

BRIEF COMMUNICATION

Divergent growth strategies between red algae and kelps influence biomechanical properties¹

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PREMISE OF THE STUDY: Morphology and material properties are the main components of the mechanical design of organisms, with species groups developing different optimization strategies in the context of their physical environment. For intertidal and subtidal seaweeds, possessing highly flexible and extensible tissues allows individuals to bend and reconfigure in flow, thereby reducing drag. Previous research has shown that aging may compromise these qualities. Tissue age increases with distance from the blade's meristem, which differs in its position on kelps and red algae. Here, we assess whether longitudinal patterns of blade material properties differ between these two algal groups according to tissue age.

METHODS: We performed tensile tests on tissues samples excised from various positions along the extent of blades in nine kelp species (basal growth) and 15 species of red algae (apical growth).

KEY RESULTS: We found that older tissues were less flexible and extensible than younger tissues in all species tested. As predicted, tissue near the basal meristem in kelp was more flexible and extensible than older tissue at the blade's distal end. The opposite pattern was observed for red algae, with the most flexible and extensible tissues found near the apical meristem at the distal ends of blades.

CONCLUSIONS: We propose that divergent patterns in the distribution of material properties along blades may have different consequences for the performance of kelps and red algae. The positioning of younger tissues at the blade base for kelps may enable these species to attain larger body sizes in wave-swept habitats.

KEY WORDS biomechanics; growth strategy; kelp; Laminariales; material properties; red algae; Rhodophyta

Wave-swept habitats are hydrodynamically stressful for marine macroalgae, with survival ultimately depending on a species' size and morphological design relative to its material properties. There is an evolutionary advantage to larger body sizes, which can afford an organism higher productivity, resistance to predation or damage, competitive ability, and reproductive output (Denny et al., 1985). A large body size may come at the expense of survival, however, because increased blade area results in a higher potential for drag in high flow environments (Denny et al., 1985; Carrington, 1990;

Friedland and Denny, 1995; Gaylord and Denny, 1997). Ultimately, wave conditions in intertidal and subtidal habitats are thought to set the upper limit of body size in macroalgae, which are smaller overall than their terrestrial counterparts (Denny et al., 1985).

Species can compensate for increases in body size by having flexible tissues. Less rigid plants can reduce the amount of drag they experience per unit surface area in wind or flowing water by going with the flow more than resisting it (Vogel, 1984; Puijalon et al., 2011). Seaweeds and flexible plants reduce drag by reconfiguring into more streamlined shapes and orientations in moving water or wind (Harder et al., 2004; Boller and Carrington, 2007; Martone et al., 2012); generally speaking, the more flexible the individual, the less drag it experiences in flow (Demes et al., 2011). High tissue flexibility may also allow an alga to achieve a low profile in the water column to take advantage of reduced flow rates in the benthic boundary layer (Koehl, 1984). Flexible tissues are therefore thought to confer a strong fitness advantage in wave-swept habitats (Harder et al., 2004). In at least some seaweed species, the ability to survive in mechanically hostile environments is largely dependent upon

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their drag reducing and/or resisting mechanisms (Demes et al., 2013a).

Tissue material properties and morphology are influenced by a variety of factors, both extrinsic and intrinsic, which in turn influence the ratio of the force required to break a macroalga to the drag it experiences, known as the safety factor (Alexander, 1968; Johnson and Koehl, 1994). Damage to macroalgal tissues through grazing or contact with the substratum can reduce an alga's safety factor by introducing flaws and causing tissue degradation that reduce tissue strength (Krumhansl et al., 2011). Resulting losses of blade area can cause mortality, if severe (Duggins et al., 2001), but in some cases may act as a pruning mechanism that ultimately increases survival through reduced drag (Blanchette, 1997; Demes et al., 2013a; de Bettignies et al., 2014). Ontogenic processes, including growth, reproduction, and aging, also influence the morphology and material properties of macroalgae. Increasing body size during development is compensated for in some species by growing into more streamlined shapes, i.e., allometric growth (e.g., Johnson and Koehl, 1994; Denny et al., 1997; Gaylord and Denny, 1997). Reproduction and tissue aging can cause a weakening and/or stiffening of tissues that may reduce the safety factor (Armstrong, 1988; Koehl, 2000; Stewart, 2006; Martone, 2007; Krumhansl et al., 2011; Demes et al., 2013b). The causes of tissue weakening with age in seaweeds have not been explicitly explored, but repetitive

