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Aerial exposure and desiccation tolerances are correlated to species composition in "green tides" of the Salish Sea (northeastern Pacific)

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Abstract

Relatively little is known about the causes of species distribution within macroalgal blooms occurring on or over soft substrata. We examine the roles of aerial exposure and desiccation in determining elevational patterns of two dominant bloom-forming ulvoid algae, *Ulva lactuca* and *Ulvaria obscura*, on the northeastern Pacific coast. These species were stressed with constant desiccation time, desiccation to a constant water potential, and desiccation to a fixed water loss. As a measure of health, we examined net photosynthesis by oxygen evolution or photosynthetic yield via pulse amplitude modulated fluorometry. By all measures, *Ulva* was physiologically superior in the intertidal zone. Under constant exposure, it desiccated more slowly than *Ulvaria*. When desiccated to a constant dryness, *Ulva* better maintained photosynthetic parameters. These observations are consistent with *Ulva*'s usual dominance over *Ulvaria* in intertidal macroalgal blooms. Given these and other observed differences between the two species, natural resource managers should not regard the two as ecologically equivalent, even though they have similar functional forms.

Keywords: desiccation; ecological redundancy; functional form; macroalgal blooms; *Ulva*; Ulvaceae; *Ulvaria*.

Introduction

Macroalgal blooms have been blamed for eradicating seagrass meadows, altering faunal community structure, and creating unsightly, malodorous piles on beaches (e.g., Valiela et al. 1997). These effects are usually associated with shading and anoxia, although extracts from some bloom-forming macroalgae are toxic (Nelson et al. 2003a). Blooms are often associated with eutrophication, although a variety of abiotic and biotic factors may limit ulvoid algal abundance and productivity (Kida 1990, Henley et al. 1991, Rivers and Peckol 1995, Anderson et al. 1996). Problematic blooms are typically reported to be monospecific (Valiela et al. 1997), with the dominant species determined by environmental conditions (Lotze et al. 2000). In the Salish Sea (the contiguous waters of Washington State, USA and British Columbia, Canada), however, *Ulva lactuca* L. often dominates the intertidal, and *Ulvaria obscura* (Kützing) Gayral dominates the subtidal bloom at the same location (Nelson et al. 2003b).

Community structure in marine environments has been examined more thoroughly in rocky intertidal areas than on the soft substrata where macroalgal blooms typically occur. In the first half of the 20th century, zonation on rocky shores was assumed to be controlled by physical factors (Chapman 1986, Robles and Desharnais 2002). In particular, the stress of low tide was presumed, and sometimes demonstrated, as causing a physiological disadvantage in species found lower on the beach. The specific cause of stress or mortality, though, can be difficult to isolate as it may be related to aerial exposure, water loss, increased light intensity, increased temperature, etc. Further, wind speed and direction, substratum moisture, and humidity can affect desiccation rate *in situ*. Laboratory experiments, in contrast, may not reflect biologically meaningful conditions in nature (Chapman 1986).

Furthermore, at least two possible explanations may account for the success of an alga exposed to drought. First, the alga may better tolerate drying. Some authors have found that photosynthetic rates in higher intertidal species recovered from greater water loss than lower intertidal species (Dring and Brown 1982, Abe et al. 2001). Skene (2004) notes that algae growing higher on the beach generally have higher rates of photosynthesis as a mechanism for time-use efficiency and that these algae are more likely to recover following desiccation than similar species ordinarily found at lower tidal elevation. Alternatively, some seaweeds typically growing higher on the beach are better at resisting water loss, rather than being physiologically more tolerant of water loss (e.g., Ji and Tanaka 2002).

In addition to desiccation, multiple other more subtle factors, including predation, competition, and refuges may determine intertidal community structure (Vadas 1977, Worm and Chapman 1996, Robles and Desharnais 2002). A handful of studies have examined the causes of spatial or temporal changes in the species composition of macroalgal blooms. Lotze et al. (1999, 2000) elegantly demonstrated the importance of recruitment timing, herbivory and nutrient supply on competition between ephemeral blooms of *Ulva* spp. (reported as *Enteromorpha* spp.) and the brown alga *Pilayella littoralis* (L.) Kjellman. Fong et al. (1996) showed that salinity and nitrogen could explain dominance patterns in *Ulva expansa* (Setchell) Setchell *et* N.L. Gardner and *Ulva intestinalis* L. [reported as *Enteromorpha intestinalis* (L.)

Nees]. Nelson et al. (2008) suggested that tolerance to low salinity might allow *U. lactuca* to dominate the intertidal in Washington State, but that biotic factors, most likely resistance to grazing, allow *Ulvaria* to dominate the subtidal.

Soft substratum marine macroalgal communities have not been as thoroughly examined as those in the rocky intertidal. Further, studies of bottom-up processes, particularly eutrophication, influencing biomass accumulation on soft substrata have predominated. Various other physical and biological factors have been used to explain changes in macroalgal biomass, but they have rarely been used to explain differences in species composition. Green tide species are generally reported to have broad tolerance ranges for salinity, irradiance, and temperature (Taylor et al. 2001). In addition, the functional form hypothesis suggests that similar-appearing species are ecologically equivalent, and that thin-bladed species are expected to grow faster and be preferred by grazers compared to thick-bladed or crustose forms (Littler and Littler 1980). The location and extent of ''green tides'' (i.e., ulvoid algal blooms) may be predictable as a functional form group, but understanding the causes of species-specific distribution patterns is more difficult (Steneck and Dethier 1994).

