

Seasonal changes in abundance and shifts in dominance of life history stages of the carrageenophyte *Sarcothalia crispata* (Rhodophyta, Gigartinales) in south-central Chile^{**}

Ricardo D. Otaíza^{*}, Sebastián R. Abades & Antonio J. Brante Facultad de Ciencias, Universidad Católica de la Santísima Concepción, Casilla 297 Concepción, Chile

(*Author for correspondence; e-mail rotaiza@david.ucsc.cl)

Received 18 November 1999; revised 14 November 2000; accepted 23 November 2000

Key words: Chile, gametophytic dominance, Gigartinaceae, life history, resorcinol, Sarcothalia crispata, self-seeding

Abstract

The population dynamics of the carrageenophyte *Sarcothalia crispata* is described from subtidal beds at two localities in south-central Chile. Seasonal fluctuations in total density and biomass were not evident. Fronds were identified to phase by the presence of reproductive structures and the resorcinol reaction. The monthly changes in abundance of each kind of frond were determined. Permanent gametophytic or sporophytic dominance was not evident: the more exposed site showed a seasonal shift from sporophytic dominance in summer to gametophytic dominance in winter, whereas the more protected site showed an interannual shift from gametophytic to sporophytic dominance. The differences between localities and years suggest a very local population dynamics with large contribution of self-seeding to the maintenance of the *S. crispata* beds.

Introduction

Isomorphic species of the Gigartinaceae have been shown to differ in the relative abundance of gametophytes to sporophytes in the natural environment. It has been proposed that changes in the proportional abundance of the life history phases would be evident through several years for species where a perennial disk is present (Dyck et al., 1985; May, 1986) explaining, for example, the different results obtained for *Mazzaella splendens* (Hansen & Doyle, 1976; Hansen, 1977; Dyck et al., 1985; May, 1986; De Wreede & Green, 1990) and *Chondrus crispus* (Craigie & Pringle, 1978; Bhattacharya, 1985; McLachlan et al., 1988; Scrosati et al., 1994). On the other hand, in species where the population renewal is mainly from spores rather than regrowth from perennating structures, changes in relative abundance should be detectable in shorter periods.

Sarcothalia crispata (Bory) Leister (Rhodophyta, Gigartinales) is an exploited carrageenophyte in Chile. Together with Mazzaella laminarioides and Gigartina skottsbergii it is harvested from natural populations and either exported or used locally for the extraction of carrageenans (Ávila & Seguel, 1993). Total landings of these species in Chile have exceeded 28×10^3 t in the last five years. Sarcothalia crispata occurs from Valparaíso (33°S) to Tierra del Fuego (~52°S), inhabiting low intertidal and shallow subtidal rocky bottoms (Santelices, 1989; Ramírez & Santelices, 1991; Hoffmann & Santelices, 1997). It has a typical triphasic life history with isomorphic free-living blades (Hoffmann & Santelices, 1997). The blades are lanceolate when complete to orbicular when broken; their distal portions are usually missing due to breakage or nec-

^{**} This paper was presented in the International Symposium 'Cultivation and Uses of Red Algae' held in Puerto Varas, Chle, in November 1999 and organized by A. Buschmann, J. Correa and R. Westermeier. The symposium was supported financially by the FONDAP Program in Oceanography and Marine Biology (Chile).

rosis after maturation; regrowth of the broken margins of the blade has not been reported (or seen in this study). The laminae have a basal adhesion disk; the larger disks (>5 mm in diameter) usually carry several whorls of small (1-5 mm long) laminae or papillae (unpublished data). Subtidal fronds grow singly from a disk in the great majority of cases, but it is common for them to produce several blades in low intertidal individuals (Hoffmann & Santelices, 1997). It has been proposed that disks have the ability to perennate (Poblete et al., 1985; Poblete & Lafón, 1987), and production of new blades from old disk could be common, although the proportion of the population which could be produced from these older disks would be very small (Ávila et al., 1996). If this were the case, rapid changes in the relative abundance of the life history phases would be expected.