loading of tissue stress seems a likely culprit, resulting in fatigue failure (Mach et al., 2007, 2011; Mach, 2009).

Macroalgal species have various growth strategies, which influence longitudinal patterns in tissue age along blades. For some species, tissue growth occurs from the basal meristem (Kogame and Kawai, 1996) (Fig. 1), so that the newest tissue always supports the blade attachment and the tissue is progressively older toward the blade apex, where it eventually erodes off the tips (Mann, 1973), analogous to a conveyor belt. Other species grow apically, with new growth occurring via meristems at their distal tips (Fig. 1). Apical growth results in the newest tissue at blade extremities and oldest tissue at the base, nearest the tissue that attaches to the rock. Therefore, the tissue holding the seaweed to the rock is not renewed throughout the blade's lifetime. A third strategy is diffuse growth, where growth occurs throughout the blade in every direction. Patterns in tissue age along blades growing basally or apically may be associated with longitudinal changes in material properties (Krumhansl et al., 2011; Paul et al., 2014), which would thus differ across macroalgal species with different growth strategies. Longitudinal patterns of tissues material properties across species have not been directly compared previously, despite potential implications for the performance of marine macroalgae.

In this study, we investigated whether shifts in material properties associated with aging were similar across macroalgal species and

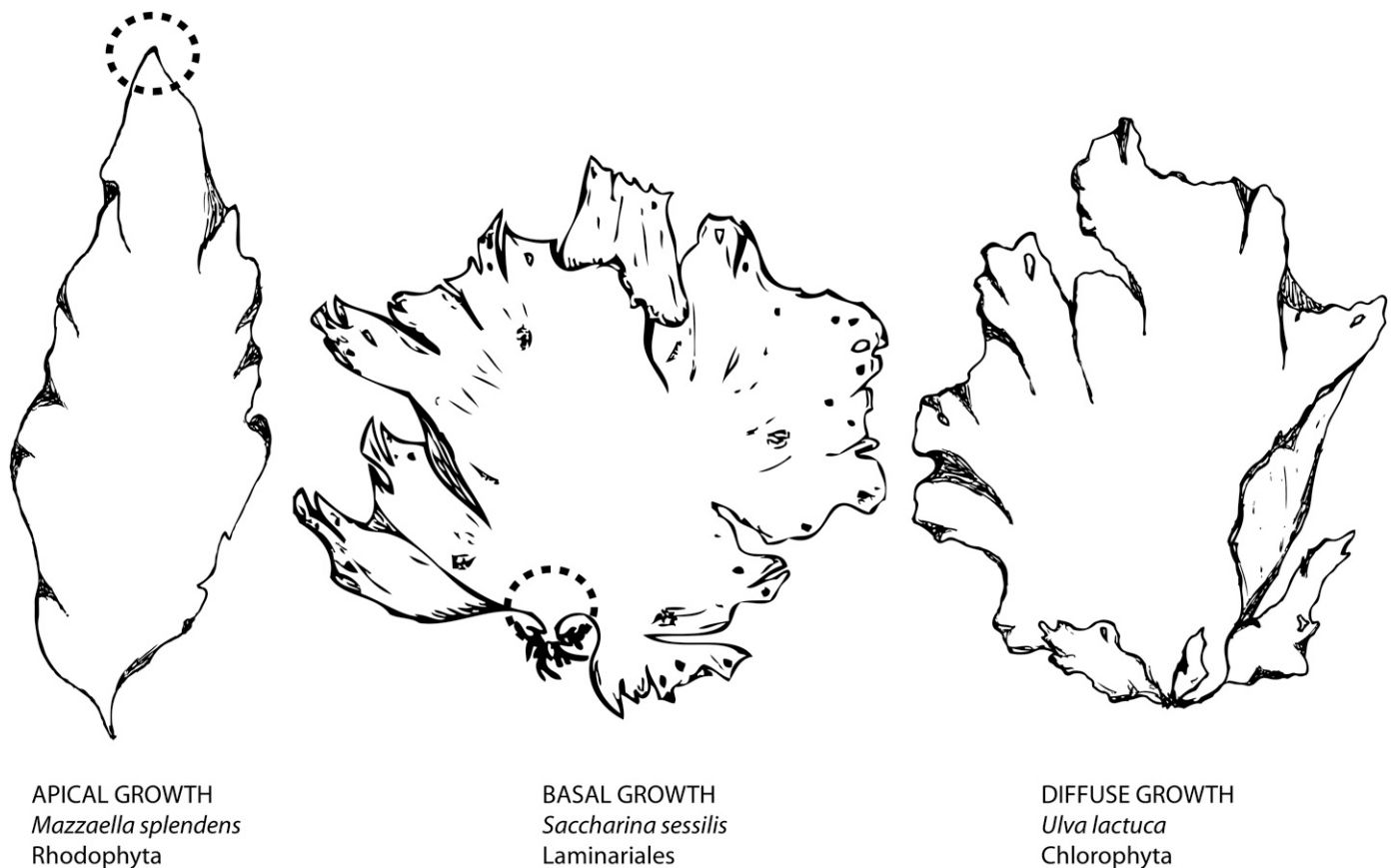


FIGURE 1 Schematic demonstrating differences in growth among morphologically similar representatives of different taxonomic groups. From left to right: *Mazzaella splendens* is a red alga (Rhodophyta) with apical growth, *Saccharina sessilis* is a kelp (Laminariales) with basal growth, and *Ulva lactuca* is a green alga (Chlorophyta) that has diffuse growth. In each species, the dashed circle(s) indicates the location of a growth meristem. *Ulva lactuca* lacks one localized meristem, and instead growth occurs in every direction from all parts of the blade.

