

THE IMPACT OF FROND CROWDING ON FROND BLEACHING IN THE CLONAL INTERTIDAL ALGA *MAZZAELLA CORNUCOPIAE* (RHODOPHYTA, GIGARTINACEAE) FROM BRITISH COLUMBIA, CANADA¹

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ABSTRACT

The importance that frond crowding represents for the survival of fronds of the clonal intertidal alga *Mazzaella cornucopiae* (Postels et Ruprecht) Hommersand (Rhodophyta, Gigartinales) was investigated in Barkley Sound, British Columbia, Canada. Frond density is high for this species, up to 20 fronds·cm⁻² in the most crowded stands. Frond crowding imposes a cost in the form of reduced net photosynthetic rates when fronds are fully hydrated as a result of reduced irradiance compared with experimental (not found naturally) low-density stands. However, the interaction between desiccation and irradiance alters this relationship between net photosynthetic rates and frond density. During a typical daytime low tide in spring, irradiance is 10–30 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ below the canopy of fronds, and frond desiccation (relative to total water content) can reach 43% at the end of the low tide. In contrast to natural stands, fronds from experimentally thinned stands are subjected to irradiances up to 2000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ because of the spatial separation among fronds and can desiccate up to 81% at the end of the same low tide. Laboratory experiments showed that negative net photosynthetic rates occur between 40% and 80% desiccation at an irradiance of 515 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and the literature suggests that strong bleaching could occur as a result. At 20 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of irradiance and desiccation levels up to 40%, simulating understory conditions of natural stands, net photosynthetic rates are never negative. Experimental thinning of stands of *M. cornucopiae* done during spring effectively resulted in a stronger extent of frond bleaching compared with natural stands. Therefore, the cost of reduced net photosynthetic rates at high frond densities when fronds are fully hydrated is counterbalanced by the protective effects of frond crowding against extensive bleaching, essential for survival at the intertidal zone. Future research will have to demonstrate the possible relationship between the frequency and duration of negative net photosynthetic rates and the extent of frond bleaching.

Key index words: bleaching; desiccation; frond crowding; Gigartinales; intertidal zone; irradiance; *Mazzaella cornucopiae*; net photosynthesis

In the intertidal zone, the regular alternation of periods of submergence and emergence results in dramatic changes in the magnitude of abiotic and biotic parameters, such as water and nutrient avail-

ability, irradiance, temperature, hydrodynamic forces, and the intensity of grazing and predation. Benthic intertidal organisms must develop strategies to cope with such variability, allowing them a continued survival in their habitat.

For intertidal seaweeds, desiccation during low tides constitutes a stress that may severely limit their photosynthetic and growth rates (Johnson et al. 1974, Brinkhuis et al. 1976, Quadir et al. 1979, Hay 1981, Hodgson 1981, Oates and Murray 1983, Oates 1985, 1986, Brown 1987, Madsen and Maberly 1990, Levitt and Bolton 1991, Bell 1993, Britting and Chapman 1993, Dudgeon et al. 1995). The simultaneous occurrence of strong desiccation and high irradiance, which may be frequent during spring and summer low tides in temperate coasts, may result in bleaching of algal tissues (Herbert and Waaland 1988, Herbert 1990, Kain and Norton 1990, Lobban and Harrison 1994). Bleaching involves the complete loss of photosynthetic pigments, constituting a disruptive stress (Davison and Pearson 1996) because the affected tissue is unable to recover.

The red alga *Mazzaella cornucopiae* (Postels et Ruprecht) Hommersand (a picture of a typical stand appears in Scrosati and DeWreede 1997) occurs frequently in the high intertidal zone of rocky areas of outer Barkley Sound, British Columbia, Canada, where it is usually a dominant species (Kim 1995, Kim and DeWreede 1996a, b, Scrosati 1997, Scrosati and DeWreede 1997). It is a clonal alga, and its thallus is composed of a crustose holdfast and several upright, foliose fronds, forming dense turfs that may cover extensive areas. During spring and summer at Barkley Sound, the upper portions of the largest fronds become completely bleached, and bleached areas are entirely lost by the end of the summer, apparently by a combination of wave action and herbivory by littorinid snails (Kim and DeWreede 1996b, Scrosati 1997).

