter, terminating the cycle with the production of carpospores. Guiry & Coleman (1982) found the maximum liberation of carpospores in winter in *G. stellata*, which corresponds with *G. skottsbergii* in southern Chile. Another carra-

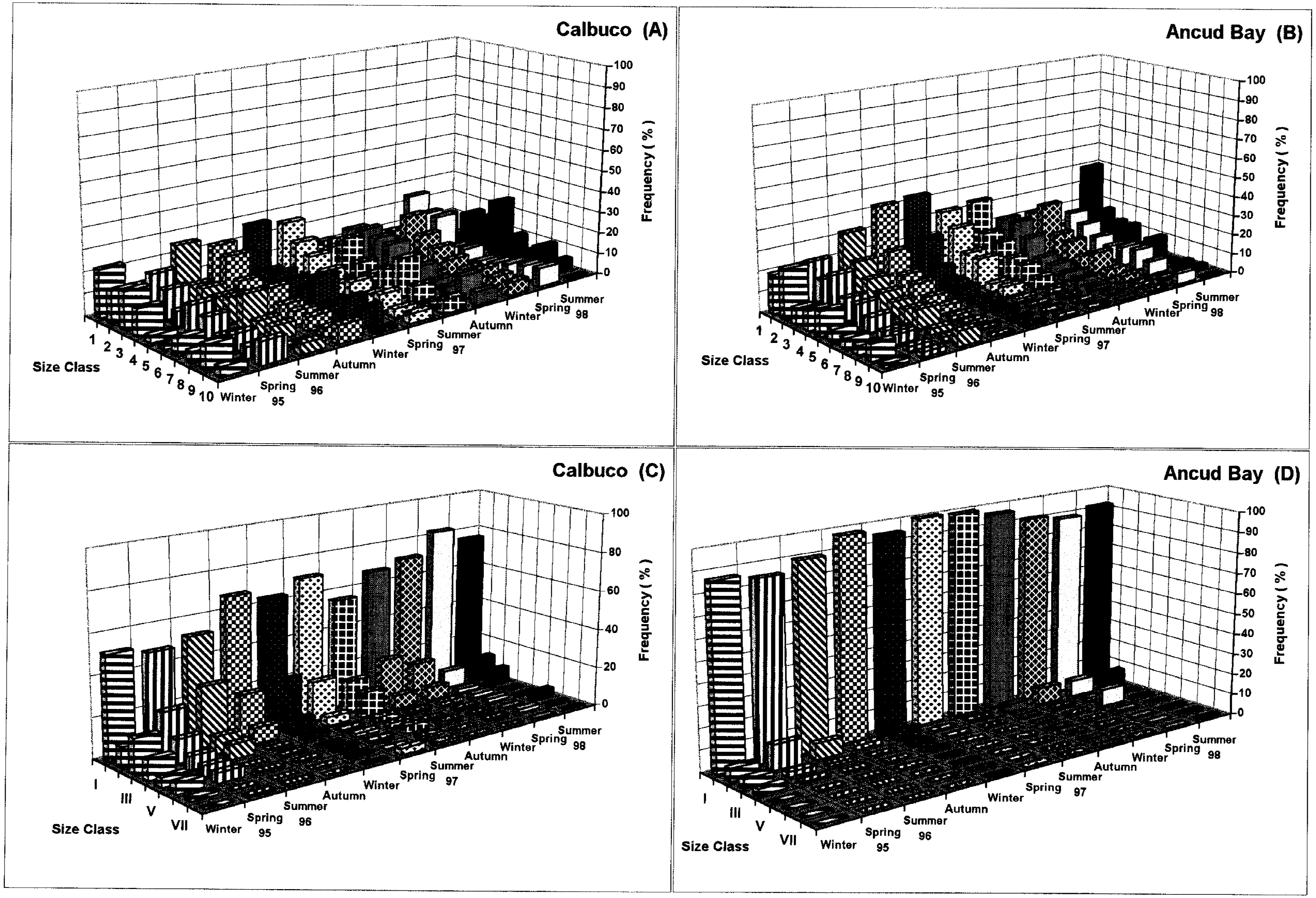


Figure 4. Seasonal variation in frond size structure of *Gigartina skottsbergii* in the study areas. (A) and (B), < 1000 cm^2; (C) and (D) all sizes. See Table 1 for size class definitions.