whether and how species growth strategy constrained longitudinal distributions of material properties along blades. We used 15 species of red seaweeds that use an apical growth strategy, one green seaweed that utilizes a diffuse growth strategy, and nine species of kelps that use a basal growth strategy to ask: (1) Are there longitudinal patterns in material properties of wave-swept macroalgae? (2) Do these patterns differ across macroalgal groups in association with their growth strategy (apical vs. basal vs. diffuse)? Testing the green algal species, *Ulva lactuca*, which possesses diffuse growth, allowed us to see whether longitudinal patterns of material properties were achieved in absence of a clear relationship between blade position and tissue age. We predicted that aging would consistently decrease breaking stress and strain and increase stiffness of tissues of all species. However, because the relationship between distance from the base of the blade and age of tissue is different between species growing basally vs. apically, we hypothesized that the two groups would display opposite trends in the longitudinal distribution of material properties and that *Ulva* (with diffuse growth) would show no trend.

MATERIALS AND METHODS

Sample collection—Specimens were collected from Port Renfrew on Vancouver Island, British Columbia, Canada (48°31'33.46"N, 124°26'50.22"W) or Friday Harbor Laboratories on San Juan Island, Washington, USA (48°32'42.62"N, 123°0'43.83"W) and thus included both wave-exposed and wave-protected species. Collections were conducted in May 2011 while species were abundant and actively growing; many of the species tested (especially the red algae) have annual blades that do not survive through winter (e.g., Bell, 1999). A total of 25 species were collected: 9 species of kelps, 15 species of red algae, and 1 species of green algae (listed, with site

of collection, in Table 1). Diversity of kelps large enough for analyses was higher in Port Renfrew (likely due to its exposed nature), while diversity of foliose red algae large enough for this study was much great at Friday Harbor Laboratories (a much more protected site). As our aim was to compare broad taxonomic groups and not to estimate variation in traits within species, we sampled only one blade of each species. We assume that this sample is representative of the species tested. After collection, specimens were placed in a flow through water table until analyses, all of which were performed within 48 h of collection.