Why is bleaching restricted to the upper portions of the largest fronds of *M. cornucopiae* without affecting more fronds or entire thalli? In this paper, we explore a possible explanation for this, one that may contribute to understanding the frequent dominance of *M. cornucopiae* in the high intertidal zone of Barkley Sound. A high frond density may prevent strong desiccation and may decrease the irradiance in the understory compared with the canopy, therefore possibly decreasing the extent of bleaching relative to hypothetical (they do not occur in nature) low-density stands. The objective of this paper is to

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assess the effects that the density of fronds of *M. cornucopiae* have on frond desiccation, understory irradiance, net photosynthetic rates, and the extent of frond bleaching, and to discuss the possible links between these processes.

MATERIALS AND METHODS

Study site and basic description of Mazzaella cornucopiae. The fieldwork was conducted in Prasiola Point (48° 49' N, 125° 10' W), a rocky outcrop located in Barkley Sound on the west coast of Vancouver Island, British Columbia, Canada. Biogeographically, this coast belongs to the cold-temperate northeastern Pacific region (Lüning 1990). Close to Prasiola Point, mean monthly temperature of the sea surface varied between 8.6° C (winter) and 16.1° C (summer) between the summer seasons of 1993 and 1995, whereas mean monthly salinity of seawater varied between 26.7‰ (winter) and 31.5‰ (summer) during the same period (Scrosati 1997). *Mazzaella cornucopiae* is one of the species located highest in the intertidal zone at Prasiola Point, occurring between about 3 and 4 m above the lowest normal tide (measurements based on Canadian Chart Datum). It is the dominant alga at the wave-exposed side (west) of Prasiola Point, but, at the relatively wave-protected site (east), it shares the substratum more evenly with two fucoid algae, namely, *Fucus gardneri* Silva and *Pelvetiopsis limitata* Gardner. The size of the largest genets (a thallus originated by a single spore) of *M. cornucopiae* is unknown, as high frond densities, possible coalescence among growing genets, and the potential breakage of one genet into independent-life clonal fragments (sensu Eriksson and Jerling 1990) prevent an accurate field identification in the largest stands. The density of fronds can be up to 20 fronds·cm⁻² in the most crowded stands. Because the tidal regime is mixed in Barkley Sound, *M. cornucopiae* is subjected to low tides twice a day. The longest of the two daily low tides occurs mostly during daytime in spring and summer and mostly during darkness in fall and winter (Scrosati 1997).

Effects of frond density on frond desiccation and understory irradiance. To test for the effects of frond density on frond desiccation during low tides, eight 4-cm² quadrats were randomly located on 19 May 1995 along a transect line placed where *M. cornucopiae* completely covered the substratum. The thalli in those quadrats were thinned to an average frond density of 1.5 ± 0.2 fronds·cm⁻² (mean ± SE, n = 8). Control (undisturbed) areas consisted of an additional eight 4-cm² quadrats that were randomly located along the same transect line. On 20 May, a similar number of fronds was collected from thinned and control quadrats (n = 44 and n = 49, respectively) and carried in closed plastic bags to the laboratory in Bamfield Marine Station, where their biomass ("desiccated biomass") was measured to the nearest milligram. Fronds were then rehydrated in seawater until maximum biomass was attained ("fully hydrated biomass"). For two groups of 15–20 fully hydrated fronds of *M. cornucopiae* (0.91 g and 1.60 g each group) from the same area, artificially induced desiccation (using lamps in the laboratory) to constant biomass indicated that the total water content of fronds was 72% (73% and 71% for the two groups of fronds, respectively).

For the fronds collected from the experimental quadrats, percentage desiccation was then estimated as follows:

$$\% \text{ Desiccation} = 100(B_h - B_d)(0.72 B_h)^{-1}$$

where B_h is "fully hydrated biomass," B_d is "desiccated biomass," and $(0.72 B_h)$ represents the estimated total water content of each frond. On 20 May, the high tide previous to the time of collection of fronds occurred at approximately 0530. Given the elevation of the experimental site (about 3.3 m above the lowest normal tide) and considering that waves were small that day, the time of emersion between the last previous wave and the time of collection of fronds (about 1530) was approximately 9.5 h. The quadrats were fully exposed to sunlight and moderate wind during that time.

