

VARIATION IN ANATOMICAL AND MATERIAL PROPERTIES EXPLAINS DIFFERENCES IN HYDRODYNAMIC PERFORMANCES OF FOLIOSE RED MACROALGAE (RHODOPHYTA)¹

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Over the last two decades, many studies on functional morphology have suggested that material properties of seaweed tissues may influence their fitness. Because hydrodynamic forces are likely the largest source of mortality for seaweeds in high wave energy environments, tissues with material properties that behave favorably in these environments are likely to be selected for. However, it is very difficult to disentangle the effects of material properties on seaweed performance because size, shape, and habitat also influence mechanical and hydrodynamic performance. In this study, anatomical and material properties of 16 species of foliose red macroalgae were determined, and their effects on hydrodynamic performance were measured in laboratory experiments holding size and shape constant. We determined that increased blade thickness (primarily caused by the addition of medullary tissue) results in higher flexural stiffness (*EI*), which inhibits the seaweed's ability to reconfigure in flowing water and thereby increases drag. However, this increase is concurrent with an increase in the force required to break tissue, possibly offsetting any risk of failure. Additionally, while increased nonpigmented medullary cells may pose a higher metabolic cost to the seaweed, decreased reconfiguration causes thicker tissues to expose more photosynthetic surface area incident to ambient light in flowing water, potentially ameliorating the metabolic cost of producing these cells. Material properties can result in differential performance of morphologically similar species. Future studies on ecomechanics of seaweeds in wave-swept coastal habitats should consider the interaction of multiple trade-offs.

Key index words: biomechanics; blade; cortex; flexural stiffness; medulla; Rhodophyta

Abbreviation: *EI*, flexural stiffness

Seaweeds have an intricate relationship with water velocity. While submerged, increased flow facilitates acquisition of CO₂ and nutrients for growth and productivity (Hurd et al. 1996, Cornelisen and Thomas 2006). However, moving water also imposes drag forces on seaweeds, calculated as follows:

$$F = 1/2\rho v^2 AC_d \quad (1)$$

where F = drag, ρ = density, v = velocity, A = projected area, and C_d = drag coefficient. Seaweed tissues must be stronger than the hydrodynamic forces they experience to avoid dislodgement and subsequent mortality. Seaweeds are able to resist hydrodynamic forces by strengthening their tissues (Lowell et al. 1991, Martone 2007) or by reducing the area exposed to flowing water by remaining small or by reconfiguring (Vogel 1984, Koehl and Alberte 1988, Armstrong 1989, Carrington 1990, Boller and Carrington 2006) to become more hydrodynamically streamlined. While seaweed strength and reconfiguration potential (indexed by flexibility) are both dependent on tissue material properties, little is known about how seaweeds produce materials of varying properties.

Unlike terrestrial plants, which produce multiple tissue types for different structural roles (Kokubo et al. 1989, Vincent 1991), macroalgae are usually limited to pigmented cortical cells at the tissue surface and nonpigmented medullary cells in the tissue center. The cortical cell layer is comparable among

¹Received 27 September 2010. Accepted 6 May 2011.

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most species, comprising one to several layers of tightly packed photosynthetic cells. Medullary tissue, on the other hand, varies greatly among taxa in terms of thickness, degree of compaction, and cell shape (Fritsch 1959). Although medullary cells are responsible for the translocation of photosynthate in kelps (Schmitz and Lobban 1976), in red macroalgae (Rhodophyta), connections between medullary cells are blocked by proteinaceous pit plugs (Pueschel 1989), leaving their function unclear.

Despite the wide-spread prevalence of nonpigmented medullary tissue among red macroalgae, little is known about its function. However, the addition of medullary cells may have significant biomechanical consequences for seaweeds. Most importantly, increasing tissue thickness should increase breaking force and EI (Vogel 2003), both of which likely affect seaweed fitness. EI is the resistance of an object to bending and is defined as the product of a material's modulus of elasticity (E) and its second moment of area (I). Increasing tissue thickness should not affect E but will greatly affect I , which increases with thickness cubed (Vogel 2003). All else being equal, thicker blades will be stiffer and therefore less easily reconfigured. Likewise, the addition of medullary cells may decrease the ability of seaweeds to reconfigure, thereby exposing them to higher hydrodynamic drag forces, which may in turn have negative effects on fitness.