There have been three studies on the temporal variation in the abundance of this species, but this information is not appropriate to evaluate changes in the composition of life history phases in subtidal populations, which are the main source of its fronds for the industry. Hannach & Santelices (1985) sampled an intertidal population in an exposed rocky shore in Pelancura close to the northern limit of geographic distribution (V Región, 33°35'S, 71°38'W); Poblete et al. (1985) sampled a subtidal bed in Punta de Parra (VIII Región, 36°40'S, 72°59'W), which showed winter burial by sand; Ávila et al. (1996) conducted a bimonthly sampling of a subtidal bed in Guapilinao (X Región, 41°58'S, 73°31'W). All three studies showed a seasonal pattern of abundance with minimum density and biomass in winter or spring and maxima in summer. Carposporic fronds were usually more abundant than tetrasporic fronds, i.e. gametophytic dominance; however, many fronds typically lacked reproductive structures, so their life history phase was not determined. In all three studies only a single complete annual cycle and a single site were sampled, so potential differences between years and localities could not be assessed.

The aim of the present study was to assess the abundance of *S. crispata* in subtidal beds without sand intrusion. In order to do this, we compared the abundance of fronds in two localities and during two consecutive growing seasons; this included identification of the two life history stages and comparison of the changes in dominance of gametophytes and sporophytes. We expected seasonal changes in abundance as indicated in previous work (Hannach & Santelices, 1985; Poblete et al., 1985; Ávila et al., 1996) and also

changes in the relative abundance of fronds and life history stages between sites and years.

Materials and methods

The study sites were located in the southern margin of the Bahía San Vicente (36°44'S, 73°08'W) in the coast of the Hualpén Peninsula, VIII Región, Chile. Their features include rocky walls and outcrops with some protected coves and small sandy beaches. A Sarcothalia crispata bed has grown in this coast for many years and traditionally has supported harvesting activity, but fishermen have abandoned seaweed extraction for other economic activities. Only on a single occasion during this study did some harvesting occur, as indicated by personnel of the Marine Coastal Station of the Universidad Católica de la Santísima Concepción located in the same coastal site. The rocky bottoms extended down to 10 m in depth, where they were replaced by sandy bottoms. Water circulation patterns in the bay are counter-clockwise (Ahumada et al., 1989), so the sites receive directly the incoming water. Two localities were chosen, about 500 m apart. S. crispata extended all over the rocky bottoms, except for the most vertical walls. The locality, Paredon, was at the base of a small cliff subjected to the currents of the bay. The bottom had a gentle slope and a depth of 6-8 m. It consisted of bedrock plus boulders of a wide size range, and extended towards the center of the bay until it was replaced by a sandy bottom. The locality, Ramuntcho, was in a more protected cove. The bottom was also bedrock with boulders with a greater slope than at Paredon. Sampling was done at a depth of 5-8 m. This cove had a small sandy beach and sand banks moved seasonally by the center; nevertheless the two sites were located in the sides of the cove. No sand bank was ever seen in any of the sampling areas on any of the fortnightly visits. The other most common organisms found were the seaweeds Grateloupia doryphora and Trematocarpus dichotomus, occasional small patches of Chondracanthus chamissoi, and a dominant cover of crustose algae, mainly corallines. The most common herbivores were the sea-urchins Tetrapygus niger, the snails Tegula spp and the chitons Chiton cumingsi and Tonicia elegans.

To facilitate sampling within each locality, two sites 50–80 m apart were chosen. Each was sampled with four 0.25 m²-quadrats placed haphazardously along the *Sarcothalia crispata* bed; a total of 16 quadrats were taken on each sampling date. Sampling

was planned to be monthly, but bad weather conditions in two occasions (July 1997 and May 1998) forced a delay producing a real sampling frequency of 3-6 weeks from May 1997 to August 1999. On each occasion all the S. crispata fronds greater than 2 cm in length within each quadrat were collected. Sampling was done by diving. In the laboratory each frond was tagged and its maximum length and width were measured individually. The phase of the life history was identified distinguishing fronds with tetrasporangial sori, fronds with cystocarps visible to unaided eye, and fronds without visible reproductive structures. A sample of each one of the latter was taken and subjected to the acetal-resorcinol reaction (Garbary & De Wreede, 1988; Shaughnessy & De Wreede, 1991) to determine the phase according to the carrageenan composition; control cystocarpic and tetrasporic fronds were included in all sets of tests. For the determination of biomass per quadrat, fronds were oven-dried at 60 °C until constant weight (2–3 days).

