Dynamics of the biomass–density relationship and frond biomass inequality for *Mazzaella cornucopiae* (Gigartinaceae, Rhodophyta): implications for the understanding of frond interactions

RICARDO SCROSATI* AND ROBERT E. DEWREEDE

*The University of British Columbia, Department of Botany,
Vancouver, BC V6T 1Z4, Canada*

This paper examines the interactions of fronds of the clonal red alga *Mazzaella cornucopiae* (Postels et Ruprecht) Hommersand. An analysis of the temporal variation of the relationship between stand biomass and frond density showed that the variables are positively correlated on an annual basis for the population studied at British Columbia, Canada. This indicates that fronds (ramets) do not undergo self-thinning even at the highest natural densities. Two of the hypotheses originally proposed to explain the lack of self-thinning among ramets of terrestrial clonal plants seem to apply also to this clonal alga, e.g. physiological integration among ramets and density-dependent formation of ramets. However, the 'ultimate biomass–density line' hypothesis does not, because biomass–density combinations for *M. cornucopiae* are higher than values predicted by this hypothesis for a given density, and these are thought to constrain biomass–density combinations for the entire plant kingdom. During the growth season for *M. cornucopiae*, frond biomass inequality decreases as fronds grow in biomass. This suggests that the growth rate of fronds is negatively related to frond size. Frond competition most likely results from the vertical gradient of irradiance within the algal stand, but competition among fronds appears to be symmetric, as opposed to asymmetric competition among nonclonal plants. The generality of our findings for clonal red algae is discussed, and comparisons with terrestrial clonal and nonclonal plants are made.

INTRODUCTION

Clonal algae are those whose individual thalli are composed of several fronds that can potentially survive on their own. When separated from the parent thallus, a frond of a clonal alga can regenerate into a new thallus if the frond remains attached to the substratum by a portion of holdfast. Fronds of clonal algae are referred to as ramets, whereas the thallus that is generated by a single spore is referred to as a genet, terms that were originally used for terrestrial clonal plants (Jackson *et al.* 1985). Within the Rhodophyta, common examples of clonal algae are species of the genera *Mazzaella* and *Chondrus* (Gigartinaceae), *Mastocarpus* (Petrocelidaceae), *Gracilaria* (Gracilariaceae), and *Gelidium* (Gelidiaceae).

Little is known about the dynamics of genets of clonal plants in general, mainly because of the difficulty in accurately identifying genets as a result of the spatial intermingling of ramets from different genets, a problem that still persists (Eriksson 1993). Conversely, the dynamics of ramets has been more commonly investigated, but the dynamics of genets of nonclonal plants is the topic that has received the greatest attention (de Kroon 1993; Hara 1994). Ramets of clonal plants have fundamentally different growth dynamics compared with those of genets of nonclonal plants. When even-aged, nonclonal plants are actively growing in crowded

conditions in monospecific stands, the smallest plants progressively die in a density-dependent fashion as a result of increased crowding due to biomass accumulation; this is known as self-thinning (Yoda *et al.* 1963; Weller 1987; Weiner 1988). Ramets of clonal vascular plants from seasonal habitats do not undergo self-thinning during growth and this difference with respect to nonclonal plants is related to the physiological integration that exists among ramets (Hutchings 1979; Pitelka 1984; Dickerman & Wetzel 1985; Lapham & Drennan 1987; Room & Julien 1994; de Kroon & Kalliola 1995).

Individual thalli (genets) of nonclonal algae also undergo self-thinning once crowded conditions are reached (Black 1974; Dean *et al.* 1989; Reed 1990; Ang & DeWreede 1992; Creed 1995; Flores-Moya *et al.* 1996). The few clonal algae for which the possible occurrence of self-thinning among fronds (ramets) has been investigated are *Mazzaella laminarioides* (Bory de Saint-Vincent) Fredericq from Chile (Martínez & Santelices 1992, as *Iridaea laminarioides*) and *Gelidium sesquipedale* (Clemente) Bornet et Thuret from Portugal (Santos 1995). Like clonal vascular plants, fronds of these algae did not undergo self-thinning at natural densities.

For *Mazzaella cornucopiae* (Postels et Ruprecht) Hommersand (Fig. 1), which occurs on coasts of the north Pacific Ocean (Abbott 1971; Hommersand *et al.* 1993; Selivanova & Zhigadlova 1997), fronds were also reported not to undergo self-thinning at natural densities (Scrosati 1996). Evidence of the lack of frond self-thinning was provided by the dynamic relationship between stand biomass and frond density (i.e.
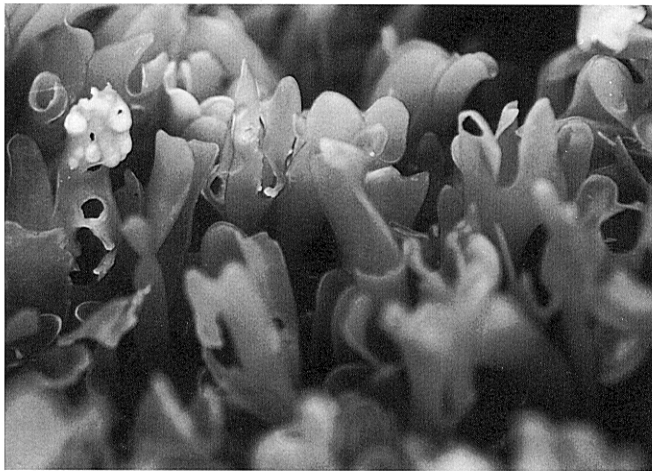
Fig. 1. Stand of *Mazzaella cornucopiae* from the high intertidal zone of Prasiola Point. The largest fronds are between 4 and 5 cm long.

both variables being repeatedly measured for the same experimental plots) calculated for one year (Scrosati 1996). The dynamic biomass–density relationship did not show a consistent pattern throughout the studied population: a positive linear relationship was found for four experimental quadrats, but no significant relationship was found for three other quadrats. We predicted that stand biomass and frond density would be positively related for the entire population once data from additional sampling dates were considered (Scrosati 1996). The first objective of this paper is to discuss the dynamic relationship of stand biomass with frond density for *M. cornucopiae* based on analysis of data collected during 2 yr using an improved estimation of stand biomass.

Our second objective is to experimentally examine the viability of two of the hypotheses that were originally proposed to explain the lack of ramet self-thinning for terrestrial clonal plants: the density-dependent formation of ramets and the 'ultimate biomass–density line' hypothesis. A density-dependent formation of ramets during the growth season is thought to prevent an overproduction of ramets that would otherwise cause self-thinning (de Kroon & Kwant 1991; de Kroon 1993). With respect to the second hypothesis, the originally named 'ultimate thinning line' describes the maximum mean biomass of individual plants that is possible for any plant density, and it is thought to constrain all plant populations, even those that do not undergo self-thinning (Weller 1989). Because it is a static constraint, the name 'thinning' originally given to this line does not describe accurately its meaning (Weller 1989). This line is the upper boundary of the interspecific biomass–density 'band', which includes all of the biomass–density pairs used to calculate self-thinning lines for different terrestrial plants, and its slope is negative (Weller 1989). It has been suggested that the highest mean biomass of ramets of clonal plants with seasonal behavior is attained when mean ramet biomass reaches this 'ultimate biomass–density line' for a given ramet density, usually at the end of the growth season. Ramets would almost stop growing at this stage, simultaneously with the occurrence of sexual reproduction and senescence. Self-thinning among ramets is thought to be prevented because mean ramet biomass would not increase more than the static constraint determined by the ultimate bio-

mass–density line for a given density (Westoby 1984; de Kroon 1993; de Kroon & Kalliola 1995). The ultimate biomass–density line for terrestrial plants is thought to be approximately $Y = -1.5X + 5.0$, where $Y = \log_{10}$(mean plant biomass) and $X = \log_{10}$(plant density) (White 1985; Weller 1989). Combinations between mean frond biomass and frond density for *M. cornucopiae* will be compared with this hypothetical line to determine if the constraint in biomass for a given density applies to this clonal alga.

