EVIDENCE OF AN EVOLUTIONARY-DEVELOPMENTAL TRADE-OFF BETWEEN DRAG AVOIDANCE AND TOLERANCE STRATEGIES IN WAVE-SWEPT INTERTIDAL KELPS (LAMINARIALES, PHAEOPHYCEAE)[1]

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Kelps are a clade of morphologically diverse, ecologically important habitat-forming species. Many kelps live in wave-swept environments and are exposed to chronic flow-induced stress. In order to grow and survive in these harsh environments, kelps can streamline (reducing drag coefficient) to avoid drag or to increase attachment and breakage force to tolerate it. We aimed to quantify the drag tolerance and streamlining strategies of kelps from wave-swept intertidal habitats. We measured drag coefficient and tenacity of populations from eight kelp species over a wide range of sizes to determine whether kelps avoid dislodgement by reducing drag coefficient or by increasing tenacity as they grow, and whether these traits are traded off. We employed phylogenetic comparative methods to rule out potentially confounding effects of species' relatedness. There was a significant negative relationship between drag avoidance and tolerance strategies, even after incorporating phylogeny. Kelps that were more tenacious were less able to reduce drag, resulting in a continuum from "tolerators" to "streamliners," with some species demonstrating intermediate, mixed strategies. Drag and tenacity were correlated with geometric properties (i.e., second moment of area) of the stipe in large kelps. Results presented in this study suggest that kelps are either strong or streamlined, but not both. This continuum is consistent with avoidance and tolerance trade-offs that have been documented in many different biological systems and may have widespread implications for the evolution of large macroalgae, perhaps driving morphological diversity within this group.

Key index words: biomechanics; foundation species; macroalgae; morphology; phylogenetic comparative methods; reconfiguration; stress avoidance; stress resistance; stress tolerance; tenacity

Trade-offs between avoidance and tolerance strategies of stress resistance have long drawn attention in the fields of evolutionary and functional biology (e.g., Storey and Storey 1986, Fineblum and Rausher 1995, Henry and Aarssen 1997, Fornoni et al. 2003, Iason and Villalba 2006, Touchette et al. 2007, Puijalon et al. 2011). Avoidance and tolerance trade-offs have been described in a variety of organisms, from amphibians (Storey and Storey 1986) and mammals (Iason and Villalba 2006) to plants in salt marshes (e.g., Touchette et al. 2007) and current-swept rivers (e.g., Puijalon et al. 2011). Although these studies addressed different types of stress and resistance, results have repeatedly demonstrated trade-offs, where tolerance or avoidance strategies incur costs to the traits that underlie the opposing strategy. This constraint could be direct, if the use of one trait directly impedes the use of another (Ballhorn et al. 2010) or indirect, if using both avoidance and tolerance strategies together is too costly (e.g., Fineblum and Rausher 1995, Fornoni et al. 2003, Baucom and Mauricio 2008).

Fluid forces exerted by moving air or water cause chronic stress for many organisms (Koehl 1982, Vogel 1994, Denny 1995, Ennos 1997, Denny and Gaylord 2002) and may impart selective pressures on the structure and morphology of plants (Norton 1991, Ennos 1997, Demes et al. 2013, Starko et al. 2015). Some plants and macroalgae can reconfigure and streamline, reorienting under waves and "going with the flow" to reduce the drag that they experience (Vogel 1989, Boller and Carrington 2006, Martone et al. 2012). Alternatively, plants and macroalgae can increase the thickness and strength (i.e., tenacity) of support tissues (Wainwright et al. 1976, Demes et al. 2013) to resist the drag that they experience. Drag tolerance traits that involve tissue thickening may directly impede drag reduction traits, if thicker tissues lead to an increase in the rigidity of fronds or basal structures, limiting bending and reconfiguration of macroalgae in flow (Koehl 1982, 1984, Demes et al. 2011).

Puijalon et al. (2011) demonstrated evidence of a streamlining–tenacity trade-off in current-swept embryophytes (see Anten and Sterck 2012 for a

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review), in which plants that experienced more drag (i.e., were less streamlined) resisted greater forces before dislodging or breaking. This constituted the first empirical evidence of an avoidance–tolerance trade-off related to mechanical stress. While the generality of this streamlining–tenacity trade-off has been scrutinized and supported (Butler et al. 2011, Puijalon et al. 2011, Anten and Sterck 2012), it remains an open question whether it can be extended to wave-exposed kelps, which are not plants and represent a distinct evolutionary trajectory (Keeling 2004).

The wave-swept intertidal zone is of particular interest for studies of mechanical stress resistance, due to the magnitude and unpredictability of wave velocities (see Denny and Gaylord 2002). Among the forces that seaweeds experience in flow, drag is the best documented and often the most important (Jensen 2014, Jensen and Denny 2015). Drag is related directly to size through the following formula:

$$\text{Drag} = \frac{1}{2}\rho U^2 A C_D \qquad (1)$$

where ρ is the mass density of the fluid (1,029 kg · m^{-3} in seawater), U is the fluid velocity (m · s^{-1}), A is the planform area (m^2), and C_D is drag coefficient, a dimensionless parameter that describes the streamlined nature of an organism (Vogel 1994). Drag forces imposed by crashing waves are not only immense (often greater than hurricane force winds) but also occur frequently, often on the scale of seconds (Denny and Gaylord 2002). This repetitive loading can cause material fatigue, often leading to dislodgement at otherwise sublethal velocities (Mach et al. 2007, 2011). Thus, selection may act to reduce drag not only under the largest waves but also under more typical conditions. Kelps and other brown seaweeds are the largest organisms to inhabit the rocky intertidal zone (Steneck et al. 2002). So how do they grow so large, if size increases drag?