The ability of macroalgae to reconfigure in flowing water and thereby reduce drag is known to be ecologically important (Koehl 1984, Carrington 1990). However, only recently have researchers attempted to quantify differences in reconfiguration potential among species and found that stipe bendiness, $(EI)^{-1}$, is largely responsible for this process in turf-forming seaweeds (Boller and Carrington 2006). Most species converge on similar maximally reconfigured shapes at high velocities that are representative of exposed intertidal sites (M. L. Boller and P. T. Martone, unpublished data); however, large differences in reconfiguration potential occur among species at lower velocities ($<2 \text{ m} \cdot \text{s}^{-1}$) that are representative of protected, high-current-exposed, or subtidal sites. Reconfiguration may come at the metabolic cost of self-shading, presenting an interesting trade-off between maximizing photosynthetic surface area incident to light (productivity) and minimizing hydrodynamic drag forces through reconfiguration (hydrodynamic forces) (Koehl and Alberte 1988, Koehl et al. 2008).

Hydrodynamic forces imposed by strong currents and breaking waves have been proposed to be a strong selective pressure in shaping the evolution of intertidal organisms (Denny 1988). Likewise, a plethora of literature exists on hydrodynamic performance of numerous species, largely focusing on mechanical limits to size (e.g., Koehl 1986, Denny 1988, Carrington 1990, Gaylord et al. 2008, Koehl et al. 2008, Martone and Denny 2008). However,

other seaweed biomechanical studies have highlighted the importance of tissue material properties (i.e., strength, extensibility, bendiness, etc.) on hydrodynamic performance (Lowell et al. 1991, Johnson and Koehl 1994, Gaylord and Denny 1997, Harder et al. 2006, Boller and Carrington 2007). Despite recent advances in this field, a paucity of data exists describing (i) variation in material properties among species (although see Koehl 2000), (ii) how variation in material properties is produced by the individual (however, see Martone 2007), and (iii) how differences in material properties affects seaweed fitness.

While previous comparative studies have provided important insight into how differences in biomechanical properties (strength, flexibility, and EI or bendiness) may affect the fitness of marine organisms, it is very difficult to disentangle the relative effects of species identity, size, shape, and environment. Furthermore, how internal growth form and thallus construction affect tissue material properties is almost entirely unexplored in these studies (however, see Koehl 1999, Martone 2007).

Foliose red macroalgae (Rhodophyta) provide an excellent way to tease apart the aforementioned confounding factors and explore effects of tissue construction on material properties because of the abundance of taxonomically distinct blades, which can be distributed growing next to one another. While all red blades are often lumped into the functional group "foliose macroalgae" (Steneck and Dethier 1994), it is possible that many different thallus constructions and tissue types could produce a bladed morphology. In this study, we quantify material properties of 16 species of foliose red macroalgae. We controlled size and shape in the laboratory to test the effects of material properties on hydrodynamic performance. Specifically, we ask: (i) Do differences in material properties exist among foliose red macroalgae? (ii) If variation in material properties exists among species, are anatomical differences responsible for such variation? (iii) Does variation in material properties explain differences in hydrodynamic performance?

MATERIALS AND METHODS

Specimen collection and processing. Table 1 lists the taxonomic placement and collection locality of species used in this study (identifications by and authorities available through Gabrielson et al. 2006). Because variation in material properties within a species has been shown to result from environmental factors (Armstrong 1987, Kraemer and Chapman 1991, Kitzes and Denny 2005), care was taken to collect specimens from locations of similar exposure. All collections were made within the San Juan Islands (Washington, USA) at moderately protected sites where largest maximum water velocities are from currents. Thirteen species were collected from the Friday Harbor Laboratories dock lines or adjacent rocks. *Prionitis* and *Smithora* were collected from docks in Roche Harbor and from eelgrass blades in False Bay, respectively. *Holmesia*, which is a

TABLE 1. Study species, taxonomic placement (order and family), and collection site of specimens used in this study. Voucher specimens are archived in the Friday Harbor Laboratory Herbarium.

