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Seasonal and Spatial Monitoring of Productivity and of Reproduction of *Chondrus canaliculatus* (Gigartinales, Rhodophyta) from Chile

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Chondrus canaliculatus (C. Agardh) Greville used to cover extensive areas at Puerto Aldea 30°16′ S, 71°30′ W), Tongoy Bay, Chile. The exploitation of this commercially-valuable alga without knowledge of its production behavior and reproductive characteristics led to its severe reduction in the area. Seasonal monitoring of biomass, reproductive capacity and reproductive potential of an intertidal and a subtidal population of *C. canaliculatus* from this locality was performed in order to gather information on how to manage this resource. Total and fertile frond biomass both have a maximum (4 and 2.5 Kg per m^2 respectively) in spring-summer and a minimum (2.4 and 1.8 Kg per m^2 respectively) during winter. Both were also higher in the subtidal (maxima of 4.2 and 2.6 Kg per m^2) than in the intertidal population (maxima of 4.0 and 2.6 Kg per m^2) and carposporic fronds were always more abundant than tetrasporic fronds. Reproductive capacity (based on the number of spores per sorus, the number of sori per frond and the fertile biomass per area unit) followed a similar seasonal pattern reaching a maximum of 5.5×10^9 spores per m^2 and was higher in the intertidal than in the subtidal and in tetrasporic rather than carposporic plants. Laboratory studies of spore settlement and survival indicated that the reproductive potential was not different between reproductive phases and between habitats. This potential, close to 30% in relative terms, is similar to those evaluated in other members of the Gigartinaceae. Maxima of total and reproductive biomass, spore production, spore settlement and juvenile survival occurred one to two months earlier in the intertidal than in the subtidal. The data available at this point suggests that the harvesting of the fronds should be done in different periods for the intertidal (early and mid-summer) and the subtidal (mid- to late summer) and approximately a month after the spore productivity peak when these have already been released, assuming that the recovery of biomass is through the growth of new individuals. Further studies on vegetative means of growth and maintenance of the populations should be added to this information in order to propose an adequate management of this resource.

Introduction

Chondrus canaliculatus (C. Agardh) Greville, containing a commercially valuable carrageenan content (Ayal and Matsuhiro 1986), is distributed on the temperate Pacific coast of South America from Chinchas Islands (14° S) to Chiloé Island (41° S) (Ramírez and Santelices 1981). This species inhabits subtidal rocky bottoms of protected bays (Eberhard 1969) as well as mid- to low intertidal, exposed and semi-exposed rocky substrates (Santelices 1989). For about two decades between 1970 and 1990, *C. canaliculatus* was abundant at Puerto Aldea, a locality in southern Tongoy Bay, Chile, where it dominated the algal biomass in an area of about 60 hectares (Vásquez and Westermeier 1993). By December 1992, a survey of this area indicated that the populations were reduced to patches by unregulated human exploitation of the resource, which consisted of the harvesting of the entire plants damaging the adhesion discs in the process. The area covered by each of these patches fluctuated between 50 m^2 and 400 m^2 for those located in the intertidal region and between 15 m^2 and 200 m^2 for those in the subtidal region. In addition, some isolated patches of the species were observed within beds of *Chondracanthus chamissoi* Kützing and *Heterozostera tasmanica* Den Hartog (González 1993). In order to allow recovery of the resource and permit science-based resource management this study was undertaken.

It should be noted that the binomial *Chondrus canaliculatus* is under recent revision, since the morphology of its cystocarp (Arakaki *et al.* 1997) and the phylogenetic analysis based on rbcL sequence (Hommersand *et al.* 1999) demonstrated that the species does not belong to *Chondrus*. Nevertheless, until a new designation of the binomial is agreed the well-established name will be used throughout this paper.

Chondrus canaliculatus has a triphasic life history, with an isomorphic alternation of generations (Kim 1976). The number of spores produced and their ability to survive and develop are assumed to be the main factors in the maintenance of populations together with vegetative propagation. In the Gigartinaceae, as in the majority of red algal species, the occurrence and frequency of sexual reproduction is difficult to evaluate (Santelices 1990), but it is assumed to occur from observations of the different reproductive phases in the field in most species. Settlement and viability of spores are almost impossible to measure directly in the field (Clayton 1992, Amsler *et al.* 1992, Vadas *et al.* 1992). Indirect methods such as reproductive capacity and reproductive potential have been used to evaluate the maintenance of algal populations by means of spores (Chopin *et al.* 1988, Mathieson 1989, Melo and Neushul 1993).

Reproductive capacity is defined as the number of spores produced by the population over a set area of substrate (Chopin *et al.* 1988). In commercially exploited algae, reproductive capacity is mainly regulated by two factors: 1) those abiotic and biotic factors (such as herbivory) that influence growth, and 2) the degree of exploitation of the resource. Factors such as temperature, irradiance, nutrients and photoperiod regulate the formation of reproductive structures, the production of fertile biomass and the occurrence of the reproductive phases (Bhattacharya 1985, Avila *et al.* 1996).

Less noticeable, but as important, is the effect of the habitat where the plant grows, as evaluated in *Mazzaella laminarioides* (Bory) Fredericq *et* Hommersand in an intertidal vertical gradient (Hannach and Santelices 1985), in *Chondrus crispus* Stackhouse in a depth gradient (Craigie and Pringle 1978), or when comparing populations that inhabit the intertidal versus the subtidal region (Fernández and Menéndez 1991). The effect of the degree of exploitation has also been evaluated in *Chondrus crispus* where plants in exploited populations had a reproductive capacity which was significantly less than those plants from non-exploited populations, due to the preferential harvest of reproductive fronds (Chopin *et al.* 1988).

Reproductive potential is defined as the capability of spores to generate viable individuals (Melo and Neushul 1993). It is also affected by the seasonality of environmental variables, the habitat, and the frond harvest (Mathieson 1989, Fernández and Menéndez 1991, Scrosati *et al.* 1994).