Kelps are flexible, allowing them to reconfigure and reorient in flow (e.g., Koehl and Wainwright 1977, Johnson and Koehl 1994, Utter and Denny 1996). Studies have shown that seaweed populations at sites with higher wave exposure may have lower drag coefficients than conspecifics from sheltered areas (e.g., Buck and Buchholz 2005, Fowler-Walker et al. 2005, Kitzes and Denny 2005, Koehl et al. 2008), suggesting a selective advantage to possessing a streamlined form, since streamlining can reduce drag and dislodgement risk. For example, the bull kelp, *Nereocystis luetkeana*, streamlines as it grows, adopting a lower drag coefficient (at a given velocity) with increased photosynthetic area to avoid a proportional increase in drag and allowing for decreased investment in support structures (Johnson and Koehl 1994). Production of increasingly streamlined forms through development may help kelps grow large and experience disproportionally less drag, potentially reducing the need for increased support and attachment.

Kelps also have continuously growing holdfasts (Oliveira et al. 1980) and stipes (similar to stalks; see Koehl 1984) to which they can add additional girth as they grow and develop (DeWreede 1986, Klinger and DeWreede 1988, Martone 2007), thereby constituting an alternative strategy to resist wave forces. Mechanical failure occurs when drag equals tenacity (see, e.g., Johnson and Koehl 1994, Utter and Denny 1996, Martone et al. 2012). Thus, investment in the holdfast or stipe could circumvent the need to streamline, allowing kelps to tolerate, rather than reduce, drag.

Kelps look similar when they are small but diversify through development, producing mature plants that are highly variable in morphology (Abbott and Hollenberg 1976), tenacity (see Starko et al. 2015), and streamlining capability (e.g., Koehl 1984, Johnson and Koehl 1994, Utter & Denny 1995). Given that streamlining and tenacity are both beneficial for survival in the intertidal zone, are drag–tolerance and streamlining strategies traded off among different kelp species living in wave-swept environments? Could a negative correlation between these capabilities help to explain the wide morphological diversity of kelps? In order to address these questions, we quantified morphogenetic changes in streamlining and tolerance over a wide range of sizes for wave-swept populations of eight kelp species, so as to determine whether increases in tenacity are associated with decreases in streamlining abilities and vice versa.

METHODS AND MATERIALS

Kelp collections and area quantification. We collected data on intertidal populations of eight kelp species (Fig. 1) from two wave-swept sites near Bamfield, British Columbia, during their peak-growing season. All collections were made between February and September (2013/2014) and included a minimum range of sizes for each species from 70 to 1,150 cm^2 (see Table 1 for additional collection information). *Alaria marginata* Postels & Ruprecht, *Egregia menziesii* (Turner) Areschoug, *Macrocystis pyrifera* (Linnaeus) Agardh, *Saccharina groenlandica* (Rosenvinge) Lane, Mayes, Druehl & Saunders, and *Laminaria setchellii* Silva were collected from wave-swept, west-facing regions of Eagle (Scott's) Bay (N 48.83376, W 125.14895). *Lessoniopsis littoralis* (Tilden) Reinke, *Costaria costata* (Agardh) Saunders, and *Saccharina sessilis* (Agardh) Kuntze were collected from a wave-exposed headland at Brady's Blowhole (N 48.82466, W 125.16148). Offshore swell (commonly 3–5 m; LaPerouse Buoy) approaches Barkley Sound from the west, and west-facing sites in Barkley Sound tend to experience similar maximum forces (Boizard 2007). For a map of the field
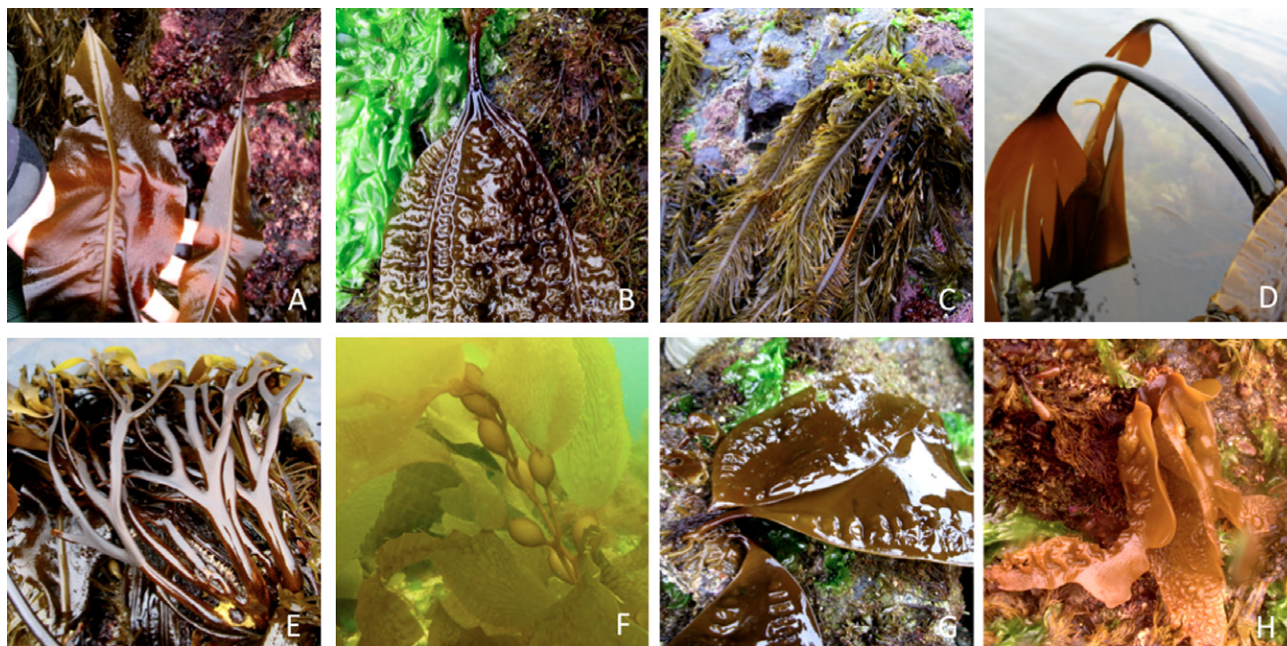
FIG. 1. Photographs of the species used in this study: (A) *Alaria marginata*, (B) *Costaria costata*, (C) *Egregia menziesii*, (D) *Laminaria setchellii*, (E) *Lessoniopsis littoralis*, (F) *Macrocystis pyrifera*, (G) *Saccharina groenlandica*, (H) *Saccharina sessilis*. Photos A–G by R.B. Munger, and photo H by S. Starko.

