RAMET DYNAMICS FOR THE CLONAL SEAWEED *PTEROCLADIELLA CAPILLACEA* (RHODOPHYTA): A COMPARISON WITH *CHONDRUS CRISPUS* AND WITH *MAZZAELLA CORNUCOPIAE* (GIGARTINALES)¹

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Little is known about the dynamics and the ecological interactions among ramets (fronds) from populations of clonal red seaweeds. Small ramets are very difficult to tag, so their growth cannot be monitored directly. The temporal variation of the relationship between stand biomass and ramet density offers information on ramet performance. We calculated this relationship for an intertidal population of Pterocladiella capillacea (Gmelin) Santelices et Hommersand (Gelidiales) from Baja California, Mexico. Biomass and density were positively correlated on an annual basis, indicating that biomass accumulated without involving self-thinning among ramets. This contrasts with nonclonal seaweeds, for which self-thinning among individuals occurs during growth, but agrees with other clonal red seaweeds, such as Chondrus crispus Stackhouse and Mazzaella cornucopiae (Postels et Ruprecht) Hommersand (both Gigartinales). The growth pattern for these members of the Gelidiales and of the Gigartinales holds despite differences in holdfast morphology and ramet branching degree and despite differences in the capacity of coalescence during early stages, known only for the Gigartinales. The positive slope for the dynamic biomass-density relationship, on a bilogarithmic scale, was statistically steeper for M. cornucopiae than for P. capillacea and for C. crispus. This suggests that the addition of new ramets during the growth season may be relatively more beneficial for biomass accumulation rates for M. cornucopiae. This would be expected for high-intertidal species subjected to strong abiotic stress, for which ramet crowding constitutes a key protection. Pterocladiella capillacea occurs at the mid-intertidal zone and C. crispus at the subtidal zone, so ramets would be relatively less important in that respect.

Key index words: allometry; *Chondrus*; clonal; Gelidiales; Gigartinales; *Mazzaella*; population ecology; *Pterocladiella*; ramet; Rhodophyta

Clonal plants are those that vegetatively produce units that have the capacity for independent life if they are separated from the parent plant. The entire organism, when it develops from a single zygote, is referred to as the genet, whereas the potentially independent units are termed ramets (Harper 1977, de Kroon and van Groenendael 1997). Nonclonal plants do not produce ramets. To understand the ecology and the evolution of plant populations, it is frequently necessary to study their dynamics. For clonal plants, information on both genet and ramet dynamics is necessary, because both levels of organization contribute to define their ecological characteristics and evolutionary potential (Eriksson and Jerling 1990, Vuorisalo et al. 1997).

The dynamics of crowded populations of nonclonal plants is relatively well understood. The growth of individuals usually involves self-thinning in a size- and density-dependent manner (Westoby 1984, Weller 1987a, b). The dynamics of genets of clonal plants are much less understood, mainly because of the difficulty in identifying genets in the field, of the long lifespan of genets, and of the possible break-up of a genet into clonal fragments, each of which includes two or more ramets (Eriksson and Jerling 1990, Eriksson 1993). Due to their ease of identification and shorter lifespan, the dynamics of ramets has been more studied than the dynamics of genets (de Kroon 1993, Hara 1994). For herbaceous clonal plants with seasonal dynamics, ramets (shoots) generally do not undergo self-thinning during growth (Suzuki and Hutchings 1997). This was thought to apply to all kinds of clonal plants, but recent studies showed that the growth of longer lived woody clonal plants may actually involve self-thinning among ramets (Peterson and Jones 1997).

The dynamics of seaweeds have been less investigated than that of terrestrial plants. Individual thalli of nonclonal seaweeds, such as many kelps and fucoids (Phaeophyceae), do undergo self-thinning when they grow in crowded conditions (Black 1974, Chapman and Goudey 1983, Dean et al. 1989, Reed 1990, Ang and DeWreede 1992, Creed 1995, Flores-Moya et al. 1997, Creed et al. 1998). The dynamics of genets of clonal seaweeds, however, remain largely unknown. A few studies monitored the dynamics of genets of clonal red (Rhodophyta) seaweeds (May 1986, Dyck and DeWreede 1995, Scrosati 1998a) but only when genets could be easily identified due to their low densities. At high genet densities, the problems mentioned above for clonal terrestrial plants also apply, so size- and density-dependent growth patterns could not be studied.