In the present study, we examined the effects of aerial exposure and desiccation on *Ulvaria* and *Ulva* using photosynthetic parameters as a proxy for overall algal health. Since *Ulvaria* is found primarily in the subtidal, it is expected to be less desiccation tolerant than *Ulva* (Nelson et al. 2003b). Alternatively, other factors may also explain *Ulva*'s intertidal dominance, including tolerance to rainfall-induced low salinity during low tides or the nature of chemical defenses in *Ulvaria*, which may require resources that could otherwise be used to maintain high maximal growth rate made possible by increased light availability in shallow water (Nelson et al. 2008). Their similar morphologies (thin, flat blades), sizes, and demographies (isomorphic alternation of generations) suggest that cellular physiology is likely key. There is a slight anatomical difference, with *Ulva* being distromatic and *Ulvaria* being monostromatic, but this difference is mitigated by the rectangular shape of *Ulvaria* cells (vs. square in *Ulva*), leading to thalli that are approximately the same overall thickness.

To determine what role, if any, desiccation plays in the species' distributions, we used air and saline drying treatments to determine whether one species was more tolerant of desiccation than the other. As a physiological response to this stress, we examined aspects of photosynthesis by measuring oxygen evolution or pulse amplitude modulated (PAM) fluorescence.

Materials and methods

Species and site descriptions

Green tides present an interesting challenge to marine ecologists. Multiple species may be found growing together in the intertidal or subtidal, either attached to the substratum or floating freely. The greatest biomass found locally occurs in free-floating mats that remain stationary in embayments. The genera involved (*Ulva* and *Ulvaria* in Washington State, USA) are superficially similar green blades that cannot be accurately distinguished in the field. Algae were collected from sites on Blakely Island, San Juan Island Archipelago, Washington State, USA (fully described by Nelson et al. 2003b and 2008).

Beach exposure

The effect of exposure at low tide was investigated by drying algal disks *in situ* and measuring rates of photosynthesis immediately following re-immersion, and again after 24 h. For several macroalgal species, recovery is complete within only a few hours, and no further recovery can be expected beyond 24 h (Dring and Brown 1982). Thirty 9.4 cm diameter disks were cut from both *Ulva* and *Ulvaria* plants that had been collected from Seal Pup Rock, Blakely Island, WA, USA. Five replicate disks of each species were dried on a pebble/cobble beach for 0, 30, 60, 120, or 180 min. Following this desiccation treatment, four disks 2.4 cm in diameter were cut from each of the larger disks and all four were placed in a biological oxygen demand (BOD) bottle to measure the rate of photosynthesis. An oxygen electrode (YSI 59 m and YSI 5905 probe, Yellow Springs Instruments, Yellow Springs, OH, USA) was used to measure oxygen concentrations before and after a 60 min incubation period. Initial measures of photosynthesis were conducted in the field (at 800 μmol photons m^{-2} s^{-1}). Photosynthesis following recovery was measured in the laboratory using a halogen lamp (Model L-33, The Designer's Edge, Bellevue, WA, USA) as a light source (150 μmol photons m^{-2} s^{-1}). All incubations were at ambient seawater temperature (12°C). Data for photosynthesis collected after 24 h from one of the *Ulvaria* specimens initially dried for 180 min were discarded due to a problem with the oxygen electrode. Data were $\log_{10}$ transformed to minimize heteroscedasticity. Data for one of the *Ulva* specimens dried for 60 min were not included in the analysis because the specimen was inadvertently torn prior to rehydration.

Laboratory desiccation

We dried algal tissues in a laboratory setting, following techniques outlined above, but with specimens placed outdoors in a terrestrial environment. This allowed us to measure water lost from the algal tissue with laboratory balances. Drying times of 0, 3, 5 and 10 min were used, with seven replicates per drying time by species combination (n=7, N=56). Incubations were conducted in a growth chamber at 10°C with light intensity at 180 μmol photons m^{-2} s^{-1}. To minimize heteroscedasticity, water loss data were arcsine-square root transformed.

Saline desiccation

The third trial involved using various saline solutions to dry algal tissues to equivalent water potential without exposing them to high light intensity or other potentially complicating

factors. We used two different methods when exposing algae to the drying effects of saline solutions. Direct immersion was used initially. Since every cell is bathed in desiccating solution during immersion, the tissues should have achieved a water potential equilibrium with their environment in a matter of seconds. We placed tissues in hypersaline solutions for 10 min, however, to ensure that equilibrium was achieved. Five replicate specimens were used for each species by salinity treatment combination. Photosynthesis was measured as oxygen evolution following 10 min recovery in ordinary seawater and again after 24 h recovery.