To test for differences between percentage desiccation of fronds from thinned and from control quadrats, an independent *t*-test (Howell 1992) was done. To avoid pseudoreplication (Hurlbert 1984), values of percentage desiccation were averaged for

each quadrat first, as suggested by Hurlbert (1984). The *t*-test was done with SYSTAT 5.2.1 for Macintosh (Wilkinson et al. 1992).

To evaluate the effects that frond density have on the irradiance that reaches the understory of stands of *M. cornucopiae*, the irradiance was measured with a light meter (model LI-COR LI-189) probe both above and below the frond canopy and under both full cloud cover and direct sunlight on 2 June 1996.

Effects of desiccation and irradiance on the net photosynthetic rate of fronds. On 3 June 1996, fronds of *M. cornucopiae* were collected during low tide from Prasiola Point at approximately 2000, shortly before sunset. Fronds were clumped together and kept in air in a closed cooler, which was taken to the laboratory at the University of British Columbia in Vancouver. On 4–5 June, fronds were placed in a container with seawater at 12°–15° C under room light for 30–60 min before net photosynthetic rates were measured. The aerial net photosynthetic rate for fronds was measured by monitoring changes in CO₂ concentration within a closed chamber using an infrared gas analyzer (IRGA, Nortech Control Equipment Inc., Delta, British Columbia, Canada). Two irradiances were used for this experiment: a "low" irradiance of 20 μmol·m⁻²·s⁻¹, which simulated the average irradiance found below the canopy of fronds of natural stands (see Results), and a "high" irradiance of 515 μmol·m⁻²·s⁻¹, which may occur only at the canopy level of natural stands or at any level of experimentally thinned stands (see Results) because of the spatial separation among fronds. The value used here as high irradiance was chosen because it is within the range of saturation irradiances for intertidal seaweeds (400–600 μmol·m⁻²·s⁻¹; Lobban and Harrison 1994).

To measure net photosynthetic rates, fronds were blotted dry after being taken from the container with seawater and were placed inside the photosynthetic chamber. To avoid self-shading, fronds were attached along a string that was hung from the top of the chamber. The air temperature was 21.5° C and 25.0° C for the low- and high-irradiance experiments, respectively. To prevent shortage of CO₂ within the photosynthetic chamber during each experimental run as a consequence of frond photosynthesis, additional CO₂ was added at the beginning of each run by exhaling air into the chamber. The initial concentration of CO₂ was 522 ± 5 ppm (mean ± SE, n = 5) for the low-irradiance experiment, whereas the final concentration was 479 ± 5 ppm. For the high-irradiance experiment, the initial concentration of CO₂ was 512 ± 12 ppm (n = 5), and the final concentration was 466 ± 6 ppm. Only in the high-irradiance experiment did the concentration of CO₂ reach its lowest value during the experiment (435 ± 4 ppm), and it increased up to the final value mentioned above. Therefore, the concentration of CO₂ was never lower than that of atmospheric air at ground level (350–400 ppm), so it was not considered to be limiting for photosynthesis.

The air that flows within the photosynthetic chamber of the IRGA caused fronds to desiccate more rapidly than they would under natural conditions. To determine the relationship between frond desiccation and time with this particular model of IRGA, two groups of medium to large fronds were separately placed inside the photosynthetic chamber (1.60 g of total wet biomass for the low-irradiance run and 0.91 g for the high-irradiance run). During the course of both experimental runs, total frond biomass was estimated to the nearest 0.01 g at 1-min intervals for 70 min at low irradiance and for 30 min at high irradiance as desiccation proceeded. To measure total frond biomass during each run, the string that held the fronds was removed from the chamber for about 5 s every 1 min. After the 30- and 70-min periods, both groups of fronds were dried to constant biomass. Total water content was 71% and 73% of the total wet biomass for the groups of fronds under low and high irradiance, respectively. With values of total wet biomass, desiccated biomass for each time of frond weighing, and total water content, percentage desiccation of fronds (percentage of lost water relative to total water content) was calculated for each time. Percentage desiccation had a high positive linear correlation with time for both irradiances ($r = 0.997$).

