

Crowding in clonal seaweeds: Does self-thinning occur in *Mastocarpus papillatus* shortly before stand biomass peaks?

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Abstract

Fronds from crowded stands of clonal seaweeds, particularly those in which holdfasts are mostly perennial and are the major source of new fronds every year, are thought not to undergo self-thinning during the growth season, unlike those from crowded stands of unitary seaweeds. For clonal seaweeds, it is not known, however, what happens at the very end of the growth season, when crowding is highest for the year. By sampling twice more frequently than previously done for similar species, the possible occurrence of frond self-thinning was tested for *Mastocarpus papillatus* (Rhodophyta, Gigartinales, Petrocelidaceae) from western Canada during the growth season (spring) of 2003. Initially, stand biomass increased together with frond density, as found previously for similar clonal seaweeds. Shortly before stand biomass peaked for the year (June), frond density remained statistically unchanged. Thus, the increased sampling precision of this study confirms that fronds of these clonal seaweeds do not undergo self-thinning, not even shortly before crowding is highest. Frond size inequality for *M. papillatus* remained statistically similar during the growth season, which is also consistent with a model of no self-thinning. There are similarities in biomass–density dynamics and in size inequality dynamics between clonal seaweeds and clonal vascular plants.

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1. Introduction

Based on the pattern of vegetative development, two main groups of seaweeds can be recognized: clonal and unitary species. A clonal seaweed is that in which its holdfast produces a number of fronds vegetatively, each frond having the potential capacity for autonomous life if it becomes physically isolated from the rest while remaining attached to the substrate by an original portion of holdfast. The basal part (holdfast tissue) of such an isolated frond has the potential capacity for generating new holdfast tissue horizontally, which subsequently may produce new fronds. Therefore, fronds of clonal seaweeds can be referred to as ramets, a term originally developed for shoots of clonal vascular plants (Harper, 1977; de Kroon and van Groenendael, 1997). The entire thallus of a clonal seaweed (including the holdfast and fronds) that develops from one spore, zygote, or parthenogenetic gamete is referred to as the genet (Scrosati, 2002). In some groups of clonal seaweeds,

neighboring genets may fuse once their holdfasts get in contact during growth (Santelices et al., 1999, 2003, 2004), which results in chimeric thalli (thalli that are each composed of two or more genets). A unitary seaweed only produces one frond or axis from the holdfast.

The clonal or unitary nature of a macroalgal species appears to be a valuable tool to predict the basic pattern of population dynamics. For example, during the growth season, the accumulation of biomass in crowded stands of unitary seaweeds involves the progressive death of small thalli as a result of increasing competition with larger thalli, a process known as self-thinning (Black, 1974; Ang and DeWreede, 1992; Creed, 1995; Flores-Moya et al., 1997; Creed et al., 1998; Arenas and Fernández, 2000; Steen and Scrosati, 2004). Self-thinning is described by a negative temporal relationship between biomass and density (Weller, 1987). On the contrary, fronds of clonal seaweeds, specifically those from stands where holdfasts are mostly perennial and spore recruitment is minimal, do not undergo self-thinning during the growth season even in crowded conditions. This was concluded after plotting biomass–density data for consecutive sampling dates together: frond density and stand biomass covary throughout

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time following a straight line with a positive slope in a bilogarithmic scale (Santos, 1995; Scrosati and DeWreede, 1997; Scrosati and Servièrre-Zaragoza, 2000). In other words, frond density also increases as total biomass accumulates in stands, which results from the continuous vegetative production of new fronds by the relatively perennial holdfasts.

It is important to note, however, that the above studies on clonal seaweeds (Santos, 1995; Scrosati and DeWreede, 1997; Scrosati and Servièrre-Zaragoza, 2000) measured biomass and density for natural populations at intervals of two or more months. It is not known how biomass and density covary at the time of highest biomass accumulation shortly before the beginning of the die-back season (during which both variables decrease simultaneously). Shortly before stand biomass peaks, frond density might continue to increase or, alternatively, crowding levels might become so high that self-thinning might occur for a limited period. In fact, the brief occurrence of self-thinning at the end of the growth season has been recorded for some clonal herbaceous plants from seasonal habitats (Hutchings, 1979; Mook and van der Toorn, 1982). To test this hypothesis for clonal seaweeds, biomass and density should be monitored during the growth season more frequently than every two months, placing particular attention on the brief period of highest biomass accumulation. This paper reports on such a study, using *Mastocarpus papillatus* (Rhodophyta, Gigartinales, Petrocelidaceae) as a model species, as this species shares similar morphological characteristics with the clonal seaweeds studied previously. Self-thinning is also associated to a decrease in size inequality or hierarchy in a population, as only the smallest size class is predominantly suffering mortality during this process due to asymmetric competition with larger size classes (Weiner, 1988; Weiner et al., 2001). Thus, the hypothesis of a possible decrease in size inequality shortly before the annual peak in stand biomass was also tested for *M. papillatus*.