TABLE 1. Additional collection information

Family	Species	Sample size[1]	Minimum area (cm^2)	Maximum area (cm^2)
Alariaceae	*Alaria marginata*	$N_S = 21$; $N_T = 24$	50	4,660
Costariaceae	*Costaria costata*	$N_S = 12$; $N_T = 15$	70	2,220
Lessoniaceae	*Egregia menziesii*	$N_S = 15$; $N_T = 14$	60	10,380
Laminariaceae	*Laminaria setchellii*	$N_S = 12$; $N_T = 13$	50	1,150
Alariaceae	*Lessoniopsis littoralis*	$N_S = 14$; $N_T = 19$	20	3,580
Laminariaceae	*Macrocystis pyrifera*	$N_S = 13$; $N_T = 23$	25	20,860
Laminariaceae	*Saccharina groenlandica*	$N_S = 13$; $N_T = 23$	40	2,220
Laminariaceae	*Saccharina sessilis*	$N_S = 15$; $N_T = 14$	30	2,010

[1]N_S is the sample size for streamlining quantification; N_T is the sample size for tenacity quantification.

sites sampled in this study, see Figure S1 in the Supporting Information.

We measured planform area as one half of the wetted surface area (as in Carrington 1990, Boller and Carrington 2006, Martone et al. 2012) since total area is a primary predictor of drag (de Bettignies et al. 2013). Specimens were cut up as needed to lay fronds flat and get an accurate measure of planform area, and photos were taken of each specimen from above with a scale of known length. Area was quantified with ImageJ software (version 1.45s; US National Institutes of Health, Bethesda, MD, USA).

Tenacity. We quantified tenacity (in newtons) in situ using tensometers (i.e., spring scales; precision = 0.1 N) that were custom built using precision springs (Associated Spring Raymond, Maume, OH, USA). For small kelps, a cable tie was used to attach the stipe to the spring scale, while for larger individuals, the stipe (or entire holdfast in the case of *S. sessilis* and some *M. pyrifera*) was wrapped with sanding cushion, and hose clamps were used to attach the tensometer to the kelp (as in Boizard 2007). For some large *Macrocystis* individuals, the hose clamp was wrapped directly around the rhizomatous holdfast. This method was only performed when a central portion was raised above the substratum and had a gap with no attached haptera. In the case of the strongest kelps (e.g., large *L. littoralis*, *L. setchellii*, or *E. menziesii*), a winch, anchored higher in the intertidal zone, was used to apply the forces necessary for dislodgement or breakage. Kelps were pulled perpendicular to the shore, in the direction that they would most likely experience the greatest wave forces. Tenacity was recorded as maximum force to break the stipe or dislodge the holdfast. Any breakage that occurred as a result of cutting from the cable or hose clamp was not recorded.

Drag. Drag (in newtons) was measured on kelp specimens at $1\ m \cdot s^{-1}$ in the large recirculating water flume (working section: $1.0 \times 0.8 \times 12\ m$) at Bamfield Marine Sciences Centre, Bamfield, British