Studies that have evaluated algal reproductive capacity and reproductive potential suggest that populations usually have a high reproductive capacity. Nevertheless, only a small proportion of the many propagules released to the environment have the potential to germinate either due to exogenous or endogenous factors (Vadas *et al.* 1992), and an even smaller number lead to recruitment (Hoffmann 1988, Clayton 1992). Maintenance of populations by means of spores (recruitment) is important in habitats where the mortality of plants is high (McLachlan *et al.* 1988, 1989, Lazo *et al.* 1989) or in populations with open spaces available for recruitment (Lazo *et al.* 1989, Scrosati *et al.* 1994).

The goal of the present study is to evaluate reproductive capacity and reproductive potential of *Chondrus canaliculatus* at Puerto Aldea throughout the year and to compare those plants inhabiting the intertidal with those inhabiting the subtidal habitat in this locality. The results obtained through this study should indicate to what extent the reproductive propagules may contribute to the settlement of new plants and to advise the fishermen when to collect the seaweed and how to obtain the best yield by allowing the plants to release their propagules to the system before the harvest and finally, whether the strategy applied has to be different in intertidal plants versus subtidal plants.

Materials and Methods

Study site

The study site was at Puerto Aldea (30°16′ S, 71°30′ W), a fishing village located at the southern end of Tongoy Bay, 62 km south of Coquimbo (Fig. 1). The intertidal zone consisted of a rocky shore fragmented in platforms surrounded by sand and crushed shell. This mixed bottom extended into the shallow subtidal area where large rocky masses were discontinuously distributed. A peninsula protects the area from the prevailing south-southeast winds except during winter when the winds change direction to the north generating heavy surf (González 1990). Field studies were done at Caleta Verde (Fig. 1, inset), a site where *Chondrus canaliculatus*

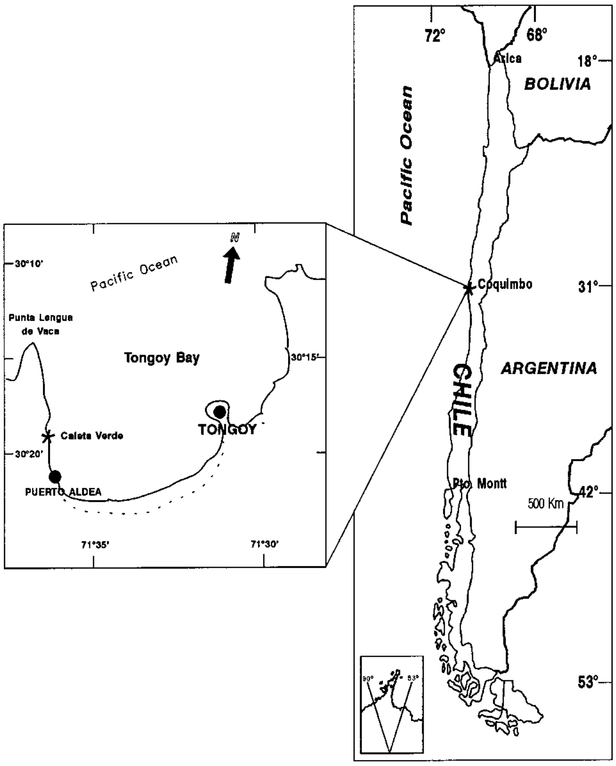

Fig. 1. Geographic location of the study area.

beds are apparently only harvested in the intertidal zone. Sampling was done in the intertidal area during the lowest monthly tides and in the subtidal area (2.5−3.5 m depth) by SCUBA diving. The intertidal (1.64 highest tidal amplitude) study area was located on a 400 m^2 rocky platform. *Chondrus canaliculatus* occurred at between 0.2 m and 1.2 m above low tide sea level, but clearly dominated both the cover and biomass between 0.2 and 0.8 m. The subtidal study area (2.5−3.5 m depth) was located 30 m directly seaward of the intertidal area and included several immersed rocks that together covered 200 m^2 where *C. canaliculatus* was also the dominant species down to a depth of 4 m. In this study 'habitat' refers to either the intertidal or subtidal location.

Field studies

Biomass was evaluated monthly from May 1993 to May 1994 using 10 quadrats of 0.25 m^2 each that were haphazardly placed on the rocky substrate in both habitats. The minimum number of quadrats required was determined by the cumulative average method (Kershaw 1964). Thalli were removed entirely, including the basal discs, with a spatula, placed in plastic bags and transported to the laboratory, located 1 h and 20 min away from the collecting site. Those plants to be used for total and reproductive biomass measurements were kept at 4 °C until analysis, those to be used for spore counts and laboratory experiments were used immediately for those purposes. At the laboratory *Chondrus canaliculatus* fronds were sorted from other algae, rinsed with filtered seawater and separated from debris, epiphytes and associated fauna. Fronds were then sorted into immature (including male gametophytes), tetrasporic, and cystocarpic fronds. Fronds were placed in a kitchen colander for 30 min and then blotted dried in paper towels. Biomass was determined by weighing the blotted fronds, separating them by reproductive phase and habitat. Biomass was expressed as wet weight per square meter of substrate.

Laboratory studies

Spore production was evaluated under controlled laboratory conditions. Ten tetrasporic sori and 10 cystocarpic sori were randomly selected, each one from a different frond, from each habitat. Selection was done by numbering all the sori within a rectangular quadrat of 2 × 3 cm placed between the apex and the first dichotomy of the frond, and using a random number table to choose the sori. Sori were cut from the fronds with a ticket punch and kept at room temperature (15 °C, 80 % humidity) for 10 min. Then the mass of spores was separated from the vegetative tissue with a surgical blade under a dissecting microscope. The spore mass was left for 30 min in 0.3 mL of saline solution (25 ‰) and then transferred to a solution of filtered seawater with methylene blue (0.2 %). Spores were counted in a hematocytometer, using the average of two counts (error fluctuated between 1 and 10 %) to extrapolate the total number of spores per mL of solution to give an estimate of the total number of spores produced per sorus. Sori production was evaluated based on the number of carposporic as well as tetrasporic sori per g of fertile frond. Ten g of cystocarpic frond and 10 g of tetrasporic fronds (from 10 fronds of each habitat) were selected monthly at random from fronds 10 cm long and longer which were those observed with reproductive structures. The number of sori in each sample were counted and divided by 10 to give the number of sori per g of fertile fronds. Monthly reproductive capacity (RC) was calculated as the product of three variables: spore production (Sp = number of spores per sorus), sori production (S = number of sori per g) and, fertile biomass (B = g per m^2). Thus reproductive capacity RC = Sp × S × B was expressed as number of spores per m^2 of substrate. No standard deviation or errors are reported in this variable since neither the fronds included for biomass evaluation nor the sori were individualized but rather formed a pool, thus the product of the three variables was not equivalent to frond A biomass multiplied by number of sori in frond A and multiplied by number of spores per each of these sori in frond A. Such a treatment of the data would have allowed the generation of an average of

Table I. Percentages of settlement, germination and germling survival in spores of *Chondrus canaliculatus* cultured under laboratory conditions.