2. Methods

The life history of *M. papillatus* involves either the alternation between gametophytes and tetrasporophytes or gametophyte recycling through direct development (Polanshek and West, 1977; Zupan and West, 1988). Gametophytic thalli are composed of a crustose holdfast and several foliose fronds (ramets) with numerous papillae, while tetrasporophytes are entirely crustose. This study focused on gametophytes. The study site was Acadia Beach (49°17'N, 123°14'W), located on the coast of Vancouver, BC, Canada. At this cold-temperate site, the maximum tidal amplitude is about 5 m. The intertidal zone is composed of several types of substrate, including sand, pebbles, cobbles and large rocks. *M. papillatus* gametophytes occur on large rocks, where the substrate is most stable on a long-term basis. Thalli occur at the high intertidal zone, between about 3.4 and 4.4 m above the lowest normal tide (Canadian chart datum). Wave action in this area is low to moderate. A dense *M. papillatus* stand and fronds of varying size are shown in Fig. 1. There are no measurements of irradiance levels for dense *M. papillatus* stands, but measure-

ments for dense stands of *Mazzaella parksii*, a morphologically similar species, indicated that irradiance may be 3–30 $\mu\text{E m}^{-2} \text{s}^{-1}$ at the understory, much lower than the irradiance reaching the canopy on sunny days at low tide in the spring, 2000 $\mu\text{E m}^{-2} \text{s}^{-1}$ (Scrosati and DeWreede, 1998).

On 7 April 2003, seven 25-cm² quadrats were randomly established in areas where *M. papillatus* gametophytes were abundant. Smaller sessile organisms, such as barnacles (*Balanus glandula*), occurred in the understory. On that date, all of the *M. papillatus* fronds were counted for each quadrat, and their length was measured to the nearest 5 mm. On 8 April, 84 fronds were randomly collected at the study site (cutting at the stipe–holdfast junction), but outside of the quadrats. The length and blotted-dry wet biomass of these fronds were measured in the laboratory to the nearest 1 mm and 1 mg, respectively. Since these fronds were collected at low tide, they were previously placed in seawater in the laboratory in order to ensure a full state of hydration before measuring their wet biomass. A power function was calculated between frond wet biomass and length (Table 1) through non-linear least squares estimation (Wilkinson et al., 1992). This function was applied to the values of frond length recorded for each quadrat to estimate the wet biomass of each frond and then stand wet biomass (by adding all values of frond wet biomass).

The mean water content of *M. papillatus* fronds was also calculated. For this, four groups of fully hydrated fronds (wet biomass range of groups = 237–447 mg) were collected at the study site, but outside of the quadrats. In the laboratory, these fronds were first hydrated fully, by placing them in seawater, and weighed (thus obtaining values of fully hydrated biomass). Then, the fronds were fully dried by placing them at a short distance under a lamp; the achievement of dry biomass was indicated when mass values remained constant after repeated weighings. This procedure indicated that the mean water content of fronds was 70.6 ± 0.9% (mean ± S.E.). This coefficient was used to estimate stand dry biomass from values of stand wet biomass. Frond density and stand dry biomass were determined for the same seven quadrats on 7 May, 6 June and 7 July 2003 (two of the seven quadrats were monitored on 8–15 July due to logistic constraints). For these additional sampling dates, frond density and length were measured as described above, but stand wet biomass was estimated using biomass–length functions that were determined specifically for each month (Table 1). Stand dry biomass was determined from values of stand wet biomass always using the 70.6% coefficient. Size inequality was determined for each quadrat and each sampling date based on the coefficient of variation (CV) for frond dry biomass. This coefficient measured the amount of variation relative to mean frond dry biomass for each quadrat, and it is expressed as the ratio between the standard deviation and the mean (Kokko et al., 1999).