The dynamics of ramets (fronds and their associated portion of holdfast) have been investigated in greater detail for clonal red seaweeds, although still for a low number of species. Even for the most crowded populations, the total biomass of stands of *Chondrus crispus* Stackhouse (Gigartinales, Gigartinaceae)

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from Prince Edward Island, Canada (Chopin et al. 1992), of *Gelidium sesquipedale* (Clemente) Bornet *et* Thuret (Gelidiales, Gelidiaceae) from Portugal (Santos 1995), and of *Mazzaella comucopiae* (Postels *et* Ruprecht) Hommersand (Gigartinales, Gigartinaceae) from British Columbia, Canada (Scrosati and DeWreede 1997) increased without involving self-thinning among ramets, actually involving an increase of ramet density. Ramet density decreased during fall and winter but simultaneously with stand biomass. Thus, the growth of ramets of these clonal seaweeds agrees better with that of seasonal clonal herbs than with that of woody clonal plants.

Three species represent, however, a small number to allow for generalizations for clonal red seaweeds. Additionally, *C. crispus, G. sesquipedale*, and *M. cornucopiae* are all from temperate habitats. We need to document ramet and biomass dynamics for more genera and for different habitats. *Pterocladiella capillacea* (Gmelin) Santelices *et* Hommersand (Gelidiales, Gelidiaceae) is one such example, because it occurs in subtropical waters from southern Baja California, Mexico. Our first objective is to examine ramet dynamics for *P. capillacea*, the hypothesis being that stand biomass increases without involving self-thinning among ramets.

Testing for self-thinning may be done by analyzing the temporal variation of the relationship between plant (or ramet) density and stand biomass (Weller 1987a), which can be referred to as the dynamic biomass-density relationship. Using mean plant (or ramet) biomass instead of stand biomass, as done frequently in the past, has some potential problems that may compromise the conclusions of analyses (Weller 1987a, Scrosati 1997). The magnitude and the sign of the slope of dynamic biomass-density relationships give information on the type and on the intensity of interactions among individuals (or ramets) during growth, suggesting ecological differences when slopes differ (Zeide 1985, Weller 1987a, b). We make the first comparison of dynamic biomass-density slopes for clonal red seaweeds, using data for P. capillacea, C. crispus, and M. cornucopiae, this constituting our second objective. Given that ramets of these species are morphologically distinct (Taylor and Chen 1973, Hommersand and Fredericq 1996, Santelices and Hommersand 1997, Scrosati and DeWreede 1997) and that morphology is related to biomass-density slopes for nonclonal terrestrial plants (Weller 1987b), the hypothesis is that biomassdensity slopes will differ between these clonal seaweeds. Data available on the temporal variation of biomass and of density for G. sesquipedale from Portugal do not describe its natural dynamics, because the studied population was subjected to commercial harvesting (Santos 1995). Therefore, its biomass-density relationship is not compared with that for the above seaweeds on a statistical basis.

MATERIALS AND METHODS

Dynamic biomass-density relationship for Pterocladiella capillacea. Stand biomass and ramet density for *P. capillacea* were periodically measured for an intertidal population from Lobos Point (23°25'N, 110°14'W), on the Pacific coast of southern Baja California, Mexico. The highest tidal amplitude is about 2 m at this site. *Pterocladiella capillacea* is the dominant species between about 30 cm and 150 cm above mean lower low water in vertical rocky walls directly exposed to waves, although its upper limit may be higher in some places due to the combined effects of topography and wave action. Water temperature in this area varied between 18° C (winter) and 29° C (summer) between March 1998 and March 1999 (R. Scrosati, unpublished data). The identification to the species level was done according to Stewart (1976). A recent taxonomic comparison based on *rbd*L gene sequences between samples of *P. capillacea* from Lobos Point and samples of *P. capillacea* from other sites of the world confirmed the taxonomic identity of the Lobos Point entity (D. W. Freshwater, Univ. of North Carolina, personal communication).

