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Population Structure and Dynamics of the Clonal Alga
Mazzaella cornucopiae (Rhodophyta, Gigartinaceae) from Barkley Sound, Pacific Coast of Canada

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The structure and the dynamics of a population of the clonal intertidal alga *Mazzaella cornucopiae* (Postels *et* Ruprecht) Hommersand (Rhodophyta, Gigartinaceae) were investigated at Barkley Sound, on the Pacific coast of Canada, between 1993 and 1995. Holdfasts of this abundant alga were mostly perennial, but fronds had higher turnover rates. Total thallus cover, frond density, mean frond length, and stand biomass varied seasonally, being generally highest in spring–summer and lowest in winter. Cystocarpic and tetrasporic (reproductive) fronds were only present during autumn and winter. On an annual basis, fronds were mostly produced by perennating holdfasts, relative to thalli that were recruited from spores. The population was numerically dominated by gametophytic (vegetative) fronds relative to tetrasporophytic (vegetative) fronds, regardless of season and the degree of wave exposure. *Mazzaella cornucopiae* conforms to a K-strategy in traits mainly studied here: (1) holdfasts are perennial and frequently dominant, (2) reproduction is delayed after recruitment, (3) thalli are iteroparous (repeated reproduction through a life time), (4) recruitment is a minor source of interannual population variation. The similarities and differences with the population dynamics of other members of the Gigartinaceae are discussed.

Introduction

The red alga *Mazzaella cornucopiae* (Postels *et* Ruprecht) Hommersand (Gigartinales, Gigartinaceae) occurs on coasts of the North Pacific Ocean from Japan to northern California (Abbott 1971, Hommersand *et al.* 1993, Selivanova and Zhigadlova 1997). In outer Barkley Sound, on the west coast of Vancouver Island, Pacific Canada, *M. cornucopiae* is often abundant in the high intertidal zone of rocky areas. At Prasiola Point, in southern Barkley Sound, *M. cornucopiae* is part of a community whose other most abundant benthic components are the fucoid algae *Fucus gardneri* Silva and *Pelvetiopsis limitata* Gardner, barnacles (*Balanus* spp. and *Chthamalus dalli* Pilsbury), limpets (*Lottia*), and herbivorous snails (*Littorina*). Important biological interactions such as competition and herbivory between *Mazzaella cornucopiae* and the above organisms have been recently studied experimentally and modelled (Kim 1995, Kim and DeWreede 1996 a, b, Kim 1997). Those studies concluded that *M. cornucopiae* is a key component of this community because of its ability ro retain space, as a food source for littorinid snails, and possibly as a refuge for snails. At the population level, however, less is known about *M. cornucopiae.* This paper examines the structure and the dynamics of the population of *M. cornucopiae* from Prasiola

Point. It is the baseline study for the analysis of more specific aspects of the ecology of this species, including the interactions among growing fronds (Scrosati and DeWreede 1997), the significance of frond crowding for survival (Scrosati and DeWreede 1998), and the response of this species to different kinds of physical disturbance (Scrosati 1997, 1998).

The thallus of *Mazzaella cornucopiae* consists of a crustose holdfast (the current use of 'holdfast' for the Gigartinaceae has been questioned by Bolton and Joska 1993) and of several foliose fronds that stand upright even at low tides. A picture of a typical stand appears in Scrosati and DeWreede (1997). *Mazzaella cornucopiae* is a clonal species, since fronds can potentially survive on their own if they are physically separated from the parent thallus while remaining attached to the substratum. Thus, fronds can be considered as ramets *sensu* Jackson *et al.* (1985) and van Groenendael and de Kroon (1990). Mature stands of *M. cornucopiae* may continuously cover the substratum for up to a couple of meters along the shore line, and frond densities are generally high. Coalescence of adjacent sporelings may occur, since this is common for other red algae (Tveter and Mathieson 1976, Tveter-Gallagher and Mathieson 1980, Maggs and Cheney 1990, Santelices *et al.* 1996). The high frond density and, possibly, holdfast coalescence prevent the accurate identification of neighboring genets (a thallus developed from a single spore) in mature stands. This is further complicated by the possible rupture of a given thallus into separate surviving

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parts (clonal fragments *sensu* Eriksson and Jerling 1990) as a result of some kind of disturbance. The two independent-life reproductive phases of *M. cornucopiae*, gametophytes and tetrasporophytes, are isomorphic, so they can only be differentiated visually when their fronds are reproductive.

This paper firstly describes the annual dynamics of the population of *Mazzaella cornucopiae* from Prasiola Point, based on a 2-year study. The periods of growth, senescence, and reproduction were identified based on a regular measurement of total thallus cover, frond density and length, stand biomass, and density of reproductive fronds. Results are compared with the dynamics of other members of the Gigartinaceae, discussing the patterns that are general for this group and those that are species- or site-specific. The regular mapping of thalli permitted an estimation of the relative role of perennating holdfasts and of spores to the persistence of the population.