Species	Order	Family	Collection site
<i>Porphyra</i> sp.	Bangiales	Bangiaceae	FHL intertidal
<i>Polyneura latissima</i>	Ceramiales	Delesseriaceae	FHL dock
<i>Holmesia californica</i>	Ceramiales	Delesseriaceae	Turn point, Stuart Is. (~9 m)
<i>Havaldiophyllum nottii</i>	Ceramiales	Delesseriaceae	FHL dock
<i>Smithora naiadum</i>	Erythropeltidales	Erythrotrichiaceae	False Bay
<i>Neodilsea borealis</i>	Gigartinales	Dumontiaceae	FHL shallow subtidal
<i>Constantinea subulifera</i>	Gigartinales	Dumontiaceae	FHL shallow subtidal
<i>Opuntia californica</i>	Gigartinales	Furcellariaceae	FHL shallow subtidal
<i>Chondracanthus exasperatus</i>	Gigartinales	Gigartinaceae	FHL dock
<i>Mazzaella splendens</i>	Gigartinales	Gigartinaceae	FHL dock
<i>Cryptonemia obovata</i>	Halymeniales	Halymeniaceae	FHL dock
<i>Prionitis lanceolata</i>	Halymeniales	Halymeniaceae	Roche Harbor
<i>Halymenia californica</i>	Halymeniales	Halymeniaceae	FHL dock
<i>Schizymenia pacifica</i>	Nemastomatales	Schizymeniaceae	FHL dock
<i>Sparlingia pertusa</i>	Rhodymeniales	Rhodymeniaceae	FHL dock
<i>Fryella gardneri</i>	Rhodymeniales	Rhodymeniaceae	FHL dock

less common species, was collected opportunistically by divers at ~9 m near Stuart Island.

Specimens were kept alive in the laboratory in seawater tables before being processed. Material property tests (described below) took place no longer than 24 h after collection and hydrodynamic performance tests (described below) were run 2–3 d after collection. For each species, voucher specimens were pressed and deposited in the Friday Harbor Laboratories Herbarium. Corresponding samples were preserved in silica gel for future molecular analyses.

Variation in anatomy and material properties. To determine anatomical variation between species, cortex thickness, medulla thickness, and total blade thickness (Fig. 1) were determined through microscopy (Olympus model BX41, Olympus, Center Valley, PA, USA). Measurements on blades thinner than 200 μm were to the nearest 10 μm , while those >200 μm were measured to the nearest 50 μm . This range represents a substantial fraction of blade thickness. However, rounding effects should be distributed randomly, adding increased error to statistical analyses and making statistical analyses more conservative. To control strain localization and accurately describe tissue properties of the different species, longitudinal test shapes (Fig. 2A) were cut from specimens after Mach (2009). Because material properties may vary along the length of blades (Armstrong 1987, Koehl 2000), especially near the stipe/blade junction (apophysis), all test shapes were cut ~5 cm above the apophysis (or stipe when apophysis absent), oriented from the center of the blade to the distal end. Tissue strength (as force to break), breaking stress (force per initial cross-sectional area), breaking strain (change in length divided by initial length), and modulus of elasticity (slope of terminal linear portion of stress vs. strain curve) were analyzed using the tensile test setting on an Instron tensometer (model 5565, Norwood, MA, USA). Test shapes were attached to the tensometer via pneumatic clamps at 60 psi lined with sand paper. For several species, soft paper was added as padding to prevent tissue breakage from the clamping apparatus. The tensometer strained the seaweeds at a constant rate of 10 $\text{mm} \cdot \text{min}^{-1}$ and measured the resisting force (N) at 1 Hz until the tissues broke. All samples were run wet, but out of water. Specimens were periodically and carefully rewetted with a paintbrush if needed. Specimens that broke at or near the clamps were not included.

Beam theory (Fig. 3) was used to measure EI (resistance of a material to bend) as described in Vogel (2003). Longitudinal

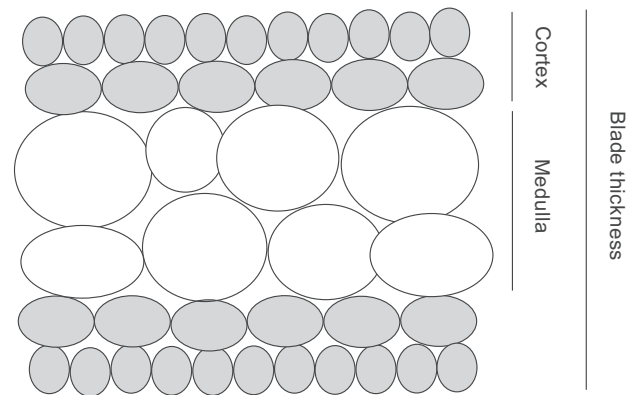


FIG. 1. Model cross-sectional view of a red blade showing anatomical measurements (blade thickness, cortex thickness, and medulla thickness). Shaded areas represent pigmentation.