To evaluate differences between localities the average density and biomass between February 1998 and August 1999 were compared with the sign test (Siegel, 1956). To test for dominance between life history phases, the percentage of gametophytes in selected months in 4 periods (two summer and two winter periods) were compared separately for Paredon and Ramuntcho. For Paredon, the four periods compared were January to March 1998, July to September 1998, November 1998 to January 1999, and June to August 1999. For Ramuntcho the four periods compared were February to April 1998, July to September 1998, December 1998 to February 1999, and June to August 1999.

A one-way Anova was applied, with season as treatment and percentage gametophytes in each pooled monthly sample as replicates. Cochran's C test was used to test for homogeneity of variance (no transformations were required), and differences were tested with SNK *a posteriori* test (Underwood, 1997). All analyses were done on the raw data; nevertheless the data in the figures are standardized to biomass per m^2 in order to permit easy comparison with other studies.

Results

Seasonal changes in abundance

Sarcothalia crispata did not show clear seasonal fluctuations in density (Figure 1). At the beginning of this study, in May 1997, there was a decline in density and biomass associated with an unusual increase in density of Grateloupia doryphora. Despite our sampling effort, S. crispata could not be found in the study sites. Only in December 1997 did S. crispata started growing again, following the decline of G. doryphora. This unusual growth of G. doryphora did not occur again. The four sites differed in some respects. Site Paredon-2 showed a longer recovery period from the G. doryphora invasion, which extended until autumn. This was the only site where the S. crispata bed declined again to zero during winter 1998. At the other sites there was only a short general decline in density in August 1998 associated with winter storms. Sudden density increases were detected in different months at some sites: December 1997 and January 1998 at Paredon-1; November and December 1998 at Paredon-2; February 1998 at Ramuntcho-1; none at Ramuntcho-2. These events were short and followed by a decline in density almost as abrupt as the increases. Biomass changes followed density very closely but fluctuations were more moderate (Figure 1). Apart from these fluctuations, there was no clear seasonal trend. Except for the single month decline in August 1998, there was a tendency for a steady increase or maintenance of the abundance of S. crispata during two growing seasons starting from spring 1997 after G. doryphora declined. The two localities had significantly different densities (n = 18, p =0.004). Density ranged between 40–80 fronds m^{-2} at Paredon and between 20-60 fronds m⁻² at Ramuntcho. No differences in average biomass were found between Paredon and Ramuntcho (n = 18, p =0.407).

We identified sporophytic fronds with and without tetrasporangial sori, and gametophytic fronds with and without cystocarps. Changes in abundance along the seasons were different for different kinds of fronds (Figure 2). In all cases the Grateloupia doryphora invasion in 1997 was noticeable, and probably distorted some patterns. The density of sporophytes (Figure 2) showed a similar pattern between years, although slightly out of phase in the 1997/8 and 1998/9 growing seasons. In Paredon, sporophytes showed low densities in late winter and early spring, increasing towards late spring and summer; a second maximum could be distinguished in autumn, followed by a decrease in winter. In Ramuntcho, density was low in winter and spring, increasing in summer. A bimodal trend was also apparent, although, unlike in Paredon, the second maximum was greater than the first. The dens-



Figure 1. Changes in abundance of *S. crispata* in each of two sites in the two localities (Paredon and Ramuntcho) sampled along two complete growing seasons. Mean (\pm SE) density of fronds (continuous line) and dry biomass (broken line).

ity of gametophytes with cystocarps also showed a similar pattern between years. In Paredon, apart from the G. doryphora invasion in 1997, cystocarpic fronds showed greater density in spring and autumn – winter, with lower densities in summer. In Ramuntcho, lower densities were also observed in summer. The density of gametophytes without cystocarps corresponded mostly to male gametophytes but also to some female gametophytes (unpublished data). In Paredon, a similar trend was observed between years: they were more abundant in summer decreasing in early autumn and showing a second maximum in late autumn to decline in winter. In Ramuntcho, the G. doryphora invasion in 1997 was long and perhaps delayed the summer growth of these gametophytes until February 1998. In 1999, density in Ramuntcho followed a similar pattern

to Paredon with a maximum in summer and a decline towards winter.