Determination of tissue material properties—Tissue material properties were determined along a longitudinal series from the point of blade attachment (i.e., stipe if present or holdfast if stipe absent) to the blade apex. Dumbbell-shaped samples without visible flaws (detailed by Mach, 2009; Demes et al., 2011) were cut from seaweed tissues longitudinally at regular intervals to ensure that 4–8 working sections (40 × 6 mm) were obtained from each species. Sampling at regular intervals (with the intervals scaled to the specimen's length) across the whole specimen allowed for the same scale of youngest to oldest tissue to be sampled in all individuals, in spite of differences in their size. The position along the length of the blade of each test-section was recorded as the distance (nearest 0.5 cm) from the center of the working section to the blade's point of attachment. Samples were tested immediately following excision from blades.

Tensile tests were conducted to determine the breaking stress (i.e., tensile strength), breaking strain (i.e., extensibility), initial and final stiffness (Young's or elastic modulus). Pneumatic grips (90 psi) were used to attach the tissue working sections to an Instron tensiometer (model 5565 Norwood, Massachusetts), which strained the samples at a constant rate of 10 mm/min. Although this rate is lower than what is observed in nature, it allowed for comparisons

TABLE 1. Summary of specimens used, collection site (FHL = Friday Harbor, WA; PR = Port Renfrew, BC), and number of samples tested (*N*) by taxonomic grouping. Also shown are the means of each material property (breaking strain, breaking stress, initial and final modulus) ± 1 SE.

Algal group	Species	Collection site	<i>N</i>	Breaking strain	Breaking stress (MPa)	Initial modulus (MPa)	Final modulus (MPa)