For the actual experiments done to measure net photosynthetic rates of fronds (5 replicate runs for each irradiance), percentage

desiccation could not be measured during the experimental runs because the photosynthetic chamber had to be closed. Rather, knowing that percentage desiccation and time are highly linearly correlated for our experimental design, the temporal variation of percentage desiccation was estimated with the linear relationship:

$$\% \text{ Desiccation} = A \cdot \text{Time} \quad (A = \text{constant})$$

The constant A was calculated for each of the 10 experimental runs, considering the two known desiccation-time pairs—the initial one (desiccation = 0%, time = 0 min) and the final one—which was different for each run.

Total initial biomass was 2.97 ± 0.04 g (mean \pm SE, $n = 5$) for the low-irradiance experiment and 2.04 ± 0.12 g (mean \pm SE, $n = 5$) for the high-irradiance experiment. The concentration of CO_2 inside the photosynthetic chamber was determined every 1 min for 60–90 min. Net photosynthetic rates were estimated from the changes in CO_2 concentration that occurred during 2-min intervals around desiccation levels separated by 10 units (0%, 10%, 20%, and so on). The net photosynthetic rate for the final desiccation levels for each run was estimated as the change in CO_2 concentration that occurred during the last 2 min. Net photosynthetic rates were finally expressed as CO_2 uptake rates in $\mu\text{mol CO}_2 \cdot \text{g}^{-1} \cdot \text{min}^{-1}$ (dry biomass) $\cdot \text{min}^{-1}$. The final average percentage desiccation for both irradiance treatments (41% for low irradiance and 80% for high irradiance) was purposely reached to simulate the percentage desiccation that was recorded for natural (43%) and thinned (81%) stands of *M. cornucopiae* from Prasiola Point after 9.5 h exposure to the air (close to the end of a daytime low tide) on 20 May 1995 (see Results).

To test for the effects of frond desiccation on net photosynthetic rates, a one-way repeated-measures analysis of variance (ANOVA; Howell 1992) was performed separately for each irradiance through randomization tests (Edgington 1987, Manly 1991) because of the violation of the normality assumption (Howell 1992). These ANOVAs were performed with the program Randomization Tests developed by Eugene S. Edgington (University of Calgary, Calgary, Alberta, Canada) for DOS. After the two ANOVAs were done, two-tailed paired t -tests were used to compare mean photosynthetic rates between consecutive desiccation levels. Additional t -tests were performed to test whether net photosynthetic rates were significantly different from zero or significantly negative, as appropriate. To test the hypothesis that the net photosynthetic rate is lower at low irradiance than at high irradiance when fronds are fully hydrated (one of the possible costs of frond crowding), a one-tailed independent t -test was used to compare photosynthetic rates under both irradiances at 0% desiccation. The t -tests were done using SYSTAT 5.2.1. The validity of using t -tests (and other tests of multiple comparisons) after an ANOVA is a highly controversial topic among statisticians; we followed Soto and Hurlbert (1991).

Effect of frond density on the extent of frond bleaching. The effect that the density of fronds of *M. cornucopiae* has on the extent of frond bleaching was assessed between the spring and the summer of 1996. On 3 June 1996, 10 4-cm² quadrats were randomly located along a permanent transect line where *M. cornucopiae* completely covered the substratum. Thalli within these quadrats were thinned, leaving only fronds longer than 1 cm (fronds can be up to 5 cm long). Eighteen additional, randomly located 4-cm² quadrats that were left undisturbed were the controls. The extent of frond bleaching was assessed for both groups of quadrats on 30 July 1996. For each quadrat, a "bleaching index" was calculated: number of fronds with their upper portions bleached relative to the number of unbleached fronds (all fronds analyzed were longer than 1 cm). An independent t -test was used to compare the bleaching indexes from the two groups of quadrats.

RESULTS

Effects of frond density on frond desiccation and understory irradiance. Percentage desiccation of fronds of *M. cornucopiae* was $81.4\% \pm 1.9\%$ ($n = 8$ quadrats; 44 fronds in total) for the thinned quadrats and $43.2\% \pm 2.0\%$ ($n = 8$ quadrats; 49 fronds in total)