Size-frequency distribution

Given the shape of the frond of *Sarcothalia crispata*, with a wider base narrowing towards the tip, and the fact that most fronds were missing the distal portions, the width of the frond rather than its length was preferred to establish the size frequency distributions. Length and width of entire fronds are highly correlated (unpublished data). Only data for Paredon is illustrated in Figure 3, but both localities followed a similar trend except for the differences described below. Immature sporophytes were strongly seasonal, occurring as a single very abrupt peak in late spring. In Paredon this was in December 1997 and November–December 1998 (Figure 3a), while in Ramuntcho it

PAREDON

RAMUNTCHO



Figure 2. Density of fronds of *S. crispata* (mean \pm SE) in different months for the two localities: Paredon (a, c, e) and Ramuntcho (b, d, f). Fronds were separated according to their reproductive state and life history phase in sporophytic (a and b: sum of sporophytic fronds with and without reproductive structures), cystocarpic (c and d: female gametophytes with cystocarps) and gametophytes without cystocarps (e and f). The phase of the life cycle of fronds without reproductive structures was identified with the acetal resorcinol reaction. Dotted line = end of the 1997 season; dashed line = 1997/1998 season; solid line = 1998/1999 season.

had the same pattern but occurred later in February 1997 and December 1998. These fronds were not all of small size, some reaching 20 cm in width (and 50 cm in length). In both localities the abundance of these fronds declined abruptly in the following months to only a few immature sporophytes until mid-autumn. Some of these fronds had a large width, presumably older fronds that had lost the portions with reproductive structures. No immature sporophytes were found from late autumn to mid spring in either locality. On the other hand, sporophytes with reproductive structures had a first maximum in abundance in late spring and early summer, coinciding with the immature sporophytes. Fronds were of a larger width range. This was particularly evident in Paredon both years (Figure 3c), while in Ramuntcho the tetrasporic fronds were more spurious during the first year. A second maximum was evident by late autumn, consisting in the increase in number of fronds in the smaller size classes. For this second maximum a preceding peak of immature fronds was not evident. This second peak was clear both years in Paredon, while in Ramuntcho it was virtually non-existent in the first year and more evident in the second year. Overall, immature sporophytes, rarely more than 30 cm in width (80 cm in length, Figure 3), whereas larger fronds were frequent in Ramuntcho in most months. Gametophytes without visible reproductive structures had also a strong seasonal component (Figure 3b). In both loc-



not they were visible to the naked eye: a) immature sporophytes; b) gametophytes without cystocarps; c) sporophytes with tetrasporangial sori; d) gametophytes with cystocarps. The columns represent the absolute number of fronds pooled for both sites in this locality (Paredon). No data were obtained in July 1997 and May 1998.



represent the spore producing fronds (cystocarpic and tetrasporic fronds), and the stippled bars represent the fronds that do not produce spores (immature or male gametophytes and immature sporophytes). The total abundance of a given life history phase for any given month corresponds to the total length of the solid and stippled bars. Density is expressed as the average number of fronds per m^{-y}) for each month for a) Paredon and b) Ramuntcho. Relative density is expressed as a percentage in relation to the total density of fronds in each month for c) Paredon and d) Ramuntcho. No data were obtained in July 1997 and May 1998. Figure 4. Absolute and relative density of fronds for the two life history phases. Gametophytes are shown above the 0 line and sporophytes below the line. In both cases the solid bars

alities and in both years there was a peak in late spring and early summer, being more abrupt in the first spring (1997) than in the following one. In Paredon a second peak was evident both years in autumn; this was much more discreet in Ramuntcho. Fronds with cystocarps had a different pattern (Figure 3d). Few were found until late autumn when a large number of fronds of all sizes showed developing cystocarps. This happened in both localities in both years.

Gametophytic dominance

The abundance of gametophytes and sporophytes changed seasonally at Paredon (Figure 4). There were significant differences in relative abundance among seasons (F = 7.69, p < 0.01). There were no differences between summers or between winters, but significantly higher values were obtained in winter 1998 than the preceding or following summer; winter 1999 had an intermediate value and differed significantly only from summer 1998. In Ramuntcho, on the other hand, in the period before the Grateloupia doryphora invasion (winter 1997) the fronds were predominantly sporophytic (Figure 4b). The relative abundance of gametophytes (Figure 4d) differed significantly among seasons (F = 34.2, p < 0.01). All paired comparisons were significant; the first year after G. doryphora declined at these sites, from summer 1998 until the following spring, fronds were predominantly gametophytic, while in the following year the sporophytes increased in abundance.