To eliminate the possibility of sodium toxicity or other artifacts of direct immersion, we performed similar experiments, but placed the thalli in plastic Petri dishes floating above hypersaline solutions in air-tight containers (hereafter, ''suspended'' treatments). This treatment creates an aerial environment with the same water potential as the saline solution itself, but without potentially confounding factors (e.g., sodium toxicity) associated with immersion. Preliminary trials indicated that overnight treatment allowed the tissues to reach equilibrium, a time frame consistent with the literature (Abe et al. 2001). Since residual water was not on the tissues when we removed them from desiccating chambers, we were able to easily determine water loss by weighing specimens prior to measuring photosynthetic rates. For these tests, seven replicates per treatment level by species combination were used (n=7, N=42).

Photosynthesis was measured in the laboratory immediately after treatment with saline solutions and, for immersed specimens only, 24 h later. Salinities tested included a seawater control and seawater +0.5, +1.0, and +2.0 M NaCl for specimens tested by immersion, and a seawater control, seawater+2 and seawater+4 M NaCl for specimens tested while suspended over the appropriate solutions.

Effects on photosynthetic yield

To examine the effects of desiccation on photosynthesis more closely, we used photosynthetic yield measured with a PAM fluorometer (PAM 102, Walz, Effeltrich, Germany) following desiccation trials in the laboratory. Specimens were placed in seawater in the dark for 5 min to recover and to become acclimated to the darkness. So-called dark-adapted yield was determined as F_v/F_m and light yield as $\Delta F/F_m'$ (e.g., Beer et al. 2000). Ulvoid specimens were placed in a culture dish with a small amount of seawater around the tissue, but not covering the surface. The culture dish was placed in a chilled water bath ($\sim$13°C) to mimic natural conditions. The tip of the PAM-102 emitter-detector unit was placed directly over the alga such that the light path was perpendicular to the thallus. A 1 s saturating pulse of white light was employed to find F_m'.

Yield was first measured in darkness, and then under saturating irradiance ($\sim$275 μmol photons m^{-2} s^{-1}) from halogen lights (Model L-33, The Designer's Edge). The two light conditions were compared to test for combined effects of recent desiccation stress and photoinhibition. For example, the efficiency of the xanthophyll cycle may be reduced in algae suffering from desiccation stress (Harker et al. 1999), leading to lower yield at high light that may not occur at lower light. Sufficient time (usually 2–3 min) was allowed to elapse between the dark and high light treatments to allow F_0' (i.e., baseline fluorescence) to reach a steady state.

Two trials were attempted. In the first, drying times of 0, 13, and 25 min were used to compare equivalent exposure, while in the second, we dried to constant mass losses of 0, 50 and 67%. The latter two values were chosen to bracket a range within which we expected to see inter-specific differences based on preliminary experiments. We used either 10 (first trial) or 6–8 (second trial) replicates of each treatment combination. In the first trial involving different drying times, yield was measured initially and after 24 h recovery. Only initial yield was measured in the second trial. Yield data were squared to reduce heteroscedasticity.

Statistical analyses

Two factor multivariate analyses of variance (MANOVA), with species and desiccation conditions treated as fixed factors, were used to test for differences between *Ulva* and *Ulvaria*, for differences between various exposure and desiccation treatments, and for interaction effects. MANOVA was used because more than one dependent variable (e.g., degree of drying and photosynthetic response) was measured in each trial. All data were analyzed for departures from normality (skew and kurtosis) and, when appropriate, equality of variance. Except when specifically noted, there were no significant departures from normality or homoscedasticity. Tukey's post-hoc test was used throughout to test significances of pairwise treatment differences. Alternative post-hoc tests (Ryan's Q and Student-Newman-Keuls) were considered, but none yielded conclusions different from the more familiar (and generally more conservative) Tukey's test.

Results

Beach exposure

All measures of desiccation tolerance indicate that *Ulvaria* is less tolerant of emersion or drying than *Ulva*. *In situ* trials resulted in decreasing rates of photosynthesis with increasing drying times (Figure 1). Both species showed declines in photosynthetic rates with increasing drying time, but the decline was more rapid in *Ulvaria* than in *Ulva*, leading to significant interaction effects. There was no significant difference between the two species in the control or for drying times of 60 min or greater (Tukey's HSD $p \geq 0.604$). *Ulvaria* had significantly lower rates of photosynthesis than *Ulva* when dried for 30 min, however (Tukey's HSD $p<0.001$). After 24 h recovery, interaction effects were still significant, with both species showing similarly reduced photosynthesis for drying times >30 min. For the 30 min drying treatment, *Ulvaria* still had significantly reduced photosynthesis relative to *Ulva* ($p<0.001$, Tukey's HSD test). No *Ulvaria* specimens that had been dried for any length of time showed net positive photosynthesis after 24 h, while most *Ulva* specimens