The ratio between gametophytes and tetrasporophytes (G : T ratio) is an important descriptor of population structure and it may vary depending on species, seasons, or site conditions for members of the Gigartinaceae (Craigie and Pringle 1978, Dyck *et al.* 1985, Lazo *et al.* 1989, Luxoro and Santelices 1989, DeWreede and Green 1990, Phillips 1994, Dyck and DeWreede 1995, Shaughnessy *et al.* 1996). The temporal and spatial variability of the G : T ratio for the population of *M. cornucopiae* from Prasiola Point is also described in this paper, relating findings with possible general patterns for the Gigartinaceae.

Materials and Methods

Study site

The study site was Prasiola Point (48°49' N, 125°10' W), on the southern coast of Barkley Sound, Vancouver Island, British Columbia, Canada (Fig. 1). The east side of Prasiola Point has a moderate wave action, because it is protected by the tip of Prasiola Point from the large waves that come from the open

Fig. 1. Location of the study site.

ocean, while the west side receives the direct impact of those large waves. This coast is washed by cold-temperate waters. Between the summer seasons of 1993 and 1995, mean monthly temperature of the sea surface varied between 8.6 °C (winter) and 16.1 °C (summer) and mean monthly salinity varied between 26.7‰ (winter) and 31.5‰ (summer) close to Prasiola Point (Scrosati 1997). Wave height was highest in winter and lowest in summer during the same period near Prasiola Point (Scrosati 1997). *Mazzaella cornucopiae* is one of the species located highest in the intertidal zone at Prasiola Point. At the moderate wave-exposure site, it occurs between 3 and 4 m above the lowest normal tide (based on Canadian Chart Datum). There, *M. cornucopiae* shares the substratum mostly with *Fucus gardneri* Silva and *Pelvetiopsis limitata* Gardner, among the seaweeds, but, at the more wave-exposed site, *Mazzaella cornucopiae* is the dominant algal species. The tidal regime is mixed in this area, and, given its location, *M. cornucopiae* spends long periods out of water. The lowest of the two daily low tides occurs mostly during daytime in spring and summer and mostly during darkness in autumn and winter.

Population dynamics

The population of *M. cornucopiae* from the moderate wave-exposure side of Prasiola Point was regularly sampled with six 100-cm² quadrats, randomly located in the intertidal zone. Total percent cover of thalli, frond density, mean frond length, stand wet biomass, and density of reproductive fronds were measured in the same quadrats during two years. There were 14 sampling dates: 4–6 June 93, 17–19 August 93, 15–17 October 93, 10–12 December 93, 24–26 February 94, 26–28 April 94, 22–24 June 94, 19–21 August 94, 5–7 October 94, 2–4 December 94, 28–30 January 95, 30 March 95, 14–16 May 95, and 11–13 July 95. Percent cover was measured for the permanent quadrats using a sampling frame with 100 divisions; divisions with 50% or more of their area covered by *M. cornucopiae* were recorded as positive for cover estimates. Because of a time limitation, frond density and frond length were measured in six 4-cm², randomly located subquadrats within each quadrat; the same subquadrats were monitored on successive sampling dates. All of the fronds present in subquadrats were counted and their length was measured to the nearest 5 mm. Stand biomass (expressed per unit area) was estimated by applying power relationships between frond length and frond wet biomass (table I in Scrosati and DeWreede 1997) to the frond density and mean frond length determined for each quadrat. The relationship between frond length and frond biomass is time-dependent for *M. cornucopiae*, so different equations were applied to different sampling dates (Table II in Scrosati and DeWreede 1997). For the estimation of frond density and stand biomass,
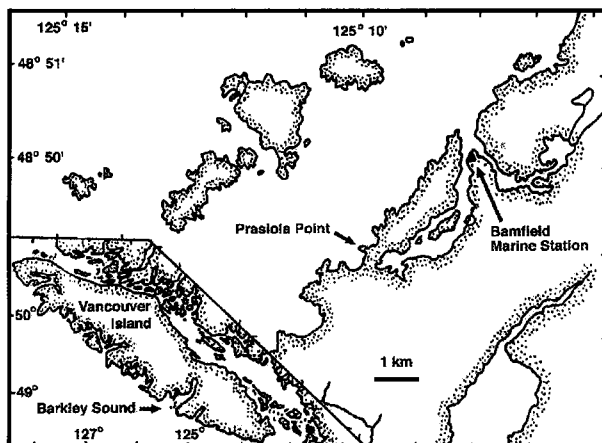
only subquadrats with more than 5 fronds were considered. The relationship between frond wet biomass and the number of cystocarps or tetrasporic sori per reproductive frond was also determined, based on a haphazard sample from the moderate wave-exposure site done on 27–28 October 1996. The perimeter of all of the thalli was regularly mapped using a waterproof marker on a 100-cm² quadrat made of transparent plastic.

