NOTE

SELF-THINNING AND SIZE INEQUALITY DYNAMICS IN A CLONAL SEAWEED (SARGASSUM LAPAZEANUM, PHAEOPHYCEAE)¹

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Fronds of clonal seaweeds with extensive holdfasts relative to frond size are known not to self-thin during growth, even in crowded stands. We tested whether frond self-thinning would occur for a clonal seaweed with large fronds relative to holdfast size, as such traits are more similar to those of unitary seaweeds, which do self-thin in crowded conditions. We used Sargassum lapazeanum Setch. et N. L. Gardner (Fucales, Phaeophyceae) from the Pacific coast of Mexico, for which we first confirmed its clonal nature by performing a regeneration experiment in culture tanks. During the growth season (winter to late spring), S. lapazeanum stand biomass increased, while frond density and size inequality (Gini coefficient for frond biomass) decreased. These results indicate that self-thinning occurred at the frond level. We propose a conceptual model for frond dynamics for clonal seaweeds in general. In stands of clonal species with small fronds and relatively extensive holdfasts (particularly when holdfasts are perennial), frond dynamics would be determined mostly by intraclonal regulation, which seems to prevent excessive crowding from occurring. Such species display a positive biomass-density relationship during the growth season. On the contrary, in stands of clonal species with large fronds relative to holdfast size, frond dynamics would be determined mostly by interactions among genets. For such species, self-thinning may be detected at the frond level in crowded stands, resulting in a negative biomass-density relationship during growth.

Key index words: clonal; Gini coefficient; Sargassum; self-thinning; size inequality

The search for universal principles in seaweed population dynamics is an active research area (Collado-Vides 2002, Santelices 2004, Scrosati 2005). The clonal or unitary nature of a species is a useful trait to predict its population dynamics. A clonal seaweed is that in which the holdfast produces a number of fronds, each one having the potential for autonomous life if it becomes separated from the rest of the thallus while remaining attached to the substrate by holdfast tissue (Scrosati 2005). The holdfast tissue of such an isolated frond has the capacity to generate new holdfast tissue horizontally, which subsequently may produce new fronds. Fronds of clonal seaweeds can therefore be referred to as "ramets," a term originally developed for shoots of clonal vascular plants (de Koon and van Groenendael 1997), while the entire thallus (holdfast and fronds) that develops from one spore, zygote, or parthenogenetic gamete constitutes the genet (Scrosati 2002). A unitary seaweed only produces one frond or axis from the holdfast (Santelices 2004).

Understanding the temporal relationship between biomass and density during growth allows the prediction of population trends better than by considering density alone (Westoby 1984). This concept is important because several population models in ecology are solely based on density (Gurney and Nisbet 1998). Recent studies have shown that biomass–density dynamics differ between clonal and unitary seaweeds. In crowded stands of unitary seaweeds, stand biomass increases, involving the progressive death of small individuals because of competition with larger individuals. Such a self-thinning process determines a negative temporal relationship between stand biomass and density (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). For clonal seaweeds, biomass–density dynamics have not been studied at the genet level (genets are difficult to identify in crowded stands; Scrosati 2005), but at the frond level. In crowded populations of clonal species, fronds generally do not self-thin during growth (Santos 1995, Scrosati and DeWreede 1997, Scrosati and Servière-Zaragoza 2000, Scrosati 2006); frond density and stand biomass are actually positively related over time because of the vegetative production of new fronds by holdfasts.