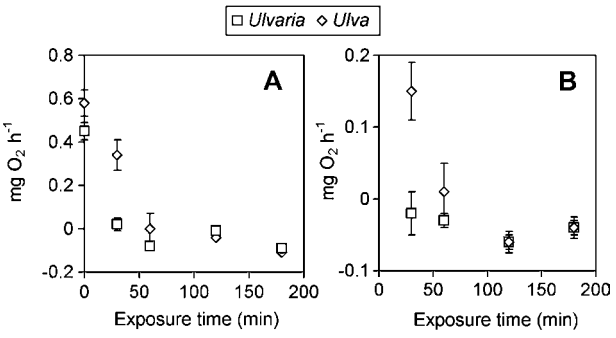

Figure 1 Net photosynthetic rates of *Ulva* and *Ulvaria* following *in situ* aerial exposure.
(A) Net photosynthesis immediately after various drying times on the beach. Exposure time, species and interaction effects were significant immediately after exposure (MANOVA, $F_{3,31}$=27.1, p<0.001, $F_{1,31}$=10.7, p=0.003, $F_{3,31}$=10.4, p<0.001, respectively). (B) Net photosynthesis in the laboratory 24 h after beach drying. Drying time, species, and interaction effects were still significant ($F_{3,31}$=13.3, p<0.001, $F_{1,31}$=11.2, p=0.002, and $F_{3,31}$=6.29, p=0.002, respectively). Tukey's HSD indicated only significant interspecific differences at 30 min drying time both before and after the recovery period (p<0.001 both before and after 24 h recovery). Values are means±SE.

dried 30 or 60 min had recovered sufficiently to at least display low positive net photosynthesis.

Laboratory desiccation

Ulva and *Ulvaria* both ultimately responded to desiccation in the laboratory with significant decreases in photosynthetic rate, but the rate dropped farther and at shorter desiccation time in *Ulvaria* than in *Ulva* (Figure 2). Neither species showed a significantly lower rate of photosynthesis relative to its conspecific control until dried for 10 min, when photosynthesis in *Ulva* and *Ulvaria* declined 73% and 112%, respectively. Interestingly, *Ulva* had a significantly higher rate of photosynthesis when dried for 3 min than in controls (Tukey's HSD p=0.002). In all drying treatments and controls, *Ulva* had slightly (though not always significantly) higher rates of photosynthesis than *Ulvaria*, with the greatest difference (107%) at a drying time of 10 min (Tukey's HSD p=0.002 for the interspecific comparison at 10 min). The controls showed the least interspecific difference (<3%, Tukey's HSD p>0.999).

Increasing drying time caused a significant decrease in water content, with mass losses ranging from zero in controls to 62% in specimens dried 10 min. There were no significant differences between the species, although in preliminary experiments (not reported here), *Ulvaria* lost significantly more water than *Ulva* when dried for 3 or 5 min.

Saline desiccation

Immersion in hypersaline solutions caused photosynthesis to track downward in both species with increasing salinity, but the decrease was greater in *Ulvaria* than in *Ulva* (Figure 3). In comparison with controls, rates of photosynthesis in both

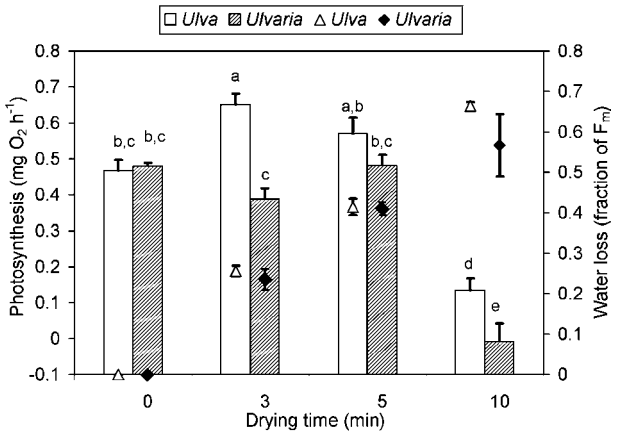

Figure 2 Net photosynthesis (bars) and mass lost to desiccation (symbols) in *Ulva* and *Ulvaria* following aerial exposure in the laboratory.
Photosynthesis varied significantly with species, desiccation time, and the interaction between these factors (MANOVA $F_{1,47}$=13.3, $F_{3,47}$=11.2, and $F_{3,47}$=6.29, respectively; p<0.001 for each). Shared letters indicate subsets of treatment combinations that are not significantly different from each other for photosynthetic measures (Tukey's test, p>0.05). Only desiccation time significantly impacted water loss (MANOVA, $F_{3,47}$=197, p<0.001 for time; $F_{1,47}$=0.942, p=0.337 for species; $F_{3,47}$=0.395, p=0.757 for interaction effects). Each drying time had significantly different water loss from every other drying time (Tukey's HSD p<0.05). Values are means±SE (symbols) or means+SE (bars).