Fig. 2. A schematic of the recirculating flume set-up used to measure drag.
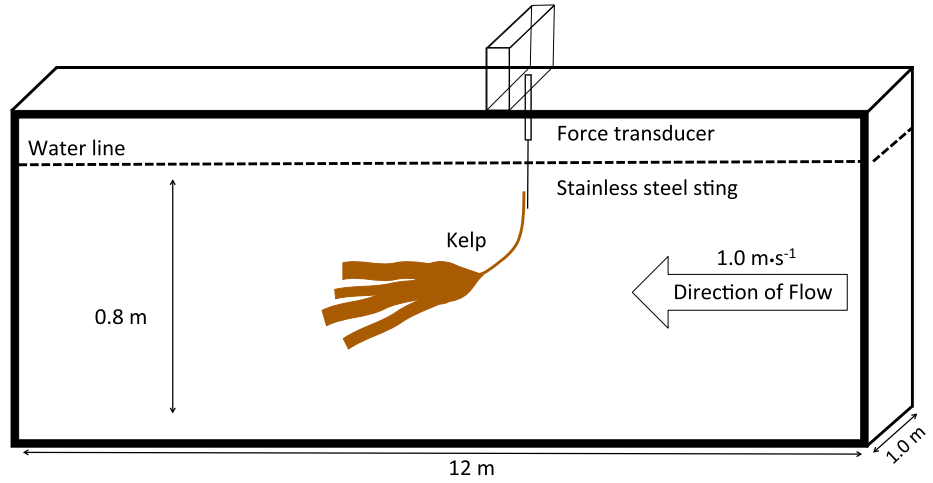
Columbia (Fig. 2). This one velocity ($1 \, \mathrm{m \cdot s^{-1}}$) – the maximum flow rate of the flume – was selected to standardize comparisons among all sizes and species of kelps. Kelps were affixed to a single-axis force transducer (model # FORT5000; World Precision Instruments, 10 Hz sampling rate, Sarasota, FL, USA) with a stainless steel sting that extended 10 cm into the water from above. A small portion of the stipe (1 cm) was affixed to the sting exactly 2 cm from the tip, perpendicular to the direction of flow (Fig. 2). For measurements of *M. pyrifera* and *S. sessilis*, the holdfast was whittled down as small as possible and affixed directly to the sting at the same position. After each drag measurement, kelp blades were removed, leaving only the holdfast or stipe attached to the sting, as well as any wire or string used to tether the kelp. Drag experienced by this "blank" was subtracted from the initial measurement to account for any drag effects of the attachment method.

Streamlining and tolerance indices. Avoidance and tolerance strategies were quantified as the slope of the line fitted to data on drag coefficient versus area or tenacity versus area, respectively. The drag avoidance strategy of each kelp population was quantified as *streamlining index* (*S*): the negative scaling coefficient of drag coefficient and area ($C_D \propto A^{-S}$). This value was used even when the slope was not statistically significant, since *S* is mathematically equivalent to the difference from unity of the scaling relationship between drag and area ($D \propto A^{1-S}$), which was always significant. *Tolerance index* (*T*) was defined as the scaling coefficient of tenacity and area (Tenacity $\propto A^T$). *S* and *T* were quantified using the slopes of the lines fitted to log–log curves. We tested for a correlation between *S* and *T* using a type II linear model fit in R (v3.0.2; R Foundation for Statistical Computing, Vienna, Austria) with the "lmodel2" package (Legendre 2004). In order to determine whether species had significantly different streamlining and tolerance indices, we conducted ANCOVAs of drag coefficient and tenacity as a function of area, species, and a species-by-area interaction.

Predicting avoidance and tolerance at different sizes. In order to determine whether more tenacious kelps also experienced more drag, generalized additive models were fit on log–log axis between drag (at $1.0 \, \mathrm{m \cdot s^{-1}}$) and planform area, as well as tenacity and planform area, using the "mgcv" package in R (Wood 2011). Size-specific drag and tenacity were then predicted (with standard error) from these models at two sizes (70 and 1,150 cm^2); these sizes were chosen because they were minimum and maximum sizes that were collected of all species and thus do not include the maximum range of some larger species (Table 1). Type II linear models were used to test for a correlation between tenacity and drag (on log-transformed axis) at these sizes.

Second moment of area. To determine whether streamlining and tolerance were predictably related to the tissue thickening of the stipe or base of blade, we quantified second moment of area (*I*) of basal structures for each species. The tendency of a structure to bend depends on its flexural stiffness (*EI*), the product of *I*, and material flexibility (*E*). Second moment of area takes into account both cross-sectional area and shape. Thus, it directly describes the structural (i.e., nonmaterial) resistance to bending of a beam. Stipes are approximated elliptical in cross-section, and thus, *I* was calculated using the following formula:

$$I = \frac{\pi d_1^3 d_2}{64} \qquad (2)$$

where d_1 is stipe diameter parallel to the direction of flow, and d_2 is stipe diameter measured perpendicular to flow. For *S. sessilis*, *I* was quantified for the portion of the blade that was fused with the holdfast. For all other kelps, diameter measurements were taken at the base of the stipe, directly above where the stipe begins to taper out toward the holdfast. Although kelp stipes can vary

significantly in material stiffness (E = 5–40 MPa; Hale 2001), EI is proportional to the fourth power of stipe thickness (eq. 2). Thus, changes in stipe thickness over the lifetime of a growing kelp would likely have the greatest impact on overall flexural stiffness (EI). For this reason, I was used as an index for the rigidity of basal structures. The relationship between I and planform area was quantified in R using generalized additive models. Estimates of I were then predicted at 70 and 1,150 cm^2 (see previous section) and regressed against predicted values of drag and tenacity. For *M. pyrifera* and *S. sessilis*, larger kelps may have multiple independent bases; however, within the size range used for predictions of I, drag, and tenacity, kelps had a single stipe (for *M. pyrifera*) or blade (for *S. sessilis*). Relevant comparisons of I were not possible for larger kelps with multiple stipes or bases.

Phylogenetic comparative methods and statistics. In order to account for potentially confounding effects of the kelp species' relatedness, we constructed a phylogeny and employed multiple phylogenetic comparative techniques. Sequence data were downloaded from GenBank and Barcode of Life Database (Table S1 in the Supporting Information) for ITS (ITS1, 5.8 rRNA, ITS 2, 26S rRNA partial) and CO1-5P regions and aligned first in Geneious, using the built-in algorithm, but then checked by eye. From downloaded sequences, we created a 1,373 base-pair alignment. Phylogenetic inference was conducted in MrBayes (3.2.3) using models separately determined for each gene by JModeltest and data on *Chorda filum* (Linnaeus) Stackhouse as an outgroup. We used Blomberg's K (Blomberg et al. 2003) to test for a phylogenetic signal on tolerance and avoidance traits, and phylogenetic generalized least squares (P-GLS) models were used along with linear models in all multispecies comparisons (S and T; drag and tenacity). These phylogenetic methods were conducted in R using "phytools" (Revell 2012) and "ape" (Paradis et al. 2004) packages, respectively.