Discussion

Three studies (Hannach & Santelices, 1985; Poblete et al., 1985; Ávila et al., 1996) on the abundance of Sarcothalia crispata have all found a clear seasonal change with minimum values of density and biomass in winter and maximum ones in summer (see also Hannach & Waaland, 1986). Usually carposporic fronds are more abundant than tetrasporic fronds. In the three studies a single site was sampled through a single complete annual cycle. Our results show a positive trend for the total monthly density and biomass. Fluctuations did occur, but were synchronous only when a decrease was likely to be produced by a major external phenomenon. There was a decrease in abundance from winter to spring 1997, but it was clearly related to the unusual growth of Grateloupia doryphora; once it declined, S. crispata grew. The abundance of G. doryphora did not increase during the following winters and S. crispata was present. The expected decline in abundance during the following winters was very short and occurred only in August 1998, coinciding with periods of frequent occurrence of heavy swells. On the other hand, abrupt increases in abundance such as those in late spring were of short duration and not detected every year at particular sites. Our results show that the density of the different kinds of fronds differed in their seasonal fluctuations. While sporophytes and gametophytes without cystocarps increased in abundance in early summer, gametophytes with cystocarps had minimum values then. Later on, all fronds increased in density towards mid autumn, but while sporophytes declined thereafter, gametophytes with and without cystocarps were still abundant in late spring. As a result, the overall abundance of S. crispata showed no seasonal trend. The decrease in abundance in the S. crispata bed studied by Poblete et al. (1985) was also due partly to a catastrophic external phenomenon, which was the sand invasion suffered in their study site and strong winter swells. Likewise, the winter decline in abundance reported by Hannach & Santelices (1985) for a low shore, exposed rocky platform could be explained as the effect of winter swells that may have dislodged or broken the S. crispata thalli. On the other hand, the results of Ávila et al. (1996) in a sheltered bay in southern Chile showed seasonality apparently unrelated to catastrophic events. The annual cycle was given by growth followed by reproduction and subsequent disappearance of the blades, presumably after senescence (see Hansen, 1977). Perhaps winter conditions preclude growth of fronds due to physical factors (e.g. temperature and light) occurring below the threshold levels required to support growth. Therefore, seasonality in density or biomass reported as of common occurrence elsewhere for S. crispata could be the result of external catastrophic phenomena or physical factors. Our results show that a lack of strong seasonal fluctuations in the total abundance is also possible as a result of complementary seasonal changes in abundance of the fronds of the different life history phases.

The most important difference between localities was the change in the relative abundance of sporophytes and gametophytes. At Paredon, alternation was from a sporophytic to a gametophytic maximum within the same year. At Ramuntcho, on the other hand, alternation in dominance between phases occurred between years. Earlier work in *Sarcothalia crispata* could not identify a phase of the blades lacking visible reproductive structures, although these were usually very abundant (Hannach & Santelices, 1985; Poblete et al., 1985; Ávila et al., 1996). In these studies, a greater abundance of cystocarpic fronds was found. De Wreede & Green (1990) found no differences when only reproductive fronds were used or when all fronds were identified to life history phase using the resorcinol-acetal test.

