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Chondracanthus chamissoi (Rhodophyta, Gigartinales) in northern Chile: ecological aspects for management of wild populations**

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Abstract

Abiotic and biotic factors affecting seasonal variations in the biomass and reproductive condition of *Chondracanthus chamissoi* were evaluated in a population at La Herradura Bay, northern Chile. During spring, increase in temperature, light, and photoperiod favored the reproductive activity of *C. chamissoi*, contributing to its growth and production of reproductive biomass. During summer, extremes of temperature and light availability were accompanied by bleaching of the thalli, followed by decomposition and biomass loss, significantly lowering production. Epiphytism and herbivory showed were then at their maximum. Analysis of fertility showed that *C. chamissoi* was in reproductive condition throughout the year, with maximum for cystocarpic and tetrasporic plants during spring, significantly correlated with total biomass production. Production and liberation of spores and other values for reproductive capacity showed the highest values in spring. The results of the study, coupled with information from the literature, recommend two commercial harvests during spring, at a time when standing crops are the highest, and values for reproductive condition predict adequate expression of the sexual phase. The time of the year suggested as adequate for commercial harvest of this alga probably coincides with the highest quality of its carrageenans, and would precede the phase of local growth cycle, where its biomass begins to deteriorate due to bleaching, epiphytism and herbivory.

Introduction

Chondrachanthus chamissoi (C. Agardh) Kützing is a marine algal species endemic to the Pacific coast of South America, distributed from Paita, Perú (5° S) to Ancud, Chile (42° S) (Ramirez & Santelices, 1991). It occupies exposed intertidal rocky habitats, as well as the shallow subtidal zone of protected bays with rocky bottoms to 15 m depth (Santelices, 1989). This seaweed is harvested commercially in northern and central-southern Chile as raw material for the extraction of carageenan, and is exported to Asian countries for human consumption (González et al., 1997).

Harvesting of *Chondracanthus chamissoi* has been variable since the begining of its commercialization in the 1980s (SERNAP, 1980–1999). This variability seems related to time and area harvested, with harvest volumes driven by demand cycles at the international markets (Vásquez & Westermeier, 1993). Commercial harvest of *C. chamissoi* in northern Chile is restricted to three subtidal populations: Caldera (27°4′S), La Herradura (29°58′S) and Puerto Aldea (30°15′S). The main volume is, however, harvested from intertidal

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and shallow subtidal beds in south and central Chile, between 35° and 38°S (SERNAP, 1980–1999).

Recent research on this species has assessed the development of tetrasporophytes and gametophytes under controlled conditions in the laboratory, describing the effects of photoperiod, irradiance, and temperature (González & Meneses, 1996; Bulboa, 1998). *In situ* observations of bathymetric and seasonal occurrence of the different reproductive phases were made by (González et al., 1997). Recent studies in the population of Puerto Aldea in northern Chile (Macchiavello et al., 1999) suggested that propagation from spores was significantly more important than vegetative propagation by free-living plants.

Alveal et al. (1999), in studies of laboratory-induced sporulation, found that cystocarpic plants produced massive release of carpospores during the first 24–48 h, whereas in contrast, tetrasporic plants gave maximum sporulation at 96 h after induction. Initial growth was more rapid in plants arising from carpospores, although no significant differences were found between plant growth from carpospores and tetraspores over the first three months of growth (González & Meneses, 1996; Alveal et al., 1999).

In spite of the socioeconomic importance of this seaweed, there has been no experimentation on its *in situ* cultivation, nor have been efforts directed at management of wild populations. This has resulted in serious problems of over-exploitation of this resource due to extensive commercial harvesting (González et al., 1997). The main goal of the present study was to evaluate, *in situ*, the effects of key biotic (benthic herbivores and epiphytic algae) and abiotic factors (temperature, light and photoperiod), on the production and reproductive phenology of *Chondracanthus chamissoi*. This biological and ecological baseline, together with information from the literature, was used to suggest a management plan for the maintenance of a sustainable production of this red alga.

Materials and methods

Study area

La Herradura (29°58′S – 71°22′W) is a bay protected from the prevalent S-W winds characteristic of the central and southern regions of Chile, having a surface area of about 3.27 km^2. Its mouth is about 0.8 km wide and has a maximum internal width of 1.9 km. *Chondracanthus chamissoi* co-exists in the study area with *Ulva* spp. and *Rhodymenia howeana* on boulders, gravel and shelly sand (Salinas, 1997).

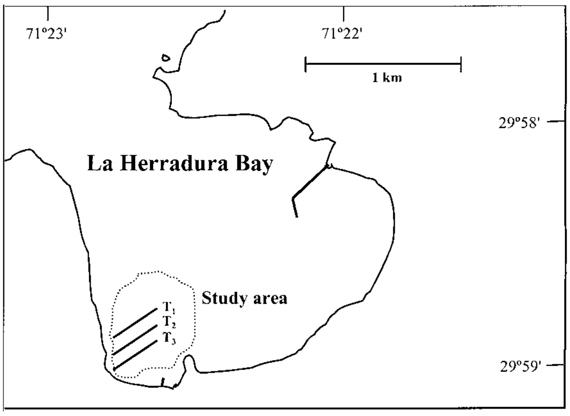

Figure 1. Study area showing sampling sites and position of the transects (T_1, T_2, T_3).