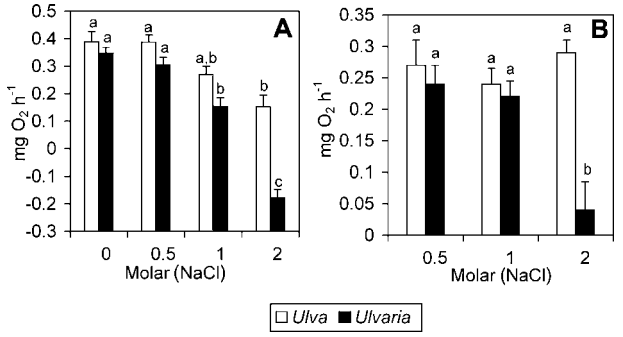

Figure 3 Net photosynthesis of *Ulva* and *Ulvaria* following immersion in hypersaline solutions.
(A) Net photosynthesis following desiccation in various concentrations of NaCl added to seawater. Salinity, species, and interaction effects on rates of photosynthesis were significant (MANOVA, $F_{3,32}$=75.9, p<0.001, $F_{1,32}$=50.2, p<0.001, $F_{3,32}$=10.3, p<0.001, respectively). (B) Net photosynthesis after 24 h recovery. Salinity, species and interaction effects were still significant (ANOVA, $F_{2,24}$=5.36, p=0.012, $F_{1,24}$=18.0, p<0.001, $F_{2,24}$=10.4, p=0.001, respectively). Shared letters indicate subsets of treatment combinations that are not significantly different from each other (Tukey's test, p>0.05). Values are means+SE.

species declined with increasing salinity through +1.0 M NaCl additions, with no significant difference in interspecific pairwise comparisons at these lower salinities (Tukey's HSD p=0.968, 0.470, and 0.101, respectively, for increasing salinities). The seawater+2.0 M NaCl treatment caused negative

net photosynthesis in *Ulvaria*, while *Ulva* had significantly higher and positive net photosynthesis (Tukey's HSD $p<0.001$ for the pairwise comparison). Following 24 h recovery, this pattern remained unchanged. Two of the *Ulvaria* specimens that had been exposed to the seawater+2.0 M NaCl were clearly dead as evidenced by the discoloration that is typical at death in the local variety of this species [*U. obscura* var. *blyttii* (J.E. Areschoug) Bliding, Gabrielson et al. 2000].

In suspended hypersaline treatments, both species lost more water at higher salinity (Figure 4, Tukey's HSD $p<0.001$ for all pairwise comparisons with the conspecific control), but there were no significant interspecific differences in water loss except in the highest salinity (4 M NaCl) treatment, where *Ulvaria* lost 70.2±0.01% [mean±standard error (SE), here and hereafter] of its mass, while *Ulva* lost only 64.1±0.02% of its mass (Tukey's HSD $p=0.008$ at 4 M NaCl, $p\geq0.421$ at lower salinity). Photosynthetic rates dropped with increasing salinity for both species, but were consistently higher in *Ulva* than in *Ulvaria* at all tested salinities (Tukey's HSD $p<0.046$). This difference was greatest at the intermediate salinity (+2 M NaCl) where photosynthetic rates were 96% lower in *Ulvaria* than in *Ulva* ($p<0.001$). *Ulvaria* had significant decreases in photosynthesis in both salinity treatments relative to the control ($p<0.001$), although there was no further decrease from +2 to +4 M NaCl (Tukey's HSD $p=0.999$), while *Ulva* only showed a significant decline in the +4 M NaCl treatment ($p<0.001$ compared to lower salinity treatments).

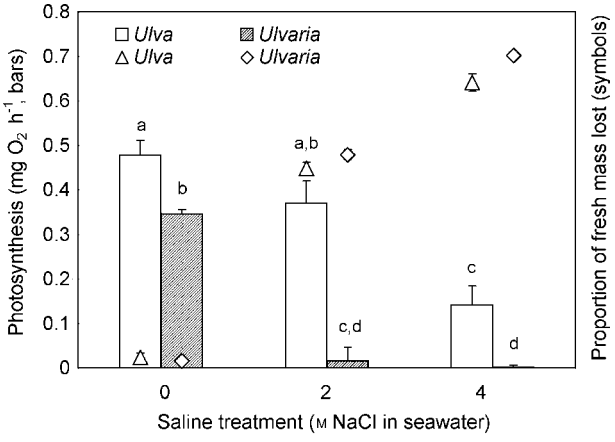

Figure 4 Net photosynthesis (bars) and mass lost to desiccation (symbols) in *Ulva* and *Ulvaria* following suspension over hypersaline solutions.
Species, drying treatment and interaction effects significantly affected water loss (MANOVA, $F_{1,36}=8.91$, $p=0.005$; $F_{2,36}=1660$, $p<0.001$; and $F_{2,36}=4.31$, $p=0.021$, respectively) and rate of photosynthesis ($F_{1,36}=68.99$, $p<0.001$; $F_{2,36}=62.77$, $p<0.001$; and $F_{2,36}=8.24$, $p=0.001$, respectively). Shared letters indicate subsets of treatment combinations that are not significantly different from each other for photosynthetic measures (Tukey's test, $p>0.05$). Water loss was not significantly different between the species at zero and 2 M NaCl addition, but was significantly different in the 4 M treatment. Values are means±SE (symbols; some error bars fall within the symbol outlines), or means+SE (bars).

Photosynthetic yield

Constant drying time *Ulvaria* specimens lost more water and showed a greater reduction in photosynthetic yield when dried for the same length of time than *Ulva* specimens (Figure 5). All measured responses to desiccation (tissue water loss; dark-adapted and high light yield, measured before and after 24 h recovery) showed significant differences caused by the species, drying time, and interaction effects (MANOVA $p<0.001$ for all tests except for interaction effects on water loss, where $p=0.003$). Both species lost water with increasing drying time, but *Ulvaria* lost more water than *Ulva* when dried for the same length of time (41.4% vs. 37.5% of mass at 13 min, and 63.4% vs. 55.7% at 25 min), albeit only significantly more at the longer drying time (Tukey's HSD $p=0.144$ and $p<0.001$ for short and long drying times).