In other isomorphic Gigartinaceae, differences in dominance of one life history phase has been reported along environmental gradients, such as exposure to wave action, intertidal height or depth (Craigie & Pringle, 1978; Dyck et al., 1985; Hannach & Santelices, 1985; Lindgren & Åberg, 1996). In our study, while it is true that a gradient of physical and/or biological factors could exist between the two localities, the change in relative abundance observed between years cannot be explained with this argument. Other explanations for dominance include preferences by herbivores or pathogens, differential performance of the haploid or diploid phases in different sets of physical variables, differential production or performance of their spores, or different cellular processes like apomeiosis or apogamy (Hansen & Doyle, 1976; Craigie & Pringle, 1978; Van der Meer et al., 1983; Hannach & Santelices, 1985; May, 1986; McLachlan et al., 1988; Luxoro & Santelices, 1989; De Wreede & Green, 1990; Correa & McLachlan, 1992; González & Meneses, 1995; Piriz, 1996; Zamorano & Westermeier, 1996; González et al., 1997). At present none of these possible explanations can be ruled out; any factors would have had to affect one locality in a seasonal manner and the other with differences between years to explain the patterns of change observed between localities and years. We suggest that the S. crispata populations showed characteristics of closed populations (Gotelli, 1995) with a preponderance of self-seeding due to poor dispersion (Hoffmann, 1987; Santelices, 1990; Norton, 1992). Sarcothalia crispata apparently has most fronds originating via settlement of locally produced propagules rather than regeneration from holdfasts (Ávila et al., 1996; see also McLachlan et al., 1988; Ang et al., 1990) and, being an organism with obligate alternation of generations (although see Kim, 1976), the proportion of life history phases in each cohort would be the result of the relative abundance and reproductive success of the preceding cohort. Therefore, the main difference between localities may reside in the capacity to support growth and maturation of blades

producing a more dynamic change in Paredon than in Ramuntcho.

In isomorphic species with mainly short lived (annual) individuals growing predominantly from spores, changes in proportional composition of life history phases may be frequent, like Sarcothalia crispata in this study, whereas in species with longer lived individuals where generations overlap widely and fronds or disks are perennial, these changes may be detectable in longer term periods (Dyck et al., 1985; May, 1986). The latter may be the case with Mazzaella splendens (Hansen & Doyle, 1976; Hansen, 1977; Dyck et al., 1985; May, 1986; De Wreede & Green, 1990), M. laminarioides (Santelices & Norambuena, 1987; Westermeier et al., 1987; Gómez & Westermeier, 1991), M. capensis (Bolton & Joska, 1993), M. cornucopiae (Scrosati, 1998), Chondrus crispus (Craigie & Pringle, 1978; Tveter-Gallagher et al., 1980; Bhattacharya, 1985; McLachlan et al., 1988; Scrosati et al., 1994; Lindgren & Åberg, 1996) and Chondracanthus canaliculatus (García-Lepe et al., 1997) where differences in dominance have been recorded in different geographical locations or different seasons. Several alternative explanations for these differences have been proposed (see above). Seasonal changes in abundance may result from differential rates of increase and decrease in density (Dyck & De Wreede, 1995). Permanent dominance, like is the case for Gigartina skottsbergii, where nearly 90% of the fronds are gametophytes (Zamorano & Westermeier, 1996; Piriz, 1996), may result from apomixis or lower survival of sporophytes (Piriz, 1996). In other cases, such as Chondracanthus chamissoi (González & Meneses, 1995; González et al., 1997) perhaps longer-term studies and over a wider habitat range may reveal slow changes in dominance.

Populations of species like *Sarcothalia crispata*, with obligate alternation of gametophytes and sporophytes and which lack vegetative reproductive and perennating structures, may exhibit rapid changes in the relative abundance of fronds of the life history phases. These changes are greater in species where the individuals are short-lived and populations are primarily self-seeding. *S. crispata* showed population changes at small (seasonal) temporal and local scales.

It was also shown that there are seasonal differences in the abundance of the spore-producing (sporophytic and female gametophytic) fronds. Seasonal restrictions to harvesting due to weather conditions or management practices could impose stronger pressure on one phase of the life history, with unexpected effects on the population dynamics. This should be considered when management plans or harvest programs are proposed.

Acknowledgements

This research was supported by FONDECYT project 1970839. We thank L. Cruz, and L. Escobar for assistance in the field.