Previous studies have shown high uncertainty in the topology of kelp phylogenies (e.g., Lane et al. 2006). For this reason, we also conducted a Bayesian character correlation analysis using BayesTraits software (V2; Meade and Pagel 2014) in order to incorporate uncertainty in tree topology into our analysis. This analysis was conducted using 10,000 iterations over all MCMC trees (after burnin) produced during tree-space exploration, with an uninformative (uniform) prior probability distribution of negative one to one. Because BayesTraits requires rooted trees, and MrBayes outputs unrooted ones, we first performed rooting at the outgroup in Mesquite (Maddison and Maddison 2015).

RESULTS

There was a significant interaction of area and species on drag coefficient (ANCOVA area × species:

$F_{15,99}$ = 7.3722, P < 0.0001) and tenacity (ANCOVA area × species: $F_{15,129}$ = 3.8007, P = 0.0009). In other words, streamlining and tolerance indices differed between species. For example, *Lessoniopsis littoralis* was a representative tolerator and *Alaria marginata* was a representative streamliner (Fig. 3). As they grow larger, *Alaria* shows a greater ability to streamline (C_D α Area$^{-0.2}$) than *Lessoniopsis* (C_D α Area$^{0.01}$), whereas *Lessoniopsis* becomes much more tenacious (*A. marginata*: Tenacity α Area$^{0.29}$; *L. littoralis*: Tenacity α Area$^{0.54}$). Both streamliners and tolerators were identified at each field site, suggesting that the pattern was not site specific. For complete results on modeling streamlining and tolerance, see Tables S2 and S3 and Figures S2 and S3 in the Supporting Information.

Streamlining and tolerance indices were negatively correlated (type II linear model: $r_{1,6}$ = −0.8485, P = 0.00774; Fig. 4), and although there was no significant relationship between drag and tenacity in the smaller size class (70 cm^2; type II linear model; $r_{1,6}$ = 0.1456, P = 0.7308; Fig. 5A), there was a strong correlation between drag and tenacity at the larger size (1,150 cm^2; type II linear model; $r_{1,6}$ = 0.8136, P = 0.01401; Fig. 5B). See Table S4 and Figure S4 in the Supporting Information for a summary of models used to predict drag at different sizes. There was a significant, positive relationship between I and drag (linear model: $F_{1,6}$ = 15.58, P < 0.01), as well as I and tenacity (linear model: $F_{1,6}$ = 20.98, P < 0.01) at the larger size class (Fig. 6), but not at the small size class (70 cm^2; I vs. drag – linear model: $F_{1,6}$ = 0.9133, P > 0.05; I vs. tenacity – linear model: $F_{1,6}$ = 2.502, P > 0.05; see Tables S5 and S6 in the Supporting Information).

The consensus tree output from MrBayes was not fully dichotomous and failed to resolve the deeper branches between the four families represented in this study (Fig. 7). In general, however, it did agree with the topology of previously published phylogenies of the kelps (e.g., Lane et al. 2006), with small differences in the Laminariaceae (in particular, branching between *Saccharina, Laminaria,* and *Macrocystis*); 6,670 distinct MCMC trees were produced from the analysis and were used as the input for our analysis in BayesTraits.