Abiotic factors

The following abiotic factors were recorded daily during the study period: 1) sea surface temperature; 2) photoperiod (daylight hours) from data on sunrise and sunset given in the Chilean Coastal Tide Tables (Anonymous, 1994–1995); 3) light measured as PAR using a LI 190 SB-COR Quantum Sensor. Correlation analyses between variables used monthly averages of each of the selected abiotic factors.

Biomass production and reproductive phenology

Between July 1994 and August 1995, three permanent parallel transects, each 60 m long, and separated by a distance of 15 m, were set perpendicular to the shore and across the whole width of the subtidal algal assemblage. These transects were sampled monthly by SCUBA diving. Sampling stations were positioned at 10-m intervals along the transects. Sampling stations at equal distances along each transect were treated as replicates because of the uniformity of the algal cover. To avoid the effects of previous quadrat sampling, every month the samples were taken one meter away from the previous sampling (detail of study area in Vásquez et al., 1998a) (Figure 1). The transects passed through a stand of mixed algae occurring in a band between the intertidal zone and the beginning of the Bay's sandy bottom (Vásquez et al., 1998a), which was dominated by *Gracilaria chilensis* and *Sarcodiotheca gaudichaudii*.

On given sampling dates, all algae contained in 0.25 m^2 quadrants were collected in pre-labeled plastic bags, and returned to the laboratory for analysis. Fronds of *Chondracanthus chamissoi* were rinsed in seawater, separated from other algae, cleaned of encrusting invertebrates and epiphytes, weighed, and separated according to reproductive phase. Female gametophytes were identified by the presence of cystocarps, and tetrasporophytes by the presence of tetrasporangial sori. Fronds without visible reproductive structures were considered vegetative or male gametophytes. The total biomass and total fertile biomass were expressed in kg m^{-2} (90% wet weight).

Temporal variability of *Chondracanthus chamissoi* reproduction in the field was determined as a function of monthly reproductive capacity (RC), expressed as number of spores m^{-2} of rocky substrate area calculated as: $RC = E \cdot S \cdot FB$ where E represented spore production per sorus, S sorus production per gram of fertile biomass, and FB the fertile biomass per m^2.

Spore production (E) was evaluated under controlled conditions in the laboratory, based on spore counts in carposporic and tetrasporic sori. Forty tetrasporic and 40 carposporic sori were collected randomly from reproductive fronds and maintained at ambient temperature (15 °C, 80% relative humidity) for 10 min. The spore mass from each sorus was then separated from vegetative tissue under a steroscopic microscope using a scalpel, aspirated into a 1.5-mL Eppendorf pipette with 0.3 mL saline solution at 25%, and transferred to a second pipette containing 0.7 mL of filtered seawater containing 0.2% methylene blue dye. The spore count was done in a hemocytometer using 0.01-mL samples. Two counts were done for each sorus, and the total number of spores per sorus was calculated.

From the total biomass of *C. chamissoi* collected each month, 10-g sub-samples were randomly obtained from 40 samples of cystocarpic and 40 samples of tetrasporic fronds, representing all different plant sizes present in the study area. The production of sori (S) was estimated by determining the number of either carposporic sori or tetrasporic sori per gram of fertile frond.

Biotic factors

The diversity and abundance of epiphytic algae associated with *Chondracanthus chamissoi* was determined monthly. The epiphytes were identified to species level, and weighed to ± 0.01 g. The results were expressed as g epiphytes (Ep) per g wet weight of host alga (Ha).

Densities of the main benthic herbivores associated with *Chondracanthus chamissoi* were determined monthly. These included gastropod snails of the genus *Tegula* and *Fissurella* spp., and the decapod crabs *Acanthonix petiveri* Milne Edwards and *Taliepus marginatus* Bell. To evaluate the possible effects of these herbivores on *C. chamissoi*, we analyzed their stomach contents, quantifying the relative abundance of ingested items in a reticulate Petri dish with 30 intersecting points. The presence of the items at the intersection points provided an estimate of the relative abundance of the food items in the diet of each species of grazer analyzed (Vásquez et al., 1984; Santelices et al., 1986).

A non-parametric correlation (Spearman R) was used to evaluate the relations between monthly biomass values for *Chondracanthus chamissoi*, the abundance of epiphytes, herbivore densities and abiotic variables (temperature, PAR, photoperiod) during the study period (Brower et al., 1998).

Data on temporal variability of biomass, spore production, ruptured sori, epiphytes and associated grazers were tested using a one-way analysis of variance after prior analysis of normality of the data using a Kolmogorov-Smirnov test, values of skewness and homogeneity of variance using a Bartlett test (Sokal & Rohlf, 1981). Tukey comparisons were used for *a posteriori* analysis (Sokal & Rohlf, 1981) in order to detect time-related differences in the distribution of biological variables.