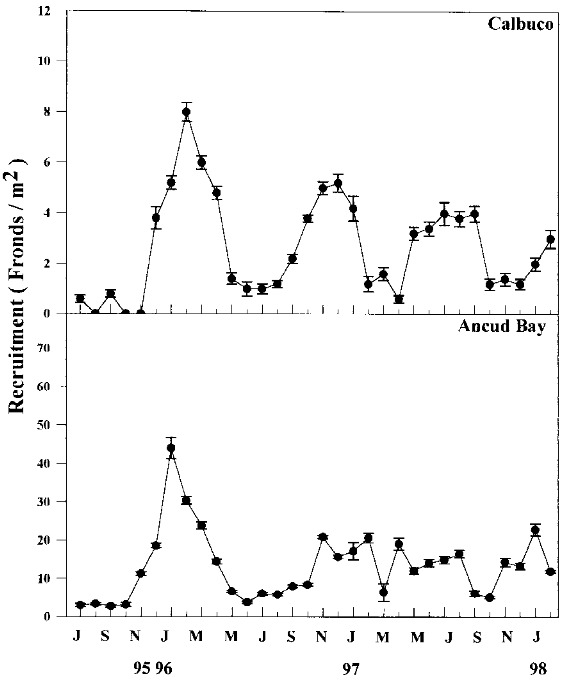


Figure 5. Monthly variation in recruitment of *Gigartina skottsbergii* in the study areas. Bars, SE.

genophyte, *Eucheuma*, showed maximum recruitment upon increase of turbulence in winter periods, which would be equivalent to the tetrasporic phase in the areas studied.

G. skottsbergii showed a growth rate average of 15% area/mo (0.5% area day^{-1}), which included all size classes at both stations. In *Chondrus crispus*, Taylor (1972) obtained a rate of 1.2% area day^{-1}, while the rate for *Constantinea subulifera* was 3.1% area day^{-1} (Powell, 1964). This indicated that *G. skottsbergii* has a lower growth rate, related to its morphological characteristics. Its maximum rates were 2.3% area day^{-1} at Ancud (Oct) and 1.4% area day^{-1} at Calbuco (Dec). In *Iridaea laminaroides* the major rates of net growth occurred in winter months, except when a maximum was reported for January with 54.7% (Gómez & Westermeier, 1991).

Other species such as *Gracilaria*, *Ulva* (Rosenberg & Ramos, 1982), *Chordaria flageliformis* (Probyn & Chapman, 1982, 1983) and *Macrocystis pyrifera* (Westermeier & Moller, 1990) showed highest growth rates in spring/summer. Piriz (1996), working with *G. skottsbergii* in the Atlantic, reported the highest biomass at the end of spring, relating his results to the length of day and increase in radiation.

Table 2. Mortality and growth rates in thallus area of *G. skottsbergii* over a periods of 27 and 12 months respectively

Class	Mortality (% month^{-1})		Growth rate (% month^{-1})	
	Calbuco	Ancud	Calbuco	Ancud
A	7.81	5.64	22.57	29.81
B	5.22	5.25	17.17	10.75
C	3.99	4.87	14.23	6.84
D	4.24	7.71	8.77	3.44
Mean	5.3	5.9	15.7	12.7

In contrast to its close relatives, the holdfast of *G. skottsbergii* is formed of haptera. It appears that a germination disc forms only in the early stages, after which haptera originate towards the substratum, where the attachment surface is increased. A possible method of management of this species/resource is postulated via maintenance of haptera and pruning of these, hopefully cultivating vegetative growth (Westermeir in prep.). At the same time we have observed *in situ* appearance of new fronds sharing the niche in the basal zone of *G. skottsbergii*. These observations differ from those of Piriz (1996), who suggests it may not be possible to obtain the renewal of fronds using this system of attachment. This undoubtedly requires further research; it may be that new fronds arise from previously settled spores.