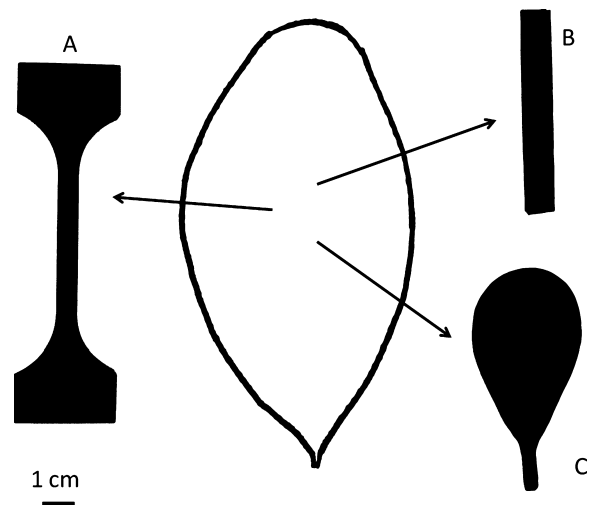


FIG. 2. Standardized test shapes cut out of specimens for (A) tensile tests, (B) flexural stiffness measurements, and (C) hydrodynamic performance measurements in the flume. Cutouts are drawn to scale.

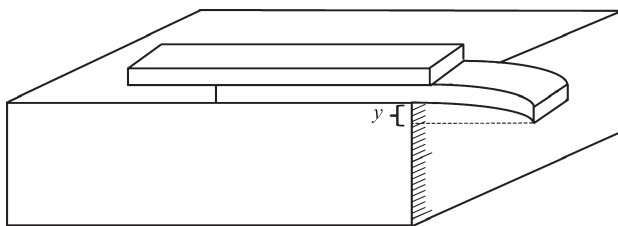


FIG. 3. Empirical measurement of tissue flexural stiffness (EI) through beam theory deflection. All samples were of constant width so that deflection (y) varied only as a result of beam length and the force applied on that beam by its weight.

rectangular shapes cut from blades (Fig. 2B) were sandwiched between a glass microscope slide and a flat edge along a 90° edge, demarcated with a mm scale. Test shapes (cantilever beams) were then incrementally pulled from the slides until deflection (measured to the nearest 0.5 mm of deflection) reached $\sim 10\%$ of the beam length (species for which $<10\%$ deflection was not achieved were left out of analyses). EI was determined for three replicates within each species using the following equation:

$$EI = FL^3/8y \quad (2)$$

whereby EI = flexural stiffness, F = weight of unsupported beam, L = length of unsupported beam, and y = deflection (Vogel 2003). Beam mass was measured to the nearest 1 mg using an analytical scale. Weight was then calculated by multiplying the mass by gravity and was assumed to be uniformly loaded across the beam.

Hydrodynamic performance. To test the effects of material properties on hydrodynamic performance, without the confounding effects of shape and size, blades were cut longitudinally into standardized shapes (Fig. 2C). The hydrodynamic test shape was chosen as a morphologically nondescript foliose rhodophyte; size ($\sim 12 \text{ cm}^2$) was constrained by the smallest blade used (*Smithora naiadum*). The hypothetical stipe portion of the sections was attached directly to a force transducer using super glue and placed in a high-speed recirculating flume developed by Boller and Carrington (2006). Drag force was measured directly by the force transducer for five replicate test shapes of each species at $1.71 \text{ m} \cdot \text{s}^{-1}$.

To determine the effect of flow-induced reconfiguration on planform surface area (perpendicular to flow), which would not affect drag but would theoretically be exposed to sunlight and be capable of photosynthesizing, photos were taken from below the seaweeds using a mirror secured at a 45° angle to the flume. Surface area was measured using ImageJ photo analysis software (U.S. National Institutes of Health, Bethesda, MD, USA).