Results

Abiotic factors, biomass production and reproduction phenology

The superficial water temperature, photoperiod, and light (PAR) of La Herradura Bay showed marked seasonality over the study period, with maxima in summer months and minima during the winter period, which is typical of these parameters in other temperate regions (Figure 2).

Non-parametric correlation analyses (Spearman R) between monthly biomass production of *Chondracanthus chamissoi* and both the abiotic and biotic variables studied (Table 1) showed no significant relations. A significant correlation was observed between the biomass of the most abundant epiphyte (*Polysiphonia*)

Table 1. Non-parametric correlation (Spearman R) between *Chondracanthus chamissoi, Polysiphonia japonica* and *Chondria californica* biomass versus abiotic variables and density of benthic herbivores. * p <0.05; ** p <0.01; ns, not significant

Variable	*Chondracanthus chamissoi*		*Polysiphonia japonica*		*Chondria californica*	
	R	p	R	p	R	p
Temperature	0.09	0.759 ns	0.62	0.019 *	–0.02	0.958 ns
PAR	0.30	0.303 ns	0.85	0.000 **	–0.44	0.120 ns
Photoperiod	0.31	0.288 ns	0.73	0.003 **	–0.23	0.433 ns
Polysiphonia	0.49	0.075 ns	–	–	–0.59	0.028*
Chondria	–0.54	0.048 ns	–0.59	0.028 *	–	–
Tegula	0.29	0.314 ns	0.40	0.151 ns	–0.10	0.725 ns
Fissurella	0.15	0.605 ns	0.09	0.759 ns	–0.56	0.044*
Acanthonix	–0.38	0.175 ns	0.02	0.958 ns	0.15	0.615 ns
Taliepus	–0.20	0.483 ns	–0.24	0.401 ns	0.61	0.021*

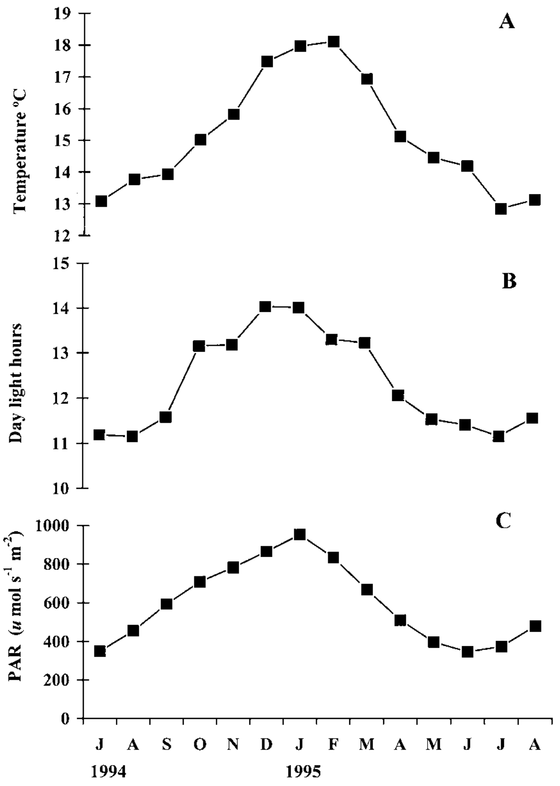

Figure 2. Temporal changes in environmental factors at the study area: A) temperature; B) photoperiod; C) light intensity (PAR).

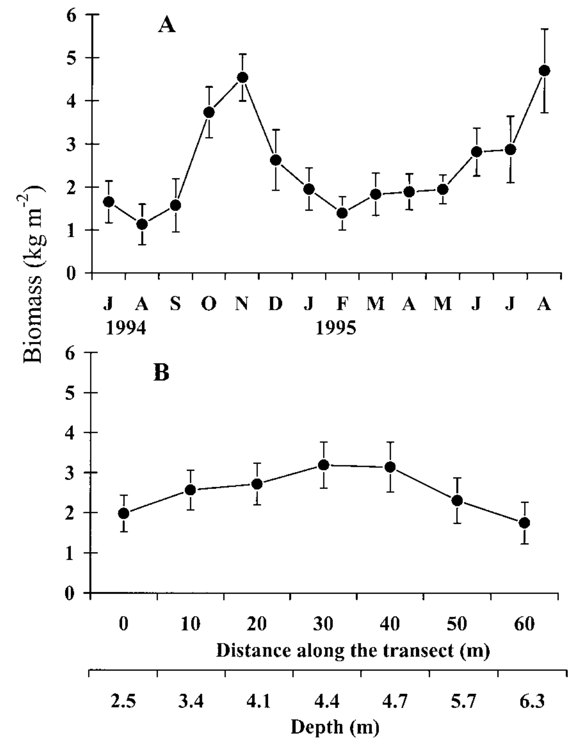

Figure 3. A) Seasonal and B) bathymetric production of biomass of *Chondracanthus chamissoi* ($\bar{X} \pm$ 2 SE).

on *C. chamissoi* and the physical variables studied (Table 1); this Table also lists the negative correlation between these variables and the frequency of *Chondria californica*. The abundance of *Chondria* was negatively correlated with the presence of *Fissurella* spp, and positively correlated with the presence of *Taliepus marginatus* (Table 1).

