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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.

Keywords: Clonal; Crowding; Gigartinales; *Mastocarpus*; Petrocelidaceae; Self-thinning; Size inequality

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

On 7 April 2003, seven 25-cm^2 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 $70.6 \pm 0.9\%$ (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