Sampling dates were 26 March 1998, 24 May 1998, 21 July 1998, 19 September 1998, 19 November 1998, and 18 January 1999. On each date, all algal biomass was collected during low tide from ten 25-cm² quadrats randomly distributed across a representative area of the population. In the laboratory, all algal material was submerged in seawater to enable it to rehydrate fully. Total wet biomass (to the nearest mg) was then determined. All ramets were counted for each quadrat. Dry biomass was used for statistical analyses rather than wet biomass. To estimate dry biomass, the total water content of ramets was determined for an independent set of 61 ramets collected randomly from the population during low tide on 1 January 1999. In the laboratory, those ramets were allowed to rehydrate completely in seawater, while still alive, after which they were placed under a lamp until water loss was complete, indicated by the lack of further variation of measured biomass. The total water content estimated was 70 \pm 1% (mean \pm SE), so values of wet biomass for each quadrat were multiplied by 0.3 to obtain dry biomass.

The annual dynamic biomass-density relationship was determined by plotting stand biomass against ramet density for all of the quadrats in a bilogarithmic scale. The strength of the linear association between \log_{10} (stand biomass) and \log_{10} (ramet density) was assessed with the Pearson correlation coefficient (r). Random sampling is a necessary condition to test for the significance of correlation coefficients (Howell 1992). For this study, each monthly group of 10 samples was collected at random, but sampling dates were separated by regular intervals of about 2 months. The significance of r was estimated through a randomization test with 1000 random permutations, because this test does not assume random sampling (Edgington 1987, Manly 1997). The functional relationship between biomass and density was calculated through principal components analysis, because both variables are random and subject to measurement error (Weller 1987a). A 95% confidence interval was calculated for the slope of the functional relationship (Sokal and Rohlf 1995). The randomization test was done with the Randomization Tests program for DOS, written by Eugene S. Edgington (University of Calgary, Canada). All of the other analyses were done with SYSTAT 5.2.1 for Macintosh (Wilkinson et al. 1992).

Dynamic biomass-density relationship for Chondrus crispus. Data on biomass and on density for *C. crispus* were obtained by Chopin et al. (1992) between May 1985 and April 1986 from a subtidal population off Rustico ($46^{\circ}30'$ N, $63^{\circ}19'$ W), Prince Edward Island, Canada. The other site monitored in their study, a subtidal population off Miminegash, Prince Edward Island, was subjected to commercial harvesting during the study, so its data are not analyzed here. For each month sampled, only mean stand dry biomass and mean ramet density were provided by Chopin et al. (1992), without indicating variability within months. Their quadrat size was 0.25 m^2 . Mean ramet density appears in their Table 1, whereas we estimated mean stand dry biomass from their Figure 4. The biomass-density relationship for *C. crispus* was calculated for the first time here; statistical analyses were done as for *P. capillacea*.

Dynamic biomass-density relationship for Mazzaella cornucopiae. Data on biomass and on density for *M. cornucopiae* were obtained between June 1993 and July 1995 from an intertidal pop-

ulation at Prasiola Point (48°49'N, 125°10'W), British Columbia, Canada. This is a cold-temperate site described in more detail in Scrosati (1998b). The methodology to estimate stand biomass and ramet density appeared in Scrosati and DeWreede (1997). For our study, dry biomass was used rather than the originally reported wet biomass, for which wet biomass was multiplied by 0.28 for every quadrat, because the average water content of ramets is 72% for this species (Scrosati and DeWreede 1998). For our study, the dynamic biomass-density relationship for M. cornucopiae was determined separately for the 2 years monitored. Scrosati and DeWreede (1997) pooled the data from both years and determined separate relationships for 7 permanent quadrats. Our approach excluded the effects of interannual variability on slopes and thus gave results comparable with those for *P. capillacea* and for *C. crispus*. In brief, each annual biomass-density relationship for M. cornucopiae included data obtained approximately every 2 months from seven 100-cm² permanent quadrats randomly placed across the population (Scrosati and DeWreede 1997). Statistical analyses were as for P. capillacea.