To test for significant differences in frond density, stand dry biomass, and frond size inequality (CV for frond dry biomass) among months, repeated-measures analyses of variance (RM-ANOVAs; Howell, 2002) were performed, since these variables were measured for the same sampling units over time. The assumption of normality of scores was tested with normal

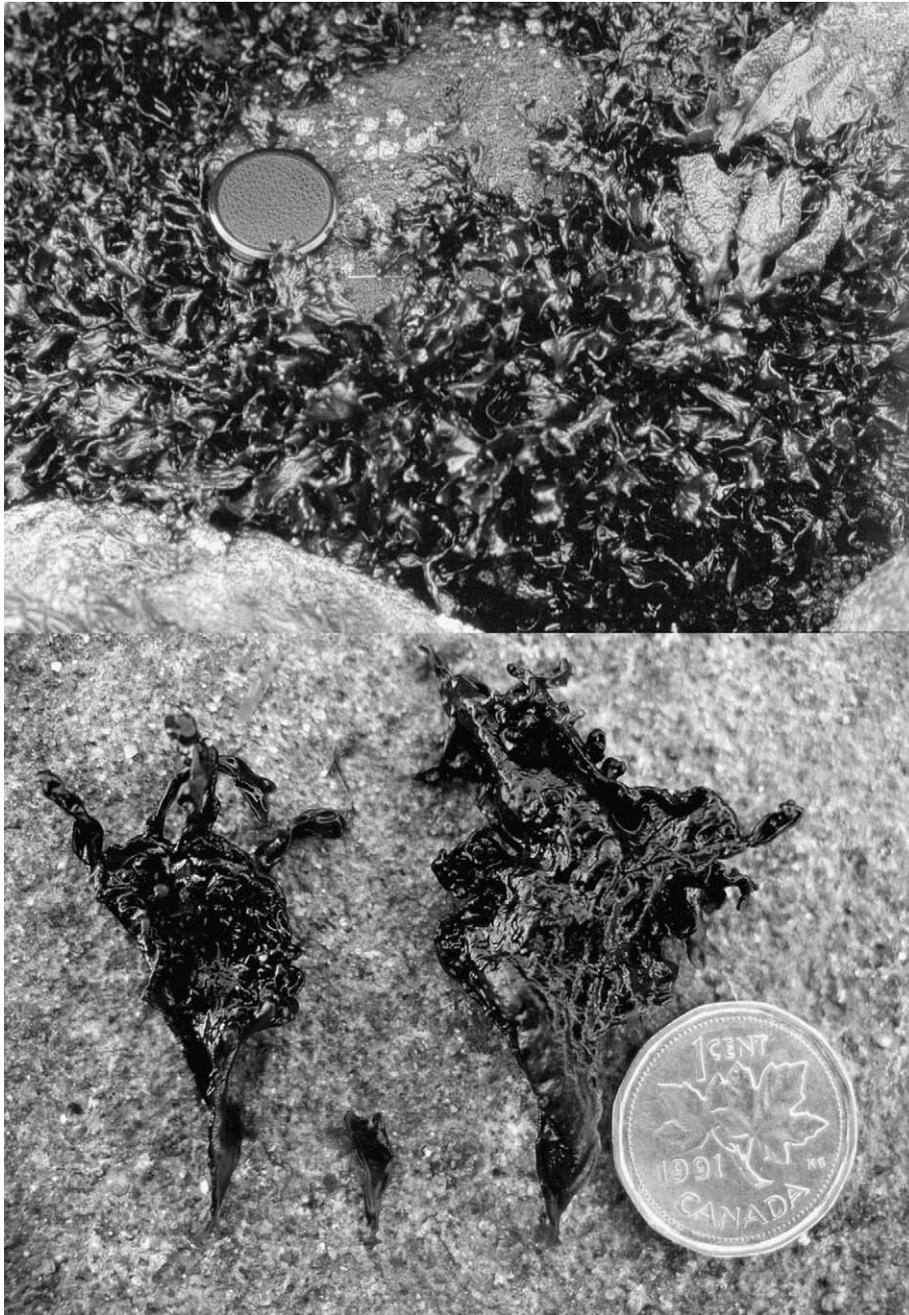


Fig. 1. Top: Dense stand of *Mastocarpus papillatus* from Acadia Beach; lens cap is 5 cm in diameter. Bottom: *M. papillatus* fronds of different sizes removed from the stand for clear view; coin is 1.8 cm in diameter. Photographs by the author.