	Settled (24 h)	Germinated (1 week)	Juveniles (1 month)
Intertidal carpospores			
Winter	57.8	40.4	27.7
Spring	71.8	50.0	34.1
Summer	54.3	37.8	24.1
Autumn	46.7	31.6	27.0
Subtidal carpospores			
Winter	50.6	34.4	28.7
Spring	52.8	39.5	28.3
Summer	64.2	42.3	29.5
Autumn	68.4	44.0	29.1
Intertidal tetraspores			
Winter	60.1	41.2	28.2
Spring	64.3	41.2	29.0
Summer	61.4	42.8	28.7
Autumn	61.2	41.8	28.0
Subtidal tetraspores			
Winter	65.1	44.2	28.4
Spring	64.5	45.4	28.2
Summer	68.7	51.1	28.5
Autumn	66.4	45.5	28.0

values with its corresponding deviation. Spores were obtained by rinsing healthy fertile fronds for 2 min in freshwater followed by a filtered seawater rinse and then drying in air for 60 min. Ten g of fertile frond tissue were kept in a beaker with 100 mL of filtered seawater (0.45 µm) for 24 h, at 15 °C and 12:$\overline{12}$ h, L:$\overline{\mathrm{D}}$ photoperiod. The spore suspension was then filtered and 3 counts were performed in a hematocytometer. Ten samples from each phase and each habitat were quantified monthly and expressed as number of spores released per g of frond.

Reproductive potential was calculated as a function of carpospore and tetraspore settlement, germination and survival to the juvenile stage. Final values obtained for reproductive potential are not expressed with standard errors due to the same reasons given for reproductive capacity. A spore suspension of approximately 30,000 spores per mL of each phase was prepared by incubating them in a beaker with 200 mL of the culture medium (Provasoli 1965). To avoid sedimentation and spore settlement, this suspension was mechanically agitated (80 rpm). Five mL of this solution were added to each of three Petri dishes with 3 cover slips on the bottom of each. These were incubated at constant temperature (15 °C), flux density (50−60 µE m^{-2} s^{-1}) and photoperiod (12:$\overline{12}$ h, L:$\overline{\mathrm{D}}$). Spore settlement was measured as the number of spores attached per coverslip after 24 h. All non-attached spores were discarded by changing the culture medium. Constant conditions, as well as no water movement, were explored in this experiment since we were evaluating the ‘intrinsic potential’ of the spores to be able to settle, germinate and survive without considering conditions of the field as an external variable that may also affect these processes. Spore germination was evaluated one week after inoculation; a spore was considered to have germinated if at least one cellular division had occurred, and if color (changes from homogeneous red to dark brown in the center and yellowish brown in the margins occur when spores germinate) and form (changes from round to oval or outgrowths on one side of the spore) had changed.

Germlings were cultured in the Petri dishes with weekly changes of medium. Their survival was determined by counting healthy plants one month after inoculation. Individuals were considered healthy when the tissue did not show signs of bleaching and when they remained attached at the time of change of culture medium. All counts mentioned above were done using 3 microscopic fields at 100 × magnification of the cover slips from each of the 3 Petri dishes. Each variable measurement was repeated in autumn (May), winter (August), spring (November) and summer (February) with fronds collected from the intertidal and the subtidal habitats.

Statistical methods

Data were analyzed with either a T-test for means comparison or with a one-way or multifactorial analysis of variance (ANOVA). In other cases non-parametric tests such as Kruskal-Wallis or Wilcoxon were applied according to previous assessments of normality and homocedasticity of the data. Normality was tested using Kolmorogov-Smirnoff and Bias values (Sokal and Rohlf 1981). Variance heterogeneity was examined using Bartlett’s test. The ANOVAS were followed by Tukey test in order to detect the treatment pairs where significant differences occurred. Kruskal-Wallis analyses were followed by a multiple comparison non-parametric test (Siegel and Castellan 1988).

Results

Field studies

Total and fertile biomass

Biomass of *Chondrus canaliculatus* varied intra-annually with two distinct periods (Tukey HSD, $P < 0.05$), 1) a low biomass period during autumn-winter and 2) a high biomass period during spring-summer (Fig. 2A). Maximum biomass values were approxi-

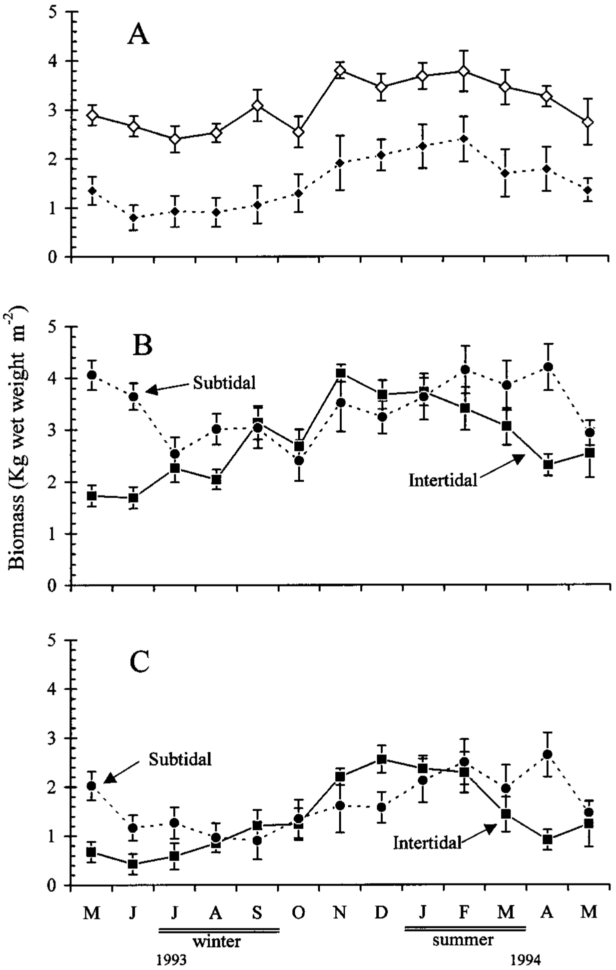

Fig. 2. Seasonal distribution of (A) total frond biomass and reproductive frond biomass (dashed line) (B), total biomass per habitat and (C) reproductive biomass per habitat of *C. canaliculatus* in the study area.

mately 4.0 Kg per m^2. Reproductive plants occurred throughout the year with seasonal changes similar to those in total biomass. Peak biomass of reproductive fronds was approximately 2.5 Kg per m^2.