Self-thinning was reported at the frond level for a clonal seaweed (Asparagopsis armata; Flores-Moya

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et al. 1997). Then, what are the conditions necessary for self-thinning to occur in clonal seaweeds? The clonal species observed not to self-thin (Chondrus crispus, Gelidium sesquipedale, Mastocarpus papillatus, Mazzaella parksi, and Pterocladiella capillacea) have perennial holdfasts that grow extensively. Their fronds are up to 5–20 cm long, and pronounced self-shading develops under a mature canopy (Scrosati and DeWreede 1998). Fronds are mostly produced by the perennating holdfasts, recruitment from spores being limited (Santos and Duarte 1996, Scrosati 1998). The density-dependent production of fronds (Scrosati and DeWreede 1997) and the widespread mortality from abiotic stress when biomass peaks annually are thought to explain self-thinning avoidance (de Kroe 1993, Scrosati 2005). Other clonal species, however, have large fronds relative to holdfast size, so small genets could be suppressed in crowded stands, resulting in their progressive mortality. If self-thinning did occur at the genet level for such clonal seaweeds, it could be detected at the ramet (frond) level, as shown by studies on clonal vascular plants whose genets undergo self-thinning (Kays and Harper 1974, Lonsdale and Watkinson 1982, Makita 1996). Thus, we investigated biomass and density dynamics at the frond level for a clonal seaweed with large fronds relative to holdfast size, under the hypothesis that self-thinning would occur during the growth season. In self-thinning populations of land plants, size inequality decreases over time, as only the smallest size class predominantly suffers mortality due to asymmetric competition with larger size classes (Hara 1988, Weiner et al. 2001). Size inequality also decreases in self-thinning stands of unitary seaweeds (Creed et al. 1998, Arenas and Fernández 2000), so we also hypothesized that frond size inequality would decrease for our study seaweed during the growth season.

We used S. lapazeanum, an endemic species from the Gulf of California, on the Pacific coast of Mexico (Setchell and Gardner 1924, Dawson 1944, Núñez-López and Casas-Valdez 1997, Paul-Chávez and Riosmena-Rodríguez 2000). The study was conducted at Piedras Coloradas (24° 21' N, 110° 40' W), near San Juan de la Costa, on the coast of La Paz Bay. Thalli of S. lapazeanum occur on rocks between the low intertidal zone and the shallow subtidal zone across a belt that is 2–3 m wide. A description of this subtropical coast and a map indicating the study site are in Rivera and Scrosati (2006). Before our study, it was uncertain whether S. lapazeanum is a clonal or unitary species. At Piedras Coloradas, several fronds may arise from a given holdfast, which suggests that S. lapazeanum is clonal, although the same pattern could also result from the hypothetical coalescence of neighboring holdfasts in a unitary species. To answer this fundamental question, we performed an experiment. On 7 April 2004, we collected rocks with S. lapazeanum. In the laboratory, we removed frond and holdfast material until only one frond and its basal holdfast tissue were left attached to a rock. We produced a total of 61 such “unifrond” individuals. These rocks were kept in tanks with running seawater under a natural light regime until 31 May 2004. The possible clonal nature of S. lapazeanum would be indicated by the horizontal regeneration of holdfasts and subsequent production of new fronds.

The annual cycle of population dynamics for S. lapazeanum from Piedras Coloradas was studied between February 2000 and February 2001 (Rivera and Scrosati 2006). The growth season occurred between winter and late spring, while dieback occurred in summer and autumn. Rivera and Scrosati (2006) measured frond density and stand biomass at regular time intervals for thirty 0.25 m² (50 cm × 50 cm) quadrats randomly placed on each date across the middle of the S. lapazeanum belt, where this species virtually constitutes a monospecific stand. The monthly means for density and biomass reported in Rivera and Scrosati (2006) were based on 30 quadrats, including those without thalli, because the objective of that study was to document abundance across the entire habitat. However, self-thinning tests must only use means calculated from quadrats with thalli. The number of quadrats with S. lapazeanum was six in February, 18 in March, 12 in April, 11 in May, 13 in June, and 12 in August. To measure frond density and stand wet biomass, all S. lapazeanum material was removed from such quadrats. Frond density was determined by counting the fronds, and stand wet biomass by weighing the collected material, previously eliminating epiphytes and drying frond surfaces with paper towels. We tested for self-thinning by comparing frond density and stand wet biomass early and late (when stand biomass peaked) in the growth season using t-tests (Sokal and Rohlf 1995). The sampling date representing the annual biomass peak was May (Fig. 1). Self-thinning would be indicated by an increasing stand biomass and decreasing frond density.