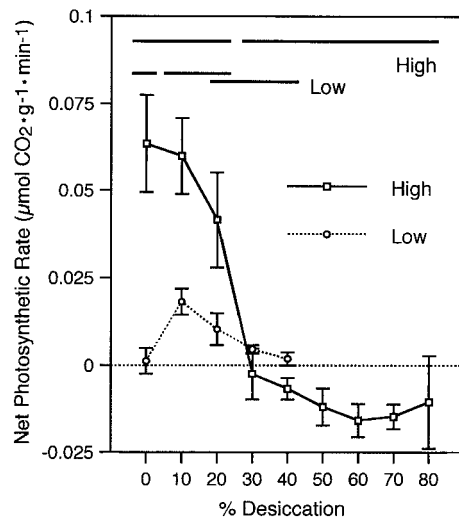


FIG. 1. Net photosynthetic rates in air (CO_2 uptake rates in $\mu\text{mol CO}_2 \cdot \text{g}^{-1} \cdot \text{min}^{-1}$ [dry biomass] $\cdot \text{min}^{-1}$; mean \pm SE, $n = 5$) of fronds of *Mazzaella cornucopiae* under $20 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ of irradiance (low) and under $515 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ of irradiance (high) as a function of percentage desiccation (relative to total water content). Desiccation levels that are grouped by a bar have statistically similar values of net photosynthetic rate (two-tailed paired t -tests done for consecutive desiccation levels, $P < 0.05$). The upper two bars (high) correspond to the experiment under high irradiance, whereas the lower three bars (low) correspond to the one under low irradiance.

for the control quadrats approximately 9.5 h after the last wave of the previous high tide reached the site. Percentage desiccation of fronds was significantly higher in thinned quadrats than in control quadrats ($P < 0.001$, two-tailed independent t -test).

On 2 June 1996, between 0930 and 1000, the highest irradiance recorded above the canopy of *M. cornucopiae* was about $2000 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ under direct sunlight and about $800 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ under full cloud cover. Below the canopy, the irradiance was $20\text{--}30 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ during sunny periods and about $10 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ under total cloud cover. During cloudy periods, the irradiance was as low as $3 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ near the holdfast.

Effects of desiccation and irradiance on the net photosynthetic rate of fronds. Fronds of *M. cornucopiae* were capable of photosynthesis when they were experimentally exposed to the air, which simulated a low tide. Frond desiccation significantly affected the net photosynthetic rate of fronds ($F = 4.07$, $P = 0.043$ for the low irradiance, and $F = 15.30$, $P = 0.001$ for high irradiance, ANOVAs through randomization tests). The highest rates of net photosynthesis occurred at low desiccation levels for both irradiances: at 10%–20% desiccation under low irradiance (a low value was obtained at 0% desiccation) and at 0%–20% desiccation under high irradiance (Fig. 1). At increasing desiccation levels, net photosynthetic rates declined; the decline was more pronounced under high irradiance than under low irradiance (Fig. 1). The net photosynthetic rate became statis-

tically similar to zero at 40% desiccation under low irradiance ($P < 0.01$, two-tailed t -test) and at 30% desiccation under high irradiance ($P < 0.01$, two-tailed t -test). Net photosynthetic rates under high irradiance were significantly negative at 40%, 50%, 60% ($P < 0.05$, one-tailed t -tests), and 70% ($P < 0.01$, one-tailed t -test) desiccation. When fronds were fully hydrated (0% desiccation), the net photosynthetic rate was significantly lower under low irradiance than under high irradiance ($P < 0.01$, one-tailed independent t -test).

Effect of frond density on the extent of frond bleaching. On 3 June 1996, frond density was 4.4 ± 0.3 fronds \cdot cm $^{-2}$ (mean \pm SE, $n = 10$) in thinned quadrats, whereas 8.5 ± 1.4 fronds \cdot cm $^{-2}$ ($n = 18$) were recorded in control quadrats. On 30 July 1996, the upper portions of several medium and large fronds appeared bleached. The bleaching index was 0.91 ± 0.13 (mean \pm SE, $n = 10$) for thinned quadrats, which was significantly greater ($P = 0.01$, two-tailed independent t -test) than the bleaching index for control quadrats: 0.46 ± 0.08 ($n = 18$). This indicates that the high frond density characteristic of natural stands of *M. cornucopiae* protects a higher proportion of medium to large fronds from becoming bleached.