Statistical analyses. To determine if variation among species existed in breaking force, breaking stress, breaking strain, modulus of elasticity, EI , and planform area at $1.71 \text{ m} \cdot \text{s}^{-1}$, one-way analysis of variance (ANOVA) was performed on species identity. To test the relative contribution of increasing cortex versus medulla tissue in thicker blades, analysis of covariance (ANCOVA) homogeneity of slopes test was used with tissue type as a fixed factor, blade thickness as the covariate, and tissue thickness as the response variable. Significantly different slopes would suggest that one tissue type over the other contributes more to blade thickening. Linear regression analysis was used to determine if hydrodynamic performance (drag) could be explained by anatomical and material properties. Nonlinear regression analysis, exponential rise to maximum,

$$y = a[1 - \exp(-bx)] \quad (3)$$

was used instead for planform area in flowing water because values were constrained by the surface area of the test shape, which they could not exceed. Finally, power curve fitting was used to test the effects of blade thickness on EI , given the a priori expectation that stiffness will increase with thickness cubed. Levene and Shapiro-Wilk tests were used to test assumptions of homogeneity of variance and normality, respectively. If assumptions could not be met after data transformations, nonparametric analyses were used instead. A result was considered to be significant with $\alpha = 0.05$ and $P < 0.05$. All statistical analyses were performed in R Statistical Package 2.10.1 (R Foundation for Statistical Computing, Vienna, Austria).

RESULTS

Variation in material properties. Material property data are summarized in Table 2. Tissue breaking stress ranged from 0.56 MPa in *Halymenia* to 4.1 MPa in *Opuntia* and was significantly different among species ($F_{15,65} = 11.140$, $P < 0.001$). Breaking strain was also different across species ($F_{15,65} = 34.513$, $P < 0.001$) and ranged from 0.074 in *Polyneura* to 0.8 in *Mazzaella*. Because residuals were not normally distributed for modulus of elasticity, data were analyzed with ANOVA on ranks. Modulus of elasticity varied from 17.5 MPa in *Polyneura* to 0.89 MPa in *Halymenia* and was significantly different among species ($P < 0.001$). Log transformation was required to meet the homogeneity of variance assumption of ANOVA for EI . EI was highly variable within a species, likely because, to maintain 10% deflection of beam length, 0.5 mm resolution proved somewhat crude given the flexibility of the specimens. Nonetheless, a significant effect ($F_{11,24} = 6.03$, $P < 0.001$) of species identity was still detected with mean values ranging from 6.0×10^{-6} in *Holmesia* to $7.5 \times 10^{-4} \text{ Nm}^2$ in *Neodilsea*. Deflections under 10% could not be achieved for *Smithora*, *Porphyra*, *Haraldiophyllum*, and *Spartingia*, and therefore these species were not included in analyses.

Anatomical sources of variation in material properties. Large variation was present in internal anatomy across species with monostromatic blades (composed of a single cell layer) 25 μm thick (*Smithora*) to leathery blades 500 μm thick (*Neodilsea*). Furthermore, increasing cross-sectional thickness was found to be driven primarily by increasing thickness of medullary tissue rather than cortical tissue (Fig. 4), such that thicker seaweeds had disproportionately thicker medulla ($F_{3,28} = 65.99$, $P < 0.001$). In other words, medulla thickness increased faster with increasing cross-sectional area than did cortex thickness.

Breaking force was positively correlated with blade thickness (Fig. 5; $P < 0.001$). In an analysis containing all species, increasing blade thickness did not increase EI ($R^2 = 0.171$, $P = 0.063$). Evident in Figure 6, *Polyneura* and *Holmesia* are outliers, being much stiffer than expected by just blade thickness

TABLE 2. Tissue material properties. Summary of red algal blade material properties ($N = 3$ for all flexural stiffness tests). ND = not determined. Values are mean \pm SE.

Species	N	Breaking strain	Breaking stress (MPa)	Modulus of elasticity (MPa)	Flexural stiffness (μNm^2)
<i>Chondracanthus</i>	3	0.44 ± 0.03	1.7 ± 0.2	4.1 ± 0.2	493 ± 248
<i>Constantinea</i>	5	0.20 ± 0.02	1.5 ± 0.1	7.9 ± 0.6	285 ± 136
<i>Cryptonemia</i>	5	0.39 ± 0.05	2.1 ± 0.3	6.1 ± 0.6	9 ± 3
<i>Fryeella</i>	3	0.07 ± 0.02	0.4 ± 0.1	4.7 ± 0.6	129 ± 63
<i>Halymenia</i>	3	0.35 ± 0.03	0.3 ± 0.03	0.9 ± 0.1	64 ± 19
<i>Haraldiophyllum</i>	4	0.15 ± 0.03	2.0 ± 0.4	14.6 ± 0.5	ND
<i>Holmesia</i>	5	0.15 ± 0.02	1.6 ± 0.4	11.6 ± 2.2	6 ± 1
<i>Mazzaella</i>	5	0.8 ± 0.03	1.9 ± 0.1	3.1 ± 0.1	17 ± 6
<i>Neodilsea</i>	5	0.41 ± 0.02	1.9 ± 0.3	4.7 ± 0.4	749 ± 329
<i>Opuntiaella</i>	5	0.43 ± 0.05	3.5 ± 0.4	6.9 ± 0.3	299 ± 210
<i>Polyneura</i>	5	0.07 ± 0.01	1.2 ± 0.3	3.1 ± 0.1	558 ± 230
<i>Porphyra</i>	4	0.40 ± 0.07	1.3 ± 0.2	4.4 ± 0.3	ND
<i>Prionitis</i>	3	0.37 ± 0.03	2.6 ± 0.1	7.2 ± 0.2	282 ± 216
<i>Schizymenia</i>	5	0.38 ± 0.03	0.40 ± 0.1	1.5 ± 0.1	33 ± 5
<i>Smithora</i>	3	0.11 ± 0.03	0.49 ± 0.2	6.4 ± 1.2	ND
<i>Sparlingia</i>	4	0.17 ± 0.04	1.2 ± 0.3	7.4 ± 0.3	ND