An increase of frond crowding, which occurs between winter and late spring or summer for *M. cornucopiae* (Scrosati 1997a), is likely to result in competition among fronds because of the decreasing irradiance below the canopy and, possibly, because of a reduction in nutrient circulation rates among fronds. However, because frond crowding does not result in frond self-thinning for clonal red algae (Martínez & Santelices 1992; Santos 1995; Scrosati 1996), the mode of competition among fronds should differ from that among nonclonal plants for which self-thinning does occur as a result of crowding. The dynamics of the inequality (= hierarchy or variability) of a given size parameter (e.g. biomass or length) as related to changes of plant density and size offers information about the kind of competition that growing plants undergo (Weiner & Solbrig 1984; Hara 1988; Weiner 1988; Bendel *et al.* 1989). Two measures of size inequality are the coefficient of variation and the Gini coefficient. Both coefficients have advantages and disadvantages, but they are highly correlated (Weiner 1988; Knox *et al.* 1989). The third objective of this paper is to analyze the dynamics of the inequality of frond biomass for *Mazzaella cornucopiae* during the growth season and to discuss its implications for the understanding of the competitive interactions among fronds. This will enable us to compare what is known about competition among fronds of clonal red algae (Martínez & Santelices 1992; Santos 1995; this study) with competition models for ramets of terrestrial clonal plants and nonclonal plants.

MATERIALS AND METHODS

Study site and basic description of *Mazzaella cornucopiae*

Measurements done on *Mazzaella cornucopiae* were taken from a population at Prasiola Point (48°49′N, 125°10′W), which is located in Barkley Sound, on the west coast of Vancouver Island, British Columbia, Canada. This coast is washed by the cold-temperate waters of the northeast Pacific ocean. At the high intertidal zone of Prasiola Point, *M. cornucopiae* occurs along a discontinuous belt between 3 and 4 m above lowest normal tide (based on Canadian Chart Datum). Thalli of *M. cornucopiae* may cover large areas of the rocky substratum. Individual genets are almost impossible to identify by visual inspection due to high frond densities (Fig. 1), possible coalescence of growing sporelings, and the potential breakage of one thallus into two or more independent entities (clonal fragments). Holdfasts are crustose, thin, and mostly perennial. They produce foliose fronds year-round, but at higher rates between midwinter and late spring or summer. The contribution of spores to the annual production of fronds is less than 3% (Scrosati 1997a).

Table 1. Functional relationships between frond wet biomass (B, g) and frond length (L, cm) for *Mazzaella cornucopiae* from Prasiola Point.

Date	Function	r^2	n
29 Apr 1994	$B = 0.011L^{1.698}$	0.86	167
5 Dec 1994	$B = 0.004L^{2.813}$	0.92	162
30 Jan 1995	$B = 0.004L^{2.728}$	0.92	168
3 Apr 1995	$B = 0.008L^{1.977}$	0.93	172
21 May 1995	$B = 0.009L^{1.948}$	0.89	164
14 Jul 1995	$B = 0.012L^{1.848}$	0.94	180
28 Oct 1995	$B = 0.007L^{2.569}$	0.91	118

Table 2. Dates for which the relationship between frond wet biomass and frond length was determined (Determination date) and dates of samples of frond density and mean frond length to which these relationships were applied to estimate stand biomass (Application date).

Determination date	Application date
29 Apr 94	26–28 Apr 1994
5 Dec 94	10–12 Dec 1993, 2–4 Dec 1994
30 Jan 95	24–26 Feb 1994, 28–30 Jan 1995
3 Apr 95	30 Mar 1995
21 May 95	4–6 Jun 1993, 14–16 May 1995
14 Jul 95	17–19 Aug 1993, 19–21 Aug and 22–24 Jun 1994, 11–13 Jul 1995
28 Oct 95	15–17 Oct 1993, 5–7 Oct 1994

Estimation of the dynamic biomass–density relationship

Stand wet biomass and frond density were estimated for the same seven permanent 100-cm^2 quadrats, nondestructively subsampled with six random 4-cm^2 quadrats referred to in Scrosati (1996) for an additional year. Frond density was calculated as in Scrosati (1996), but we improved the estimation of stand biomass for the present paper. In Scrosati (1996), stand biomass was estimated by applying a unique relationship between frond wet biomass and frond length (determined only for April 1994) to the mean frond length and frond density that had been found for each quadrat on each of the seven sampling dates then considered. We later found that the relationship between frond biomass and frond length varies seasonally (Table 1). Hence, for the present paper, we estimated stand biomass by a time-dependent relationship between frond biomass and frond length determined from fronds collected haphazardly on appropriate dates (Table 2). There were 14 sampling dates for the present paper, selected at approximately bimonthly intervals between June 1993 and July 1995 (Table 2). Stand biomass was preferred over mean frond biomass as the variable to be plotted against frond density to avoid potential problems of interpretation of results (Weller 1987; Scrosati 1997b).

The significance of the Pearson correlation coefficients obtained separately for the seven experimental quadrats was assessed using parametric tests (Fisher & Yates 1963) and randomization tests (Edgington 1987; Manly 1991). Randomization tests were used because the assumption of random sampling was violated (biomass–density combinations were repeatedly measured for a same quadrat to calculate each r). Randomization tests are distribution-free statistical tests that can be applied to test for the significance of any statistic; assumptions regarding random sampling, normality, and homogeneity of variance are not required for these tests (Edgington 1987; Manly 1991). Analyses were done with the Randomization Tests DOS program developed by Eugene S. Edgington (University of Calgary, Alberta, Canada). Given the number of data pairs for each replicate quadrat (n = 13–14), the number of posible data permutations (2^n) is high, so 1000 random permutations were done for each quadrat. Probability values for correlation coefficients using randomization tests were compared with those obtained by using Fisher & Yates' (1963) table to see how nonrandomness affects parametric tests of significance for our case. The linear relationship between $\log_{10}$(stand biomass) and $\log_{10}$(frond density) was determined for each quadrat separately through principal components analysis (PCA), because neither variable can be considered as a fixed variable (Weller 1987). The statistical sim-

ilarity among the seven slopes obtained was determined by comparing 95% confidence intervals for each slope; overlapping of confidence intervals indicated statistical similarity (Weller 1987; Sokal & Rohlf 1995).

Density-dependent formation of fronds

In an area with a high cover of *Mazzaella cornucopiae*, 10 4-cm^2 quadrats were randomly located along a permanent transect line on 1 April 1995. Experimental thinning was done in those quadrats by removing fronds from their holdfasts using scissors. Ten additional, unmanipulated 4-cm^2 quadrats were randomly selected along the same transect line and were used as controls. On 1–2 April and 14–16 May 1995, total frond density was measured for both groups of quadrats. The rate of formation of fronds between April and May 1995 was expressed as the difference in total frond density between both dates relative to the initial frond density, i.e. the proportional increase of frond density. Tagging the small fronds to follow their individual survival was impossible owing to their size. For the estimation of the rate of formation of new fronds, we assumed that no significant losses of fronds occurred during the study period. This assumption is supported by the following observations: frond density increased for both groups of quadrats, fronds appeared healthy, and holdfast scars that indicate frond losses (observed during fall and winter) were not seen during the experiment. To test for a differential rate of formation of new fronds between the experimentally thinned and control quadrats, an independent t-test was performed using SYSTAT 5.2.1 for Macintosh (Wilkinson *et al.* 1992).

Comparison of biomass–density data with the ultimate biomass–density line

Mean frond biomass and frond density were determined for 56 thalli of *Mazzaella cornucopiae* from Prasiola Point and Nudibranch Point (about 400 m apart). Thalli were collected on 17 October 1993, 28–29 April 1994, and 21 August 1994 by scraping the rock surface with a knife, thus collecting both the holdfast and the fronds. The outline of each holdfast was drawn on a transparent plastic surface before collection. In the laboratory, paper pieces with the shape of holdfasts were weighed and, by comparing their biomass with the biomass of a paper piece of known area, the area of holdfasts was calculated. Fronds were counted for each thallus and thallus biomass was measured to the nearest 10 mg to calculate mean

frond biomass and frond density (referred to holdfast area). It is important to note that the problems derived from using mean frond biomass to study self-thinning through correlation against frond density (Weller 1987; Scrosati 1997b) do not apply for this section, because the nature of the ultimate biomass–density line is static and not dynamic.