Photosynthetic yields for *Ulva* were unaffected by drying time, while *Ulvaria* yields were reduced with drought. *Ulvaria* specimens dried for 25 min had reduced dark-adapted yield relative to controls, to specimens dried for 13 min, or to any *Ulva* treatments, both before and after a 24-h recovery period (Tukey's HSD $p<0.001$ for all comparisons). Dark-adapted *Ulva* specimens did not show any significant differences in yield in response to drying time either initially (Tukey's HSD $p\geq0.293$) or after 24 h recovery ($p\geq0.997$). Dark-adapted *Ulvaria* controls were not significantly different from any of the *Ulva* treatments (Tukey's HSD $p\geq0.077$). However, *Ulvaria* specimens dried for 13 or 25 min initially had reduced yield relative to conspecific controls and to each other (Tukey's HSD $p<0.001$ for comparisons between drying times). There was no significant difference between species at the shorter drying time (Tukey's HSD $p=0.115$), but there was a significant difference between species with longer drying time ($p<0.001$). After 24 h recovery, dark-adapted yield in *Ulvaria* specimens dried for the shorter time period had returned to equal the control, but specimens of *Ulvaria* dried for 25 min still had significantly lower yields than any other species by drying time combination ($p<0.001$ for all comparisons).

At high light intensity, *Ulvaria* initially had lower yield than *Ulva* regardless of drying time, and yield decreased with increasing drying time. Yield for *Ulva* did not differ between drying times ($p\geq0.995$), while *Ulvaria* yields significantly decreased with each drying time ($p<0.001$ for all comparisons). After 24 h recovery, this pattern had not changed substantially.

Drying to constant desiccation state Specimens dried to 50–67% mass loss had reduced dark-acclimated yield with increased desiccation regardless of species (Figure 6, Tukey's HSD $p<0.001$ for pairwise comparisons between desiccation states). At high light, both species showed reduced yield with increasing desiccation, but the response was greater in *Ulvaria* at intermediate desiccation. *Ulva* and *Ulvaria* controls