Biomass production of *Chondracanthus chamissoi* was markedly seasonal, with maximum values observed during the spring and early summer (Figure 3A). Values for this parameter, although not nu-

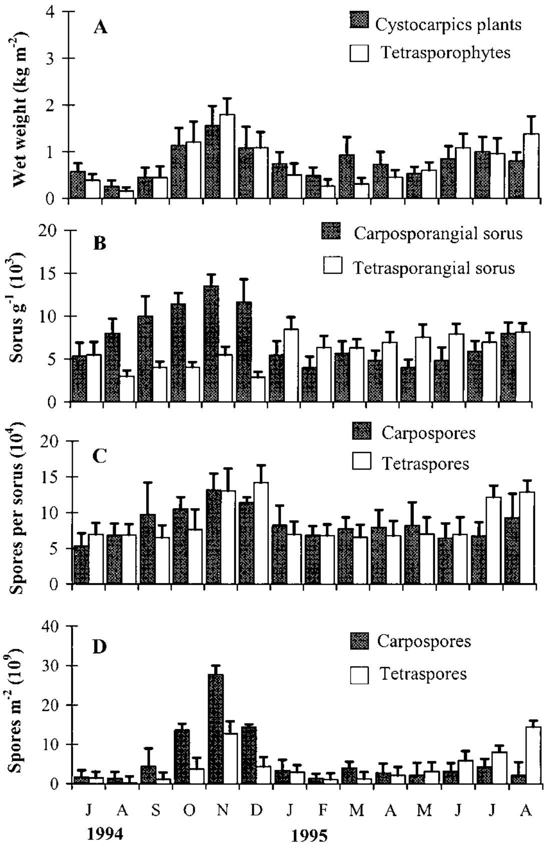

Figure 4. Seasonal changes in the fertility of *Chondracanthus chamissoi*. ($\bar{X} \pm 2$ SE). A) biomass of reproductive thalli; B) number of sori per per g of fertile thalli; C) number of spores per sorus; D) number of spores per unit area.

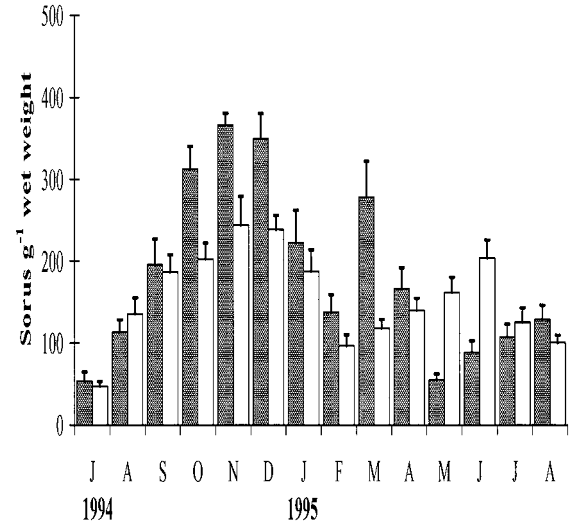

Figure 5. Seasonal changes in the number of ruptured sori of *Chondracanthus chamissoi* ($\bar{X} \pm 2$ SE).

merically correlated with any of the abiotic factors (Table 1), were observed to decline during summer months, when maximum values were obtained for sea surface temperature, photoperiod and PAR. During the summer months a majority of the *C. chamissoi* plants became bleached and experienced breakage of thalli. It was noted that bathymetric distribution of the annual average biomass of *C. chamissoi* was significantly higher at 4.4 and 4.7 m depth, diminishing toward the limits of the bed (Figure 3B).

Analysis of the different parameters of fertility evaluated in this study showed *Chondracanthus chamissoi* to be in a reproductive state throughout the year (Figure 4), with maxima in the biomass of cystocarpic and tetrasporic plants during the spring (Figure 4A). Biomass of reproductive plants (cystocarpic and tetrasporic thalli), was correlated ($p < 0.05$) with total biomass production during the entire study period (Figure 3A–4A). The maxima in biomass of cyctocarpic and tetrasporic plants showed marked seasonality, and production of sori over time differed significantly between the phases ($p > 0.05$, Figure 4B). The production of carposporangial sori was significantly greater from August to December 1994 ($p < 0.05$), while production of tetrasporangial sori was significantly greater ($p < 0.05$) between January and July 1995 (Figure 4B).

The production of spores (S) evaluated as number of spores per sorus (Figure 4C), as well as reproductive capacity (RC) (N° of spores m^{-2}, Figure 4D) showed patterns of temporal variability which coincided with variability of both phenological phases. Although the production of carpospores and tetraspores occur all year round, maximal production of carpospores during springtime of 1994, could explain the increase in the biomass of tetrasporophytes for the subsequent reproductive period (Figure 4).

The number of open sori per reproductive frond of both phases (an index of spores release), was significantly higher ($p < 0.05$) during the spring months. There was, however, a second significant increase ($p < 0.05$) in March 1995 for the carposporangia, and during June 1995 for the tetrasporangia (Figure 5). In this context, our data on spore production, reproductive capacity, and open sori per reproductive frond strongly suggest that *Chondracanthus chamissoi* have an alternated frequency of both phenological phases during a year cycle.