Size inequality may be described by the Gini coefficient (Kokko et al. 1999), which ranges between a minimum of 0, when all individuals are equal in size (perfect equality), and a theoretical maximum of 1 in an infinite population in which every individual, except one, has a size of 0 (perfect inequality). We analyzed the temporal variation in frond biomass inequality. For each quadrat, we measured the length of each frond from the base of the stipe to the tip of the longest primary branch. Then, we calculated frond wet biomass using biomass–length functions (Table 1) determined with fronds collected outside of the quadrats (functions were parameterized through nonlinear least-squares regression). We programmed the formula to calculate the Gini coefficient (see Kokko et al. 1999) in MatLab 5.3 and then calculated this coefficient for each
To test whether size inequality decreased during the growth season, we compared the Gini coefficient early and late (when stand biomass peaked) in the growth season using a t-test. The experimental unifrond individuals regenerated holdfast tissue across the rocky surfaces. On 19 April, the first upright structure was visible in one of the regenerating holdfasts. On 31 May, 36 of the 61 originally unifrond individuals (59%) had produced each at least one upright structure equal in form to the young fronds from natural populations. Therefore, the frond of *S. lapazeanum* can be considered as the ramet, and this species is confirmed to be clonal. The temporal variation in frond density, stand biomass, and frond size inequality is shown in Figure 1. In tests of self-thinning, statistical comparisons between any two monthly means must be done at the appropriate temporal scale. Using intervals that are too long might exceed the growth season, while using intervals that are too short might not allow temporal differences (positive or negative) to be detected on statistical grounds. Thus, not all monthly means are statistically compared, but all monthly values are shown in Figure 1 for completeness. In late winter (between February and March), frond density ($t = 2.45$, $P = 0.029$), stand wet biomass ($t = 3.30$, $P = 0.004$), and frond size inequality ($t = 6.89$, $P < 0.001$) increased. During the main growth period (between March and May), stand biomass kept increasing ($t = 2.36$, $P = 0.035$), but frond density ($t = 1.97$, $P = 0.030$) and size inequality ($t = 2.25$, $P = 0.035$) decreased. In May, the *S. lapazeanum* canopy covered nearly 100% of the substrate where this species occurred. Between late spring and midsummer (between May and August), stand biomass decreased ($t = 3.40$, $P = 0.007$), indicating the beginning of the dieback season, while frond density showed no significant change ($t = 0.99$, $P = 0.336$), and size inequality decreased ($t = 5.36$, $P < 0.001$).

In summary, stand biomass of *S. lapazeanum* increased, while frond density and size inequality decreased during the growth season. In self-thinning plant populations, size inequality decreases as a result of the predominant mortality of the smallest size class (Hara 1988, Weiner et al. 2001). The temporal changes in frond size structure for *S. lapazeanum* were reported in a previous paper (Rivera and Scrosati 2006), but it is worth highlighting here that the mortality rate for the smallest size class was higher than that for any of the larger size classes between March and May. These results indicate that self-thinning occurred for *S. lapazeanum*. Because genets were impossible to identify, we cannot state whether frond density decreased because of self-thinning among genets, among fronds within genets, or through both processes. In any case, it is now clear that self-thinning may occur for some clonal seaweeds. Our findings thus add to the first report of self-thinning for a clonal seaweed (Flores-Moya 2006).

### Table 1. Parameters for the power relationship between frond wet biomass ($B$, in g) and frond length ($L$, in cm), $B = aL^b$, for *Sargassum lapazeanum* from La Paz Bay.