Differences among monthly means of percent cover, frond density, mean frond length, and stand biomass were tested using separate one-way, repeated-measures analyses of variance (ANOVAR, Howell 1992). The Huynh-Feldt adjustment for probability values (which corrects for the lack of compound symmetry of the covariance matrix, Howell 1992) was preferred over the Greenhouse-Geisser adjustment because it is considered to be more powerful and reliable (Myers and Well 1991, Howell 1992). The assumption of normality of scores within each sampling date was tested using the 'Probability Plot-Normal' option in SYSTAT 5.2.1 for Macintosh (Wilkinson et al. 1992), and it was satisfactory for all cases. Regarding the assumption of homogeneity of variance, the criterion of Howell (1992) was followed: if data distributions are symmetric, and if the largest variance is no more than four times the smallest, the analysis of variance is most likely to be valid. This was applicable to my data set. To graphically describe the temporal trend for the population parameters measured, monthly means were smoothed following the LOWESS algorithm (Cleveland 1979 in Wilkinson et al. 1992), which involves a locally weighted robust regression. This was done using SYSTAT 5.2.1, with a tension factor of 0.5.

Gametophyte : tetrasporophyte (G : T) ratio

From the moderate wave-exposure side (east) of Prasiola Point, 135 fronds were collected haphazardly on 29 April 1994 and on 20–21 May 1995 to characterize the studied population. To test for possible seasonal differences of the G : T ratio, frond sampling was repeated at the same site on 22 December 1995 (n = 105). To test for a possible effect of the degree of wave exposure on the G : T ratio, 100 fronds were haphazardly collected from the wave-exposed side (west) of Prasiola Point on 20 May 1995 and on 28 October 1995. To determine if the G : T ratio changes with elevation, fronds from the wave-exposed site were sampled from both the high zone (n = 50) and the low zone (n = 50) of the *M. cornucopiae* belt (about 1 m of difference in elevation). Fronds sampled from the high zone were part of thalli that covered most of the substratum. These fronds were collected more than 10 cm apart from one another to ensure as much as possible that they represented different genets (although the size of mature genets is still unknown for *M. cornucopiae*).

Fronds sampled from the low zone were in different clumps clearly separated from one another.

Collected fronds were air dried and kept until laboratory analyses were done at the University of British Columbia, in Vancouver. The reproductive phase for each frond was determined according to the resorcinol method (Garbary and DeWreede 1988). The accuracy of the resorcinol method for determining phases of *Mazzaella cornucopiae* depends on the experimental protocol used (Shaughnessy and DeWreede 1991). For my samples, frond fragments of about 0.5–1 mg of dry weight were placed in test tubes with 2 mL of the resorcinol reagent, then submerged for 2 min in a water bath at 70–75 °C, and immediately transferred to a cold bath. Solutions containing gametophytic material were dark red, while the ones containing tetrasporophytic material were light orange, pink, or transparent. For the few fronds for which the resorcinol test did not show clearcut results, colors were compared with the color obtained using reproductive fronds, for which the phase was known with certainty. The percentage of doubtful identifications using this protocol was 0–5% for the different groups of fronds analyzed.

Results

Population dynamics

Mazzaella cornucopiae was present continuously at Prasiola Point between June 1993 and July 1995. Percent cover, frond density, mean frond length, and stand biomass varied significantly among months: Huynh-Feldt-adjusted probability values for the separate ANOVARs done for these parameters (degrees of freedom = 13 for each ANOVAR) were $p = 0.004$ (F = 3.16) for percent cover, $p = 0.007$ (F = 3.40) for frond density, $p = 0.031$ (F = 2.04) for mean frond length, and $p < 0.001$ (F = 12.09) for stand biomass. These population parameters generally followed a seasonal trend, with maximum values between midspring and summer and minimum values in winter (Fig. 2). Unexpectedly, percent cover and mean frond length did not show an increasing trend during spring and summer of 1995. Monthly mean percent cover of thalli varied between 48.8 ± 11.7% and 80.2 ± 5.8% (mean ± SE, n = 6). Monthly mean frond density varied between 5.2 ± 0.8 fronds cm⁻² and 10.4 ± 1.5 fronds cm⁻². Monthly mean frond length varied between 0.7 ± 0.1 cm and 1.1 ± 0.1 cm. Monthly mean stand biomass varied between 15 ± 5 mg cm⁻² and 115 ± 15 mg cm⁻².