When comparing intertidal versus subtidal biomass (Fig. 2B), production occurred over a longer period in the subtidal than in the intertidal area, thus overall biomass production was higher in the subtidal area (Two-way ANOVA, df = 1, F = 86.931, $P < 0.05$). Total biomass reached a peak of 4.0 Kg per m^2 in both habitats. Total biomass in the subtidal area had its lower values during winter months (between June and September), whereas in the intertidal the low production extended through autumn and winter (April to August).

Although biomass of reproductive fronds reached a peak of approximately 2.5 Kg per m^2 in both habitats (Fig. 2C), the production of reproductive fronds in the subtidal area extended four months longer than that in the intertidal area. Therefore, overall production of reproductive fronds was higher in the subtidal area (Two-way ANOVA, df = 1, F = 18.124, $P < 0.05$).

A more detailed observation of the biomass of reproductive fronds indicated that in both habitats carposporic frond biomass was higher than tetrasporic frond biomass (Wilcoxon test, z = 5.925 $P < 0.05$) and that the highest values were recorded for the subtidal area (1.6 Kg per m^2 versus 2.0 Kg per m^2, Wilcoxon test, z = 8.326, $P < 0.05$). The highest production occurred during the summer (Kruskal-Wallis test, z = 80.233, $P < 0.001$) for the carposporic frond biomass (approximately 1.4−1.6 Kg per m^2) and tetrasporic frond biomass (approximately 0.6−0.9 Kg per m^2) in the intertidal area. In the subtidal area, the highest carposporic frond biomass (approximately 1.6−2.0 Kg per m^2) was recorded between February and May (Kruskal-Wallis test, z = 66.887, $P < 0.001$), whereas the tetrasporic frond biomass was higher (Wilcoxon test z = 0.45, P = 0.651) during spring and summer months reaching values similar to those in the intertidal area (approximately 0.6−0.9 Kg per m^2) (Figs 3A, B).

Sori production per fertile biomass

The number of sori per g of fertile fronds in the total study area of both habitats (Fig. 4A) was the highest (≈ 280) in January, and the lowest (≈ 140) in April (multifactorial ANOVA of three factors, F = 14.158, $P < 0.05$) independent of the habitat (habitat × months interaction non-significant, F = 1.272, Tukey test, $P < 0.05$, for both months). Production of total sori (Fig. 4A) was always higher in the subtidal area (T-test, $P < 0.05$). Tetrasporic sori were always more abundant than carposporic sori (3.5 to 1 in total), 4:1 in the intertidal area and 3:1 in the subtidal area. To obtain these rates we took the average number of tetrasporic sori per g of fertile fronds and divided it by the average number of carposporic sori per g of fertile fronds (Figs 4B, C). On the other hand, carposporic sori production was different to tetrasporic sori production throughout the year (Figs 4B, C). Sori per g of tetrasporic fronds reached the highest values (≈ 310) in August (end of winter) and January (mid-summer) in the intertidal (Tukey test, $P < 0.05$), decreasing up to ≈ 260 sori per g during the months between these two peaks. Lowest production of tetrasporic sori (≈ 220−230) was observed during late summer and winter (Tukey test, $P < 0.05$, Fig. 4B). In the subtidal area, the production of tetrasporic sori fluctuated between a minimum of approximately 310 to a maximum of 400 sori per g of fertile frond from May to February, decreasing from March to next May to approximately 260 sori per g of fertile frond. Carposporic sori production was less variable throughout the year showing the highest production (≈ 100 sori at the intertidal and ≈ 120 sori at the subtidal) during the spring and summer months (Tukey test, $P < 0.05$) in both habitats. In the intertidal area, minima (≈ 20 sori) were detected from May to October and from March to May (Tukey test,

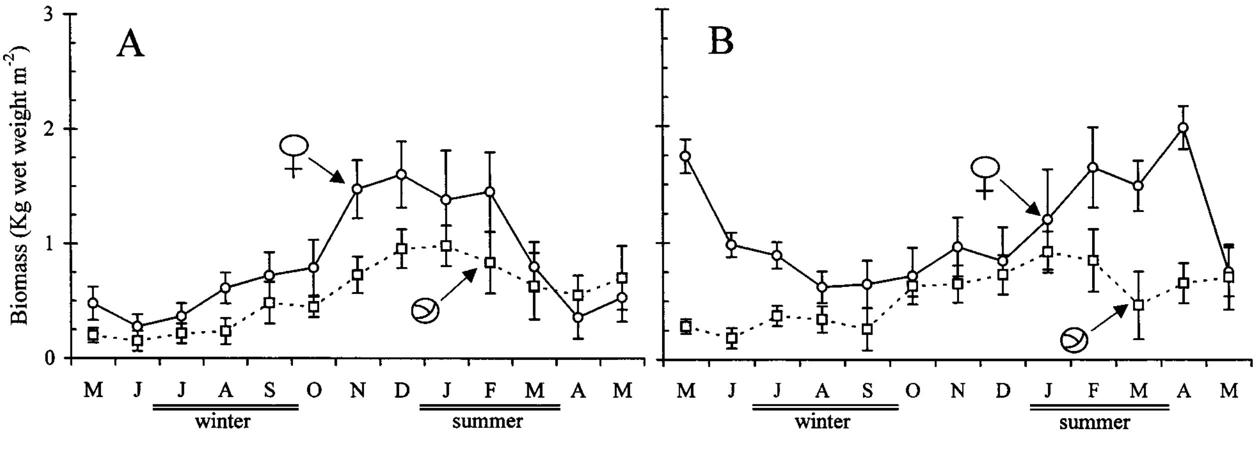

Fig. 3. Seasonal variation of fertile biomass by reproductive phase. ♀ = carposporic, ⊘ = tetrasporic, (A) intertidal, (B) subtidal.