Table 1
 Biomass–length power relationships ($M = aL^b$) for fronds of *Mastocarpus papillatus*

Collection date	Function	N	r	P	95% Confidence intervals	
					a	b
8 April 2003	$M = 3.044L^{2.868}$	84	0.96	<0.001	1.996–4.092	2.606–3.131
7 May 2003	$M = 4.839L^{2.480}$	80	0.91	<0.001	2.037–7.642	2.144–2.816
6 June 2003	$M = 15.293L^{2.015}$	68	0.90	<0.001	6.604–23.982	1.727–2.304
7 July 2003	$M = 3.909L^{2.819}$	66	0.96	<0.001	1.264–6.555	2.458–3.180

M, frond wet biomass (mg); L, frond length (cm).

probability plots and considered satisfactory for each of the three variables. Another assumption to meet in repeated-measures designs is that of compound symmetry of the variance–covariance matrix, which refers to a pattern of constant variances (one value per month) on the diagonal of this matrix and constant covariances (one value for each possible pair of months) off the diagonal (Howell, 2002). To correct for a possible lack of compound symmetry, the degrees of freedom can be adjusted before calculating probability values. The Huynh–Feldt adjustment is preferable over the Greenhouse–Geisser adjustment because it is considered to be more powerful and reliable (Myers and Well, 1991; Howell, 2002). Thus, the Huynh–Feldt adjustment was used for the RM-ANOVAs for frond density, stand dry biomass, and frond size inequality.

Since the three RM-ANOVAs detected significant differences, pairwise comparisons were done between consecutive months to locate when exactly the significant differences occurred. For this, three paired *t*-tests (April–May, May–June and June–July comparisons) were done for each variable, adjusting critical values to keep a familywise error rate of 0.05 for each variable (Howell, 2002). All of the statistical analyses were done with SYSTAT 5.2 for Macintosh (Wilkinson et al., 1992).

3. Results

Frond density ($F = 18.86$, $P < 0.001$, Huynh–Feldt $\varepsilon = 0.68$), stand dry biomass ($F = 25.22$, $P < 0.001$, Huynh–Feldt $\varepsilon = 0.55$) and frond size inequality ($F = 4.75$, $P = 0.013$, Huynh–Feldt $\varepsilon = 1$) varied significantly for *M. papillatus* during the study period (Fig. 2). For Acadia Beach, the growth season can be identified as the period until the June sampling date, since stand biomass increased significantly between April and May ($t = 4.72$, $P = 0.003$) and between May and June ($t = 5.29$, $P = 0.002$). Crowding conditions were reached then, as indicated by the fact that the canopy (constituted by large fronds) normally covered the substrate entirely, thus shading the small fronds because of the opaque nature of the canopy (Fig. 1). The beginning of the die-back season can be identified as the period after the June sampling date, since stand biomass ($t = 6.31$, $P = 0.001$) and frond density ($t = 6.42$, $P = 0.001$) significantly decreased simultaneously between June and July. Such a decreasing trend persisted until the following winter, when biomass and density reached their lowest levels for the year (R. Scrosati, personal observation).

To test whether self-thinning occurred at the very end of the growth season, the comparison focused on the last time interval sampled before the June sampling date. In the month comprised between May and June, stand biomass increased significantly, as stated above, but frond density remained statistically unchanged ($t = 1.27$, $P = 0.253$). Earlier in the growth season, between April and May, a significant increase in frond density ($t = 10.84$, $P < 0.001$) accompanied the above-mentioned increase in stand biomass. Thus, no evidence of self-thinning was found for any time interval during the growth season.

The temporal changes in frond size inequality were in agreement with a model of no self-thinning during the growth