There was no significant phylogenetic signal for either streamlining ($K_{1,6}$ = 0.5467, P = 0.694) or tolerance ($K_{1,6}$ = 0.7244, P = 0.493) indices, and there remained a significant negative relationship between streamlining and tolerance indices, even when correcting for both phylogeny (P-GLS model; $t_{2,6}$ = −5.1530, P = 0.0021) and uncertainty in the phylogeny (Bayesian character correlation; log Bayes factor = 18.3036). Size-dependent correlations between tenacity and drag were also robust to phylogenetic corrections (P-GLSM 1,150 cm^2: $t_{2,6}$ = 4.844, P = 0.0029; P-GLSM 70 cm^2: $t_{2,6}$ = −0.0002, P = 0.9998).
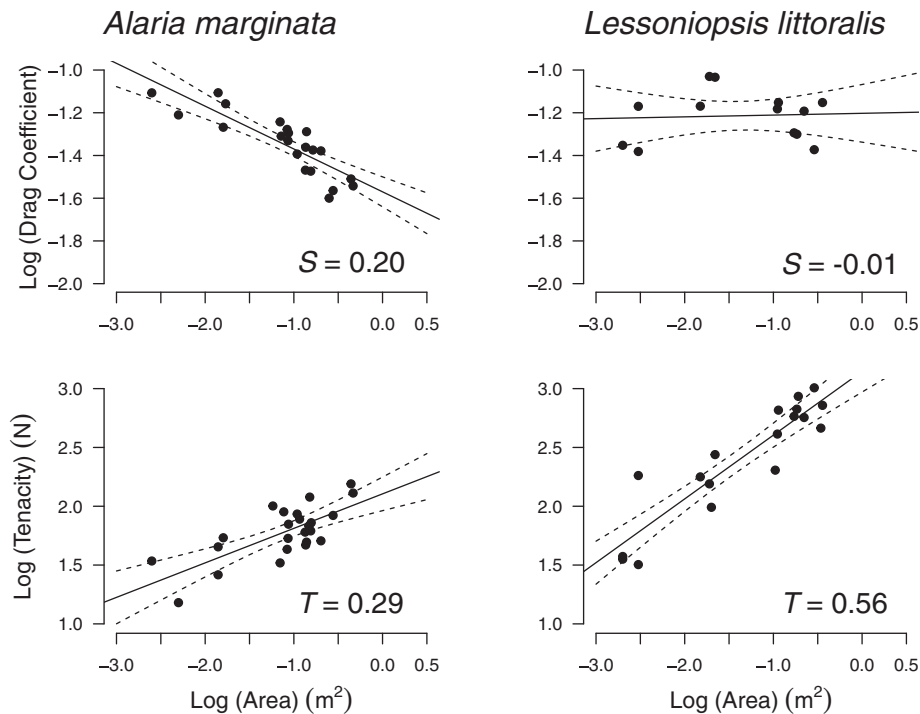
FIG. 3. An example of closely related species (Alariaceae family) with alternate strategies. *Alaria marginata* shows a strong ability to streamline with increased size, whereas *Lessoniopsis littoralis* does not streamline but becomes much more tenacious with increased size.
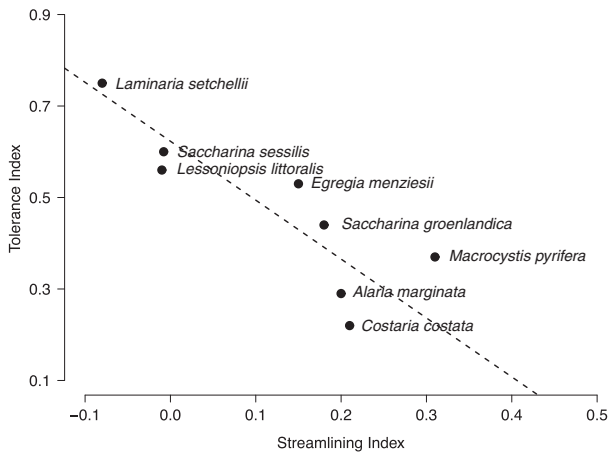

FIG. 4. Negative correlation between tolerance and streamlining indices. The dotted line represents the line of best fit from a type II model ($T = -1.288*S + 0.623$).

DISCUSSION

Support for a streamlining–tolerance trade-off. In this study, we present evidence of a mechanical trade-off between streamlining and tolerance strategies of wave-swept kelps, consistent with that demonstrated in aquatic plants (Puijalon et al. 2011, Anten and Sterck 2012). Species that became more tenacious through development were also those that showed smaller changes in drag coefficient, and species that were better at streamlining did not attach as strongly.

By incorporating phylogeny into our analysis, we demonstrate that relatedness among kelp species cannot explain the observed patterns of streamlining and tolerance (see Blomberg et al. 2003) and that low tolerance–high streamlining or high tolerance–low streamlining strategies have appeared repeatedly throughout the evolution of these kelp species (see Fig. 7). In addition, species that are not strictly "tolerators" or "streamliners" (e.g., *S. groenlandica* and *E. menziesii*) fall along the same regression line, suggesting that some kelps have intermediate strategies, but none can exist at both ends of the avoidance–tolerance spectrum simultaneously (i.e., achieving maximum values for streamlining and tolerance). This is consistent with the concept of an avoidance–tolerance continuum as described in previous studies (e.g., Iason and Villalba 2006, Puijalon et al. 2011).

Perhaps not surprisingly, the trade-off is principally observed in adult thalli. At the large size class (1,150 cm^2), more tenacious kelps were predicted to be less able to streamline and, therefore, experience more drag. However, this trend did not hold true for kelps that were small (70 cm^2). Small kelps possess similar morphologies, possibly explaining why drag estimates and tenacities were similar among species. Moreover, some factors underlying streamlining and tolerance may be size dependent. For example, larger individuals may have a greater scope for reconfiguration, since they have more area that can potentially reorient, fold up, and compress (see Wernberg 2005).
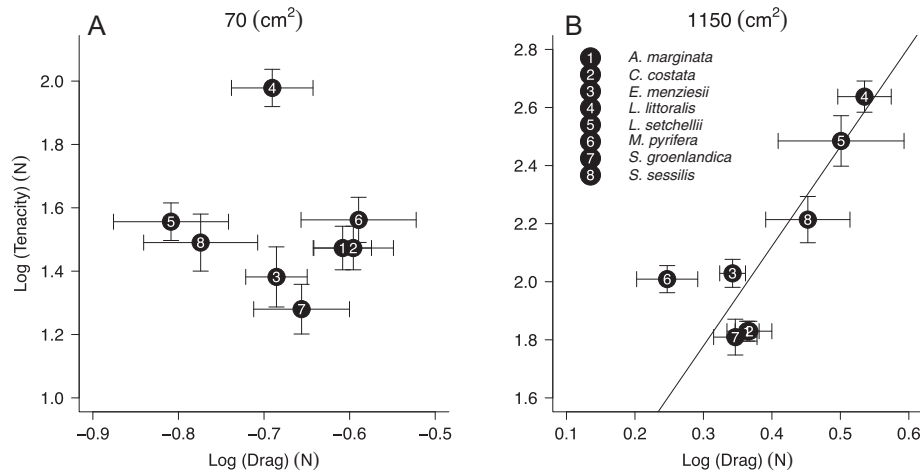
Fig. 5. Drag and tenacity for all species at 70 (A) and 1,150 cm^2 (B) as predicted by generalized additive models. Error bars represent standard error, as predicted with a Bayesian algorithm in "mgcv".
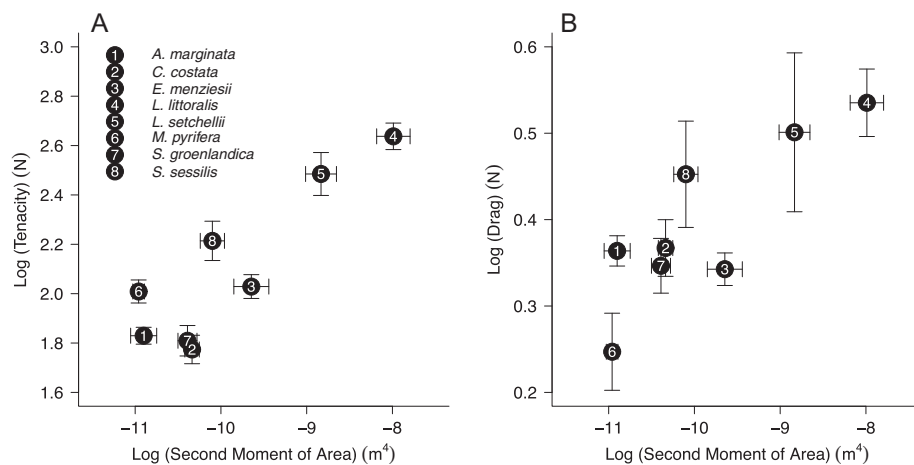