During autumn and winter, the entire fronds of *M. cornucopiae* were dark red. During spring and summer, only small fronds or the base of medium and large fronds that were in the understory of the algal mat were dark red, while the upper parts of medium and large fronds were yellow-green. During late spring and summer, the upper portions of most medium and large fronds became bleached. By the end
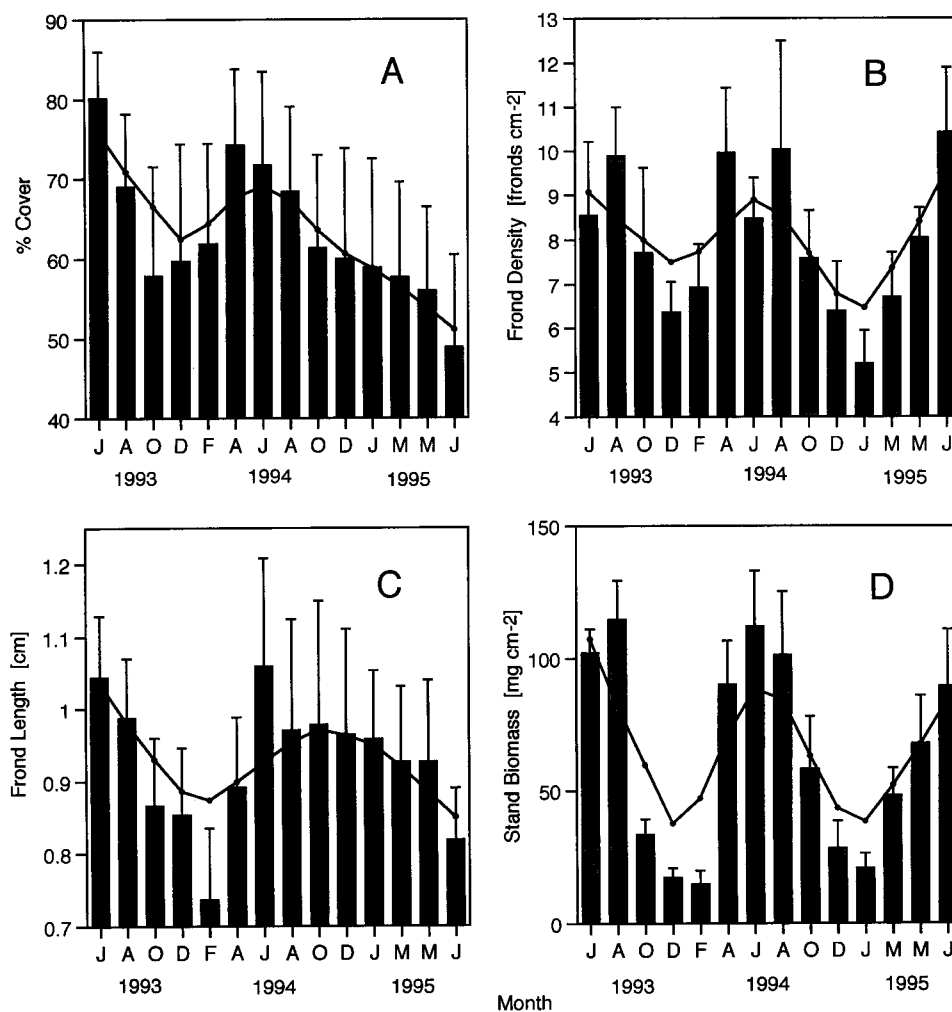
Fig. 2. (A) Temporal variation of percent cover (mean + SE, n = 6) of *Mazzaella cornucopiae* from Prasiola Point. (B) Temporal variation of frond density (fronds cm^{-2}, mean + SE, n = 6). (C) Temporal variation of frond length (cm, mean + SE, n = 6). (D) Temporal variation of stand biomass (mg cm^{-2}, mean + SE, n = 6). The functional relationships were calculated through the LOWESS algorithm.

of the summer, all of the bleached areas were completely lost, apparently mainly by a combination of herbivory by littorinid snails and wave action.

Reproductive fronds appeared during autumn and winter and were absent during spring and summer (Fig. 3). The few cystocarps observed during the spring of 1994 seemed empty or in poor condition, given their light color, and apparently they were remains of the previous reproductive season. Cystocarpic fronds were more abundant than tetrasporic fronds at all sampling dates, and cystocarps appeared before tetrasporangia for both reproductive seasons studied. Large fronds had more reproductive structures than small ones (Fig. 4). The functional relationships shown in Figure 4 were the ones that best fitted the data.

The accurate identification of thalli recruited from spores during the study period was not possible mainly due to their small size and, secondarily, by the presence of other organisms in the quadrats and the sometimes-difficult sampling conditions under rain
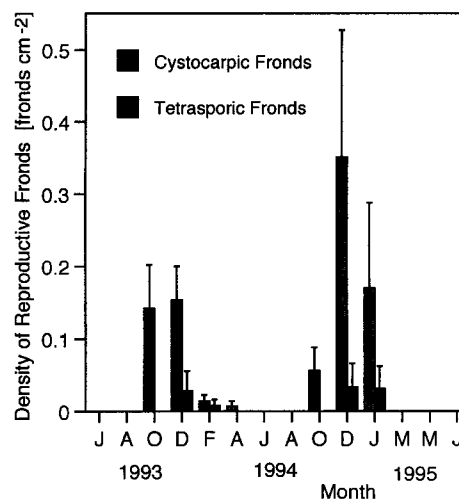