Table 2. Epiphytic algal species on *Chondracanthus chamissoi* and their relative abundance (g kg^{-1} *C. chamissoi*: mean ± SD)

Species	x	SD
Chlorophyta		
Ulva rigida C. Agardh	0.21	0.33
Ulva taeniata (Setchell) Setchell and Gardner	0.20	0.30
Ulva costata (Howe) Hollenberg	<0.01	
Bryopsis plumosa (Hudson) C. Agardh	<0.01	
Rhodophyta		
Acrosorium uncinatum (J. Agardh) Kylin	1.95	3.26
Anthithamnion densum (Surh.) Howe	<0.01	
Antithamnionella ternifolia (Hooker and Harvey) Lyle	<0.01	
Branchioglossum bipinnatifidum (Montagne) Wynne	<0.01	
Callophyllis variegata (Bory) Kütz.	0.01	0.09
Centroceras clavulatum (C. Agardh) Montagne	<0.01	
Ceramium rubrum (Hudson) C. Agardh	0.02	0.10
Chondria californica (Collins) Kylin	2.78	6.65
Gracilaria chilensis Bird, McLachlan and Oliveira	0.40	2.61
Griffithsia chilensis Montagne	<0.01	
Heterosiphonia subsecundata (Suhr) Falkenberg	<0.01	
Nytophyllum peruvianum (Montagne) Howe	0.02	0.10
Phycodrys quercifolia (Bory) Skottsberg	<0.01	
Plocamium cartilagineum (L.) Dixon	0.04	0.23
Polysiphonia japonica Harvey	4.72	4.72
Pterosiphonia dendroidea (Montagne) Falkenberg	<0.01	
Rhodymenia howeana Dawson	0.18	0.56
Sarcodiotheca gaudichaudi (Montagne) Gabrielson	0.11	0.47
Stenogramme interrupta (C. Agardh) Montagne	0.03	0.24
Phaeophyta		
Colpomenia sinuosa (Mertens ex Roth) Derbés and Solier	<0.01	
Hincksia granulosa (J.E. Smith) Silva	<0.01	

Biotic factors

A total of 25 algal species were identified as epiphytic on *Chondracanthus chamissoi*, including Chlorophyta (4), Rhodophyta (19), and Phaeophyta (2). Of these, two species of Rhodophyta, *Polysiphonia japonica* and *Chondria californica*, accounted for 80% of the epiphyte biomass (Table 2), and had maxima in biomass during January 1995 and April 1995 respectively (Figure 6).

The distribution and abundance of the benthic herbivores associated with *Chondracanthus chamissoi* varied with time, with maxima in abundance during summer months (Figure 7A). The gastropods *Tegula* and *Fissurella* spp., and the decapods *Taliepus marginatus*, and *Acanthonix petiveri* were the only conspicuous herbivores, most of them juveniles living on the thalli of *C. chamissoi. Tegula* spp increased significantly in abundance during January and February ($p < 0.05$, Figure 7B). *Fissurella* spp., showed two maxima in abundance, late winter (1994 and 1995) and spring-early summer 1994 (Figure 7C). The abundance of *Acanthonix petiveri* was variable among different months with no pattern in temporal variability (Figure 7D). In contrast, *Taliepus marginatus*, increased significantly in abundance ($p < 0.05$) from March to June (Figure 7E).

Analyses of stomach contents of benthic herbivores associated with *Chondracanthus chamissoi* showed epiphytic algae to be the most important part of their diets (Table 3). *C. chamissoi* was of secondary dietary importance to the benthic herbivores, not exceeding 12% of their stomach contents. Other items

Table 3. Gut contents (%: mean ± SD) of the main benthic herbivores associated with *Chondracanthus chamissoi*

Prey items	*Fisurella* spp.		*Tegula* spp.		*Taliepus marginatus*		*Acanthonix petiveri*	
	x	SD	x	SD	x	SD	x	SD
Ch. chamissoi	11.7	4.7	11.7	4.3	7.4	5.1	7.0	4.8
epiphytes	54.5	9.2	41.3	6.0	37.3	11.3	53.6	8.2
diatoms	13.7	5.2	5.5	2.5	0.0	0.0	2.9	2.4
spores of Rhodophyta	12.7	10.3	6.4	2.9	7.0	6.9	4.5	6.9
Cyanophyta	3.7	1.5	1.8	1.6	0.0	0.0	0.0	0.0
calcareous crusts	2.8	3.1	2.6	2.5	1.9	1.9	0.0	0.0
non-calcareous crusts	3.4	3.8	0.7	1.0	0.0	0.0	0.0	0.0
invertebrates (incl. larvae)	3.0	2.3	2.5	2.0	28.0	5.1	25.5	4.2
empty spaces	7.7	4.1	14.3	4.1	18.3	4.6	6.4	3.8
Total Individuals	127		88		54		34	