Fig. 6. Predicted drag (A) and tenacity (B) for kelps 1,150 cm^2 in size, plotted against second moment of area (*I*). Error bars represent standard error, as predicted with "mgcv".
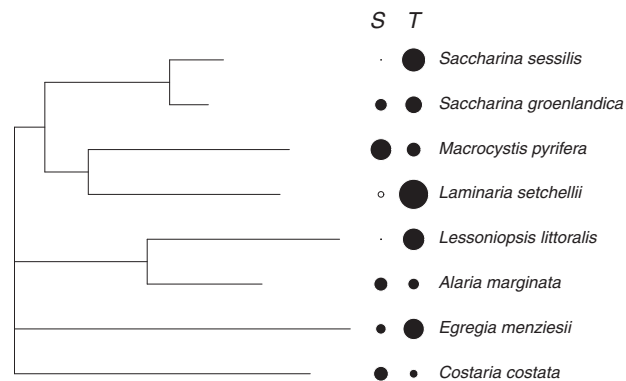

Fig. 7. Bayesian phylogram of the eight species used in this study constructed from a 1,373 base-pair concatenated alignment of ITS and CO1-5P sequence data in MrBayes 3.2.3. Streamlining (S) and tolerance (T) indices have been scaled for visualization. White circles represent negative values, while black dots represent positive values. The root is present at the polytomy.

Factors driving the trade-off. In previous studies, there have generally been two potential explanations for the evolution of avoidance–tolerance trade-offs. One possibility is that avoidance and tolerance strategies are partially or fully redundant and that both incur costs on the function and/or productivity of the organism. Under this condition, use of both strategies would be at an unnecessary cost, and selection could act to reduce redundancy, explaining the occurrence of the trade-off (as in Fineblum and Rausher 1995, Fornoni et al. 2003, Baucom and Mauricio 2008). Indeed, streamlining and tolerance are partially redundant, in that they both aim to resist dislodgement from wave action. So selection to reduce extraneous costs could explain the trade-off between drag avoidance and tolerance.

However, both drag and tenacity increase with increased *I* (Fig. 6). Consequently, our data suggest that the tolerance-streamlining trade-off results, at least in part, from a direct interaction between the traits that underlie each strategy (as in Ballhorn et al. 2010): kelps with high tolerance indices may be physically less able to streamline. Strength and stiffness tend to covary in plant materials (e.g., Niklas 1993), and the rigidity (i.e., flexural stiffness) of a structure depends largely on its thickness (e.g., Demes et al. 2011, eq. 2). As tenacity increases, tissues near the holdfast thicken, increasing second moment of area at the base of the kelp (see Fig. 6); in this way, species that are drag tolerant may be

more rigid and less capable of reconfiguring to reduce drag. Indeed, I varies by more than four orders of magnitude in large kelps of the same size (Fig. 6). For example, two of the most tolerant species, *Laminaria* and *Lessoniopsis*, possess thick, stiff stipes capable of holding the kelps upright, which could hinder reconfiguration and increase forces experienced by the holdfast. These were both the strongest kelps and those that experienced the most drag at 1,150 cm^2. *Saccharina sessilis*, another tolerant species, lacks a stipe altogether and instead has dissected blades arising directly from a large holdfast. This too could prevent reconfiguration, since the wide blade base might prevent complete bending of the frond into the direction of fluid flow. The three most streamlined species, *M. pyrifera*, *A. marginata*, and *C. costata*, all have thinner, less rigid stipes that could bend and allow for increased reconfiguration in flow.