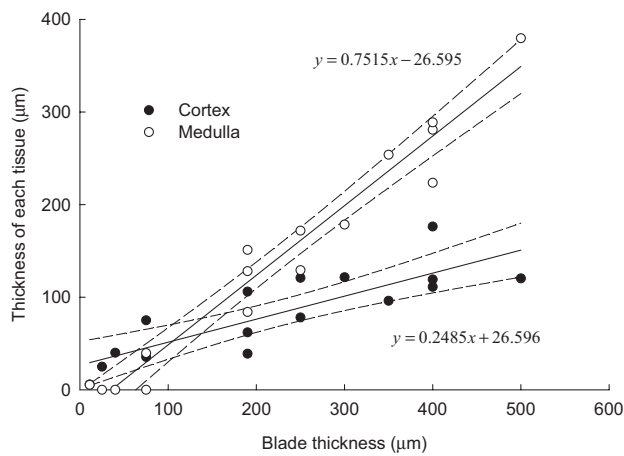


FIG. 4. As blade thickness increases, thickness of medullary tissue increases at a faster rate than cortex tissue. In other words, thicker blades exhibit disproportionately larger medulla.

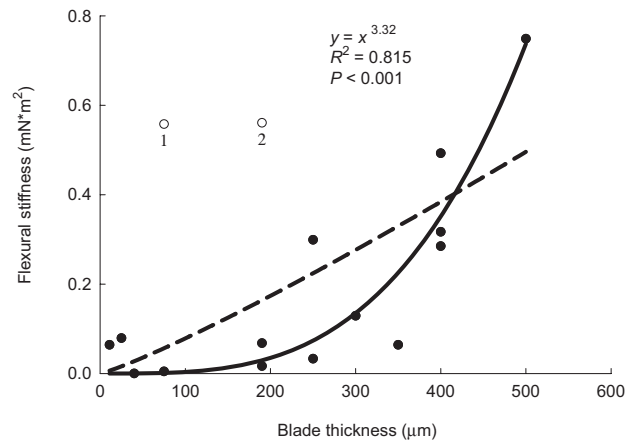


FIG. 6. Flexural stiffness as a function of blade thickness. Line represents partial model (filled circles only) excluding *Polyneura* and *Holmesia*. Equation and statistics derived from partial model.

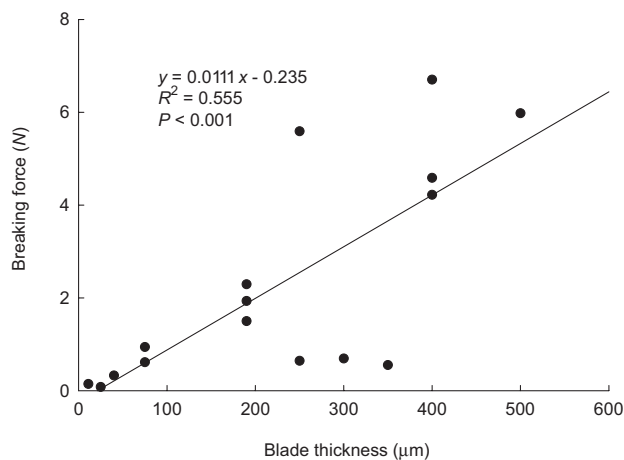


FIG. 5. Blade thickness is positively associated with force (N) to break tissue.

alone. Analysis without these two species found a significant relationship between blade thickness and EI ($R^2 = 0.777$, $P < 0.001$). Furthermore, the cubic exponent predicted by increases in EI due to second moment of area, was not significantly different than the exponent observed in the partial model (3.37 ± 0.756). None of the anatomical characters measured was found to predict tensile modulus of elasticity, breaking stress, or breaking strain ($P \gg 0.05$).