Temporal variation of frond biomass inequality, frond density, and mean frond biomass

The temporal variation of the inequality of frond biomass (expressed as the coefficient of variation for frond biomass), frond density, and mean frond biomass for *Mazzaella cornucopiae* from Prasiola Point was analyzed during the growing seasons of 1994 and 1995 (midwinter to late spring and/or summer, Scrosati 1997a). For this purpose, the density and length of fronds were repeatedly determined for the seven permanent quadrats mentioned above on 24–26 February, 26–28 April, 22–24 June, and 19–21 August 1994, and on 28–30 January, 30 March, 14–16 May, and 11–13 July 1995 as in Scrosati (1996). Using power relationships between frond biomass and frond length found for comparable dates (Tables 1 and 2), the biomass of each frond was estimated. Frond biomass was preferred over frond length for the calculation of size inequality because biomass is a better descriptor of size than length, because length only represents one dimension.

To test for significant temporal changes of frond biomass inequality, frond density, and mean frond biomass, one-way repeated-measures analyses of variance (ANOVAR, Howell 1992) were performed separately for the two growth seasons analyzed. The homoscedasticity assumption was considered satisfactory if the largest variance was less than four times the smallest variance for each ANOVAR (Howell 1992), whereas the normality assumption was tested using the Probability Plot-Normal option of SYSTAT 5.2.1. Data transfomations were done if necessary to meet these assumptions (see Results). Trend analyses (Howell 1992) were done after each ANOVAR. The analyses above were performed using SYSTAT 5.2.1. For testing possible temporal differences for frond density for the 1994 growing season, the ANOVAR was done through a randomization test with 1000 random permutations (Edgington 1987; Manly 1991), because data transformations did not help to meet the assumptions for parametric ANOVAR; the program Randomization Tests was used for this purpose.

RESULTS

Estimation of the dynamic biomass–density relationship

Between June 1993 and July 1995, the mean monthly stand biomass of *Mazzaella cornucopiae* from Prasiola Point oscillated between 13.4 ± 4.5 mg cm^{-2} (mean $\pm$ SE, n = 7) and 112.4 ± 12.5 mg cm^{-2}, whereas mean monthly frond density oscillated between 5.1 ± 0.7 fronds cm^{-2} (n = 7) and 10.5 ± 1.2 fronds cm^{-2}. The highest values of both variables occurred in spring and summer and the lowest values occurred in winter. The temporal variation of the relationship between $\log_{10}$(stand biomass) and $\log_{10}$(frond density) between June 1993 and July 1995 was described by a straight line with positive slope for the seven experimental quadrats (Fig. 2).

The significance of Pearson correlation coefficients obtained by randomization tests was the same as those obtained using parametric tables. Stand biomass was expressed as g m^{-2} and frond density was expressed as fronds m^{-2} in Fig. 2 to allow a comparison with results reported by previous researchers, mainly for terrestrial plants. Our results demonstrate that self-thinning among fronds of *M. cornucopiae* did not occur during the growth season, even at the highest densities observed.

The slopes of the dynamic biomass–density relationships that were determined by PCA for the seven experimental quadrats ranged between 2.85 and 7.42 and were statistically similar to one another (95% confidence intervals for slopes, Table 3). The calculation of confidence intervals (Sokal & Rohlf 1995) results in the difference between the upper confidence limit for a given slope and that slope being much larger than the difference between the lower limit and the slope. On the other hand, confidence intervals are inversely related to the correlation coefficient between both variables. The correlation coefficients for quadrats 4 and 6 were the lowest obtained: 0.48 and 0.52, respectively (Fig. 2). The upper confidence limit for quadrat 4 was -19.21 (corresponding to an angle of 92.98°), whereas that for quadrat 6 was -275.95 (corresponding to an angle of 90.21°), far different from the obtained slopes 5.07 and 5.40, respectively (Table 3). The negative portion of the confidence interval for slope 4 (between 90° and 92.98°) represents 10.6% of the entire confidence interval (between 64.75° and 92.98°), whereas the negative portion of the confidence interval for slope 6 (between 90° and 90.21°) represents only 1% of the entire confidence interval (between 68.81° and 90.21°). Given these low percentages, the positive slopes obtained for all of the quadrats, and the positive 12 confidence limits, we believe that these two negative confidence limits resulted from the variability of our data and the way in which confidence intervals were calculated. Therefore, we are confident that the dynamic biomass–relationship for *M. cornucopiae* is positive.

Density-dependent formation of fronds

Frond density was 5.5 ± 0.5 fronds cm^{-2} (mean $\pm$ SE, n = 10) in thinned quadrats right after experimental thinning and 8.3 ± 0.6 fronds cm^{-2} in control quadrats on 2 April 1995, a significant difference (independent t-test, p = 0.003). The density of fronds increased in both groups of quadrats between April and May 1995, but the rate of formation of new fronds was higher in thinned quadrats than in control quadrats. Thinned quadrats had a proportional increase of 2.24 ± 0.49, whereas control quadrats had a proportional increase of 0.42 ± 0.11, a significant difference (independent t-test, p = 0.005). This shows a density-dependent formation of new fronds of *M. cornucopiae* during the growth season.