Kelp	<i>Agarum fimbriatum</i>	FHL	7	0.19 ± 0.03	1.8 ± 0.2	26.7 ± 3.2	3.8 ± 0.5
	<i>Alaria marginata</i>	PR	16	0.30 ± 0.02	2.9 ± 0.1	26.9 ± 2.3	4.3 ± 0.3
	<i>Costaria costata</i>	FHL	6	0.42 ± 0.03	1.3 ± 0.1	6.6 ± 0.5	1.5 ± 0.2
	<i>Laminaria complanata</i>	FHL	7	0.27 ± 0.03	1.3 ± 0.1	8.1 ± 0.7	2.4 ± 0.2
	<i>Laminaria setchellii</i>	PR	6	0.43 ± 0.05	3.0 ± 0.3	17.6 ± 3	3.5 ± 0.4
	<i>Laminaria sinclairii</i>	PR	11	0.30 ± 0.02	2.9 ± 0.1	21.4 ± 1.6	4.4 ± 0.8
	<i>Macrocystis pyrifera</i>	PR	5	0.18 ± 0.03	0.9 ± 0.1	5.2 ± 0.9	3.6 ± 0.6
	<i>Pterygophora californica</i>	PR	5	0.37 ± 0.05	2.5 ± 0.2	13.6 ± 1.8	3.7 ± 0.8
	<i>Saccharina sessilis</i>	PR	10	0.52 ± 0.04	1.9 ± 0.2	4.4 ± 0.3	3.7 ± 0.5
	<i>Ulva lactuca</i>	FHL	6	0.15 ± 0.03	2.4 ± 0.4	26.3 ± 2.6	11.4 ± 4.2
Green							
Red	<i>Callophyllis pinnata</i>	FHL	5	0.29 ± 0.02	3.2 ± 0.4	15.3 ± 2.8	7.7 ± 1.0
	<i>Chondracanthus corymbifera</i>	FHL	6	0.39 ± 0.03	1.3 ± 0.1	3.5 ± 0.6	3.8 ± 0.5
	<i>Chondracanthus exasperatus</i>	FHL	7	0.33 ± 0.04	1.5 ± 0.1	5.2 ± 0.6	5.0 ± 0.3
	<i>Cryptonemia borealis</i>	FHL	5	0.28 ± 0.04	2.5 ± 0.4	10.3 ± 1.6	7.2 ± 1.2
	<i>Cryptopleura ruprechtiana</i>	FHL	3	0.23 ± 0.01	7.0 ± 2.1	51.1 ± 22.4	16.7 ± 3.6
	<i>Mastocarpus papillatus</i>	FHL	4	0.44 ± 0.03	3.2 ± 0.3	4.5 ± 1.3	8.0 ± 0.6
	<i>Mazzaella splendens</i>	FHL	6	0.56 ± 0.09	2.0 ± 0.1	1.5 ± 0.2	4.6 ± 0.2
	<i>Neodilsea borealis</i>	FHL	4	0.30 ± 0.05	1.8 ± 0.4	5.0 ± 0.9	7.8 ± 0.6
	<i>Opuntia californica</i>	FHL	4	0.29 ± 0.03	2.9 ± 0.4	11.8 ± 1.1	7.6 ± 0.8
	<i>Palmaria hecatensis</i>	PR	6	0.27 ± 0.08	1.2 ± 0.2	4.0 ± 0.3	5.5 ± 0.2
	<i>Palmaria mollis</i>	FHL	6	0.29 ± 0.01	1.7 ± 0.3	5.5 ± 1	5.4 ± 0.4
	<i>Polyneura latissima</i>	FHL	4	0.11 ± 0.01	1.5 ± 0.1	16 ± 3.5	9.4 ± 2.3
	<i>Schizymenia pacifica</i>	FHL	5	0.29 ± 0.03	2.2 ± 0.2	4.7 ± 0.4	8.8 ± 1.5
	<i>Sparlingia pertusa</i>	FHL	6	0.29 ± 0.03	3.8 ± 0.4	16.2 ± 3.5	11.4 ± 0.9