RESULTS

Dynamic biomass-density relationship for Pterocladiella capillacea. Thalli of P. capillacea were always present at Lobos Point between March 1998 and March 1999 (only a visual inspection was done in March 1999). Stand dry biomass and ramet density were generally higher in May and July and lower in other months (Fig. 1). Monthly means of stand dry biomass ranged between 21.6 \pm 4.0 mg·cm⁻² (mean \pm SE; n = 10) in November and 53.9 \pm 6.8 mg·cm⁻² in July, with a highest absolute value of 86 mg·cm⁻². Monthly means of ramet density ranged between 6.9 ± 1.2 ramets cm⁻² in November and 15.8 ± 1.4 ramets \cdot cm⁻² in May, with a highest absolute value of 22 ramets cm⁻². Logarithmically transformed values of stand biomass were positively correlated to equivalent values of ramet density (r =0.74, P = 0.001, n = 56; Fig. 1). In Figure 1, stand biomass was expressed in g·m⁻² and ramet density in ramets m⁻² to allow for direct comparisons with studies on terrestrial plants and on other seaweeds. Only one quadrat contained no biomass during the study period. Three outliers, identified with boxplots (Howell 1992), were excluded from the analysis. The positive relationship between biomass and density indicates that self-thinning did not occur among ramets of P. capillacea. The functional relationship between stand dry biomass (B) and ramet density (N) was

$$\log_{10}B = 0.68\log_{10}N - 0.91\tag{1}$$

and 95% confidence limits for the slope were 0.52 and 0.86.

Dynamic biomass-density relationship for Chondrus crispus. Chondrus crispus was always present at the subtidal site off Rustico between May 1985 and April 1986 (Chopin et al. 1992). Stand dry biomass and ramet density were generally higher in spring and summer and lower in fall and winter (Fig. 2). Monthly means of stand dry biomass oscillated between 12 mg·cm⁻² (April 1986) and 26 mg·cm⁻² (July 1985). Monthly means of ramet density oscillated between 0.13 ramets·cm⁻² (January 1986) and 0.31 ramets·cm⁻² (September 1985). Data variability within months was



FIG. 1. Temporal variation of the relationship between \log_{10} (stand dry biomass) and \log_{10} (ramet density) for *Pterocladiella capillacea* from western Mexico between March 1998 and January 1999. Each data point represents one sampled quadrat. The functional relationship was calculated through principal components analysis.

not indicated by Chopin et al. (1992). Logarithmically transformed values of mean stand biomass were positively correlated to equivalent values of mean ramet density (r = 0.85, P = 0.007, n = 8; Fig. 2). The functional relationship between stand dry biomass and ramet density was

$$\log_{10}B = 0.75\log_{10}N - 0.20 \tag{2}$$

and 95% confidence limits for the slope were 0.37 and 1.34.

Dynamic biomass-density relationship for Mazzaella cornucopiae. Mazzaella cornucopiae was always present at Prasiola Point between June 1993 and July 1995. Stand dry biomass and ramet density were generally higher in spring and summer and lower in fall and winter (Figs. 3 and 4). Monthly means of stand dry biomass ranged between $3.8 \pm 1.3 \text{ mg} \cdot \text{cm}^{-2}$ (mean $\pm \text{SE}$; n =7) in February 1994 and $31.5 \pm 3.5 \text{ mg} \cdot \text{cm}^{-2}$ in August 1993, with a highest absolute value of 57.5 mg·cm⁻². Monthly means of ramet density ranged between 5.1 \pm 0.7 ramets cm⁻² in January 1995 and 10.5 \pm 1.2 ramets \cdot cm⁻² in July 1995, with a highest absolute value of 21 ramets cm⁻². Logarithmically transformed values of stand biomass were positively correlated to equivalent values of ramet density between June 1993 and June 1994 (r = 0.39, P = 0.005, n = 49; Fig. 3) and between August 1994 and July 1995 (r = 0.49, P <0.001, n = 49; Fig. 4). The annual relationship between stand dry biomass and ramet density was