$P < 0.05$), whereas in the subtidal area (≈ 90 sori) minima were detected from May to September (Tukey test, $P < 0.05$) and again from March to May (Tukey test, $P < 0.05$).

Spore production per sorus

Total monthly production of spores (≈ $10.5-12 \times 10^3$ spores per sorus) is shown throughout the year (Fig. 5A) with peaks in spring-summer-autumn months (Tukey HSD, $P < 0.05$). Production of spores per sorus was higher in the subtidal (T-test, $P < 0.05$) and carpospore production per sorus was significantly higher (≈ 10.3×10^3 spores per sorus) than tetraspore production per sorus (≈ 9.5×10^3 spores per sorus, T-test, $P < 0.05$) in both habitats.

When comparing seasonality of spore production between habitats, results showed that in the intertidal as well as in the subtidal area, there was an increase in spore production between spring and summer months (Fig. 5A). The monthly high production of spores (≈ 11.000 to 12.000 spores per sorus) persisted in the subtidal until April, whereas in the intertidal area it dropped in March (Tukey test, $P < 0.05$).

Carpospore production showed less month to month variability than tetraspore production, highest production in carpospores (Tukey test, $P < 0.05$) was from October to February in the intertidal (≈ 11.500 spores per sorus, Fig. 5B) and from January to March in the subtidal area (≈ 12.500−13.000 spores per sorus, Fig. 5C). Average tetraspore production was approximately 9.22×10^3 spores per sorus in the intertidal and 9.83×10^3 spores per sorus in the subtidal area.

Reproductive capacity

Total reproductive capacity (both tetraspores and carpospores) per month of *Chondrus canaliculatus* in the study area (Fig. 6A) showed a peak in summer between November and February (≈ $4-6 \times 10^9$ spores per m^2). When comparing between habi-

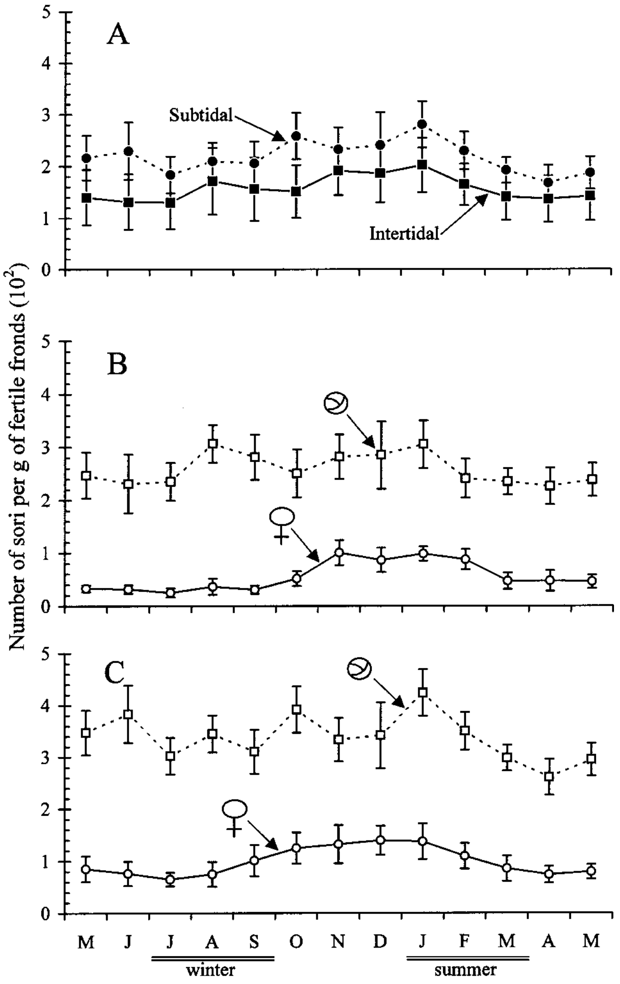

Fig. 4. Seasonal sori production in fertile fronds of *C. canaliculatus* in both habitats (A), and by reproductive phase in the intertidal (B) and in the subtidal (C).

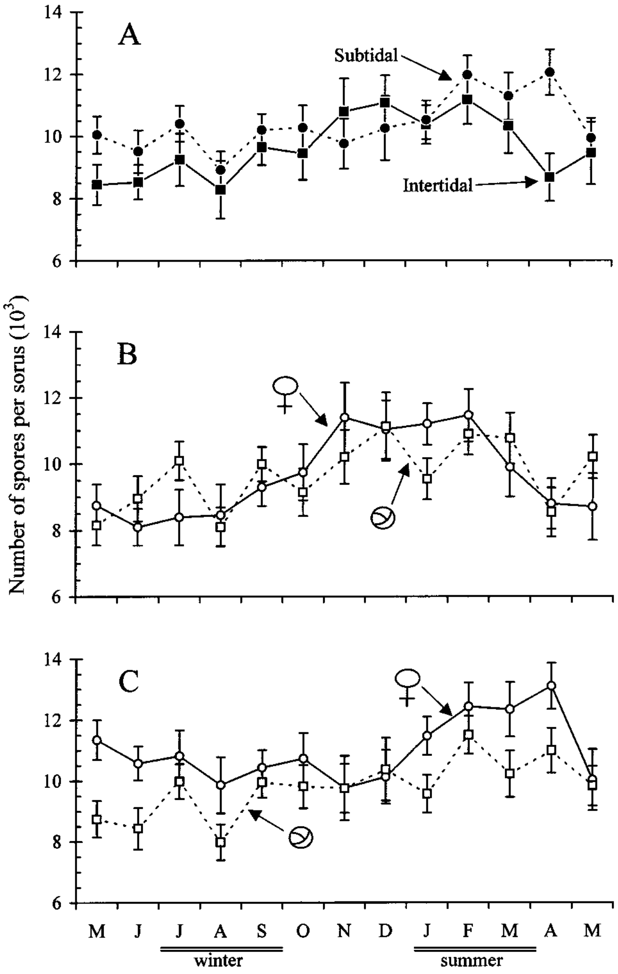

Fig. 5. Monthly pattern of total spore production per sorus in both intertidal and subtidal habitats (A), monthly spore production per tetrasporangial sorus and per carposporangium for intertidal (B), and subtidal (C) habitats.