across species, which was the goal of this study, and is consistent with strain rates in similar studies (Hale, 2001; Harder et al., 2004; Boller and Carrington, 2007; Demes et al., 2013a, b). The resisting force (N) and displacement (± 0.1 mm) of tissue was measured at 10 Hz until tissue failure occurred. Width and cross-sectional area of working sections were measured before tensile tests to the nearest 0.1 mm using digital calipers. Significant grip slip would have been detectable by sampling at 10 Hz, but was not observed in visual inspection of tensile test data. All tensile tests were performed on tissues while submerged in 10°C seawater from Friday Harbor Laboratories.

Strain was calculated as the change in length of the tissue divided by the initial length. Breaking strain and force to break samples were recorded as the final strain and force values, respectively. Force values were converted to stress (Pa) by dividing by initial tissue cross-sectional area, and breaking stress was calculated as the final stress value. Modulus was calculated as the slope of the stress vs. strain curve. Since algal tissues do not yield linear stress vs. strain curves (Hale, 2001), the modulus was determined at the initial and terminal portions of the curve, and defined hereafter as initial and final Young's modulus, respectively.

Statistical analyses—Position along the length of the blade and the tissue material property data were standardized for each specimen using $x_i - \bar{x} / \bar{x}$, where \bar{x} is the mean value across blade positions for each species. Thus, a value of zero represents the mean for that species, negative values represent values below the mean for that species, and positive values represent values greater than the mean for that species. Data were standardized in this manner because tissue material properties (as well as length of specimens) vary among species within a phylum (Demes et al., 2011) and among phyla (Martone, 2007). Linear mixed effects models were then performed on standardized data to test the hypothesis that material properties varied along the length of blades in red algae and kelps. To test this hypothesis, position along the length of the blade was included as a fixed factor, while species was included as a random factor. To test the hypothesis that variation in growth strategies between red algae and kelps results in differential trends in material properties along the length of blades, linear models included group (red algae vs. kelps) and position along the length of the blade as fixed factors and species as a random factor nested within group. A group \times distance interaction term was included as an explicit test of the differences in the relationship between position along the length of the blade and the given mechanical property for kelps and red algae. Because only one species of green alga (Chlorophyta) was large enough to obtain mechanical data at multiple positions along the length of the blade, the green alga *U. lactuca* was analyzed separately from the red algae and kelps. Statistical analyses were performed using R Statistical Package 2.15.1 (R Foundation for Statistical Computing, Vienna, Austria) and considered significant with $\alpha = 0.05$ and $P < 0.05$. Linear mixed effects models were performed in the lme4 package (Bates et al., 2008), and the significance of fixed effects was determined using Wald χ^2 tests implemented with the car package (Fox and Weisberg, 2010).

RESULTS

Breaking strain in kelps decreased significantly with distance from the blade base, while initial and final modulus significantly increased

(Table 2; Fig. 2A–D, gray points and lines). For the red algae, the opposite trend was found for each tissue material property: breaking strain increased significantly with distance from the blade's base, and initial and final modulus decreased significantly toward the blade's apex (Table 2; Fig. 2A–D, black points and lines). Thus, in specimens of both kelp and red algae, older tissue was stiffer and less extensible. In kelps, breaking stress increased significantly with distance from the blade base, but there was no significant relationship between breaking stress and distance in red algae. For the green alga tested, *Ulva lactuca*, position on blade ($N = 5$) was not significantly associated with any material properties: breaking strain ($R^2 = 0.04$, $P = 0.745$), breaking stress ($R^2 = 0.07$, $P = 0.658$), initial modulus ($R^2 = 0.341$, $P = 0.224$), and final modulus ($R^2 = 0.001$, $P = 0.961$; data not shown). Means and standard deviations of each material property by species are given in Table 1.

In the hierarchical model analysis, taking species into account as a random factor nested within taxonomic group, a significant growth strategy group \times position on blade interaction term was detected for all tissue mechanical properties tested (Table 3). The sign of the relationship between distance from the base of the blade of the tissue to its material properties (i.e., breaking strain, tissue breaking stress, and initial and final modulus) was opposite for kelps and red algae in all material properties (Table 2, Fig. 2A–D).

DISCUSSION

Material properties varied longitudinally along the length of blades in red algae and kelp. For both groups of macroalgae, we observed decreased breaking strain (i.e., extensibility) and increased initial and final modulus (i.e., stiffness) with distance from the meristem, corresponding to increases in tissue age. Previous studies have shown similar trends in material properties with tissue age (Armstrong, 1988; Koehl, 2000; Stewart, 2006), corroborating the notion that aging compromises the extensibility and flexibility of seaweed tissues. Consistent with our predictions, material properties did not vary longitudinally along the blades of the green alga *Ulva lactuca*, likely because its diffuse growth strategy does not allow blade position to serve as a proxy for tissue age. Our inability to detect such relationships may have resulted from an inherent lack of aging effects on tissue mechanical properties, but does appear to support our overall result that longitudinal patterns in materials properties are determined by growth strategy. An alternate approach to testing for aging effect in species with diffuse growth could be to compare blade material properties during periods of rapid growth (newer tissues) to periods of slow growth (older tissues).

TABLE 2. Variation in material properties (first standardized by species) explained by position on blade (distance from blade's attachment point) for each algal species group separately (red algae and kelps). Analyses were run in a mixed effects modeling framework with species included as a random variable.