DISCUSSION

Frond crowding represents a cost for fronds of *M. cornucopiae* when they are fully hydrated, because the aerial net photosynthetic rate under an irradiance observed at the understory of natural stands is lower than under an irradiance equivalent to experimental conditions of low frond density. However, the interaction between desiccation and irradiance modifies this relationship between net photosynthetic rates and frond density. The average desiccation of fronds of natural stands of *M. cornucopiae* was 43% after 9.5 h (almost at the end of the low tide) of exposure to sunny and windy conditions on a spring day at Prasiola Point. Under an experimental irradiance of $20 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, which is commonly observed below the canopy of natural stands, the net photosynthetic rate of fronds is not significantly different from zero at 40% desiccation. The average desiccation of fronds of experimentally thinned stands was much higher after the same period of 9.5 h at the same site, 81%. Under an experimental irradiance of $515 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, which can be observed both at the canopy level of natural stands and at any level in thinned stands, net photosynthetic rates are negative for desiccation levels between 40% and 70% (at 80% desiccation, the net photosynthetic rate was also negative, although not statistically significant).

The negative net photosynthetic rates observed under strong desiccation and high irradiance may be a result of photoinhibition (Herbert and Waaland 1988, Herbert 1990, Lobban and Harrison 1994), and photoinhibition often involves bleaching

of algal tissues (Kain and Norton 1990). Based on this, our observed net photosynthetic rates suggested that bleaching could be potentially stronger in experimentally thinned stands than in natural stands. The experimental thinning done in stands of *M. cornucopiae* in late spring confirmed our prediction. In midsummer, a greater percentage of medium and large fronds had bleached upper portions in thinned stands than in natural stands. Therefore, frond crowding protects fronds of *M. cornucopiae* against strong bleaching, and this may be so because of the protective effects of frond crowding against strong desiccation and high irradiance during low tides. To actually confirm the apparent relationship among negative net photosynthetic rates, possible photoinhibition, and the extent of bleaching for *M. cornucopiae*, further research will be needed. The importance of high frond density for the prevention of strong desiccation and subsequent bleaching was also indicated for tropical algae such as *Dictyota bartayresii* (brown alga), *Halimeda opuntia* (green), and *Laurencia papillosa* (red) (Hay 1981) and for the temperate alga *Corallina vancouveriensis* (red) (Pardilla 1984, Taylor and Hay 1984).

It is worth noting that there is a vertical gradient of color in fronds of *M. cornucopiae* from Prasiola Point during spring and summer. Fronds of medium and large size that are not bleached go from yellow-green in the upper portion to dark red in the lower portion (in winter, they are entirely dark red). This vertical distribution of colors also occurs for some tropical intertidal red algae, such as *Ahnfeltiopsis concinna* (J. Agardh) Silva et De Cew and *Laurencia mcdermidiae* (J. Agardh) Abbott from Hawaii, as a consequence of photoacclimation (Beach and Smith 1996a), which results in these areas of the fronds having some differences in photosynthetic and respiration rates (Beach and Smith 1996b). Our measurements of net photosynthetic rates for *M. cornucopiae* were done with entire fronds that generally showed some degree of the color gradient referred to above. Therefore, the net photosynthetic rates that we recorded represent a value between the rates for lower and upper portions of fronds. However, based on results obtained for *A. concinna* (Beach and Smith 1996b), which occurs in the high intertidal zone (*L. mcdermidiae* occurs in the low intertidal zone, so it may not be ecologically comparable with *M. cornucopiae* because of different emersion stresses; see Beach and Smith 1996b), we believe that our main conclusions remain valid. At low irradiance, the net photosynthetic rate (measured in seawater) for dark tissues of *A. concinna* is higher than that for light tissues. If this pattern holds true also for *M. cornucopiae*, our values of net photosynthetic rates at low irradiance would be higher had we used only dark portions of fronds. However, this does not modify our finding that net photosynthetic rates are never negative at desiccation levels found within high-density stands. Additionally, the maxi-

mum net photosynthetic rate (referred to both fresh and dry biomass) for *A. concinna* is unaffected by tissue color. Assuming that our "high" irradiance of $515 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ is close to the saturation irradiance for *M. cornucopiae* (see Lobban and Harrison 1994), the photosynthetic rate would be similar for dark and light tissues at the high irradiance tested if these two high intertidal algae have a similar physiological pattern. Then our values of net photosynthetic rates at high irradiance would remain similar had we used only light tissues.

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