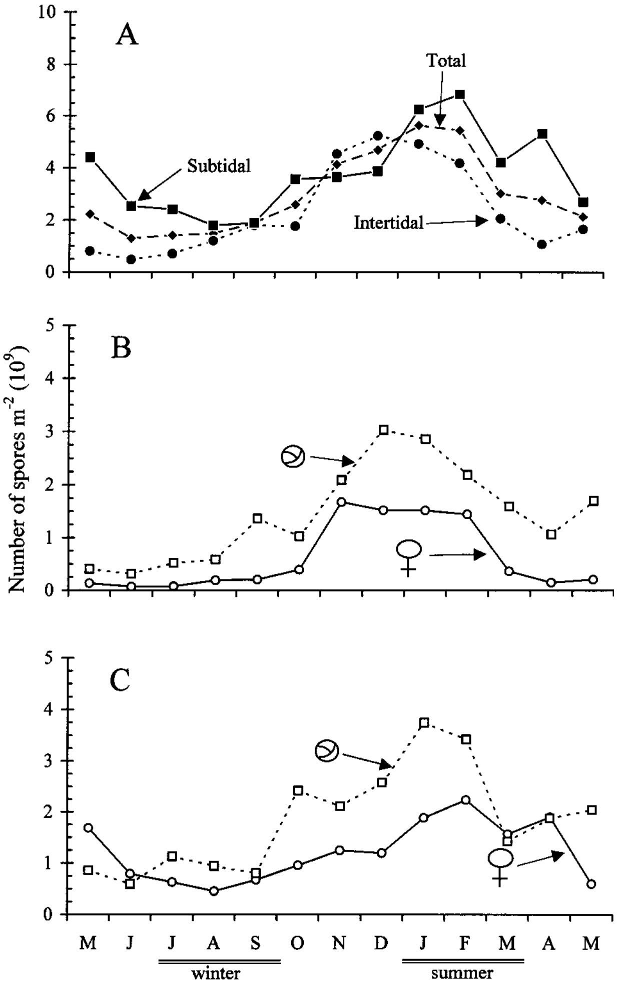

Fig. 6. Monthly values for total reproductive capacity of *C. canaliculatus* in the study area and for both habitats (A), for both tetraspores and carpospores in the intertidal (B), and in the subtidal (C).

tats, monthly reproductive capacity was higher in the intertidal area and, in the subtidal area monthly reproductive capacity had a slightly earlier peak in the year (December) than in the intertidal area (February).

Reproductive capacity of tetrasporic thalli was higher than that of carposporic thalli in both the intertidal and in the subtidal areas, although the annual pattern of spore production of both phases was not the same in both habitats. The intertidal tetrasporic plants increased spore production sharply from October to November (up to approximately 3.2×10^9 spores per m^2), followed by a gradual decrease (Fig. 6B). A similar pattern was seen in the subtidal plants (Fig. 6C) although the peak in production was in January ($\approx 3.9 \times 10^9$ spores per m^2). Intertidal carpospore production increased sharply in November and then it leveled on to February (Fig. 6B). Subtidally, carpospore production increased during spring-summer peaking in February (Fig. 6C).

Laboratory studies

Spore release

Release of carpospores ($\approx 796{,}000 \pm 24{,}360$ spores per month) was significantly higher (Wilcoxon test, $z = 3.95$ and $z = 7.51$, $P < 0.05$ intertidal and subtidal fronds, respectively) than release of tetraspores ($\approx 665{,}140 \pm 35{,}000$ spores per month) in fronds from both habitats (Figs 7A, B), and both types of spores were produced in greater number in the subtidal area (Wilcoxon test, $z = 7.87$ and $z = 2.10$, $P < 0.05$ carpospores and tetraspores, respectively). The maximum number of spores released ($\approx 760{,}000-1, 40{,}000$ spores) by both types of fronds occurred between November and February (Kruskal-Wallis test, $z = 180.051$ and $z = 154.487$, $P < 0.05$) carpospores and tetraspores, respectively). Tetraspore release began earlier and carried on for a longer period in the subtidal (Fig. 7B) than in the intertidal area.

Spore settlement

Chondrus canaliculatus did not show significant differences in spore settlement between fronds from both habitats (multifactorial ANOVA of three factors – habitat, phase, season –, $df = 2.0$, $F = 3.887$, $P = 0.0508$). Also, total spore settlement did not change significantly during seasons of the year (ANOVA, $df = 3.0$, $F = 2.234$, $P = 0.0874$). When comparing spore settlement seasonally in each habitat, results indicated that in the intertidal area, settlement of spores was significantly higher (53–82%) in spring (Tukey test, $P < 0.005$ between spring and the other three seasons), whereas in the subtidal area it was significantly higher (Tukey HSD, $P < 0.05$ between summer and spring and summer and winter, non-significant between summer and autumn) during summer (50–81%) and autumn (53–86%).

Spore germination

Spore germination rate depended on the native habitat of the parental plant (T-test $t = -2.13469$, $P = 0.0345$). Significantly higher germination rates ($\bar{X} = 43.3 \pm 1.5$) occurred for spores from subtidal thalli and here, the tetraspore rate of germination was significantly higher than for carpospores (T-test, $P < 0.05$). This was not the case in the intertidal thalli. Both intertidal and subtidal spore germination rates differed significantly (ANOVA, $df = 3.0$; $F = 6.240$, $P = 0.0008$ and ANOVA, $df = 3.0$; $F = 4.670$, $P = 0.005$ for intertidal and subtidal, respectively) during the year. Germination was higher in spring in the intertidal spores ($45.6 \pm 1.8\%$, Tukey HSD, $P < 0.0505$) while in the subtidal spores it was higher during the summer (Tukey HSD, $P < 0.0505$). Carpospores had a higher incidence of germination in spring ($44.8 \pm 1.99\%$, Tukey HSD, $P < 0.05$), for tetraspores this occurred in summer ($47 \pm 1.18\%$, Tukey HSD, $P < 0.0505$).