Property	Reds		Kelps	
	Slope	P	Slope	P
Breaking strain	1.53 e^{-1}	0.039	-3.35 e^{-1}	<0.001
Breaking stress	-8.55 e^{-2}	0.247	1.43 e^{-1}	0.002
Initial modulus	-4.09 e^{-1}	<0.001	2.48 e^{-1}	<0.001
Final modulus	-6.53 e^{-2}	0.279	5.25 e^{-1}	<0.001

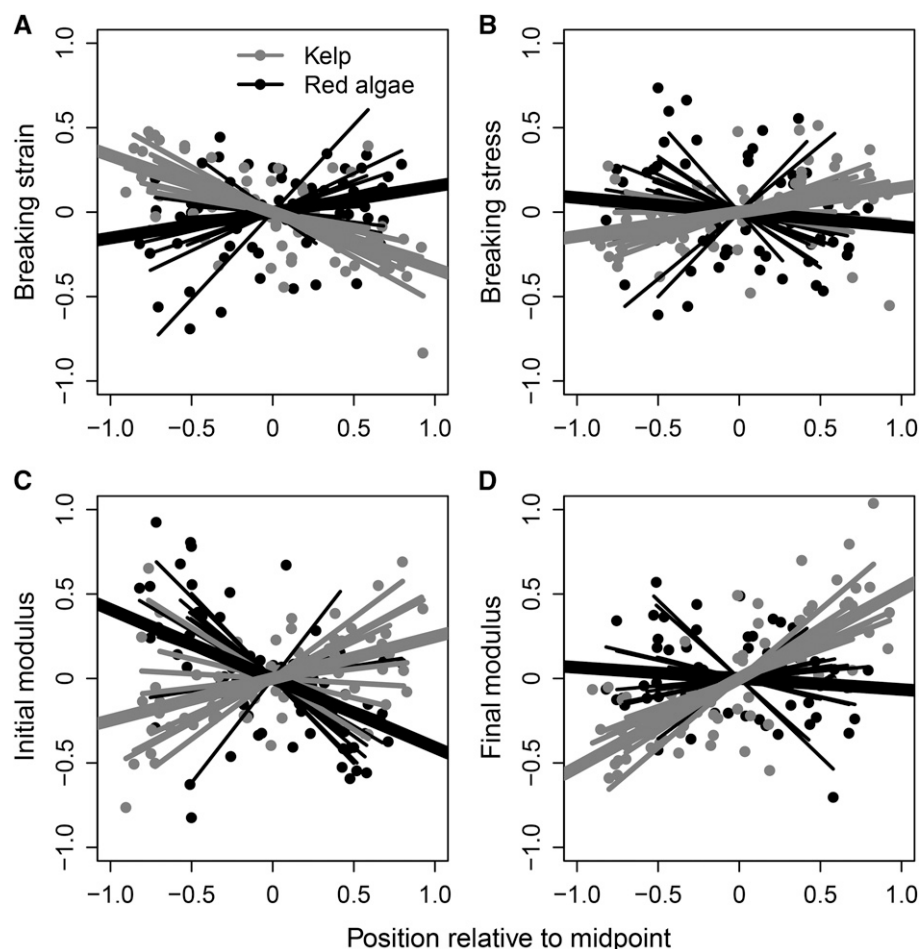


FIGURE 2 Tissue material properties vary along the lengths of blades of kelps (gray coloring) and foliose red algae (black coloring): (A) Breaking strain. (B) Breaking stress. (C) Initial modulus. (D) Final modulus. Dots represent results of individual tests at each blade position for each species, thin solid lines represent estimated linear fit by species, while thick solid lines represent estimated linear fit by group (red algae or kelp). All values are standardized to allow comparison among species and taxonomic groups. The x-axis is a standardized position on blade with zero representing the center of the blade, negative values representing areas closer to the blade's base, and positive values representing distal portions of the blades. Slopes for the green alga *Ulva lactuca* were not significantly different from zero and were excluded from graphs.