Fig. 3. Temporal variation of the density of reproductive fronds (fronds cm^{-2}, mean + SE, n = 6) of *Mazzaella cornucopiae* from Prasiola Point.
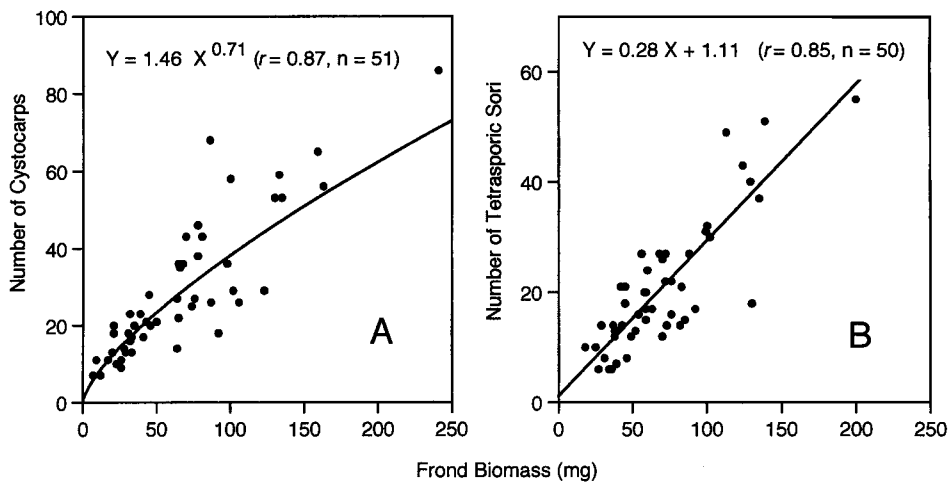
Fig. 4. (A) Number of cystocarps per frond of *Mazzaella cornucopiae* from Prasiola Point versus frond biomass (mg). (B) Number of tetrasporic sori per frond versus frond biomass (mg).

or snow at night. However, regular mapping of thalli showed that holdfasts detected in the first sampling date were mostly perennial and that they were the main source of total thallus cover relative to recruited thalli. Perennating holdfasts changed shape across time by vegetative growth of some areas and disappearance of others.

Gametophyte : tetrasporophyte (G : T) ratio

Gametophytic (vegetative) fronds of *Mazzaella cornucopiae* were more abundant than tetrasporophytic (vegetative) fronds at Prasiola Point regardless of site and season (Table I). At the moderate wave-exposure side (east) of Prasiola Point, the G : T ratio was similar between sampling dates. The G : T ratio varied more at the high wave-exposure site (west) between sampling dates, although this might be a result of

Table I. Relative abundance of gametophytic (G) and tetrasporophytic (T) vegetative fronds of *Mazzaella cornucopiae* in Prasiola Point, determined by the resorcinol method applied to frond samples.

Collection date	Site	% G-% T	G : T ratio	n
29 Apr 1994	E	77-23	3.3	135
20–21 May 1995	E	68-32	2.1	135
20 May 1995	W (all)	60-40	1.5	100
20 May 1995	W (high)	62-38	1.6	50
20 May 1995	W (low)	58-42	1.4	50
28 Oct 1995	W (all)	81-19	4.3	100
28 Oct 1995	W (high)	90-10	9.0	50
28 Oct 1995	W (low)	72-28	2.6	50
22 Dec 1995	E	72-28	2.6	105

The east (E) side of Prasiola Point is generally protected from large waves, whereas the west (W) side is generally exposed to strong wave action. 'Low' and 'high' refer to the low and the high zone of the *Mazzaella* belt, respectively, and 'all' represents both data sets combined.

poor replication there. The relative abundances of gametophytes and tetrasporophytes apparently changed with elevation at the wave-exposed site: the proportion of gametophytic fronds was higher at the high zone of the *M. cornucopiae* belt than at the low zone. During the reproductive season monitored at the wave-exposed site (October 1995), fertile gametophytic (cystocarpic) fronds were predominantly found at the high zone of the *M. cornucopiae* belt, whereas fertile tetrasporophytic (tetrasporic) fronds were mostly found at the low zone.

Discussion and Conclusions

Population dynamics

Holdfasts of *Mazzaella cornucopiae* from Prasiola Point were mostly perennial and produced fronds year-round between June 1993 and July 1995, as suggested by the continuous presence of small fronds (< 0.5 cm long). The rate of formation of new fronds was strongly seasonal, however; the strongest initiation occurred between early or mid-winter and late spring or early summer. As a result, maximum frond density occurred between mid-spring and mid-summer. The largest fronds (3–5 cm long) were most abundant during mid-spring, and stand biomass was highest in late spring and summer. Subsequently, the increase of mortality rates of fronds of all size-classes and the decrease of formation rates of new fronds resulted in the progressive decrease of frond density and stand biomass. Frond bleaching (Scrosati and DeWreede 1998), herbivory by littorinid snails (see Kim and DeWreede 1996 b), wave action, and natural senescence were likely factors that increased the mortality rates of fronds. Frond density and stand biomass reached their lowest values in early or mid-winter, after which the annual cycle of strongest frond initiation and growth resumed.

Percent cover and mean frond length for *M. cornucopiae* only alternated between high values in

spring—summer and low values in winter until the beginning of 1995. Both parameters did not increase during spring and summer of 1995, as the previous trend suggested. Fronds, however, grew in biomass during that period (Scrosati and DeWreede 1997) as for the equivalent period of 1994. Changes in frond biomass are a better descriptor of frond growth than changes in frond length, since length represents only one dimension, so the first half of the year can be adequately identified as the growth season for *M. cornucopiae*. With respect to percent cover, it was 23 ± 10% (mean ± SE) on the same six quadrats on 30 July 1996, which represented the lowest value for any of the summer seasons studied. The causes for this progressive decrease in cover are not clear. May 1995 and July 1996 were sunnier, dryer, and warmer compared with the same months of previous years. At the end of July 1996, bleaching of fronds was unusually strong and even many holdfasts were bleached, which was not seen in previous years. A simultaneous increase in desiccation, irradiance, and temperature (see Scrosati 1997, Scrosati and DeWreede 1998) may partially account for the high mortality rates observed between 1995 and 1996.