$$\log_{10}B = 7.38\log_{10}N - 33.99\tag{3}$$

for 1993–1994 (with 4.36 and 22.64 as 95% confidence limits for the slope), and

$$\log_{10}B = 4.76 \log_{10}N - 21.10 \tag{4}$$



FIG. 2. Temporal variation of the relationship between \log_{10} (stand dry biomass) and \log_{10} (ramet density) for *Chondrus crispus* from eastern Canada between May 1985 and April 1986. Each data point represents a monthly mean for replicate quadrats. The functional relationship was calculated through principal components analysis.

for 1994–1995 (with 3.11 and 9.69 as 95% confidence limits for the slope).

DISCUSSION

Dynamic biomass-density relationship for Pterocladiella capillacea. Pterocladiella capillacea is the fourth clonal red seaweed, after C. crispus (Chopin et al. 1992), G. sesquipedale (Santos 1995), and M. connucopiae (Scrosati and DeWreede 1997), for which stand biomass was found to increase without involving self-thinning among ramets. Moreover, these four species showed a positive dynamic biomass-density relationship throughout the year, with the highest values observed generally in spring and summer and the lowest in fall and winter. Thus, this growth pattern could be characteristic of clonal red seaweeds that may include, at least, members of the Gelidiaceae and of the Gigartinaceae.

It is important to note that this growth pattern holds despite important morphological differences between the species. Both *G. sesquipedale* and *P. capillacea* (Gelidiaceae) have stoloniferous holdfasts and thin highly branched ramets (Dixon 1958, Hommersand and Fredericq 1996, Santelices and Hommersand 1997). Instead, *C. crispus* and *M. cornucopiae* have crustose holdfasts and usually less-branched broader ramets. The largest ramets of *M. cornucopiae* may be divided into a few apical lobes (Scrosati and DeWreede 1997), whereas medium-sized and large ramets of *C. crispus* usually have more lobes, which can vary greatly in width and in the degree of branching (Taylor and Chen 1973).

Another difference between the Gelidiaceae and the Gigartinaceae is the capacity of sporelings to coalesce during early development, which appears to occur only for members of the Gigartinaceae (Santelices et al. 1999). This difference, however, does not result



FIG. 3. Temporal variation of the relationship between \log_{10} (stand dry biomass) and \log_{10} (ramet density) for *Mazzaella cornucopiae* from western Canada between June 1993 and June 1994. Each data point represents one sampled quadrat. The functional relationship was calculated through principal components analysis.

in major differences in growth patterns for ramets from mature stands, as shown here.

For *C. crispus* from Ireland and for a member of the Phyllophoraceae (Gigartinales), *Mastocarpus stellatus* (Stackhouse) Guiry, also from Ireland, a positive relationship between stand biomass and ramet density was also found, but in a static context, because data were collected for different stands that were not monitored repeatedly (Pybus 1977). Biomass and density were also measured for *Mazzaella laminarioides* (Bory de Saint-Vincent) Fredericq from Chile (Martínez and Santelices 1992), but also in a static context. There-



FIG. 4. Temporal variation of the relationship between \log_{10} (stand dry biomass) and \log_{10} (ramet density) for *Mazzaella cornucopiae* from western Canada between August 1994 and July 1995. Each data point represents one sampled quadrat. The functional relationship was calculated through principal components analysis.

fore, the dynamic biomass-density relationships for *Mastocarpus stellatus*, for *Mazzaella laminarioides*, and for this Irish population of *C. crispus* remain unknown because dynamic relationships cannot be inferred from static ones directly (Weller 1989).