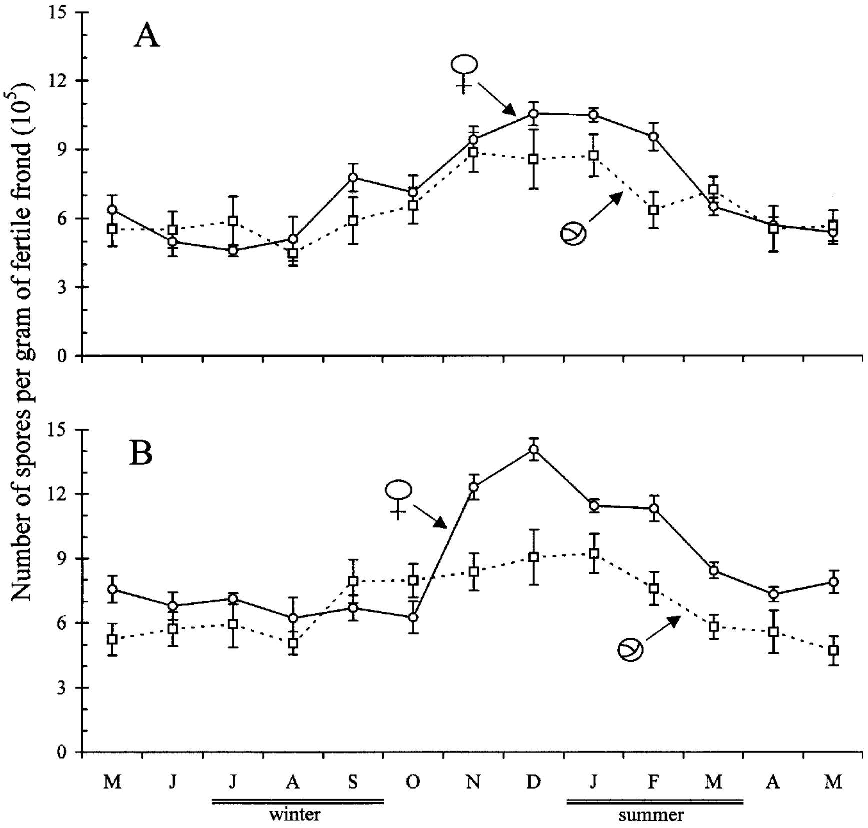

Fig. 7. Carpospores and tetraspores artificially released from reproductive fronds from the intertidal (A), and from the subtidal (B) of *C. canaliculatus*.

Germling survival

Total survival of germlings (28.54 ± 0.024) from intertidal versus subtidal parents was not significantly different (T-test, $t = -0426768$, $P = 0.670195$). Also, there was no difference (T-test, $t = 0.312525$, $P = 0.7551$) in the survival of germlings originating from tetraspores (28.4 ± 0.0276) versus carpospores (28.7 ± 0.0626) when comparisons were made without considering seasons. Nevertheless, juveniles originating from carpospores of intertidal plants had a significantly higher survival rate (31.2 ± 0.017) in spring (ANOVA, $df = 3$, $F = 3.180$; $p = 0.0293$, Tukey HSD, $P < 0.05$), but those from tetraspores showed no significant differences (ANOVA, $df = 3$, $F = 4.10$; $P = 0.7463$) in survival rate at different seasons. In the subtidal fronds the highest percentage of juvenile survival ($\approx 30\,\%$) was observed in summer and autumn (Tukey test, $P < 0.005$) for those germlings originating from carpospores (sporophytes), juvenile gametophytes did not show differences during the year.

Reproductive potential

Sixty percent of all spores settled in the first 24 h (Table I). However, after one week of culture only 40 % germinated and developed a basal disc. After one month of culture 30 % of the settled spores developed into juvenile thalli.

The quantity of juveniles obtained per g of fertile frond varied depending on the reproductive phase, the habitat of the parental plant, the season of the year and the number of spores released. Overall, reproductive fronds of *Chondrus canaliculatus* from Puerto Aldea averaged 74.4 ± 19.3 released spores per g of fertile frond, and 45.7 ± 13.7 of these became settled, 31.5 ± 9.4 germinated and 21.2 ± 5.8 reached the age of one month. In summary, the estimated reproductive potential of *C. canaliculatus* is 10^9 spores/m^2/month.

Discussion

Chondrus canaliculatus is one of the many marine resources used by fishermen of Tongoy Bay (including Puerto Aldea), along with scallops, various species of sea snails, patella, octopus, several species of local fish and *Gracilaria chilensis* Bird, McLachlan *et* Oliveira, *Chondracanthus chamissoi* Kützing and *Lessonia* spp. among seaweeds. *Chondrus canaliculatus* harvesting is made during that time of the year when high stocks of the alga are detected making it a temporary resource. Unfortunately, unless a serious training program is developed, the species stock will be further reduced due to the lack of knowledge about the reproductive phenology of the species and to the harvesting method which consists in scraping off the whole thallus.

Total biomass production of *Chondrus canaliculatus* changed seasonally at the same time as reproductive biomass did. This poses a problem when harvesting has to be optimized without depleting the resource by eliminating its recovery through reproductive propagules. However, managing *C. canaliculatus* as a temporary resource at Puerto Aldea may be done by collecting the fronds after the peak in biomass has been reached. In this manner reproductive fronds would be allowed to release those spores that have the highest chance to settle, germinate and give rise to new thalli. Such a decision has to be taken when considering the results obtained in the study of these later processes and the differences that resulted from the original habitat of the fronds (intertidal versus subtidal) and the reproductive phase of each.