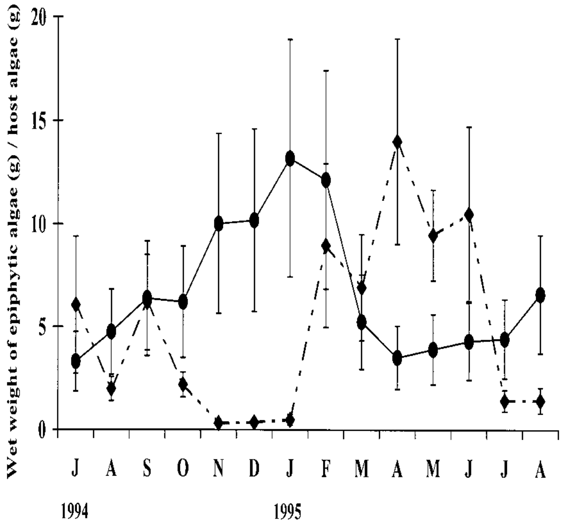

Figure 6. Seasonal changes in the epiphytes biomass (Ep/Hg) associated with *Chondracanthus chamissoi* ($\bar{X}$± 2 SE). A) Biomass of *Polysiphonia japonica* (● B) Biomass of *Chondria californica* (♦).

discovered in the herbivore stomachs varied according to the species, and included crustose algae, spores, diatoms and invertebrate larvae (Table 3).

Monthly variability in the diet of *Tegula* spp. (Figure 8A), *Fissurella* spp. (Figure 8B), *Acanthonix petivery* (Figure 8C) and *Taliepus marginatus* (Figure 8D) showed some maxima in consumption of epiphytic algae during spring. This dietary category was important in the stomach contents of the herbivores analyzed, fluctuating between 30 and 70% (Figure 8). Conversely, the consumption of *C. chamissoi* did not show seasonal patterns, and the frequency of this algae in total herbivore stomach contents did not exceed 20%.

Discussion

The population of *Chondracanthus chamissoi* in La Herradura Bay showed a seasonal pattern in the biomass abundance similar to that reported from nearby subtidal beds in Puerto Aldea (González, 1993; González et al., 1997), and was typical of other subtidal beds of Gigartinales in other temperate regions of the world (Mathieson, 1989; Lüning, 1990). Seasonality in the production of algal biomass in temperate regions is regulated principally by the combined effects of primary abiotic and biotic factors (Lüning & Diek, 1989; Lüning, 1990; Pizarro & Santelices, 1993), and accordingly, *C. chamissoi* had maximal biomass values in spring, as well as a maximum number of plants with reproductive structures. Due to the shallow subtidal distribution of *C. chamissoi* in La Herradura Bay, the maximum biomass production occurred prior to the summer maxima of temperature, light and photoperiod. During the summer, extremes observed in the above mentioned environmental variables produced bleaching of the *Chondracanthus* thalli, which become soft and fragile, accompanied by a sharp drop in total biomass. Bleaching of the plant tissue during the summer may be produced by physiological stress due to photoinhibition or because nutrient levels drop to critical thresholds in the ecosystem (Davison & Pearson, 1996). Given the constant input of nutrients due to permanent upwelling not far from the study area

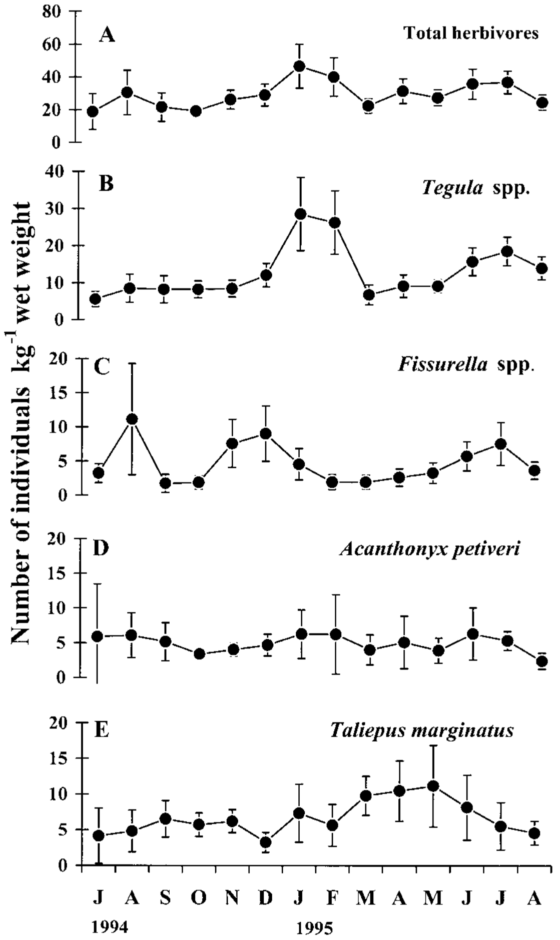

Figure 7. Seasonal changes in the density of benthic hervibores associated with *Chondracanthus chamissoi*. ($\bar{X} \pm$ 2 SE). (A) Total herbivore density; (B) density of *Tegula* spp.; (C) density of *Fissurella* spp.; (D) density of *Acanthonyx petiveri*; (E) Density of *Taliepus marginatus*.