The dynamics of ramets of C. crispus, G. sesquipedale, M. cornucopiae, and P. capillacea is similar to that of shoots of clonal perennial herbs (Suzuki and Hutchings 1997) and of some clonal aquatic ferns (Room and Julien 1994) in that they generally do not undergo self-thinning during the growth season. The production of new shoots while stand biomass increases is also common among these clonal vascular plants (Hutchings 1979, Mook and van der Toorn 1982, Room and Julien 1994). Negative relationships were observed, however, between mean ramet biomass and ramet density for a few herbs for some time intervals (Hutchings 1979), but not all of the existing ramets were considered in his analyses. Additionally, for negative relationships, increases of mean ramet biomass may erroneously indicate that ramets are growing when they may not, the use of stand biomass being a better alternative (Weller 1987a, Scrosati 1997). The negative relationships between mean ramet biomass and ramet density reported for ramets of an additional herb for some time intervals (Kays and Harper 1974) were accompanied by the mortality of genets. The number of ramets per genet actually increased during that time. Thus it is not possible to assess whether the overall decrease of ramet density resulted from their direct interaction or simply from genet mortality. Negative relationships between stand biomass and ramet density were reported for the herb Phragmites australis (Cav.) Trin. ex Steudel (Poaceae), but only late in its growth season (Mook and van der Toorn 1982), unlike for nonclonal plants and woody clonal plants, for which selfthinning is a dominant process during growth (Peterson and Jones 1997, Suzuki and Hutchings 1997).

What can explain the lack of self-thinning among ramets of clonal red seaweeds? Research on the better-studied clonal herbs suggests possibilities, although the causes for the general lack of shoot self-thinning are not clear even for them (Westoby 1984, de Kroon 1993, de Kroon and Kalliola 1995, Suzuki and Hutchings 1997). The physical connection among ramets allows for the exchange of photoassimilates, nutrients, and other substances among ramets (Alpert and Stuefer 1997, Jónsdóttir and Watson 1997). The translocation of photoassimilates from large to small shaded ramets would prevent the mortality of small ramets, but the generality of this hypothesis was later questioned based on experimental data (de Kroon 1993). Translocation of assimilates was recently demonstrated for Gracilaria cornea J. Agardh (Gracilariales, Gracilariaceae; Gonen et al. 1996), which supports the applicability of the above hypothesis for clonal red seaweeds. More research is evidently needed here. The synchronization of ramet growth during spring was also proposed to result in the lack of ramet selfthinning for seasonal species (de Kroon 1993), but

this has been recently questioned too (Suzuki and Hutchings 1997). Considering that each plant population has its own hypothetical self-thinning line, related to morphological variables (Weller 1987b, Osawa and Allen 1993), a third proposed explanation is that ramet growth would be regulated in seasonal species so that these hypothetical self-thinning lines are not reached at the end of the growth season, when senescence occurs (Westoby 1984, de Kroon 1993, de Kroon and Kalliola 1995). This hypothesis also remains unproven for clonal plants in general.

A fourth proposed explanation is the negative density-dependent production of new ramets, which would prevent an overproduction of ramets (de Kroon 1993). This may also apply to clonal red seaweeds, because a negative density-dependent production of new ramets occurs for *M. cornucopiae* (Scrosati and DeWreede 1997). Whether this regulation responds to internal or external factors is unclear (Suzuki and Hutchings 1997). A fifth proposed explanation is that the asymmetrical competition between large and small ramets would be moderated by the resources that the perennating structures of genets store during the unfavorable season and allocate later to new ramets (de Kroon 1993, Suzuki and Hutchings 1997). Holdfasts of perennial clonal red seaweeds, whether crustose (e.g. Gigartinales) or stoloniferous (e.g. Gelidiales), are generally thin and unlikely to store much energetic reserve. The potential role of resource allocation by these holdfasts to the production of new ramets also needs to be investigated. A sixth possible explanation for the lack of ramet self-thinning for clonal seaweeds involves the possible acclimation of the smallest ramets to the low understory irradiance (Scrosati and DeWreede 1997). The scarce evidence that exists for clonal red seaweeds, however, is contradictory, because the small ramets appear to be severely light limited for some species but not for others (Scrosati 2000).