In processing factories, the minimum frond size utilized is 20 cm^2, which implies lowering the potentially harvestable biomass in subsequent periods, and reduction of the possibility of reproductive generations of new thalli. From our results, it can be concluded that the strategy for management of this resource should include restriction to the sole removal of plants exceeding 600 cm^2 (25 cm length) between December and February. This would signify a substantial contribution of reproductive material to the different cohorts, which would ensure later recruitment. It is possible to suggest permanent monitoring, except in winter, to extract plants of this size. The type of harvesting to which this resource is exposed may produce major reductions of biomass over a short time period, which suggests the need for more conservative harvesting. It is also recommended that the harvest be done by pruning (cutting), conserving the basal fixation system, as the thallus is capable of regenerating new tissue by action of the meristems involved (Westermeier in prep.).

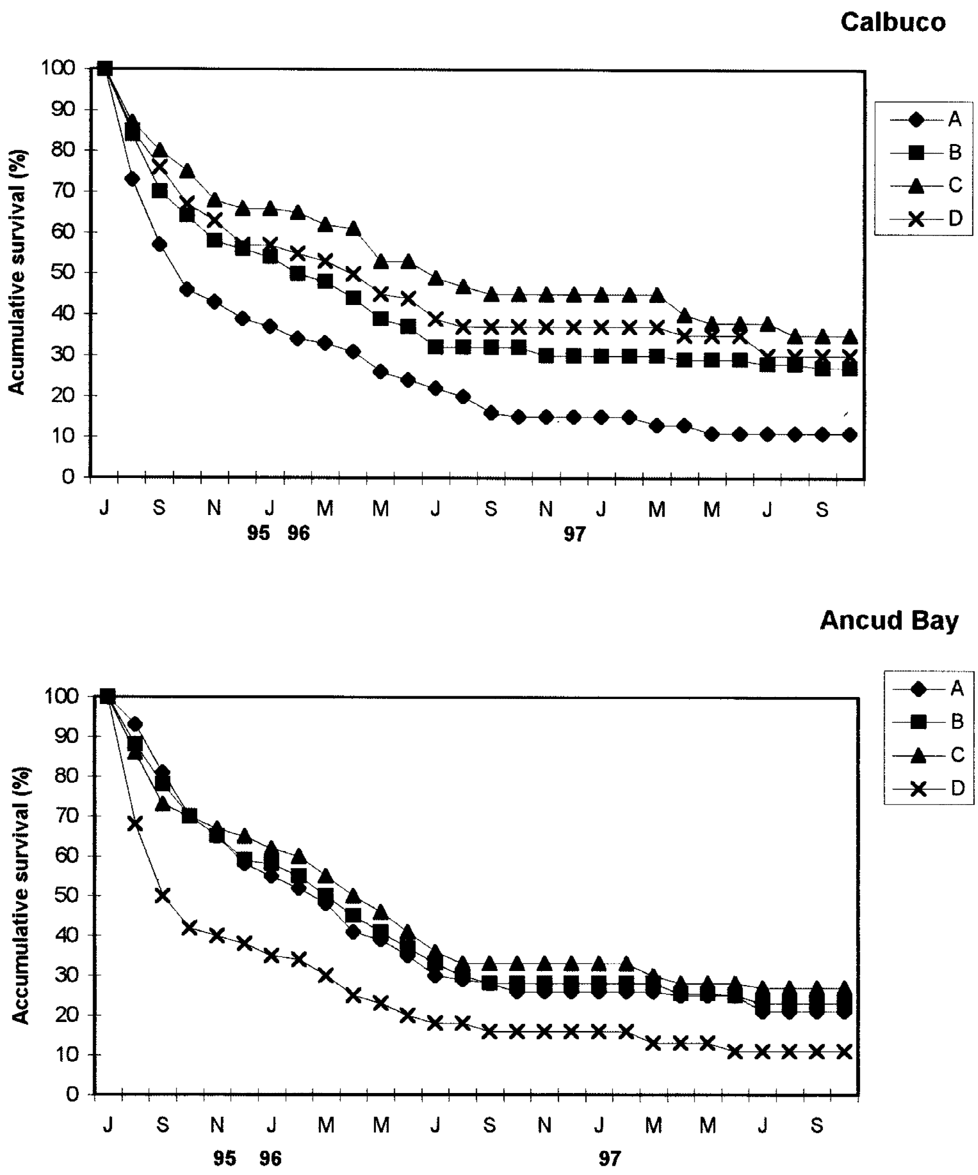


Figure 6. Cumulative survival curves of *Gigartina skottsbergii* in the study areas. See Table 1 for definitions of size classes A–D.

In future activities related to the culture of this resource, it is proposed that exposed areas such as the Gulf of Ancud be used as areas for spore capture, where the recruits, after reaching sizes of 100 cm^2 (10 cm length) are transplanted to protected areas such as Calbuco to complete their growth.

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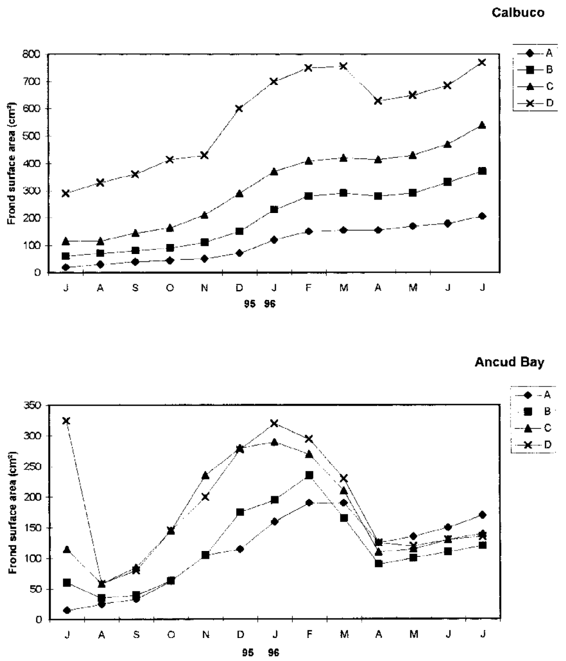

Figure 7. Growth curves of *Gigartina skottsbergii* in the study areas. See Table 1 for definitions of size classes A–D.

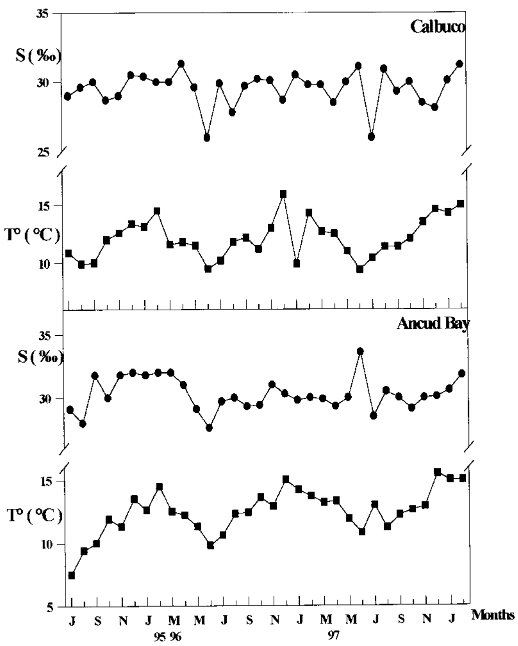

Figure 8. Monthly variation in temperature (°C) and, salinity (‰) of the water column in the study areas.

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