Biomechanical consequences of branching in flexible wave-swept macroalgae

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Summary

- Wave-swept macroalgae present an excellent system for studying the effects of chronic physical stress on the morphological evolution of plants. Wave-induced water velocities impose great drag forces, leading to a morphological tradeoff between light interception and drag reduction/tolerance. What are the hydrodynamic consequences of morphological diversification, such as increased branching?
- Drag was measured on artificial macroalgae of constant 'photosynthetic' area, but differing branching patterns, in a high-speed flume at water velocities up to 3.5 m s^{-1}. A meta-analysis was used to compare dislodgement forces of branched and unbranched species of comparable sizes in the field to determine if drag-prone morphologies had greater attachment strengths.
- Branched fronds experienced greater drag than unbranched fronds of the same size. Greater drag in branched forms was not the result of increased projected area but probably resulted from greater pressure or friction drag. In the field, branched species resisted greater dislodgement forces than unbranched species of comparable size, suggesting that branched species compensate for increased drag with stronger attachment to the substratum.
- Branching has clear biomechanical consequences, increasing drag and the need for increased attachment. This raises questions about physiological and ecological advantages that may have driven the repeated evolution of biomechanically costly, branched morphologies.

Introduction

Forces imposed by high wind and water velocities are a source of physical stress that can have significant effects on the survivorship of terrestrial and aquatic plants (e.g. Grace, 1977; Koehl, 1982; Denny, 1994, 1998; Vogel, 1994; Blanchette, 1997; Ennos, 1997; Denny & Gaylord, 2002; Butler *et al.*, 2012). Among these forces, drag has been the best characterized and the most well studied, although forces resulting from rapid acceleration and wave impingement have also been demonstrated (Gaylord, 2000; Gaylord *et al.*, 2008). Unable to adjust behavior like most animals, wind- and wave-swept plants adjust their morphology and biological structure as they grow to mitigate the effects of drag. For example, within a wide repertoire of growth strategies, plants may reduce drag by changing branch architecture (Niklas, 1994; Sterck & Bongers, 1998; Bruchert & Gardiner, 2006), reducing size (Denny *et al.*, 1985; Wolcott, 2007; Martone & Denny, 2008), and passively reorienting in flow (Vogel, 1989; Boller & Carrington, 2006; Martone *et al.*, 2012); alternatively, plants may resist drag by fortifying support tissues (Martone, 2007; Speck & Burgert, 2011) and reinforcing their attachment to the substratum (Ennos, 2000; Milligan & DeWreede, 2000; Clair *et al.*, 2003; Anderson *et al.*, 2006). For > 100 yr, most studies of drag reduction and drag resistance have explored patterns and adaptations in terrestrial plants (see overview in Niklas *et al.*, 2006). Yet, aquatic flow conditions can be significantly more stressful than aerial flow conditions, particularly in the intertidal zone where wave-induced water velocities may exceed 25 m s^{-1}, applying forces much greater than hurricane winds (Denny & Gaylord, 2002). Thus, macroalgae ('seaweeds') living in the wave-swept intertidal zone are excellent test subjects for investigating the effects of drag on plant evolution.

Most macroalgae are flexible, allowing photosynthetic thalli to reorient and reconfigure under breaking waves to reduce drag (Koehl, 1986; Gaylord *et al.*, 1994; Denny & Gaylord, 2002; Boller & Carrington, 2006; Demes *et al.*, 2011; Martone *et al.*, 2012). Branched and unbranched macroalgae live side by side on rocky coastlines, suggesting that flexibility may be sufficient to permit a wide range of morphologies to persist (Harder *et al.*, 2004; Martone *et al.*, 2012). However, recent work on flow-induced reconfiguration has started to differentiate the way branched and unbranched macroalgae resist wave-induced drag. Data suggest that flexible macroalgae utilize two coordinated methods for reducing drag as they reconfigure, changing frond

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shape (reducing drag coefficients) and reducing frond area projected into the flow (Boller & Carrington, 2006; Martone *et al.*, 2012). These two processes are related, but distinct, and macroalgae can specialize in one mode or the other to effectively reduce drag: branched algae are sometimes better able to reduce area projected into flow, whereas unbranched algae are better able to change shape and reduce drag coefficient (Martone *et al.*, 2012). Moreover, unbranched fronds may have a slight hydrodynamic advantage over branched forms, generally experiencing less drag in flow (Boller & Carrington, 2007; Albayrak *et al.*, 2012; Martone *et al.*, 2012). Unfortunately, because size, shape, and flexibility of fronds vary widely within and among macroalgal species (Abbott & Hollenberg, 1976; Carrington, 1990; Hale, 2001; Boller & Carrington, 2007), the effects of these factors on drag are confounding and difficult to interpret from previous studies. Thus, a controlled experiment using artificial seaweeds is necessary to clarify and isolate the effect of frond shape on drag (see Albayrak *et al.*, 2012).

In general, aquatic plants that experience more drag also tend to have greater attachment strengths, suggesting a biomechanical tradeoff between attachment strength and drag reduction and a constraint on these redundant traits (Puijalon *et al.*, 2011). But this pattern has not been clearly demonstrated for the diversity and extreme hydrodynamic stress of wave-swept macroalgae. Larger macroalgae experience more drag (Denny *et al.*, 1985; Gaylord *et al.*, 1994; Wolcott, 2007; Martone & Denny, 2008) and have greater attachment strengths (Thomsen & Wernberg, 2005). But, accounting for size, what is the effect of frond shape on drag and attachment? If fronds with certain branching patterns are more susceptible to flow-induced drag, are they also more firmly attached for a given size?