Morphological responses of kelps to environmental factors may also drive the persistence of a streamlining–tolerance continuum. Frond shape and material properties are known to directly affect drag (e.g., Boller and Carrington 2006, Demes et al. 2011, Martone et al. 2012, de Bettignies et al. 2013, Starko et al. 2015), and seaweeds with drag-prone morphologies tend to be more strongly attached to the substratum (e.g., Starko et al. 2015). If thallus morphologies develop to improve some aspect of ecophysiological performance, such as light capture or nutrient acquisition (see Hurd et al. 2014), this may result in thalli that are inherently poor at streamlining (e.g., Koehl et al. 2008). These kelps might counterbalance this increase in drag by augmenting tenacity to tolerate these increased forces. Kelp morphology is known to vary across gradients of wave exposure (e.g., Duggins et al. 2003, Roberson and Coyer 2004, Koehl et al. 2008), depth (e.g., Gerard 1988, Molloy and Bolton 1996, Demes et al. 2013), and various other biotic and abiotic factors (e.g., Thomsen et al. 2004, Charrier et al. 2012), with marked intraspecific variation occurring over both small and large spatial scales (Wernberg et al. 2003, Thomsen et al. 2004, Fowler-Walker et al. 2005, Lane et al. 2007, Wernberg and Vanderklift 2010), as well as between seasons (e.g., Milligan and DeWreede 2000). Thus, avoidance and tolerance strategies may differ between populations of the same species due to combined effects of plasticity, local adaptation, and random disturbance from the environment. Future work should document the intraspecific variability in ontogenetic streamlining and tolerance strategies in order to better understand the factors contributing to each strategy and to the trade-off.

All drag measurements in this study were made at 1.0 m · s^{-1}, a water velocity commonly experienced along wave-swept coastlines, but representing only low-velocity wave surge. Nevertheless, interspecific comparisons of wave-swept seaweeds (e.g., Boller and Carrington 2007, Martone et al. 2012) show that differences in drag measured at 1 m · s^{-1} tend to be maintained as water velocity increases, suggesting that measurements taken at 1 m · s^{-1} may be sufficient to compare hydrodynamic performance at higher velocities. Conversely, drag experienced by certain species at higher velocities can be difficult to predict (see Martone et al. 2012), and differences in drag observed in morphological variants of some species may disappear at higher velocities (de Bettignies et al. 2013). Our results cannot rule out convergence upon a narrow range of drag coefficients as water velocity increases. At a minimum, "streamliners" likely experience less drag than "tolerators" under sublethal conditions. This could, in turn, reduce the risk of long-term fatigue failure (Mach et al. 2007, 2011).

The phylogenetic comparative methods used in this study allow us to conclude that the streamlining–tolerance continuum is not an artifact of data nonindependence (i.e., species' relatedness; see Felsenstein 1985, Blomberg et al. 2003). Unlike previous work on avoidance and tolerance of aquatic tracheophytes (e.g., Puijalon et al. 2011), our methods failed to detect any effect of phylogeny on either streamlining or tolerance strategies. Some closely related species demonstrate very different streamlining and tolerance strategies (see Fig. 7). For example, *Alaria* and *Lessoniopsis* are relatively closely related but exhibit entirely opposing strategies (see Fig. 3). Furthermore, even the two congeneric *Saccharina* species fail to fall together on the continuum (see Fig. 4). Thus, streamlining and tolerance strategies may be highly evolvable in the kelps, unlike aquatic tracheophytes, and forgone disruptive selection may have caused some closely related species to exhibit divergent strategies.

Ecoevolutionary implications. One major goal in the study of evolution is to recognize and understand the factors selecting for and maintaining the diversity of traits, particularly those that are ecologically important. For habitat-forming kelps, morphology is particularly important, since it can determine the organisms that can be supported by the new habitat, ultimately influencing community composition (e.g., Hughes 2010). The selective advantages of both tolerance and streamlining strategies are clear. In the absence of a trade-off, it would be expected that species growing on wave-exposed coasts would be both strong and streamlined; this could limit morphological diversity and drive convergence toward a form that is both hydrodynamically optimal (i.e., experiencing less drag than other forms) and maximally strong to tolerate forces generated by the most powerful waves. Our results suggest, however, that the use of tolerance strategies may preclude the adoption of streamlined fronds and vice versa. Given that streamlining and tolerance are partially redundant strategies, investing in one strategy could free up diversification of the other. Kelps that invest in tenacity could be free to develop any morphology because they can endure the large forces associated with that structure. Kelps that specialize in streamlining, on

the other hand, need not invest much in attachment. This kind of relief from selection could allow for diversity in the opposing trait, perhaps permitting morphologies that are favorable in some other ecological or physiological sense.

CONCLUSIONS

In our study, we provide evidence for a negative correlation between avoidance and tolerance strategies of intertidal kelps to resist dislodgement under breaking waves. Our data suggest that there is a trade-off between these strategies. This trade-off could have had substantial consequences for the evolution of brown algae, since selection for one strategy may lead to a reduced ability or need to use the alternative strategy. This, in turn, may play an important role in maintaining morphological diversity within this group. For example, investing in tenacity could release fronds from such strict morphological selection, allowing them to generate less streamlined structures and contributing to the diversity observed today.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Figure S1. Maps of (a) Barkley Sound and (b) the field sites used in this study.

Figure S2. Raw drag coefficient data for each species.

Figure S3. Raw tenacity data for each species.

Figure S4. Raw drag (at $1.0 \text{ m} \cdot \text{s}^{-1}$) data for each species.

Table S1. Database accession numbers of sequence data.

Table S2. Summary of models used to determine streamlining indices.

Table S3. Summary of models used to determine tolerance indices and tenacity predictions.

Table S4. Summary of models used to predict drag at two size classes.

Table S5. Collection information for second moment of area measurements.

Table S6. Summary of models used to predict second moment of area at different sizes.