Seaweeds of the family Gigartinaceae mostly occur in cold and warm temperate waters of the world (Kim and Norris 1981, Hannach and Waaland 1986, Hommersand *et al.* 1993, 1994), where the abiotic environment is seasonal. The population dynamics of these algae also follow seasonal patterns, which are generally similar between species. For these species, the increase of frond density starts at some time between winter and spring. It occurs in the winter for *Mazzaella heterocarpa* (Postels *et* Ruprecht) Fredericq from Prasiola Point (R. Scrosati, pers. obs.), *Mazzaella splendens* (Setchell *et* Gardner) Fredericq from California [Hansen and Doyle 1976, as *Iridaea cordata* (Turner) Bory de Saint-Vincent] and from Barkley sound (Dyck *et al.* 1985, as *I. cordata*), and *Chondracanthus pectinatus* (Dawson) L. *et* R. Aguilar from the gulf of California (Pacheco-Ruiz *et al.* 1992, as *Gigartina pectinata* Dawson), in winter—spring for *Chondrus crispus* Stackhouse from New Hampshire (Mathieson and Burns 1975) and from Ireland (Pybus 1977), and in the spring for *Mazzaella laminarioides* (Bory de Saint-Vincent) Fredericq from southern Chile (Gómez and Westermeier 1991, as *Iridaea laminarioides* Bory de Saint-Vincent). For these and additional species of the Gigartinaceae, the highest frond density and the highest stand biomass occur in spring and/or summer, whereas their lowest values occur in winter (Hansen and Doyle 1976, Hansen 1981, Hannach and Santelices 1985, Poblete *et al.* 1985, McQuaid 1985, Santelices and Norambuena 1987, Westermeier *et al.* 1987, Mathieson 1989, Bolton and Joska 1993, Dyck and DeWreede 1995, Levitt *et al.* 1995). Fronds of some species are mostly annually deciduous, with large fronds being rare in winter, such as *Mazzaella splendens* (Norris and Kim 1972, Hansen 1977, Dyck *et al.* 1985, May 1986),

whereas other species have fronds year-round, such as *M. laminarioides* and *Chondrus crispus* (Santelices and Norambuena 1987, Westermeier *et al.* 1987, McLachlan *et al.* 1988).

Production of reproductive fronds

Spore release apparently occurred during autumn and winter for *Mazzaella cornucopiae* from Prasiola Point, since cystocarps and tetrasporic sori looked healthy (dark red) during that period. Why has this apparent strategy been selected for in *M. cornucopiae*? Spore release during autumn and winter may be advantageous compared with spring and summer. During autumn and winter, there is more free substratum as a result of the mortality of many algae and benthic animals whose biomass peaked during spring and summer (Kim and DeWreede 1996a), which should increase chances of settlement for spores (Kain and Norton 1990). Additionally, frond biomass is directly related to the number of reproductive structures in a frond, but frond size is inversely related to the degree of bleaching during spring and summer (Scrosati and DeWreede 1998). Therefore, most of the reproductive material could be killed if it was produced during spring and summer.

For species of the Gigartinaceae, the seasonality of the production of reproductive fronds does not follow a common pattern. Some species have cystocarpic and tetrasporic fronds year-round, with varying degrees of seasonality, such as *Mazzaella splendens* from California (Hansen and Doyle 1976, Hansen 1977, as *Iridaea cordata*), *M. laminarioides* from southern Chile (Westermeier *et al.* 1987), *Chondrus crispus* from Massachusetts (Prince and Kingsbury 1973), and *Gigartina skottsbergii* Setchell *et* Gardner from Argentina (Piriz 1996). Spore abundance and viability, however, may significantly vary throughout the year (Prince and Kingsbury 1973, Scrosati *et al.* 1994, Santelices and Martínez 1997). Other species or the above species from different habitats show a more marked seasonal production of reproductive fronds. For them, one or both kinds of reproductive fronds are absent in certain seasons, such as for *Chondrus crispus* from New Hampshire (Mathieson and Burns 1975) and from Ireland (Pybus 1977), *C. armatus* (Harvey) Okamura and *C. pinnulatus* (Harvey) Okamura from Japan (Brodie *et al.* 1997), and *Sarcothalia crispata* (Bory de Saint-Vincent) Leister from central Chile (Hannach and Santelices 1985, as *Iridaea ciliata* Kützing). For *Mazzaella laminarioides* from central Chile, fertile fronds were reported to be absent during certain seasons (Santelices and Norambuena 1987), but later resampling in the same area found fertile fronds year-round (Santelices and Martínez 1997).