Comparison of biomass–density data with the ultimate biomass–density line

The mean biomass of fronds of *M. cornucopiae* measured for 56 thalli from Prasiola Point and Nudibranch Point was always higher than the value predicted by the ultimate biomass-density line for the frond densities found for the thalli (Fig. 3). Thus, the constraint in mean frond biomass for a given frond density predicted by the ultimate biomass–density line,
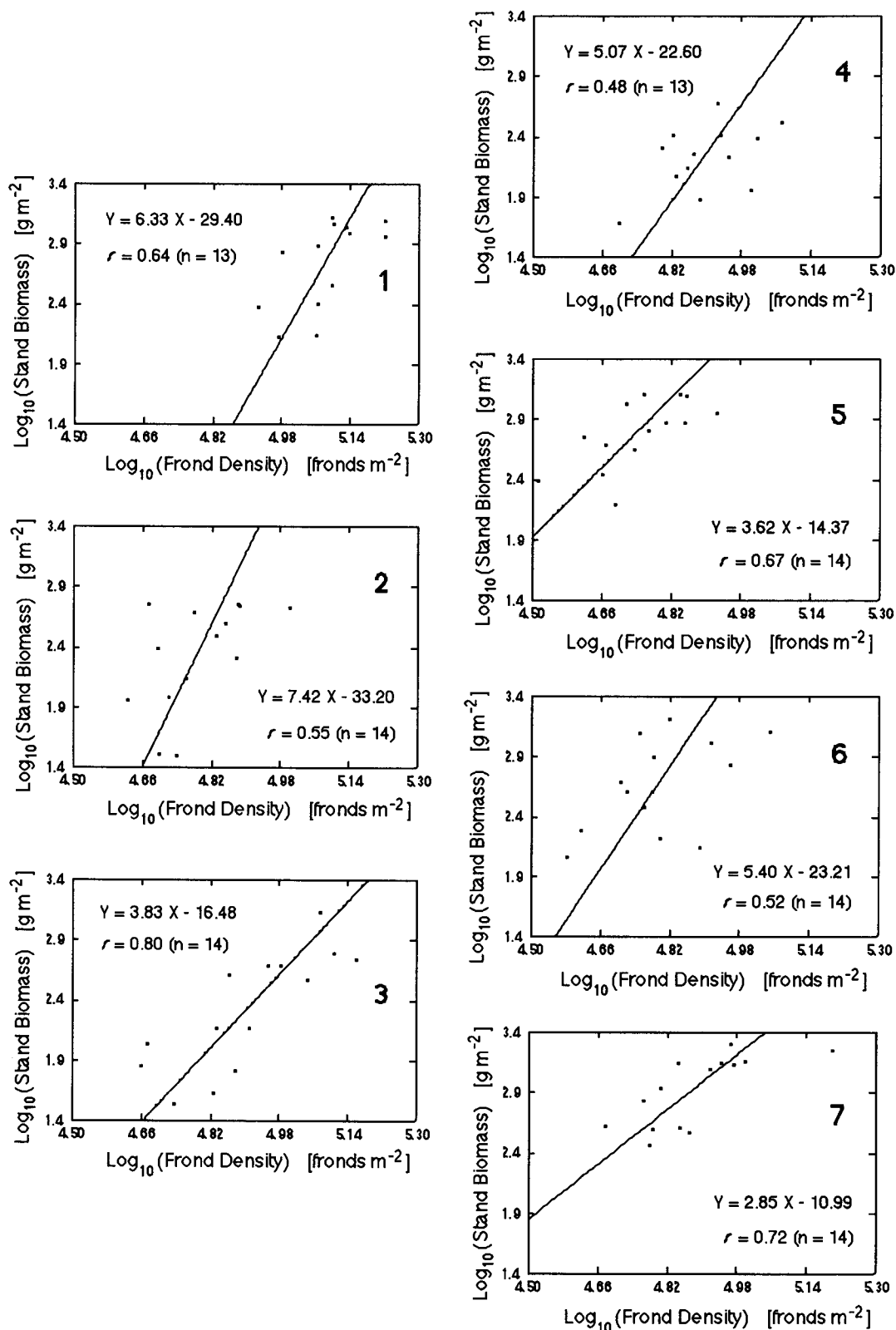
Fig. 2. Relationship between $\log_{10}$(stand wet biomass) (g m^{-2}) and $\log_{10}$(frond density) (fronds m^{-2}) of *Mazzaella cornucopiae* from Prasiola Point for seven experimental quadrats between June 1993 and July 1995.
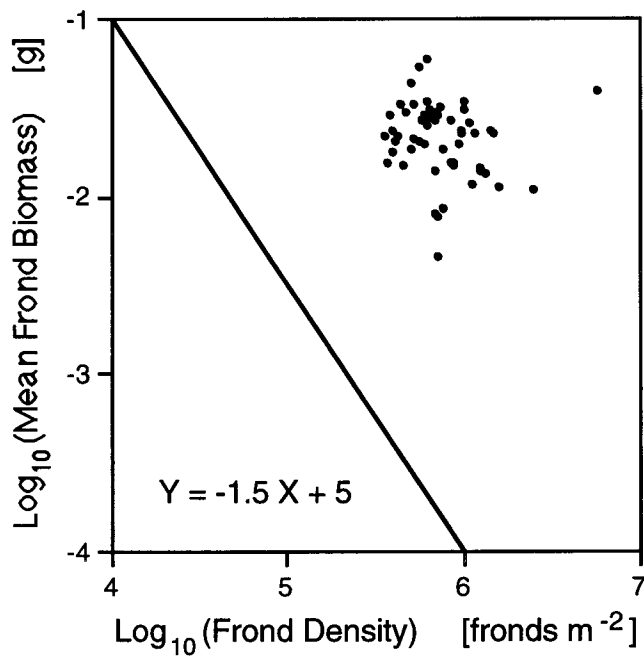
Fig. 3. Relationship between $\log_{10}$(mean frond wet biomass) (g) and $\log_{10}$(frond density) (fronds m^{-2}) for 56 thalli of *Mazzaella cornucopiae* from Prasiola Point and Nudibranch Point. The plotted line is the 'ultimate biomass–density line' proposed for terrestrial plants (see text for details).
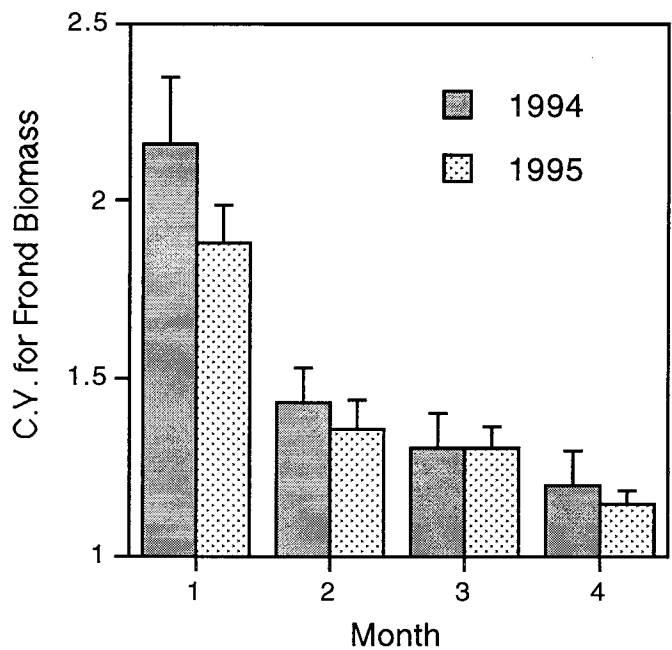

Fig. 4. Temporal variation of the coefficient of variation (CV) for frond wet biomass (mean + SE, n = 7) for *Mazzaella cornucopiae* from Prasiola Point during the 1994 and 1995 growth periods. Month numbers represent (1) Feb 94 and Jan 95; (2) Apr 94 and Mar 95; (3) Jun 94 and May 95; and (4) Aug 94 and Jul 95.

developed from work with terrestrial plants, does not apply to crowded stands of fronds of *M. cornucopiae*.

Temporal variation of frond biomass inequality, frond density, and mean frond biomass

The coefficient of variation for frond biomass significantly varied among months of the 1994 growth period (one-way ANOVAR, F = 19.69, Huynh–Feldt adjusted p < 0.001), and it followed a decreasing trend (Fig. 4), with both significant linear (F = 21.90, p = 0.003) and quadratic (F = 15.38, p = 0.008) components. For 1995, the coefficient of variation for frond biomass also varied among months (one-way ANOVAR on log-transformed data, F = 16.19, Huynh–Feldt adjusted p < 0.001), following a decreasing linear trend (F = 30.56, p = 0.001, Fig. 4).

Overall, frond density did not vary significantly during the first half of 1994 (one-way ANOVAR through a randomization test, F = 0.83, p = 0.59, Fig. 5). However, we can say that frond density increased for the population between Feb-

ruary and April, because frond density increased in six of the seven quadrats during that period. For the 1995 growth period, frond density significantly varied (one-way ANOVAR, F = 13.81, Huynh–Feldt adjusted p < 0.001), following an increasing linear trend (F = 25.67, p = 0.002, Fig. 5).
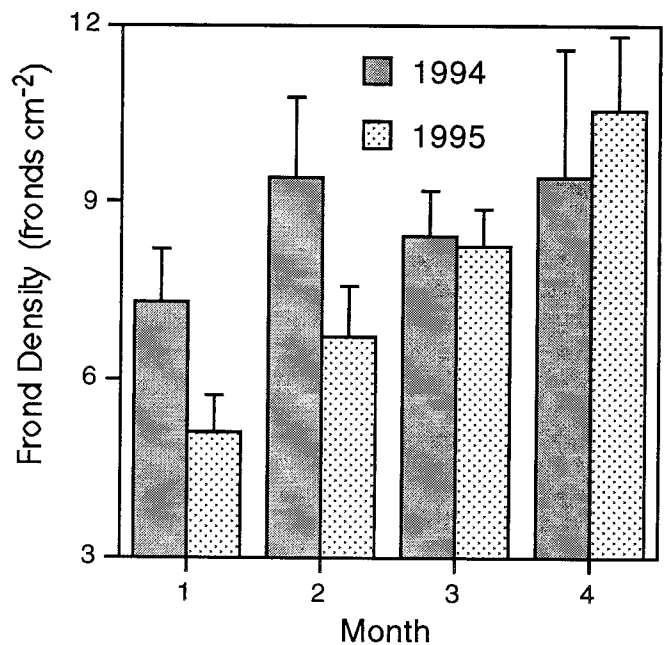

Fig. 5. Temporal variation of frond density (fronds cm^{-2}, mean + SE, n = 7) for *Mazzaella cornucopiae* from Prasiola Point during the 1994 and 1995 growth periods. Month numbers represent (1) Feb 94 and Jan 95; (2) Apr 94 and Mar 95; (3) Jun 94 and May 95; and (4) Aug 94 and Jul 95.