At Puerto Aldea, the loss of intertidal thalli biomass of *Chondrus canaliculatus* during summer follows the bleaching of fronds which later become soft and fragile. A similar phenomenon was observed in intertidal populations of *Mastocarpus papillatus* Kützing and *Chondrus crispus* Stackhouse on the east coast of North America (Davison and Pearson 1996). Frond bleaching could be explained by the high levels of irradiance during desiccation periods (see Scrosati and DeWreede 1998) in the intertidal region, especially since the thallus of this species is not a tight bushy shape, but has loosely grouped fronds with spaces among them, allowing irradiance to reach most fronds as well as facilitating water loss. However, frond bleaching also occurred in the subtidal population at the end of the summer and early autumn. In this habitat, the loss of biomass of *Chondrus canaliculatus* was the result of the detachment of most of the large-sized fronds in each thallus due to mechanical traction during periods of storm or of sand abrasion. Also, an increase in fauna associated with the thallus during reproductive and egg-laying periods of this fauna, as well as predation by invertebrates and herbivorous fish (González 1990, González 1993) contribute to the loss of biomass of *Chondrus canaliculatus.* These factors, plus endophytism, are also known to be agents of natural mortality in subtidal populations of *Chondrus crispus* in Canada (Bathacharya 1985, Chopin *et al.* 1988, Correa and McLachlan 1991).

In general, our results showed that the maxima in total biomass, reproductive biomass, sori production and spore production per sorus occurred in the months of spring and summer, often extending a month or two into autumn for fronds of the subtidal population. More important, all of these variables, except for sori production which was similar in the timing for both habitats, showed their maxima earlier in the year in the intertidal region (usually late spring months and early summer months) and later in the subtidal region (middle and late summer) indicating that harvesting may be concentrated in two different periods. The different timing of total biomass peaks in intertidal thalli of *C. canaliculatus,* and those in the subtidal, may be a consequence of summer abiotic factors (longer periods of exposure to air, temperature and/or irradiance) that cause the frond bleaching and possibly earlier mortality in the intertidal region (Mathieson and Burns 1975, Gutiérrez and Fernández 1992, Dudgeon and Johnson 1992, Davison and Pearson 1996).

Although no estimations of growth have been made on *Chondrus canaliculatus* from Puerto Aldea, differential timing in all the variables between intertidal and subtidal fronds may be explained as a differential timing of growth in their vertical gradient of distribution. This has been reported in *C. crispus* populations from the coasts of France, where intertidal fronds reach their maximum productivity before subtidal fronds (Chopin and Floc'h 1992).

The period of maximum release of spores, from intertidal as well as from subtidal fronds, is comparatively long involving four months from November (end of spring) until February (end of summer). Spore release in seaweeds is often seasonal, with a peak in spore viability in a period of the year when the new individuals have higher probabilities of development (Mathieson 1989, Amsler *et al.* 1992, Brawley and Johnson 1992, Clayton 1992, Vadas *et al.* 1992, Melo and Neushul 1993, González *et al.* 1997).

According to the peaks of settlement that resulted from spores originated in fronds from both habitats, those originated from intertidal fronds that settled in spring would be the ones released during November. On the other hand, spores which settled in summer and autumn originated from subtidal fronds and would be those released during the two last months of the summer period. In other words, although spores are released over a long period, those released at the beginning of the period have higher probabilities of settling in the intertidal region while those released at the end of the period have the higher probability of settling in the subtidal region.

These results impose a difficult constrain upon the optimal period for harvesting since this should not be done during the entire period of spore release, in order to allow the availability of spores for settlement in both habitats. Nevertheless this is solved by a differential timing in harvesting, earlier in the intertidal and later in the subtidal region.

After the spores have settled, the germination timing followed a similar pattern to that of settlement. Germination of spores from intertidal fronds do better in spring, in other words, those that settled in spring would have better probabilities of germinating during the same season. Spores from subtidal fronds settle in summer and autumn and those that settled in summer would show a higher percentage of germination during the same season. Nevertheless, high mortality rates due to factors such as herbivory, parasitism and density-dependent interactions may be observed during pre- and post- settlement processes (Amsler *et al.* 1992, Vadas *et al.* 1992). These variables were not measured in this study. Again, germination peaks were earlier in the year for the intertidal than for the subtidal spores and this reinforces the suggestion of a differential timing in harvest between the intertidal and the subtidal populations.

The proportion of juveniles surviving was the same for those originating from spores released from intertidal and subtidal fronds and the survival of gametophytes did not depend on the original habitat of the frond that provided the corresponding spore. On the other hand, tetrasporophytes did show a higher success in surviving during spring for the intertidal and during summer-autumn for the subtidal areas, confirming the time difference for the entire process from spore release to germling survival between the two habitats.

According to these data harvesting periods should be concentrated in late December and January. In addition, they may be extended to February depending on the balance between fishing effort and algal yield in those intertidal areas next to Puerto Aldea, particularly Caleta Verde (our study site). The harvesting period in the subtidal area of the same locality should last from late January to February. The different timing of harvesting in these two habitats will lead to the maximum yield of the alga and will allow the release of those spores better suited for settlement and germination from fronds of each habitat. It will also extend the entire harvesting period of the alga in the locality.

Although we have evaluated the potential of the spores to generate new thalli, none of these measurements included those external factors that could be extremely important for the final outcome of these *Chondrus canaliculatus* beds. In fact, settlement may be strongly affected by water movement and currents in the area as well as the time the spores are able to remain viable in the water column (Hoffmann 1988, Santelices 1990).

Since a third of the released spores may be able to achieve the juvenile stage (as indicated by the reproductive potential evaluation), further information is needed on whether this proportion of juveniles is sufficient for the replacement of fronds lost annually. In *Chondrus crispus* the reported reproductive potentials were variable; Mathieson (1989) obtained between 68 and 92 % of viable juveniles depending on the season, whereas Scrosati *et al.* (1994) observed a spore viability ranging between 15 and 30 %. In California the reproductive potential of *Gelidium robustum* (Gardn.) Hollenberg *et* Abbott was 60 % in spring-summertime and decreased to less than 10 % in wintertime. The population of *Chondracanthus chamissoi* at Puerto Aldea had a reproductive potential of 50 % (González and Meneses 1996). It is likely that the reproductive potentials in red algae are variable between species and between localities for the same species. It is also understood that the reproductive potential, only based on reproductive propagules obtained in this study, is probably underestimated, since a number of variables, such as the occurrence of microhabitats in nature, could improve the possibilities of spores to settle and of juveniles to persist. Finally, harvesting methods involving the pruning of fronds in those months of maximum biomass (Vega *et al.* unpublished) have been studied to propose a basic management for the population of *Chondrus canaliculatus* in order to allow recovery and preserve this resource.

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