Role of recruitment and holdfast perennation for population persistence

Perennating holdfasts of *Mazzaella cornucopiae* were the principal source of new fronds at Prasiola Point;

recruitment from spores contributed relatively very little. The perennial nature and extensive horizontal growth of holdfasts appear to be mechanisms that allow *M. cornucopiae* to be competitively dominant in the high intertidal zone (see also Kim 1995, Kim and DeWreede 1996 a). Recruitment from spores becomes relatively more important for population persistence when a strong disturbance (e. g. dislodgment of the surface layer of substratum, strong bleaching) completely removes holdfasts from a given area (Scrosati 1998). The importance of spores of *M. cornucopiae* as recolonizing agents depends on the size of the disturbance (Kim and DeWreede 1996a) and their role in recolonization is complemented by perennating holdfasts that may border the disturbed area (Scrosati 1998).

The high importance of holdfasts for population persistence is also observed for species of the Gigartinaceae from similar habitats such as *Mazzaella laminarioides* from Chile (Santelices and Norambuena 1987, Gómez and Westermeier 1991) and *Chondrus crispus* from Atlantic Canada (Bhattacharya 1985). Related species but from different habitats may show different strategies. For the low intertidal to shallow subtidal species *Mazzaella splendens* from Vancouver Harbour, British Columbia, matrix models that simulated its demography suggested that recruitment of thalli from spores is the major contributor to the production of fronds on an annual basis (Ang *et al.* 1990, as *Iridaea splendens*). Why does the proposed relative importance of spores of *M. splendens* for population maintenance differ from that of *M. cornucopiae*? Holdfasts of *M. splendens* are much smaller than those of *M. cornucopiae*. Therefore, a particular absolute decrease in holdfast area due to partial mortality is more likely to increase the probability of mortality for the entire holdfast of *M. splendens* than for one of *M. cornucopiae*. Then, spores would be expected to be more important for the population maintenance of *M. splendens* than for *M. cornucopiae*. For *M. splendens* from central California, though, the great majority of annually produced fronds were reported to derive from perennating thalli (Hansen and Doyle 1976, Hansen 1977). Causes for the differences between the observed pattern for central California and the predicted pattern for southern British Columbia are unknown, but is has to be noticed that we are comparing field observations for one area with model-based predictions for the other area.

Gametophyte : tetrasporophyte (G : T) ratio

Vegetative gametophytic fronds of *Mazzaella cornucopiae* were more numerous than vegetative tetrasporophytic fronds at Prasiola Point at all seasons and under different degrees of wave exposure. This coincides with the predominance of cystocarpic fronds over tetrasporic fronds observed during both repro-

ductive seasons. Studies based on the presence of reproductive fronds and/or resorcinol tests of field samples showed that the overall annual dominance of gametophytic fronds in populations of the Gigartinaceae is common, as found for *Mazzaella capensis* (J. Agardh) Fredericq, *M. laminarioides*, *M. splendens*, *Chondrus crispus*, *Gigartina skottsbergii*, and *Sarcothalia crispata* (Mathieson and Burns 1975, Hannach and Santelices 1985, Poblete *et al.* 1985, Santelices and Norambuena 1987, Luxoro and Santelices 1989, Bolton and Joska 1993, Dyck and DeWreede 1995, Piriz 1996). Studies based on resorcinol tests of fronds of *Chondrus crispus* collected between spring and autumn also showed a predominance of gametophytic fronds (Craigie and Pringle 1978, Bhattacharya 1985, Lazo *et al.* 1989, Scrosati *et al.* 1994, Lindgren and Åberg 1996).

To infer the G : T ratio at the genet level from the G : T ratio at the frond level, it is necessary to assume that fronds have been collected from separate genets. For *Mazzaella cornucopiae*, it was attempted to achieve this by collecting fronds separated from one another by, at least, 10 cm, when they were located in a same large stand, or that belonged to different clumps, spatially separated from one another. This problem may also occur for other species of the Gigartinaceae such as *M. laminarioides* and *Chondrus crispus* because of their similar growth habit (R. Scrosati, pers. obs.).

A number of hypotheses have been proposed to explain the frequent dominance of gametophytes in populations of the Gigartinaceae through ecological differences between both reproductive phases (Bhattacharya 1985, Hannach and Santelices 1985, May 1986, Lazo *et al.* 1989, Luxoro and Santelices 1989, Fernández and Menéndez 1991, González and Meneses 1996, Lindgren and Åberg 1996, Piriz 1996), under the not-always-explicit assumption that the G : T ratio should be 1 were both phases ecologically similar. However, demographic models based on potential spore output for each phase predict that the G : T ratio is generally higher than 1 even when both phases do not differ ecologically (Scrosati 1997). Nonetheless, the ecological differences that were indeed observed between gamegophytes and tetrasporophytes of some species of the Gigartinaceae would be important in determining the G : T ratio for a particular species at a given site.