Table 3. Slopes and 95% confidence intervals for the dynamic relationship between $\log_{10}$(stand wet biomass) (g m^{-2}) and $\log_{10}$(frond density) (fronds m^{-2}) for *Mazzaella cornucopiae* from Prasiola Point.

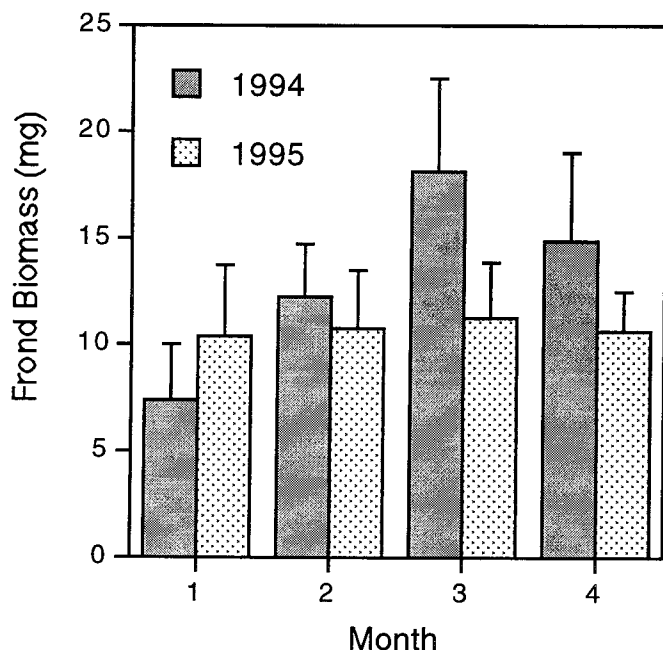| Quadrat	Slope	Confidence interval		
1	6.33	3.57	to	24.85
2	7.42	3.81	to	88.14
3	3.83	2.58	to	7.06
4	5.07	2.12	to	−19.21
5	3.62	2.07	to	11.15
6	5.40	2.58	to	−275.95
7	2.85	1.72	to	6.69

Fig. 6. Temporal variation of mean frond wet biomass (mg, mean + SE, n = 7) for *Mazzaella cornucopiae* from Prasiola Point during the 1994 and 1995 growing seasons. Month numbers represent (1) Feb 94 and Jan 95; (2) Apr 94 and Mar 95; (3) Jun 94 and May 95; and (4) Aug 94 and Jul 95.

Mean frond biomass significantly varied during the 1994 growth period (one-way ANOVAR, F = 10.68, Huynh–Feldt adjusted p = 0.002), and it followed an increasing trend (Fig. 6) with both significant linear (F = 15.36, p = 0.008) and quadratic (F = 8.30, p = 0.028) components. Mean frond biomass did not change significantly during the 1995 growth period (one-way ANOVAR, F = 0.16, Huynh–Feldt adjusted p = 0.86, Fig. 6).

DISCUSSION

Randomization tests and parametric tests of significance of r

Parametric tests and randomization tests of the significance of a given statistic usually agree when observations seem to come from a normal distribution. This agreement gives some justification for using parametric tests on nonrandom samples (Manly 1991). The similar significance levels obtained by both methods for the linear correlation between $\log_{10}$(stand biomass) and $\log_{10}$(frond density) for *M. cornucopiae* support, by this approach, the valid use of parametric tables for the significance of r for our data set, even considering that sampling was not done at random. This is important to consider for the analysis of other data sets that also come from nonrandom samples.

Relevance of the dynamic biomass–density relationship

The analysis of additional sampling dates with respect to the preliminary results reported in Scrosati (1996) indicated that the positive linear relationship between $\log_{10}$(stand biomass)

and $\log_{10}$(frond density) for *M. cornucopiae* is true for all of the experimental quadrats, i.e. for the entire population from Prasiola Point. The lack of a negative relationship between the variables indicates that fronds of *M. cornucopiae* did not undergo self-thinning even at the highest densities observed. No frond self-thinning was reported for *Mazzaella laminarioides* from Chile (Martínez & Santelices 1992) or for *Gelidium sesquipedale* from Portugal (Santos 1995). However, the evidence for *M. laminarioides* is indirect, because biomass–density combinations were measured for different stands at a single instant, i.e. a static relationship, which may or may not describe the dynamic relationship (Weller 1989). A positive dynamic relationship between stand biomass and frond density might also occur for *Chondrus crispus* Stackhouse and *Mastocarpus stellatus* (Stackhouse) Guiry from Ireland, for which a positive static biomass–density relationship was found (Pybus 1977, *M. stellatus* as *Gigartina stellata*).

Linear models between $\log_{10}$(stand biomass) and $\log_{10}$(frond density) would be useful for the estimation of stand biomass from a count of fronds for a given area; it is quick and avoids the destructive sampling necessary with other methods. The statistical similarity among the seven slopes determined for our experimental quadrats suggests that there is only one functional relationship between biomass and density for the population from Prasiola Point. However, 95% confidence intervals for slopes were generally large. This prevents a reliable estimation of stand biomass, so this method cannot be recommended. On the other hand, a great deal of the statistical similarity among the seven slopes results from the variation observed for the data (correlation coefficients for biomass–density relationships ranged between 0.48 and 0.80). Moderate correlation coefficients result in the overlapping of confidence intervals for slopes; therefore, they are unable to detect significant differences between seemingly different slopes (the largest was 7.42 and the smallest was 2.85). In spite of statistical results, these apparently different slopes suggest that the dynamic biomass–density relationship might be site dependent. This would agree with the fact that a given species of terrestrial plant has different self-thinning lines depending on site conditions (Weller 1987). The biotic and abiotic factors that affect *Mazzaella cornucopiae* are continuously varying in their relative intensity, which may be responsible for the high variability in biomass–density combinations. As a result, the dynamic biomass–density relationship would differ each year and would also depend on the site considered.

We will now discuss hypotheses generated to explain the lack of frond self-thinning for *M. cornucopiae* and additional clonal red algae in light of our own results and the recent literature.

Physiological integration among fronds

Ramets of terrestrial clonal plants show varying degrees of physiological integration (Pitelka & Ashmun 1985; Marshall 1990; Hester *et al.* 1994; Stuefer *et al.* 1994; Alpert 1996). For most of the terrestrial clonal plants studied, interconnections among ramets are thought to reduce mortality of the smallest ramets (up to a certain point, see de Kroon 1993) by allowing translocation of assimilates from large ramets to small ramets, which become increasingly shaded as plants

grow (Hutchings 1979; Pitelka 1984; Pitelka & Ashmun 1985; Marshall 1990).

Fronds of clonal red algae that arise from the same holdfast may have a certain degree of physiological integration (Maggs & Cheney 1990). Recent evidence (Gonen *et al.* 1996) indicates that translocation of photoassimilates occurs within thalli of the red alga *Gracilaria cornea* J. Agardh (Gracilariales). For *M. cornucopiae,* an indirect indication that physiological integration may occur is the existence of short (<5 mm) frond-like projections that occasionally grow downward from the lower surface of holdfasts and penetrate crevices. These projections are almost colorless, and the low to nil irradiance that occurs beneath the holdfasts suggests that these projections should be nourished from the upper regions of thalli, involving a certain degree of translocation. The physiological integration hypothesis therefore remains potentially viable for clonal red algae and provides a basis for future research.