<table>
<thead>
<tr>
<th>Month</th>
<th>a</th>
<th>b</th>
<th>r</th>
<th>P</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>February</td>
<td>0.024</td>
<td>1.669</td>
<td>0.77</td>
<td>&lt;0.001</td>
<td>113</td>
</tr>
<tr>
<td>March</td>
<td>0.007</td>
<td>2.101</td>
<td>0.86</td>
<td>&lt;0.001</td>
<td>264</td>
</tr>
<tr>
<td>May</td>
<td>0.005</td>
<td>1.333</td>
<td>0.68</td>
<td>&lt;0.001</td>
<td>220</td>
</tr>
<tr>
<td>August</td>
<td>0.018</td>
<td>1.743</td>
<td>0.76</td>
<td>&lt;0.001</td>
<td>220</td>
</tr>
</tbody>
</table>

Fig. 1. Temporal variation in (A) frond density, (B) stand wet biomass, and (C) frond size inequality (Gini coefficient for frond wet biomass) for *Sargassum lapazeanum* during and after its growth season in La Paz Bay, Mexico. Data are monthly means ± SE.
et al. 1997), ours being the first report for a brown clonal species.

The relative size of fronds and holdfasts appears to help predict whether a clonal seaweed will self-thin or not. Holdfasts of the clonal species that do not self-thin (Santos 1995, Scrosati and DeWreede 1997, Scrosati and Servière-Zaragoza 2000, Scrosati 2006) are generally larger than fronds and are perennial, being the main source of new fronds (Santos and Duarte 1996, Scrosati 1998). As a result, frond dynamics appear to be determined more by regulatory processes within genets than by interactions among neighboring genets (Fig. 2). For such species, fronds do not self-thin likely because of density dependence in the vegetative production of fronds (Scrosati and DeWreede 1997) and the extensive mortality from abiotic stress when stand biomass peaks every year (Scrosati and DeWreede 1998), as such mechanisms prevent excessive crowding. The few genets that are recruited every year could be competitively excluded by large genets in noncoalescing clonal species (Santelices et al. 1999) or absorbed by large genets in coalescing clonal species (Santelices et al. 2004). Overall frond density would change little in the first case and likely by nothing in the second case. This conceptual model is in line with current views for clonal vascular plants that do not self-thin (de Kroon 1993, Suzuki and Hutchings 1997). The physiological mechanisms responsible for intraclonal regulation are still unclear (Tomlinson and O’Connor 2004).

Clonal seaweeds with large fronds relative to holdfasts are a different case, because small genets may be shaded by larger genets (Fig. 2) and competitively excluded. In other words, frond dynamics would be determined more by interactions among neighboring genets than by intraclonal regulation. Fronds longer than 50 cm are common in mature S. lapazaeum stands (up to 1.34 m at Piedras Coloradas; Rivera and Scrosati 2006), while holdfasts are usually <10 cm in diameter. Coalescence with large genets might prevent small ones from dying, but they would all have to make direct contact for that to occur, which is unlikely; in any case, whether coalescence occurs for S. lapazaeum is unknown. Overall, the occurrence of self-thinning for S. lapazaeum supports the above theory. Future research should investigate if small genets undergo significant mortality in crowded populations, as predicted by this conceptual model.

Self-thinning, thought for some time not to occur for clonal vascular plants (de Kroon and Kalliola 1995), is common during the growth phase for a clonal bamboo (Sasa kurilensis) that has large ramets and small basal structures (rhizomes), analogous to S. lapazaeum. For S. kurilensis, self-thinning resulted from genet mortality in crowded stands (Makita 1996). Interestingly, the rhizomes of another bamboo species (Sasa tsuboiana) grow extensively across the substrate, and ramet dynamics are determined mostly by intraclonal regulation. In an analogy with the clonal seaweeds with large holdfasts relative to frond size, biomass and ramet density increase together (a positive relationship) during the growth phase for S. tsuboiana (Makita 1996). Self-thinning does occur at the end of the growth phase for S. tsuboiana, but this species grows for several years, as opposed to fronds of the above-mentioned clonal seaweeds, which suffer widespread mortality from abiotic stress when biomass peaks every year. The challenge ahead is to determine the convergences in biomass–density dynamics between vascular plants and seaweeds, which should result in a more predictive population ecology for primary producers in general.

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