Comparison of dynamic biomass-density relationships between Pterocladiella capillacea, Chondrus crispus, and Mazzaella cornucopiae. For *M. cornucopiae*, slopes describing the joint variation of stand biomass and of ramet density for 1993–1994 (7.38) and for 1994–1995 (4.76) do not differ statistically, as indicated by the overlap of their confidence intervals. The relatively high variability of data resulted in relatively large confidence intervals. This inability to detect interannual differences for the slope of the dynamic biomass-density relationship adds to the lack of statistical differences among the slopes for the 7 permanent quadrats sampled, although data variability was important for each quadrat too (Scrosati and DeWreede 1997). Data variability, therefore, is a problem for detecting differences among biomassdensity slopes at spatial and temporal scales for M. cornucopiae from Prasiola Point.

The slope of the dynamic biomass-density relationship for *P. capillacea* from Lobos Point (0.68) is statistically indistinguishable from the slope for *C. crispus* from the subtidal site off Rustico (0.75) because confidence intervals for the slopes overlapped. Both slopes were, however, statistically different from the two annual slopes determined here for *M. cornucopiae*, indicated by the lack of overlap between confidence intervals. What does this difference in slopes suggest about the possible effects that the increase of ramet density has on biomass accumulation for each species? These effects cannot be assessed by manipulating ramet densities and measuring their resulting growth rates. The small ramets (of a few milligrams) are impossible to tag without damaging or removing them, so their size cannot be monitored through time. This is particularly true for intertidal sites where wave action is strong, such as Prasiola Point and Lobos Point.

The slopes indicate that stand biomass increased more for *M. cornucopiae* than for *P. capillacea* and for *C.* crispus for every new ramet produced by holdfasts. Moreover, given the bilogarithmic nature of graphs, slopes also indicate that the increment of stand biomass per ramet produced increased as ramet density increased for M. cornucopiae but that it decreased for P. capillacea and for C. crispus. Are there biological differences between these species that could explain this difference in growth? This is difficult to assess because these species occur in different geographical areas and were sampled in different years, so slope differences could result from habitat or time differences in addition to possible biological differences. However, a few hypotheses can be made based on a morphological comparison.

Strong desiccation and irradiance during low tides are stressful factors that may negatively affect the growth and the survival of intertidal seaweeds (Lobban and Harrison 1994, Davison and Pearson 1996). For M. cornucopiae, laboratory experiments done under strong desiccation and irradiance, simulating conditions for experimentally thinned stands (which do not occur in nature), suggested that low ramet densities are associated with negative net photosynthetic rates for long periods during low tides, unlike natural ramet densities (Scrosati and DeWreede 1998). This suggests that growth would be relatively limited at low ramet densities. Although the daily carbon balance has not been determined for thinned and for natural stands of M. cornucopiae, field experiments indicated that strong desiccation and irradiance result in the loss of photosynthetic pigments (bleaching) after 2 months between spring and summer (Scrosati and DeWreede 1998), indicating that growth is effectively limited at low ramet densities.

Ramets of *P. capillacea* are highly branched and their axes and branches are thin (Hommersand and Fredericq 1996, Santelices and Hommersand 1997), whereas ramets of *M. cornucopiae* are unbranched and relatively broad (Scrosati and DeWreede 1997). A hypothesis to explain the difference in biomass–density slopes between *P. capillacea* and *M. cornucopiae* is that each new growing ramet of *M. cornucopiae* would confer a higher capacity of holding moisture during low tides to thalli of this species than equivalent ramets of *P. capillacea* to their own thalli, because of the differences in ramet morphology. As ramets of M. cornucopiae grow and get broader, this protecting effect would increase progressively more than for P. capilla*cea.* The protective effects of the production and growth of new ramets against irradiance stress during low tides would differ similarly between both species. Thus, through a faster decreasing degree of abiotic stress as ramet density increases for *M. cornucopiae*, the average growth rate of ramets would increase faster than for P. capillacea under the same increase of ramet density. This would result in a steeper slope of the biomass-density relationship. To test this hypothesis, field manipulations of desiccation and of understory irradiance and measurements of growth rates should be done. Again, the growth rate of small ramets has been impossible to measure in the field. A reliable technique to determine field growth rates of small ramets is therefore needed.