Density-dependent formation of fronds

During the growth period for ramets of terrestrial clonal plants, the formation of ramets is density dependent (Hutchings 1979; Hartnett & Bazzaz 1985; Briske & Butler 1989; de Kroon & Kwant 1991; de Kroon 1993; Hara *et al.* 1993). It has been hypothesized that regulation of ramet formation prevents overproduction that would otherwise cause self-thinning (de Kroon & Kwant 1991; de Kroon 1993). During the growth period for *M. cornucopiae* from Prasiola Point, i.e. between midwinter and late spring or summer (Scrosati 1997a), the continuous formation of fronds is also density dependent, which may contribute to the lack of frond self-thinning for this species as has been suggested for terrestrial clonal plants. This could occur for other clonal red algae as well.

The cause of the density-dependent formation of ramets of clonal terrestrial plants remains unclear. Some authors suggest that it may result from the inhibiting effects of the low irradiance and the low red : far-red ratio occurring near the bottom of ramets on the development of basal axillary buds (Casal *et al.* 1985; Solangaarachchi & Harper 1987; de Kroon 1993). However, recent experiments with the bunchgrass *Schizachyrium scoparium* var. *frequens* (Hubb) Gould did not support this hypothesis (Murphy & Briske 1994). Like terrestrial plants, seaweeds have a variety of physiological responses to the light regime. Some marine algae produce phytochrome (although its presence in red algae is in doubt) and other pigments possibly related to photomorphogenesis (Dring 1988; Lobban & Harrison 1994). Therefore, light might affect the density-dependent formation of fronds of *M. cornucopiae* and other clonal red algae.

Comparison of biomass–density data with the ultimate biomass–density line

Combinations between mean frond biomass and frond density for *Mazzaella cornucopiae* are not constrained by the ultimate biomass–density line proposed as universal for the plant kingdom (White 1985; Weller 1989). Additional measurements done for 32 gametophytic thalli of *Mastocarpus papillatus* (C. Agardh) Kützing from Vancouver Harbor, British Columbia (Scrosati 1997a) also showed that the mean biomass of fronds was always higher than predicted by the ultimate biomass–density line for a given frond density.

Whether the constraint for combinations between mean frond biomass and frond density that is specific for clonal red algae is different remains to be determined. Numerous terrestrial plant species had to be studied to detect the existence of the ultimate biomass–density line, although the functional relationship is not well known (Weller 1989). Several clonal algal species should be studied to determine possible constraints for the maximum mean biomass of fronds for any given frond density. For the moment, the lack of self-thinning among fronds of *Mazzaella cornucopiae* cannot be explained by the ultimate biomass–density line hypothesis (Westoby 1984; de Kroon 1993; de Kroon & Kalliola 1995).

Photoacclimation of the smallest fronds to low irradiance

Another hypothesis that could explain the lack of frond self-thinning for *M. cornucopiae* is acclimation of the smallest fronds to the low irradiance close to the holdfasts of crowded stands: 3–30 μmol m^{-2} s^{-1} depending on distance to holdfasts and cloudiness (Scrosati 1997a). If the light compensation point for the smallest fronds is lower than such irradiance levels, growth is possible, thus preventing self-thinning, regardless of the intensity of physiological integration or the degree of density-dependent formation of fronds. However, if the light compensation point for the smallest fronds is higher, then causes of the lack of frond self-thinning should be related to physiological integration among fronds or to the density-dependent formation of fronds. The light compensation point and understory irradiance for algae that occur in the high intertidal zone have been reported only for the tropical red species *Ahnfeltiopsis concinna* (J. Agardh) Silva et De Cew from Hawaii (Beach & Smith 1996a, 1996b). For this alga, the compensation point for understory tissue (26.3 μmol m^{-2} s^{-1} measured underwater) is higher than the irradiance observed at the understory (usually less than 10 μmol m^{-2} s^{-1}). This suggests that crowding could limit the growth of the smallest fronds of this alga through shading. The reported compensation point for *A. concinna* could be higher during low tides because photosynthetic rates generally decrease as thallus desiccation increases (Johnson *et al.* 1974; Quadir *et al.* 1979; Hay 1981; Oates 1985, 1986; Madsen & Maberly 1990; Bell 1993; Britting & Chapman 1993; Dudgeon *et al.* 1995; Scrosati 1997a), so the hypothesis of growth limited by low irradiance is reinforced.

Under certain conditions, self-thinning can occur among ramets of terrestrial clonal plants. Self-thinning was recently reported to occur among shoots of the clonal perennial grass *Gynerium sagittatum* (Aublet) Palisot de Beauvois from tropical floodplains in Amazonian Peru (de Kroon & Kalliola 1995). These authors suggested that, in seasonal habitats, the periodic density-independent mortality would not allow shoots to reach a self-thinning stage. On the contrary, a low seasonality of the environment (such as in the Amazon, compared with temperate environments) would allow shoots to undergo self-thinning after years of continuous growth, as would be the case of *G. sagittatum* (de Kroon 1993; de Kroon & Kalliola 1995). However, to accept this hypothesis fully, one should consider the degree of physiological integration that remains among ramets after prolonged growth. If physiological integration is eventually reduced to a minimum or nonexistent level after years of growth, ramets would relate to

one another like nonclonal plants, thus effectively leading to the mortality of small ramets. Only if physiological integration remains strong after prolonged growth would self-thinning among ramets not occur.

Competition among fronds

Field growth rates are not possible to measure for all frond sizes of *M. cornucopiae*. The smallest fronds are impossible to tag due to their size, so their growth cannot be monitored through time. However, data on the temporal variation of frond biomass inequality, frond density, and mean frond biomass during the growth periods of 1994 and 1995 allow us to infer growth rates for fronds of different sizes relative to each other. For 1994, the fact that frond biomass inequality was decreasing while fronds were growing in biomass suggests that the growth rate of small fronds was higher than that of large fronds. For 1995, there is an indirect indication that fronds were also growing in biomass, despite the fact that mean frond biomass did not increase significantly. Frond density clearly increased during the 1995 growth period by the addition of small fronds. For mean frond biomass to remain unchanged through time, the ratio between stand biomass and frond density should not vary. The proportional increase of frond density is higher than the proportional increase of stand biomass when small fronds are being continuously formed. Therefore, growth of existing fronds is the only alternative to keep mean frond biomass similar through time. The increase in frond biomass inequality during the 1995 growing season, together with the growth in biomass of fronds, suggests that growth rates for small fronds were higher than for large fronds, as for the previous year.

The dynamics of frond biomass inequality of *M. cornucopiae* during growth, and its implications for the kind of competition that exists among fronds, differs from that for the much better studied nonclonal terrestrial plants. During the early stages of growth of even-aged, nonclonal terrestrial plants, plant size inequality increases mainly as a consequence of competition for light among plants (Hara 1988; Weiner 1988, 1990). This is evidence of one-sided or asymmetric competition, in which large plants progressively suppress the growth of the smallest plants. When self-thinning commences, plant size inequality starts to decrease because of the mortality of the smallest plants (Schmitt *et al.* 1986; Weiner & Thomas 1986; Weiner 1988, 1990; Knox *et al.* 1989).

The increasing frond crowding that results from the formation of new fronds and the growth of existing fronds results in a progressive reduction of the irradiance that reaches the small fronds in the understory. The net photosynthetic rate of fronds is significantly lower under an irradiance of about 20 μmol m^{-2} s^{-1}, which is observed in the understory, compared with about 500 μmol m^{-2} s^{-1} measured at the canopy level (Scrosati 1997a). This suggests that increased crowding induces greater competition among fronds for light. However, because mortality of the smallest fronds of *M. cornucopiae* does not occur, but frond size inequality decreases during growth, competition among fronds does not appear to be asymmetric as for individuals of nonclonal plants. Rather, frond competition for *M. cornucopiae* would respond to the symmetric (two-sided) model. Symmetric competition occurs when the growth increment of ramets per unit time is propor-

tional to, independent of, or negatively related to ramet size (for asymmetric competition, this relationship is described by a concave curve, de Kroon *et al.* 1992; de Kroon 1993; Hara *et al.* 1993). The growth increment of fronds per unit time appears to be negatively related to frond size for *M. cornucopiae*. Symmetric competition occurs among ramets of terrestrial clonal plants, for which ramet size inequality either decreases or remains constant as ramets grow and their density increases (de Kroon 1993).