References

- Ahumada R, Rudolph A, Madariaga S, Carrasco F (1989) Descripción de las condiciones oceanográficas de la bahía San Vicente y antecedentes sobre los efectos de la contaminación. Biol. pesq. 18: 37–52.
- Ang P, De Wreede RE, Shaughnessy F, Dyck L (1990) A simulation model for an *Iridaea splendens* (Gigartinales, Rhodophyta) population in Vancouver, Canada. Hydrobiologia 204/205: 191–196.
- Ávila M, Otaíza R, Norambuena R, Núñez M (1996) Biological basis for the management of 'luga negra' (*Sarcothalia crispata* Gigartinales, Rhodophyta) in southern Chile. Hydrobiologia 326/327: 245–252.
- Ávila M, Seguel M (1993) An overview of seaweed resources in Chile. J. appl. Phycol. 5: 133–139.
- Bhattacharya D (1985) The demography of fronds of *Chondrus* crispus Stackhouse. J. exp. mar. Biol. Ecol. 91: 217–231.
- Bolton JJ, Joska MAP (1993) Population studies on a South African carrageenophyte: *Iridaea capensis* (Gigartinaceae, Rhodophyta). Hydrobiologia 260/261: 191–195.
- Correa JA, McLachlan JL (1992) Endophytic algae of *Chondrus crispus* (Rhodophyta). IV. Effects on the host following infections by *Acrochaete operculata* and *A. heteroclada* (Chlorophyta). Mar. Ecol. Progr. Ser. 81: 73–87.
- Craigie JS, Pringle JD (1978) Spatial distribution of tetrasporophytes and gametophytes in four Maritime populations of *Chondrus crispus*. Can. J. Bot. 56: 2910–2914.
- De Wreede RE, Green LG (1990) Patterns of gametophyte dominance in *Iridaea splendens* (Rhodophyta) in Vancouver Harbour, Vancouver, British Columbia, Canada. J. appl. Phycol. 2: 27–34.
- Dyck L, De Wreede RE, Garbary D (1985) Life history phases in *Iridaea cordata* (Gigartinaceae): relative abundance and distribution from British Columbia to California. Jap. J. Phycol. 33: 225–232.
- Dyck LJ, De Wreede RE (1995) Patterns of seasonal demographic change in the alternate isomorphic stages of *Mazzaella splendens* (Gigartinales, Rhodophyta). Phycologia 34: 390–395.
- Garbary DJ, De Wreede RE (1988) Life history phases in natural populations of Gigartinaceae (Rhodophyta): quantification using resorcinol. In Lobban S, Chapman DJ, Kremer BP (eds), Experimental Phycology: A Laboratory Manual. Cambridge University Press, Cambridge, pp. 174–178.
- García-Lepe MG, Ballesteros-Grijalva G, Zertuche-González JA, Chee-Barragán A (1997) Annual variation in size and reproductive phenology of the red alga *Chondracanthus canaliculatus* (Harvey) Guiry at Punta San Isidro, Baja California, Mexico. Cien. mar. 23: 449–462.
- Gómez IM, Westermeier RC (1991) Frond regrowth from basal disk in *Iridaea laminarioides* (Rhodophyta, Gigartinales) at Mehuín, southern Chile. Mar. Ecol. Progr. Ser. 73: 83–91.