Hydrodynamic performance. Flexural stiffness was the best predictor of drag force and explained 68% of the variation at $1.71 \text{ m} \cdot \text{s}^{-1}$ (Fig. 7; $P < 0.001$). However, seaweeds which experienced higher drag forces required more force to break (Fig. 8; $R^2 = 0.326$, $P = 0.021$). Because EI could not be determined for all species (particularly the thinner, more flexible species that are likely more susceptible to folding), the effect of blade thickness (which

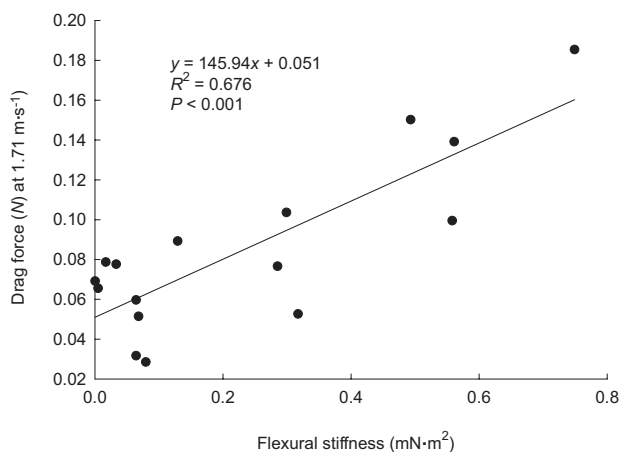


FIG. 7. Blades with higher flexural stiffness experience higher drag forces. Flexural stiffness values are in $10^{-3} \text{ N} \cdot \text{m}^2$ to increase axis clarity.

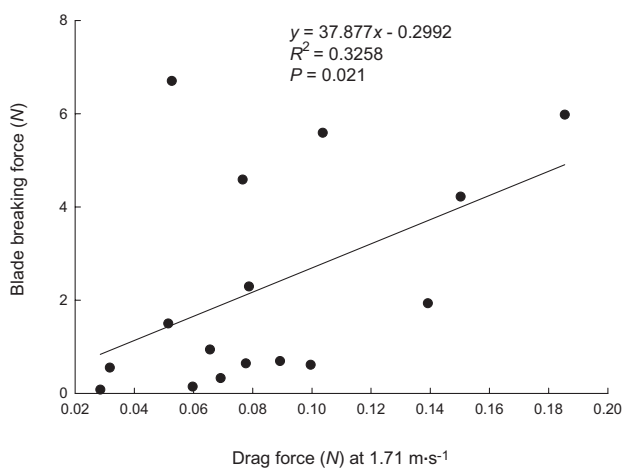


FIG. 8. Blades that experience higher drag forces are also stronger and can withstand larger forces before tissue failure.

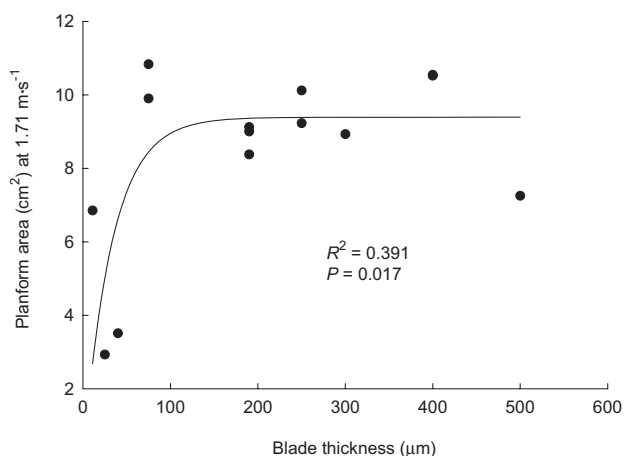


FIG. 9. Planform area at $1.71 \text{ m} \cdot \text{s}^{-1}$ as a function of blade thickness. Thicker blades have higher surface area exposed to sunlight while waves pass.

was shown to be positively associated with EI) on planform surface area was analyzed instead. Significant variation in planform area at $1.71 \text{ m} \cdot \text{s}^{-1}$ was detected ($F_{13,41} = 21.830$, $P < 0.0001$) among species. This variation was partly explained by blade thickness, such that thinner blades reconfigured more readily in flow and exhibited decreased planform area (Fig. 9; $R^2 = 0.391$, $P = 0.017$).