Genetic differences among nonclonal plants are one of the causes of the increase of plant size inequality during early stages of growth (Weiner 1988, 1990). For *M. cornucopiae*, genetic differences among fronds from the same genet are likely absent, so the decrease of frond size inequality and the lack of asymmetric competition among fronds during the growth period would be facilitated. The proposed negative relationship between growth rate and frond size for *M. cornucopiae* may be explained by the fact that frond crowding confers important benefits for the growth and survival of this high intertidal alga, but these benefits, such as protection against strong desiccation, high irradiance, and bleaching, apply primarily to the fronds that are protected by the canopy, i.e. fronds of small and medium size (Scrosati 1997a). Physiological integration among fronds may also partially contribute to the higher growth rate of small fronds relative to large fronds by allowing translocation of photosynthates from large to small fronds.

Frond size inequality for *M. cornucopiae* may also be reduced by a combination of frond bleaching, herbivory, and wave action. Snails of the genus *Littorina* are common inhabitants of *M. cornucopiae* stands (Kim & DeWreede 1996). Between midspring and summer, the tips of the largest fronds become bleached (Scrosati 1997a), and littorinid snails graze frequently on the bleached tips (Scrosati 1997a). The combined effects of grazing and removal of damaged tips by waves may reduce the frond size inequality by selectively reducing the size of the largest fronds.

Little is known about the dynamics of frond size inequality and its implications for the understanding of the interactions among fronds of clonal red algae in general. For *Gelidium sesquipedale* from Portugal, frond length inequality also decreases between winter and summer (Santos 1995). This suggests that fronds of *G. sesquipedale* may compete following the symmetric model proposed for *M. cornucopiae*. Frond size inequality was also determined for *M. laminarioides* from Chile (Martínez & Santelices 1992), but only once for the spring and once for the fall, so its temporal variation during the growth season cannot be discussed. To increase our understanding of how fronds of clonal algae interact, including competition models, it will be necessary to develop tagging techniques for all frond sizes, so their growth can be adequately monitored.

REFERENCES

ABBOTT I.A. 1971. On the species of *Iridaea* (Rhodophyta) from the Pacific coast of North America. *Syesis* **4**: 51–72.

ALPERT P. 1996. Nutrient sharing in natural clonal fragments of *Fragaria chiloensis. Journal of Ecology* **84**: 395–406.

ANG P.O. & DeWREEDE R.E. 1992. Density-dependence in a population of *Fucus distichus. Marine Ecology Progress Series* **90**: 169–181.

BEACH K.S. & SMITH C.M. 1996a. Ecophysiology of tropical rhodophytes. I. Microscale acclimation in pigmentation. *Journal of Phycology* **32**: 701–710.

BEACH K.S. & SMITH C.M. 1996b. Ecophysiology of tropical rhodophytes. II. Microscale acclimation in photosynthesis. *Journal of Phycology* **32**: 710–718.

BELL E.C. 1993. Photosynthetic response to temperature and desiccation of the intertidal alga *Mastocarpus papillatus. Marine Biology* **117**: 337–346.

BENDEL R.B., HIGGINS S.S., TEBERG J.E. & PYKE D.A. 1989. Comparison of skewness coefficient, coefficient of variation, and Gini coefficient as inequality measures within populations. *Oecologia* **78**: 394–400.

BLACK R. 1974. Some biological interactions affecting intertidal populations of the kelp *Egregia laevigata. Marine Biology* **28**: 189–198.

BRISKE D.D. & BUTLER J.L. 1989. Density-dependent regulation of ramet populations within the bunchgrass *Schizachyrium scoparium:* interclonal versus intraclonal interference. *Journal of Ecology* **77**: 963–974.

BRITTING S.A. & CHAPMAN D.J. 1993. Physiological comparison of the isomorphic life history phases of the high intertidal alga *Endocladia muricata* (Rhodophyta). *Journal of Phycology* **29**: 739–745.

CASAL J.J., DEREGIBUS V.A. & SÁNCHEZ R.A. 1985. Variations in tiller dynamics and morphology in *Lolium multiflorum* Lam. vegetative and reproductive plants as affected by differences in red/far-red irradiation. *Annals of Botany* **56**: 59–65.

CREED J.C. 1995. Spatial dynamics of a *Himanthalia elongata* (Fucales, Phaeophyta) population. *Journal of Phycology* **31**: 851–859.

DEAN T.A., THIES K. & LAGOS S.L. 1989. Survival of juvenile giant kelp: the effects of demographic factors, competitors, and grazers. *Ecology* **70**: 483–495.

DE KROON H. 1993. Competition between shoots in stands of clonal plants. *Plant Species Biology* **8**: 85–94.

DE KROON H., HARA T. & KWANT R. 1992. Size hierarchies of shoots and clones in clonal herb monocultures: do clonal and non-clonal plants compete differently? *Oikos* **63**: 410–419.

DE KROON H. & KALLIOLA R. 1995. Shoot dynamics of the giant grass *Gynerium sagittatum* in Peruvian Amazon floodplains, a clonal plant that does show self-thinning. *Oecologia* **101**: 124–131.

DE KROON H. & KWANT R. 1991. Density-dependent growth responses in two clonal herbs: regulation of shoot density. *Oecologia* **86**: 298–304.

DICKERMAN J.A. & WETZEL R.G. 1985. Clonal growth in *Typha latifolia:* population dynamics and demography of the ramets. *Journal of Ecology* **73**: 535–552.

DRING M.J. 1988. Photocontrol of development in algae. *Annual Review of Plant Physiology and Plant Molecular Biology* **39**: 157–174.

DUDGEON S.R., KÜBLER J.E., VADAS R.L. & DAVISON I.R. 1995. Physiological responses to environmental variation in intertidal red algae: does thallus morphology matter? *Marine Ecology Progress Series* **117**: 193–206.

EDGINGTON E.S. 1987. *Randomization Tests,* 2nd ed. Marcel Dekker, New York and Basel. 341 pp.

ERIKSSON O. 1993. Dynamics of genets in clonal plants. *Trends in Ecology and Evolution* **8**: 313–316.

FISHER R.A. & YATES F. 1963. *Statistical Tables for Biological, Agricultural and Medical Research,* 6th ed. Oliver & Boyd, Edinburgh. 138 pp.

FLORES-MOYA A., FERNÁNDEZ J.A. & NEILL F.X. 1996. Growth pattern, reproduction, and self-thinning in seaweeds. *Journal of Phycology* **32**: 767–769.

GONEN Y., KIMMEL E., TEL-OR E. & FRIEDLANDER M. 1996. Intercellular assimilate translocation in *Gracilaria cornea* (Gracilariaceae, Rhodophyta). *Hydrobiologia* **326/327**: 421–428.

HARA T. 1988. Dynamics of size structure in plant populations. *Trends in Ecology and Evolution* **3**: 129–133.

HARA T. 1994. Growth and competition in clonal plants—persistence of shoot populations and species diversity. *Folia Geobotanica & Phytotaxonomica* **29**: 181–201.

HARA T., VAN DER TOORN J. & MOOK J.H. 1993. Growth dynamics and size structure of shoots of *Phragmites australis,* a clonal plant. *Journal of Ecology* **81**: 47–60.

HARTNETT D.C. & BAZZAZ F.A. 1985. The regulation of leaf, ramet and genet densities in experimental populations of the rhizomatous perennial *Solidago canadensis. Journal of Ecology* **73**: 429–443.

HAY M.E. 1981. The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. *Ecology* **62**: 739–750.