- González J, Meneses I (1995) Differences in the early stages of development of gametophytes and tetrasporohytes of *Chondracanthus chamissoi* (C.Ag.) Kützing from Puerto Aldea, northern Chile. Aquaculture 143: 91–107.
- González J, Meneses I, Vázquez J (1997) Field studies in *Chon*dracanthus chamissoi (C.Agardh) Kützing: seasonal and spatial variations in life-cycle phases. Biol. pesq. 26: 3–12.
- Gotelli, N (1995) A Primer of Ecology. Sinauer Associates. 206 pp.
- Hannach G, Santelices B (1985) Ecological differences between the isomorphic reproductive phases of two species of *Iridaea* (Rhodophyta: Gigartinales). Mar. Ecol. Progr. Ser. 22: 291–303.
- Hannach G, Waaland JR (1986) Environment, distribution and production of *Iridaea*. Aquat. Bot. 26: 51–78.
- Hansen JE (1977) Ecology and natural history of *Iridaea cordata* (Gigartinales, Rhodophyta) growth. J. Phycol. 13: 395–402.
- Hansen JE, Doyle WT (1976) Ecology and natural history of *Iridaea cordata* (Rhodophyta: Gigartinaceae): population structure. J. Phycol. 12: 273–278.
- Hoffmann AJ (1987) The arrival of seaweed propagules at the shore: a review. Bot. mar. 30: 151–165.
- Hoffmann AJ, Santelices B (1997) Marine flora of central Chile. Ediciones Univ. Católica de Chile, Santiago: 275–278.
- Kim DH (1976) A study of the development of cystocarps and tetrasporangial sori in Gigartinaceae (Rhodophyta, Gigartinales). Nova Hedwigia 27: 1–146.
- Lindgren A, Åberg P (1996) Proportion of life cycle stages of *Chondrus crispus* and its population structure: a comparison between a marine and an estuarine environment. Bot. mar. 39: 263–268.
- Luxoro C, Santelices B (1989) Additional evidence for ecological differences among isomorphic reproductive phases of *Iridaea laminarioides* (Rhodophyta: Gigartinales). J. Phycol. 25: 206– 212.
- May G (1986) Life history variations in a predominantly gametophytic population of *Iridaea cordata* (Gigartinaceae, Rhodophyta). J. Phycol. 22: 448–455.
- McLachlan JL, Lewis NI, Lazo ML (1988) Biological considerations of *Chondrus crispus* Stackhouse (Rhodophyta, Gigartinaceae) in the southern Gulf of St. Lawrence, Canada. Gayana bot. 45: 29–45.
- Norton TA (1992) Dispersal by macroalgae. Br. phycol. J. 27: 293– 301.
- Piriz ML (1996) Phenology of *Gigartina skottsbergii* Setchell et Gardner population in Chubut province (Argentina). Bot. mar. 39: 311–316.
- Poblete A, Candia A, Inostroza I, Ugarte R (1985) Growth and reproductive phenology of *Iridaea ciliata* Kützing (Rhodophyta, Gigartinales) in a sublittoral population. Biol. pesq. 14: 23–31.
- Poblete A, Lafón A (1987) Nota sobre el comportamiento de los discos basales de *Iridaea ciliata* Kützing. Medio Ambiente 8: 90–94.
- Ramírez ME, Santelices B (1991) Catálogo de las algas marinas bentónicas de la costa temperada del Pacífico de Sudamérica. Monografías Biológicas 5. Publicaciones Periódicas, P. Universidad Católica de Chile, Santiago, 437 pp.
- Santelices B (1989) Algas Marinas de Chile. Distribución, ecología, utilización, diversidad. Ediciones Universidad Católica de Chile. 399 pp.
- Santelices B (1990) Patterns of reproduction, dispersal and recruitment in seaweeds. Oceanogr. Mar. Biol. ann. Rev. 28: 177–276.
- Santelices B, Norambuena R (1987) A harvesting strategy for *Iridaea laminarioides* in central Chile. Hydrobiologia 151/152: 329–333.

- Scrosati R (1998) Population structure and dynamics of the clonal alga Mazzaella cornucopiae (Rhodophyta, Gigartinaceae) from Barkley Sound, Pacific Coast of Canada. Bot. mar. 41: 483–493.
- Scrosati R, Garbary DJ, McLachlan J (1994) Reproductive ecology of *Chondrus crispus* (Rhodophyta, Gigartinales) from Nova Scotia, Canada. Bot. mar 37: 293–300.
- Shaughnessy FJ, De Wreede RE (1991) Reliability of the resorcinol method for identifying isomorphic phases in the Gigartinaceae (Rhodophyta). J. appl. Phycol. 3: 121–127.
- Siegel S (1956) Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill Kogakusha, Tokyo. 312 pp.
- Tveter-Gallagher E, Mathieson AC, Cheney DP (1980) Ecology and developmental morphology of male plants of *Chondrus crispus* (Gigartinales, Rhodophyta). J. Phycol. 16: 257–264.

- Underwood, AJ (1997) Experiments in Ecology. Cambridge University Press, Cambridge, 504 pp.
- Van der Meer JP, Guiry MD, Bird CJ (1983) Sporogenesis in male plants of *Chondrus crispus* (Rhodophyta, Gigartinales). Can. J. Bot. 61: 2261–2268.
- Westermeier R, Rivera PJ, Chacana M, Gómez I (1987) Biological bases for management of *Iridaea laminarioides* Bory in southern Chile. Hydrobiologia 151/152: 313–328.
- Zamorano J, Westermeier R (1996) Phenology of *Gigartina skott-sbergii* (Gigartinaceae, Rhodophyta) in Ancud Bay, southern Chile. Hydrobiologia 326/327: 253–258.