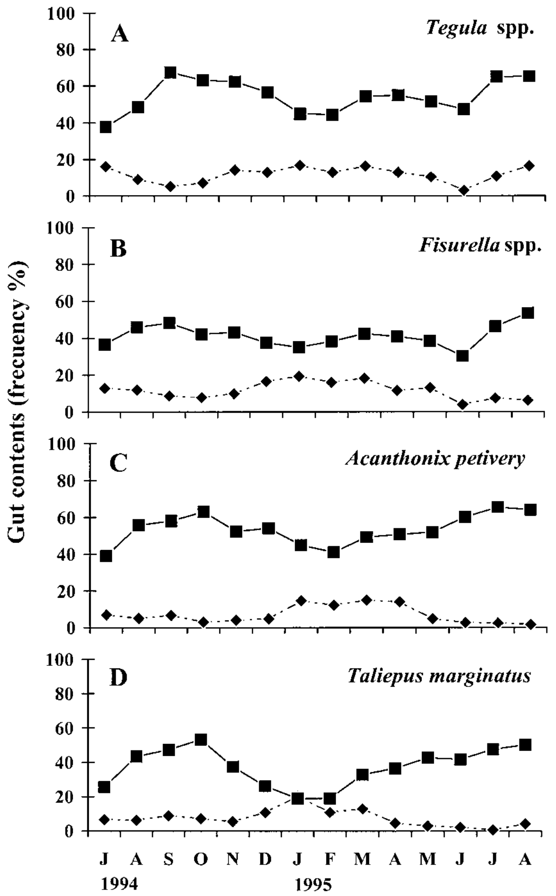

Figure 8. Monthly changes in the abundance of *Chondracanthus chamissoi* (◆) and epiphytes (■) in the the gut contents of the main benthic herbivores in *Chondracanthus* stands.

(Vásquez et al., 1998 b), we suggest that the decline in biomass of *C. chamissoi* in summer is due to factors related to temperature and light rather than nutrient limitation. The summer bleaching of *C. chamissoi* favored epiphytism in the La Herradura bed, similar to results obtained by Pizarro and Santelices (1993) for *Gracilaria chilensis* in other localities in northern Chile.

Under laboratory conditions, the vegetative growth of *Chondracanthus chamissoi* increased with increase in temperature, light, and length of the photoperiod (González & Meneses, 1996; Bulboa, 1998). However, as discussed previously, our field observations did not show this relationship during the summer, when upper ranges of temperature, light, and photoperiod severely affect the biomass of this species.

The positive relationship between fertility and vegetative growth is a common characteristics of the family Gigartinaceae (Mathieson, 1989), including *Chondracanthus chamissoi* as shown in the present study, and in that of González (1993) and González et al. (1997). Another characteristic was the year-round production of spores by *C. chamissoi* in La Herradura Bay, and major production of reproductive tissue during the spring.

As in other Gigartinales (e.g. *Mazzaella laminariodes*; Luxoro & Santelices, 1989), the total abundance of spores over a given period of time is a function of the relative abundance of each phase, size and abundance of fertile fronds, number of sori per frond, and the number of spores per sorus. Under laboratory conditions, a summer-winter comparison showed a higher percentage of liberation, settlement, and germination of *Chondracanthus chamissoi* spores during the summer (González & Meneses, 1996). Consequently, our field data on ruptured sori suggested that the greatest release of the spores occurred between October and December (spring). In this context, seasonality in the viability and production of spores is an important factor for the management of natural populations, as this defines the temporal window for the recovery of the population by means of seasonal recruitment of juveniles.

The importance of sexual reproduction over vegetative propagation by fragmentation of thalli of *Chondracanthus chamissoi* has been suggested by González et al. (1997) and Macchiavello et al. (1999) for beds in northern Chile. The production of spores per sorus, as well as the reproductive capacity, showed patterns of temporal variability which coincided with variability of both phenological phases. Although the production of carpospores and tetraspores occurs all year round, maximal production of carpospores during the spring of 1994 may explain the increase in the biomass of fertile tetrasporophytes for the subsequent maximum reproductive period. In this context, the temporal production of propagules during the whole year, with maxima during the spring, suggests that sexual reproduction is a relevant mechanism in the maintenance of wild populations of *C. chamissoi* during its annual cycle.

Epiphytism may be a serious problem for algal growth and survival, particularly in protected bays in temperate regions (D'Antonio, 1985; Arrontes, 1990; González et al., 1993; Pizarro & Santelices, 1993). *Chondracanthus chamissoi* was exploited as a substrate for the growth of foliose saxophilic algae throughout our study. Understanding this phenomenon is complicated by the changes in the relative abundance between each of the two major epiphytes of *Chondracanthus* during the year. The emergence of epiphytic algae may reduce the growth rate of *Chondracanthus* by shading, and also by competition for mineral nutrients (D'Antonio, 1985; Kuschel & Buschmann, 1991). Also, the increase of epiphytism during the summer may increase the mortality of *C. chamissoi*, by causing breakage of the thalli due to deleterious mechanical effects on the host thallus, and by debilitation of its' holdfast structures due to the mass of the epiphytes (Hallam et al., 1980; Brawley & Adey, 1981; D'Antonio, 1985; González et al., 1993). This is the first report to the effects of epiphytism on *Chondracanthus chamissoi* in northern Chile. More research on this topic should address possible methods for the reduction or mitigation of the effects of epiphytes on this important economic algal resource.