HESTER M.W., McKEE K.L., BURDICK D.M., KOCH M.S., FLYNN K.M., PATTERSON S. & MENDELSSOHN I.A. 1994. Clonal integration in *Spartina patens* across a nitrogen and salinity gradient. *Canadian Journal of Botany* **72**: 767–770.

HOMMERSAND M.H., GUIRY M.D., FREDERICQ S. & LEISTER G.L. 1993. New perspectives in the taxonomy of the Gigartinaceae (Gigartinales, Rhodophyta). *Hydrobiologia* **260/261**: 105–120.

HOWELL D.C. 1992. *Statistical Methods for Psychology,* 3rd ed. Duxbury Press, Belmont. 693 pp.

HUTCHINGS M.J. 1979. Weight-density relationships in ramet populations of clonal perennial herbs, with special reference to the −3/2 power law. *Journal of Ecology* **67**: 21–33.

JACKSON J.B.C., BUSS L.W. & COOK R.E. 1985. *Population Biology and Evolution of Clonal Organisms.* Yale University Press, New Haven and London, 530 pp.

JOHNSON W.S., GIGON A., GULMON S.L. & MOONEY H.A. 1974. Comparative photosynthetic capacities of intertidal algae under exposed and submerged conditions. *Ecology* **55**: 450–453.

KIM J.H. & DeWREEDE R.E. 1996. Distribution and feeding preference of a high intertidal littorinid. *Botanica Marina* **39**: 561–569.

KNOX R.G., PEET R.K. & CHRISTENSEN N.L. 1989. Population dynamics in loblolly pine stands: changes in skewness and size inequality. *Ecology* **70**: 1153–1166.

LAPHAM J. & DRENNAN D.S.H. 1987. Intraspecific regulation of populations of the clonal herb, *Cyperus esculentus. Journal of Applied Ecology* **24**: 1011–1024.

LOBBAN C.S. & HARRISON P.J. 1994. *Seaweed Ecology and Physiology.* Cambridge University Press, Cambridge and New York, 366 pp.

MADSEN T.V. & MABERLY S.C. 1990. A comparison of air and water as environments for photosynthesis by the intertidal alga *Fucus spiralis* (Phaeophyta). *Journal of Phycology* **26**: 24–30.

MAGGS C.A. & CHENEY D.P. 1990. Competition studies of marine macroalgae in laboratory culture. *Journal of Phycology* **26**: 18–24.

MANLY B.F.J. 1991. *Randomization and Monte Carlo Methods in Biology.* Chapman and Hall, London and New York, 281 pp.

MARSHALL C. 1990. Source–sink relations of interconnected ramets. In: *Clonal Growth in Plants: Regulation and Function* (Ed. by J. van Groenendael & H. de Kroon), pp. 23–41. SPB Academic Publishing, The Hague.

MARTÍNEZ E. & SANTELICES B. 1992. Size hierarchy and the −3/2 "power law" relationship in a coalescent seaweed. *Journal of Phycology* **28**: 259–264.

MURPHY J.S. & BRISKE D.D. 1994. Density-dependent regulation of ramet recruitment by the red:far-red ratio of solar radiation: a field evaluation with the bunchgrass *Schizachyrium scoparium. Oecologia* **97**: 462–469.

OATES B.R. 1985. Photosynthesis and amelioration of desiccation in the intertidal saccate alga *Colpomenia peregrina. Marine Biology* **89**: 109–119.

OATES B.R. 1986. Components of photosynthesis in the intertidal saccate alga *Halosaccion americanum* (Rhodophyta, Palmariales). *Journal of Phycology* **22**: 217–223.

PITELKA L.F. 1984. Application of the −3/2 power law to clonal herbs. *The American Naturalist* **123**: 442–449.

PITELKA L.F. & ASHMUN J.W. 1985. Physiology and integration of ramets in clonal plants. In: *Population Biology and Evolution of Clonal Organisms* (Ed. by J.B.C. Jackson, L.W. Buss & R.E. Cook), pp. 399–435. Yale University Press, New Haven.

PYBUS C. 1977. The ecology of *Chondrus crispus* and *Gigartina stellata* (Rhodophyta) in Galway Bay. *Journal of the Marine Biological Association of the United Kingdom* **57**: 609–628.

QUADIR A., HARRISON P.J. & DEWREEDE R.E. 1979. The effects of emergence and submergence on the photosynthesis and respiration of marine macrophytes. *Phycologia* **18**: 83–88.

REED D.C. 1990. An experimental evaluation of density dependence in a subtidal algal population. *Ecology* **71**: 2286–2296.

ROOM P.M. & JULIEN M.H. 1994. Population–biomass dynamics and the absence of −3/2 self-thinning in the clonal weed *Salvinia molesta. Australian Journal of Ecology* **19**: 26–34.

SANTOS R. 1995. Size structure and inequality in a commercial stand of the seaweed *Gelidium sesquipedale. Marine Ecology Progress Series* **119**: 253–263.

SCHMITT J., EHRHARDT D.W. & CHEO M. 1986. Light-dependent dominance and supression in experimental radish populations. *Ecology* **67**: 1502–1507.

SCROSATI R. 1996. The relationship between stand biomass and frond density in the clonal alga *Mazzaella cornucopiae* (Rhodophyta, Gigartinaceae). *Hydrobiologia* **326/327**: 259–265.

SCROSATI R.A. 1997a. *Population Ecology of the Clonal Red Alga Mazzaella cornucopiae from Barkley Sound, Canada.* PhD Thesis. The University of British Columbia, Vancouver. 189 pp.

SCROSATI R. 1997b. On the analysis of self-thinning among seaweeds. *Journal of Phycology* **33**, in press.

SELIVANOVA O.N. & ZHIGADLOVA G.G. 1997. Marine algae of the Commander Islands. Preliminary remarks on the revision of the flora III. Rhodophyta. *Botanica Marina* **40**: 15–24.

SOKAL R.R. & ROHLF F.J. 1995. *Biometry. The Principles and Practice of Statistics in Biological Research,* 3rd ed. W.H. Freeman and Company, New York. 887 pp.

SOLANGAARACHCHI S.M. & HARPER J.L. 1987. The effect of canopy filtered light on the growth of white clover *Trifolium repens. Oecologia* **72**: 372–376.

STUEFER J.F., DURING H.J. & DE KROON H. 1994. High benefits of clonal integration in two stoloniferous species, in response to heterogeneous light environments. *Journal of Ecology* **82**: 511–518.

WEINER J. 1988. Variation in the performance of individuals in plant populations. In: *Plant Population Ecology* (Ed. by A.J. Davy, M.J. Hutchings & A.R. Watkinson), pp. 59–81. Blackwell Scientific Publications, Oxford and Boston.

WEINER J. 1990. Asymmetric competition in plant populations. *Trends in Ecology and Evolution* **5**: 360–364.

WEINER J. & SOLBRIG O.T. 1984. The meaning and measurement of size hierarchies in plant populations. *Oecologia* **61**: 334–336.

WEINER J. & THOMAS S.C. 1986. Size variability and competition in plant monocultures. *Oikos* **47**: 211–222.

WELLER D.E. 1987. A reevaluation of the −3/2 power rule of plant self-thinning. *Ecological Monographs* **57**: 23–43.

WELLER D.E. 1989. The interspecific size-density relationship among crowded plant stands and its implications for the −3/2 power rule of self-thinning. *The American Naturalist* **133**: 20–41.

WESTOBY M. 1984. The self-thinning rule. *Advances in Ecological Research* **14**: 167–225.

WHITE J. 1985. The thinning rule and its applications to mixtures of plant populations. In: *Studies on Plant Demography: A Festschrift for John L. Harper* (Ed. by J. White), pp. 291–309. Academic Press, London.

WILKINSON L., HILL M.A. & VANG E. 1992. *SYSTAT: Statistics, Version 5.2 ed.* SYSTAT, Evanston, IL. 724 pp.

YODA K., KIRA T., OGAWA H. & HOZUMI K. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions (intraspecific competition among higher plants XI). *Journal of Biology, Osaka City University* **14**: 107–129.