DISCUSSION

Reconfiguration significantly reduces drag forces on seaweeds (Carrington 1990, Boller and Carrington 2006) and is essential for life in the intertidal zone (Harder et al. 2006). However, reconfiguration may also carry with it the added cost of self-shading when thallus portions fold on top of one another (Koehl and Alberte 1988). Our results show that thinner blades reconfigure more readily in flowing water than thicker blades and consequently experience lower drag but higher self-shading (lower planform surface area). On the other hand, thicker blades can withstand larger drag forces before breaking and are able to resist mechanical failure as they expose more surface area for photosynthesis and reconfigure less.

Why then are not all red blades thick? One possible explanation is a metabolic cost associated with increased medullary thickness. Thicker blades can absorb $>90\%$ of ambient light and likely reflect the rest (Beach et al. 2006). Light penetrance into tissue may therefore limit the thickness of the cortex (pigmented cells). Since medullary cells are nonpigmented, it is reasonable to assume that they rely metabolically on cortical cells. This scenario suggests a maximum medulla to cortex ratio and may set an upper limit to blade thickness. The integration of metabolic costs of tissue production into ecomechanics of seaweeds presents a fascinating and unexplored area of future research.

Although EI depends on both tensile stiffness (E) and blade thickness (I , second moment of area), both of which varied in this study, $\sim 80\%$ of the variation in EI was explained by blade thickness alone for most species. However, two species in this study displayed substantially higher EI than expected given their thickness (see Fig. 6), suggesting other mechanisms for increasing stiffness. *Polyneura latissima* is unique among the species in this study in that it possesses thickened veins running through its blade. Differentially thickened thallus portions, such as veins or midribs, may also result in higher EI . Thickness of blade tissue between veins was used in our analyses. Using the thickness of the veins instead may have provided a more accurate prediction of EI in this species. While the other disproportionately stiff species, *Holmesia californica*, does not possess veins, it stands out from the other species in regard to medullary construction. Medullary tissue in most of the species used is composed

of loosely packed spherical or filamentous cells. To the contrary, medullary tissue of *H. californica* is composed of tightly compacted cuboid cells, which may better resist bending. Contributions of venation and medullary cell type to material properties and hydrodynamic performance require data from many more species and remain unresolved.

While many of the species used in this study are not easily morphologically discerned from one another without the use of microscopy, some are very easily distinguished by anecdotal tactile tests. Phycologists are often seen in the field tugging, tearing, or rubbing foliose red macroalgae for easy field identification. This practice is supported here by differences in material properties found across species. One material property in particular, *EI*, has a significant effect on hydrodynamic performance such that increases in *EI* result in increased drag. Previously, Boller and Carrington (2007) reported that variation in reconfiguration potential in, and therefore drag forces experienced by, 10 species of taxonomically, morphologically, and ecologically dissimilar species was related to *EI* of stipe tissue. The current study further supports their findings that increased *EI* of thallus tissue results in increased drag forces between much more closely related species, while controlling for differences in size and shape.

The novelty of this study is that we controlled size and shape of seaweeds and showed how material properties alone can affect hydrodynamic performance. However, it is important to note that the species here naturally vary in size and shape to various degrees. For instance, two species of drastically different material properties may experience comparable drag forces by altering their morphology (shape and/or size). Therefore, whether material properties of seaweeds actually affect fitness (productivity or survivorship) of individuals in the field is difficult to discern from this study. Experimental studies measuring selection on intraspecific variation in material properties and phylogenetic analyses of material properties are lacking but could shed light on whether material property effects on performance are evolutionarily significant.

We are indebted to Jaquan Horton for invaluable help throughout the course of this project, Robin Elahi for collection of subtidal specimens, and Chris Harley and Jonathan Pruitt for constructive criticism on earlier drafts of this manuscript. This work was supported by the Stephen and Ruth Wainwright Endowment via fellowship to Kyle Demes, NSF through grant EF-1041213 awarded to Emily Carrington, and a Discovery Grant awarded to P. T. Martone by the Natural Science and Engineering Research Council (NSERC). Additional funds were provided by the NSERC CREATE program.

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