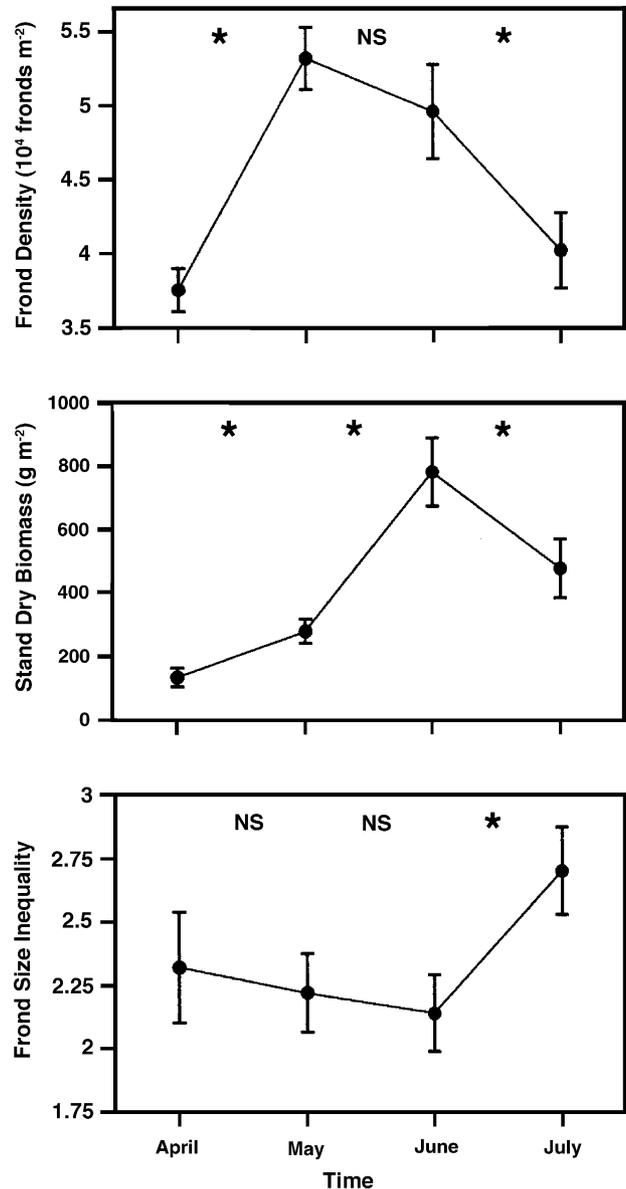


Fig. 2. Temporal variation of frond density, stand dry biomass, and frond size inequality (expressed as the coefficient of variation for frond dry biomass) for *Mastocarpus papillatus* from Acadia Beach (means \pm S.E. for all months). An asterisk (*) indicates that the means for two consecutive months differed significantly, while “NS” indicates a non-significant difference (see text for specific *P*-values).

season, since the CV for frond dry biomass remained statistically similar between April and May ($t = 0.57$, $P = 0.587$) and between May and June ($t = 1.14$, $P = 0.299$). Small fronds were more abundant than medium and large fronds for all quadrats and sampling dates.

The biomass–length allometric exponent (*b*) significantly decreased between April and June, as indicated by the lack of overlap in 95% confidence intervals for the exponent for April and June (Table 1). Between June and July, the biomass–length allometric exponent significantly increased, as indicated by the lack of overlap in 95% confidence intervals for the exponent for June and July (Table 1).

4. Discussion

4.1. Biomass–density dynamics

Among clonal seaweeds, the dynamics of the biomass–density relationship has only been studied for a few red (Rhodophyta) species. The predominant consensus is that self-thinning does not occur in stands of these algae during the growth season. This has been found for species of the Gelidiaceae (*Gelidium sesquipedale* (Santos, 1995) and *Pterocladia capillacea* (Scrosati and Servièrre-Zaragoza, 2000)), the Gigartinaceae (*M. parksii* (Scrosati and DeWreede, 1997) and *Chondrus crispus* (Scrosati and Servièrre-Zaragoza, 2000)), and now the Petrocelidaceae (*M. papillatus*). The findings of the present study are important because samplings were done twice more frequently than in past studies. Even with this increased temporal precision, however, the present study on *M. papillatus* found no statistical evidence for the occurrence of self-thinning, even shortly before the time of highest biomass accumulation in the population (June). Increasing the sampling frequency even further closely before the biomass peak would likely show also a lack of self-thinning, considering that density remained statistically similar between May and June in this study.

Given this seemingly general pattern, it is then worth analyzing why self-thinning occurs in unitary seaweeds but not in clonal seaweeds. The explanation of such a difference appears to be related to the capacity of a species to regulate density. For example, unitary seaweeds are generally unable to regulate the amount of new settlers at a site. If this amount is too high, then the stand will likely reach high levels of crowding as thalli develop during the growth season, thus causing extensive mortality among the smallest thalli, which become severely shaded by larger thalli. On the contrary, the amount of new fronds being produced each year in stands of clonal seaweeds where holdfasts are relatively perennial depends more on the holdfasts' vegetative activity than on recruitment from spores or zygotes. The production of new fronds from clonal holdfasts is density-dependent (Scrosati and DeWreede, 1997), which might prevent stands from reaching excessive levels of crowding that might otherwise result in self-thinning, in an analogy with what is hypothesized for many clonal vascular plants (de Kroon, 1993). The seasonality of the environment, which basically stops active growth at a similar time every year and decreases biomass and density through a variety of stresses, might be another factor preventing excessive levels of crowding from being reached. Physiological integration among ramets, once thought to be a possible explanation for the lack of ramet self-thinning, has been more recently put into question after re-analyzing the existing evidence (de Kroon, 1993). These ideas are discussed in more detail in a review of the studies on biomass–density relationships done for seaweeds (Scrosati, 2005).