Besides morphological differences, physical factors may also explain the difference in biomass-density slopes, such as elevation on the shore. Pterocladiella capillacea roughly occupies the mid-50% of the intertidal zone at Lobos Point (see Materials and Methods), but *M. cornucopiae* occurs in the uppermost 25% of the intertidal zone at Prasiola Point (Scrosati 1998b). The time during which an intertidal seaweed is exposed to the air increases as its elevation on the shore increases (Swinbanks 1982). The highest degree of desiccation (at the end of a low tide) could not be determined for ramets of P. capillacea, as safe access to the site is restricted only to a narrow period during the lowest tides. However, our observations suggest that ramets of P. capillacea from Lobos Point desiccate less than those of M. cornucopiae (43% of water loss in spring) (Scrosati and DeWreede 1998) during low tides. Adding new ramets to the thallus would bring more benefits at sites where desiccation is stronger, resulting in a steeper biomass-density slope, which was found for M. cornucopiae. Desiccation of ramets does not occur for the population of C. crispus sampled by Chopin et al. (1992) because it is subtidal, so its biomass-density slope would be shallower than for intertidal seaweeds, based on the above. This was true when compared with M. cornucopiae but not when compared with P. capillacea. Determining field desiccation rates for intertidal *P. capillacea* should help to test the above hypothesis.

To define inter- and intraspecific biomass-density trends for clonal red seaweeds, more species and more habitats should be investigated. It will be interesting to model the slope of the dynamic biomassdensity relationship in relation to allometric measurements of ramet geometry (as Weller, 1987b, did for nonclonal terrestrial plants) and in relation to habitat characteristics. To accomplish this, biomass-density slopes, the morphometry of ramets, and habitat characteristics should be quantified for several species of clonal red seaweeds, because theoretical models need to be tested using several examples (Weller 1987b). For interspecific biomass-density trends, phylogenetic relationships between species should be taken into account when doing the analyses (Harvey 2000).

Finally, it is interesting to note that despite displaying a similar ramet dynamics, the three species analyzed here showed different reproductive dynamics. Both the Gelidiaceae and the Gigartinaceae have the same type of life history (van den Hoek et al. 1995), including the alternation of isomorphic gametophytes and tetrasporophytes (Akatsuka 1986, Santelices 1988, Hommersand et al. 1999). However, the reproductive phenology depended on the species. Chondrus crispus off Rustico displayed reproductive ramets year-round (Chopin et al. 1988), but M. cornucopiae from Prasiola Point displayed reproductive ramets only in fall and in winter (Scrosati 1998b). Gametophytic ramets predominated over tetrasporophytic ramets for both species (Chopin et al. 1988, McLachlan et al. 1988, Lazo et al. 1989, Scrosati 1998b). Pterocladiella capillacea from Lobos Point showed reproductive ramets year-round, but the population was always dominated by fertile tetrasporophytic ramets; a few fertile gametophytic ramets appeared only in January 1999 (E. Servière-Zaragoza, unpublished data). These patterns of phase dominance agree with what is generally observed for species of the Gelidiaceae (Akatsuka 1986, Santelices 1988) and of the Gigartinaceae (Scrosati and DeWreede 1999). This suggests that the clonal habit and reproductive traits followed separate evolutionary paths. The main factors that drive the evolutionary change of vegetative phenology and of reproductive phenology of clonal plants in general are not clear and are subject to both theoretical and empirical research (Grace 1993, McLellan et al. 1997). This is particularly true for clonal red seaweeds (Hughes and Otto 1999, Scrosati and DeWreede 1999), which points out the importance of comparative studies such as this one.

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