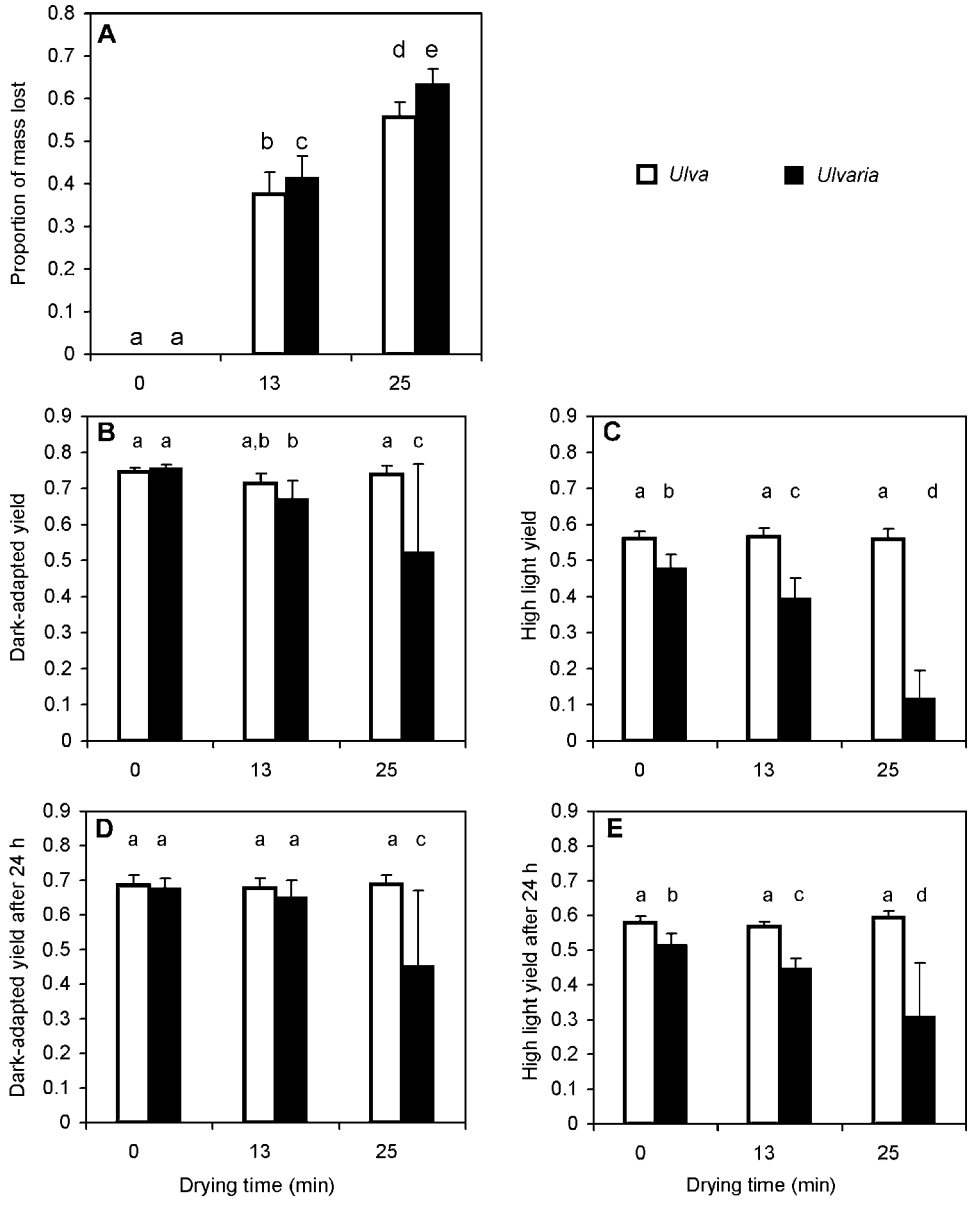

Figure 5 Mass lost (A) and photosynthetic yields (B–E) following air drying in the laboratory for different periods of time. Yield is shown after initial recovery (B, C) and after 24 h (D, E), measured under both dark conditions (B, D) and at photosynthetically saturating light intensity (C, E). Values are means+SE. For all tests, MANOVA results indicated significant species, drying time, and interaction effects (MANOVA for species $F_{1,54}$=18.9, 158, 523, 24.2, and 217 for A–E, respectively; for drying times $F_{2,54}$=1.56×10^3, 117, 64.0, 11.6, and 15.6, respectively; for interaction effects $F_{2,54}$=6.34, 121, 60.5, 13.4, 25.5, respectively; $p<0.001$ for all tests except for interaction effects on water loss, where $p=0.003$). Shared lower case letters indicate subsets of treatment combinations that are not significantly different from each other (Tukey's HSD, $p<0.05$).

and *Ulva* specimens dried to 50% mass did not have significantly different yields ($p>0.05$). Specimens of both species dried to 67% mass loss had the lowest yields (averaging 0.070±0.013), and were significantly different from all other drying treatments ($p\leq0.021$) though not significantly different from each other (Tukey's HSD $p=0.708$). *Ulvaria* specimens dried to 50% mass loss had lower yields than controls or *Ulva* dried to 50%, but higher than more desiccated specimens ($p\leq0.021$ for all pairwise comparisons, Tukey's test, $p>0.05$).

Discussion

Why do some species occur lower on the shore?

A variety of physical and biological factors control algal zonation along the shoreline, but either desiccation tolerance or desiccation resistance are clearly critical parameters in determining some species distribution (e.g., Dring and Brown 1982, Abe et al. 2001, Ji and Tanaka 2002, Skene 2004). Our experiments demonstrate that the deeper-growing

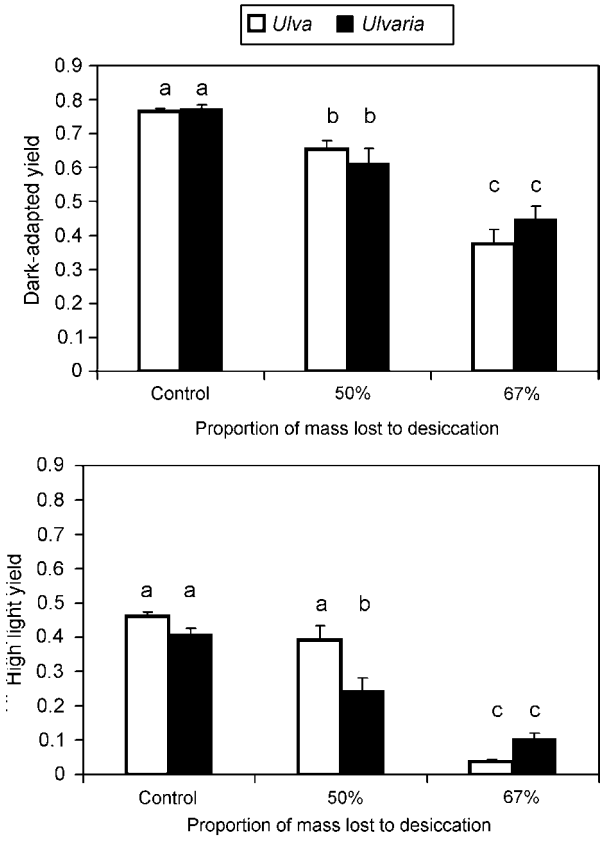

Figure 6 Photosynthetic yield under dark and high light conditions when *Ulva* and *Ulvaria* were dried to constant water loss. Dark-adapted yield did not differ significantly between species (MANOVA $F_{1,36}$=0.227, p=0.637) nor were there interaction effects between species and desiccation state (MANOVA $F_{1,36}$= 1.60, p=0.216). At high light, yield was significantly affected by species, desiccation, and interaction effects (MANOVA $F_{1,36}$=4.587, p=0.039; $F_{2,36}$=101, p<0.001; and $F_{2,36}$=8.48, p=0.001, respectively). Shared letters indicate subsets of treatment combinations that are not significantly different from each other (Tukey's test, p>0.05). Values are means+SE.