Tetrasporophytes of some species of the Gigartinaceae may become the most abundant phase during certain seasons. This occurs during the winter for *Mazzaella splendens* from British Columbia (DeWreede and Green 1990, Dyck and DeWreede 1995), during the autumn for *M. capensis* from South Africa (Bolton and Joska 1993), and also possibly during the autumn for *Sarcothalia crispata* from central Chile (Hannach and Santelices 1985). The reversal of phase dominance may occur after longer periods in other cases. For example, tetrasporophytes

of *Mazzaella splendens* from California were the dominant phase mot of the year in 1972–73 (Hansen and Doyle 1976), but resampling in 1982–83 showed a high gametophytic dominance (Dyck *et al.* 1985). A seasonal reversal of phase dominance has not been observed for species such as *M. laminarioides* (Santelices and Norambuena 1987, Westermeier *et al.* 1987) and *Chondrus crispus* (Mathieson and Burns 1975). The also lack of a seasonal reversal of phase dominance for *Mazzaella cornucopiae* from Prasiola Point may be explained by the perennial nature of holdfasts. Once established in a mature community, it would take a catastrophic event (e. g. dislodgment of rocky substratum, strong bleaching) to remove the holdfasts and to open up space that could potentially lead to a different G : T ratio. However, the dominance of gametophytes at all sites studied within Prasiola Point suggests that a final dominance of tetrasporophytes is unlikely for this species.

Tetrasporophytes may also predominate over gametophytes depending on the degree of wave action. For *Mazzaella splendens* from Barkley Sound, tetrasporophytes, whose fronds are more resistant to hydrodynamic forces than gametophytic fronds, predominate in wave-exposed sites, whereas gametophytes predominate in more sheltered areas (Dyck *et al.* 1985, Phillips 1994, Shaughnessy *et al.* 1996). Such differential distribution of phases has not been detected for *M. cornucopiae* from Prasiola Point. The largest fronds of *M. cornucopiae* (up to 5 cm long) are much smaller than those of intertidal *M. splendens* (up to about 35 cm long) and are densely packed in extensive mats, unlike those of *M. splendens*. This confers a high resistance to detachment by waves to fronds of *M. cornucopiae* (Scrosati 1997). Therefore, even if both reproductive phases of *M. cornucopiae* differ in biomechanical properties, wave action would not be as important in shaping its G : T ratio as for *M. splendens*.

A differential distribution of gametophytes and tetrasporophytes occurs on a vertical gradient for some species of the Gigartinaceae such as *Chondrus crispus* and *Mazzaella laminarioides*. Gametophytes are relatively more abundant at the upper zone of their distribution, whereas tetrasporophytes are relatively more abundant at the lower zone. Differential resistances to desiccation or herbivory were suggested as causal factors, based on laboratory experiments (Mathieson and Burns 1975, Craigie and Pringle 1978, Hannach and Santelices 1985, Luxoro and Santelices 1989). For *Chondrus crispus*, however, additional surveys did not find unequivocal differences in distribution of phases depending on elevation or depth (Bhattacharya 1985, Lazo *et al.* 1989). For *Mazzaella cornucopiae* from the coast of Oregon, gametophytes and tetrasporophytes have a similar pattern of vertical distribution compared with Prasiola Point, and field experiments suggested that differential resistance to desiccation and grazing by lim-

pets between phases may explain this pattern for that size (Olson 1990).

Strategy of population persistence

The observations described in this paper and the additional ecological information about *Mazzaella cornucopiae* that appeared elsewhere (Kim 1995, Kim and DeWreede 1996 a, Kim 1997, Scrosati 1997, 1998, Scrosati and DeWreede 1997, 1998) enables us to have a picture of the strategy of persistence of this species. Both the abiotic environment (Scrosati 1997) and the high intertidal community (Kim and DeWreede 1996 a) change in a relatively predictable way through seasons at Prasiola Point. Disturbances that remove the surface layer of the rocky substratum are uncommon at the moderate wave-exposure side of Prasiola Point. In such a habitat, species whose main life-history traits fit relatively better to a K-strategy than to a r-strategy (MacArthur and Wilson 1967, Pianka 1982) are expected to be common. *Mazzaella cornucopiae* conforms to a K-strategy with respect to some important demographic characteristics:

(1) Thalli are dominant or frequent in the high intertidal community,

(2) their holdfasts are mostly perennial, so population size does not experience high interannual variations,

(3) reproduction is delayed after recruitment (it did not occur in almost any thallus recruited from spores during the first two years after experimental clearings, Scrosati 1997),

(4) thalli are iteroparous (several reproductive events through a life time, Cockburn 1991), although fronds are usually detached after reproduction, and

(5) recruitment from spores is a minor source of annual frond production.

(6) High levels of competition are expected for K-selected species (Pianka 1982), and *Mazzaella cornucopiae* is a strong competitor for substratum with the fucoid algae and other benthic organisms (Kim 1995, Kim and DeWreede 1996 a).

Finally, the strategy of population persistence of *Mazzaella cornucopiae* from Prasiola Point is similar to that shown by vascular clonal plants. Their population dynamics are mainly determined by birth and death rates of ramets, which are continuously produced by some form of vegetative propagation. For those populations, recruitment of new genets through seed germination is infrequent (Cook 1985, Hara 1994).

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