Contrary to our predictions, we found significant increases in breaking stress (i.e., strength) with age in kelps. Interestingly, there was no clear relationship between tissue age and breaking stress in red algae. Macroalgal tissues are composed of boxes and/or spheres (cells) of varying sizes, enclosed by cell walls of varying thickness, and filled to varying degrees with water and various cellular constituents. The strength of a macroalgal tissue is related to the quantity and quality of the underlying structural materials (i.e., the cell wall). Martone (2007) demonstrated that the increased breaking stress of older segments of the red alga *Calliarthron tuberculosum* was due to a thickening of the cell walls. A similar mechanism could help explain why we detected higher tissue breaking stress among older tissues in the kelp species tested, but further study is needed to determine mechanisms specific to kelps and other macroalgal species. Differences in ontogenetic change in tissue breaking stress between red algae and kelps suggest that the mechanisms

dictating aging effects on structural materials differ between macroalgal species groups.

Because high extensibility (Koehl and Wainwright, 1977) and low stiffness (Boller and Carrington, 2007; Demes et al., 2011) are thought to be important components of seaweeds' mechanical adaptation to life in wave-swept habitats, varying longitudinal positioning of younger tissues likely has differential implications for the mechanical performance of red algae and kelps. Because the majority of foliose red algae (and all of the red algal species tested) grow from the blade apices, the oldest tissue attaches the blade to the substrate. Because this tissue is less flexible and extensible, the alga may not be able to fully bend and streamline in flow, increasing the amount of drag experienced on the algal thallus and possibly limiting the overall size that red algae can attain. The positioning of older tissue at the blade base may also increase the susceptibility of blade loss due to tissue fatigue failure (Mach, 2009). For kelp, positioning younger tissues at the blade base may enable blades to bend and streamline in flow, reducing the profile of the alga in the water column and enabling it, at least in prostrate and stipitate species, to take advantage of reduced flow near the substrate (Koehl, 1984). Extensible tissues at the blade's base can absorb energy created by this movement, reducing overall force on older tissues at the blade's distal end and increasing the safety factor of the seaweed. Tissue strengthening with age in kelps might also be an important compensatory mechanism for decreases in tissue flexibility and extensibility. Thus, we propose that the evolutionary novelty of basal growth among kelps may have contributed to their ability to obtain large blade sizes in high-energy environments and dominate wave-exposed habitats.

Growth strategy is only one of many factors that contribute to mechanical performance of seaweeds, but our results suggest that its role warrants further investigation. Although we have demonstrated that longitudinal variation in material properties exists in accordance with species growth strategy, implications for survival and breakage dynamics in the field remain unexplored. Differential blade positioning of older tissues in red algae and kelps may influence how these species reconfigure in flow, and consequently the loads that they bear. The implications of our results depend, at least in part, on the role of fatigue failure in older tissues. Positioning of newer tissues at the blade base in brown algae could be a strategy for avoiding fatigue failure, but too little is known about the occurrence and mechanisms dictating interspecies variation in susceptibility to tissue fatigue to support this supposition.

Although mechanical properties of red algae may limit their body size, their ability to thrive in these mechanically hostile environments may be related to other growth strategy and/or life history traits. For instance, many other red algal species can proliferate

TABLE 3. Variation in material properties (first standardized by specimen) explained by position on blade (distance from blade's attachment point) and the interaction between position on blade and growth strategy group (red algae vs. kelps). The main effect of growth strategy is not shown because data were standardized to a mean of 0 for each group. Analyses were run in a mixed effects modeling framework with species included as a random variable nested within growth strategy group.

Property	Position on blade		Position × Growth strategy	
	χ^2	P	χ^2	P
Breaking strain	9.6	0.002	33.4	<0.001
Breaking stress	1.2	0.265	7.2	0.007
Initial modulus	0.4	0.542	45.9	<0.001
Final modulus	46.9	<0.001	52.3	<0.001

from crustose holdfasts—these species may sacrifice blades in particularly hydrodynamically stressful times to allow the holdfast to remain attached and regenerate blades (Marshall et al., 1949; Sousa, 1985; D'Antonio, 1986; Bell, 1999). Other red algae are annual and, as their strategy for persistence, may rely on one large reproductive event before the onset of large winter swells that may dislodge them. Clearly, it is important to consider morphological, material, and life history traits when addressing adaptations of seaweeds to wave-exposed environments.

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