High macroinvertebrate species richness is normally associated with assemblages of benthic algae in protected bays of northern Chile (Alarcón, 1992; Salinas, 1997). The most abundant of these associated to *Chondracanthus chamissoi* included four taxa of benthic herbivores composed mainly of recruits and juveniles. Although the assemblage of benthic herbivores is a permanent component of the subtidal environments of La Herradura Bay, their abundance increases significantly during spring-summer coinciding with increases in epiphytes on *C. chamissoi* upon which they feed. This grazing activity removes epiphytes from *Chondracanthus* thalli, and may have a positive effect on its' growth (D'Antonio, 1985; Williams & Reed, 1992). However, in the absence of epiphytes, the herbivores consume vegetative and fertile tissue of the host plants, decreasing their growth by the reduction of the photosynthetic surface and reproductive capacity of the algae (Brawley & Adey, 1981; Williams & Reed, 1992). Herbivory may break open the sori, aiding in the liberation of spores (Buschmann, 1991) and consumption of fertile tissue favors dispersion, settlement, and germination of the macroalgal propagules as they are not affected by passage through the digestive tracts, and are dispersed with the feces (Santelices, 1992).

The results of this study plus information from the literature suggest guidelines for a management plan for the harvesting of *Chondracanthus chamissoi* in northern Chile (Figure 9). Since the maximum biomass was found to occur in spring after maximal germination and liberation of spores, this is probably the best time of the year for the scheduling commercial extraction. This is supported by the observation of declines in biomass due to bleaching and epiphytism with summer rises in temperature and increases in herbivore populations. It should be cautioned, however, that a peak in *Chondracanthus* biomass was observed in August 1995, demonstrating a potential for temporal flexibility in peak production of this alga from one year to the next.

The seasonal changes in the quality of carrageenan in *Chondracanthus chamissoi* and the concentration of carbohydrates, lipids and proteins (R. Westermeier, unpublished data), as in other Gigartinales (*Mazzaella* and *Sarcothalia* spp.), suggest that maximum carrageenan yields occur between October and February (Santelices & Norambuena, 1987). Thus, in addition

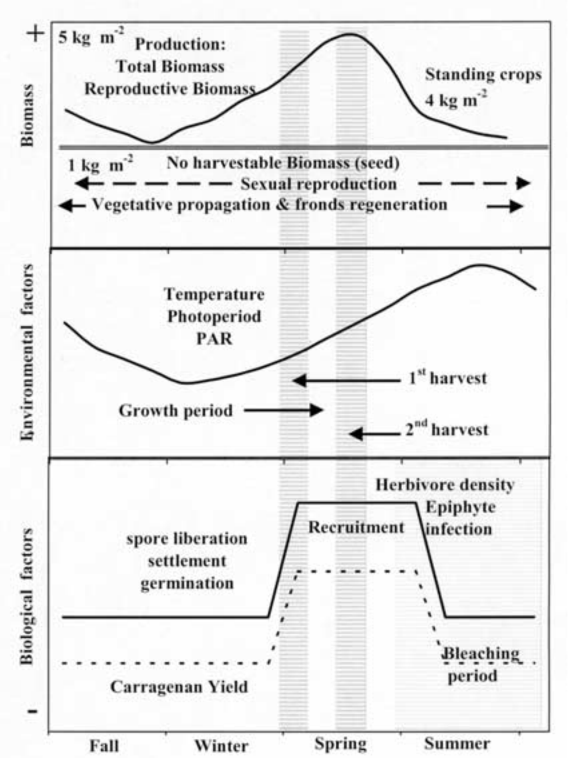

Figure 9. Ecological factors affecting the production of *Chondracanthus chamissoi* and timing for optimal harvest during an annual cycle.

to the above reasons for harvesting during the spring, it is probable that the carrageenan content may be optimal in this harvesting period. Given the growth rate for *Chondracanthus* during spring (also see Stotz & González, 1994) it is suggested that two harvests can be made, separated by a 30–45 day interval. This would permit optimal conditions for growth of the alga during this period of time, while maximizing harvest volumes. As suggested by Santelices (1989), it would be necessary to leave a 'seed' biomass equivalent to the smallest standing crop observed during the annual cycle, to allow regrowth of the alga. For *Chondracanthus* in La Herradura Bay this should be about 1 kg m^{-2}, as production in the bed during the spring is about 4 kg m^{-2}.

Future planning of commercial extractions of algal resources needs to be made independently of socioeconomic factors and requirements of international markets as mentioned by Vásquez and Westermeier (1993), and should rely more heavily on the biological and ecological attributes of the resource. A similar approach, supported by biological, ecological and environmental information, has been suggested by Santelices (1989) and Vásquez (1995) for the management of wild population of *Gracilaria* and brown seaweeds along the Chilean coasts.

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