Ulvaria is less resistant to desiccation under at least some conditions and in all cases is less tolerant of desiccation than *Ulva*. In the field, we demonstrated a negative response to low tide conditions in total. By conducting experiments in the dark and in the laboratory, we eliminated the effects of light and extreme temperature. Via saline immersion, we eliminated the effects of air alone, and by saline suspension the possible impact of sodium toxicity. Although we did not measure mortality directly here, reduction in photosynthesis may lead to either direct mortality via a net loss of carbon when integrated over multiple tidal cycles or sufficient competitive disadvantage to alter species composition.

In the present comparison both tolerance and resistance may give *Ulva* the advantage in the intertidal. It is tempting to attribute *Ulva*'s resistance to desiccation relative to *Ulvaria* to the fact that the former is distromatic and the latter monostromatic, since small differences in morphology can lead to substantial changes in function (Koehl 1996). However, Abe et al. (2001) found that *Monostroma nitidum* Wittrock is actually slower to desiccate than distromatic *Ulva pertusa* Kjellman. Thus, such a conclusion, even if valid, is not broadly applicable.

A growing body of data indicates that elevation differences in species composition in intertidal areas are often controlled by physical stress in the evolutionarily novel habitat (i.e., higher on the beach for most marine organisms, but lower for salt marsh grasses descended from terrestrial angiosperms) and biological stresses in the more familiar habitat (e.g., Nelson et al. 2008 and references therein). In the case of the species considered here, *Ulvaria* is more resistant to grazers than *Ulva* (Van Alstyne et al. 2006, Nelson et al. 2008), perhaps allowing it to dominate where grazing activity is more intense. *Ulva*, in contrast, is more tolerant of low salinity than *Ulvaria*, a characteristic associated with intertidal species that may be inundated by rainfall or terrestrial freshwater discharges (Einav et al. 1995, Nelson et al. 2008), and the more obvious drought (demonstrated here) that accompanies low tide.

Ulva's lack of response to desiccation, indeed in one trial it enhanced net photosynthesis under slight desiccation, is somewhat unexpected. Other *Ulva* species have been shown to maintain photosynthetic rates when slightly desiccated, though this is not universally true for intertidal macroalgae (Beer and Eshel 1983, Gao et al. 1999, Williams and Dethier 2005). In our tests, thalli were rehydrated prior to measuring photosynthetic parameters, preventing direct uptake of atmospheric CO_2. We cannot rule out the possibility that these thalli were able to concentrate CO_2 prior to rehydration, however, thus benefiting from the atmospheric exposure (Beer et al. 1990).

Ulvaria has lower photosynthetic yield (shown here) and rates of net photosynthesis (Nelson et al. 2008) under high light conditions than *Ulva*, regardless of desiccation state. Algae higher on the shore may have less time available for maximal photosynthesis due to reduced photosynthetic rates when dehydrated; that is, the adaptation in *Ulva* may be a question of increasing time use efficiency (Skene and Raven 2001). Alternatively, *Ulvaria* may simply be adapted to lower light environments due to desiccation intolerance, and thus has no need to devote resources to maximizing photosynthesis at light intensities it rarely experiences.

Lack of ecological redundancy

Wohl et al. (2004) describe functionally redundant species as ''biologically unique'' but contributing ''with similar intensity to the same process within an ecosystem, such as energy flow or nutrient cycling.'' Ulvoid algal species are certainly part of the same functional-form group (*sensu* Littler and Littler 1980), and are often thought of as functionally redundant. Nelson et al. (2008) point out that several physiological differences, including differences in growth rates, photosynthetic rates, tolerance of low salinity, and nitrogen physiology exist. Coupled with differences in exposure and desiccation tolerance seen here, it is clear that differences between the species can impact community structure and function, and potentially affect management decisions related

to the control of blooms. For example, both species release toxins following desiccation-induced mortality (Nelson et al. 2003a). Variation in desiccation tolerance will affect community impacts of these toxins. A similar situation exists with species of *Fucus* inhabiting Atlantic Ocean shorelines; again, similarity of functional form does not imply ecological redundancy (Barker and Chapman 1990).

Future directions

Several potential factors are not considered here that could affect the relative performance of these two species. Differences in responses to atmospheric CO_2 available at low tide, which may enhance photosynthesis for well-hydrated thalli, could impact relative performance (Einav et al. 1995). On the other hand, emersion may cause non-photosynthetic stresses, e.g., by altering nutrient uptake (Kim et al. 2008). That is, there is no guarantee that the species are responding similarly at the cellular or physiological level when damaged by desiccation. The nature of damage to desiccated thalli is not considered here, although data from PAM fluorometry in *Ulvaria* specimens exposed to high light suggests damage to the photosynthetic apparatus itself. Similarly, increased variance in photosynthetic rates for highly desiccated *Ulvaria* suggests an all-or-none response, i.e., death or substantial recovery that may involve different desiccation responses at the cellular level than those in *Ulva*.

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