It is relevant to note, however, that self-thinning was indeed reported for one species of clonal red alga, *Asparagopsis armata* (Bonnemaisoniaceae; Flores-Moya et al., 1997). Such a study did not specify whether self-thinning occurred among fronds within genet, among genet, or at both levels of

organization and the size of fronds and holdfasts was not specified either. In theory, it is possible that neighboring genet, that produce relatively long fronds, have relatively small holdfasts, and do not experience coalescence (the Bonnemaisoniales do not coalesce; Santelices et al., 1999) may undergo self-thinning in crowded conditions, thus resembling the dynamics of a stand of unitary seaweeds. If self-thinning occurred among such clonal genet, then a negative biomass–density relationship would also be observed at the ramet level (such was the case noted for some clonal vascular plants; Kays and Harper, 1974; Lonsdale and Watkinson, 1982; Makita, 1996). Flores-Moya et al. (1997) detected self-thinning by measuring frond density regardless of which genet fronds belonged to, so the above is a possible explanation for their observations. The study on *A. armata* might indicate that self-thinning might occur for groups of clonal seaweeds other than the Gelidiaceae, Gigartinaceae, and Petrocelidaceae. This points out the need of documenting biomass–density dynamics for groups of clonal seaweeds differing in frond size, holdfast size, and coalescence potential. Westoby (1984) and de Kroon and Kalliola (1995) discuss possible biomass–density trajectories for clonal vascular plants and how they may end up self-thinning or not, depending on clonal attributes and initial density. Their analyses might be useful for the needed research on clonal seaweeds.

It is also worth noting that the biomass–length allometric exponent decreased significantly between April and June. This means that fronds had less biomass per unit of length as the growth season progressed. Such a temporal change in allometry might have resulted from increasing competition levels among fronds as biomass was progressively accumulating in the population. Interestingly, the biomass–length exponent increased significantly after the peak in stand biomass (June), as would be predicted under decreasing crowding levels. Experimental tests of frond performance and competition will be needed to elucidate the mechanistic basis of these temporal changes in allometry.

4.2. Size inequality dynamics

The statistical constancy of frond size inequality observed for *M. papillatus* during its growth season also agrees with the notion that self-thinning did not occur during this period. In self-thinning stands of unitary plants, the smallest individuals progressively die as a result of asymmetric competition for light with larger individuals, causing a decrease in size inequality as stand biomass increases (Weiner, 1988; Weiner et al., 2001). Frond biomass inequality may decrease during the growth season for some clonal seaweeds, such as *M. parksii*, but not as a result of self-thinning among fronds, because this process does not occur for these algae (Scrosati and DeWreede, 1997). The decrease in size inequality for *M. parksii* might actually result from the selective loss of distal tissues in large fronds due to bleaching (Scrosati and DeWreede, 1998) and grazing of bleached tips by littorinid snails (Heaven and Scrosati, 2004). Extensive bleaching or evident signs of herbivory were not observed in the studied stands of *M. papillatus*. The statistical

constancy of frond biomass inequality during the growth season has been noted for other clonal seaweeds, such as *G. sesquipedale* (Santos, 1995).

In stands of clonal vascular plants, shoot size inequality may remain constant or even decrease during the growth season, but without being associated to shoot self-thinning, which generally does not occur in habitats where seasonal die-back occurs every year (de Kroon, 1993; Hara, 1994). Thus, there is a similarity in stand dynamics (including biomass–density dynamics and size inequality dynamics) between clonal vascular plants and clonal seaweeds that display marked seasonal growth (self-thinning may develop in stands of clonal plants that grow continuously for several years, such as in tropical habitats; de Kroon and Kalliola, 1995; Peterson and Jones, 1997). On the other hand, the dynamics of size inequality for unitary seaweeds agree well with the pattern known for unitary vascular plants, as size inequality has also been observed to decrease as a result of self-thinning in unitary seaweeds (Creed et al., 1998; Arenas and Fernández, 2000). The ecology of stand dynamics has traditionally been more studied for vascular plants than for seaweeds. Therefore, the observations described above indicate that concepts developed from ecological research on vascular plants may be more applicable to the ecological study of seaweeds than what is commonly appreciated.

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