In this study, we use artificial macroalgae of precisely the same ‘photosynthetic’ surface area to explore the effect of branching on drag experienced by wave-swept macroalgae at water velocities of up to 3.5 m s^{-1}. We then use a meta-analysis of previously published datasets to compare the attachment strengths of branched and unbranched macroalgae to determine, for a given frond size, whether macroalgae with drag-prone morphologies have evolved stronger attachment strengths to compensate for hydrodynamic disadvantages.

Materials and Methods

Sample preparation

Four artificial macroalgal shapes were designed in a computer-aided design (CAD) program, representing four increasing degrees of branching (DB) – unbranched (DB = 0), primarily dichotomous (DB = 1), secondarily dichotomous (DB = 2), and tertiarily dichotomous (DB = 3) – each chosen to represent the shapes and branch angles of real macroalgae (Fig. 1). Each shape was scaled to have identical planform areas of 48.20 cm^2. Using the CAD files, a computer-controlled laser cutter (Universal Laser Systems, Scottsdale, AZ, USA) was used to cut five replicate model macroalgae of each shape from sheets of latex rubber (0.25 mm thick). Latex models were very flexible (Young’s modulus = 1 MPa) and were used to represent the stiffness of real macroalgal fronds (Young’s modulus = 0.2–48 MPa; Hale, 2001).

Drag measurement

Model macroalgae were affixed to a single-axis force transducer that was mounted to the top of the working section of a high-speed recirculating flume. Samples were suspended into the flow via a wire hook and held parallel to flow, allowing for unrestricted reorientation and reconfiguration, similar to previous studies of reconfiguring leaves (Vogel, 1989) and macroalgae (Koehl, 2000). Drag was recorded on model macroalgae at flow speeds of 0.25, 1.0, 2.0 and 3.5 m s^{-1}. Measurements were logged at a sampling rate of 3 Hz, averaged over 5 s, and corrected for drag contributed by the wire hook.

To explore the effect of macroalgal shape on drag, one-way ANOVAs were conducted at each velocity with shape as a fixed factor (four levels) followed by Tukey’s *post hoc* comparisons, and an ANCOVA was performed with shape as a fixed factor (four levels), water velocity as a covariate, and drag$^{0.5}$ as the linear response.

Measurement of projected area

High-resolution photos (EOS Rebel XT SLR camera; Canon Inc., Tokyo, Japan) were taken of each model macroalga at 0.25, 1.0, 2.0 and 3.5 m s^{-1}, through a window in the

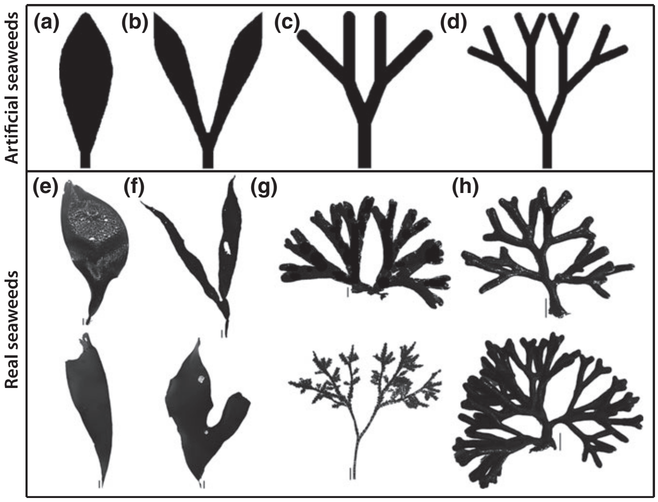

Fig. 1 Artificial macroalgal shapes (a–d) used in this study to mimic real macroalgae (e–h). Shapes had identical planform areas but different degrees of branching (DB): (a) unbranched, DB = 0; (b) primarily dichotomous, DB = 1; (c) secondarily dichotomous, DB = 2; and (d) tertiarily dichotomous, DB = 3. (e–h) Real macroalgae depicted are as follows: (e) *Chondracanthus exasperatus* (top) and *Palmaria hecatensis* (bottom); (f) *Chondracanthus harveyanus* (top) and *P. hecatensis* (bottom); (g) *Fucus distichus* (top) and *Calliarthron cheilosporioides* (bottom); and (h) *Codium fragile* (top and bottom). Bars, 1 cm.

flume located downstream of the working section. Projected areas of model macroalgae were measured using ImageJ software (version 1.43u; US National Institutes of Health, Bethesda, MD, USA) and, for each replicate ($n=5$), an average of two to three photographs was used as the final measurement. Pictures were not taken concurrently with drag measurements, but were taken of the same samples at the same velocities. In order to determine whether differences in drag were simply the result of differences in projected areas of model macroalgae in flow, we sampled with replacement five area and drag datapoints from each of the four degrees of branching ($n=20$), and tested for an effect of projected area on drag at each velocity with a linear regression analysis on 10 000 bootstrap replicates. Resampling was performed in R (v3.0.2; R Foundation for Statistical Computing, Vienna, Austria). Differences in projected areas among shapes at each velocity were tested using ANOVAs followed by Tukey's *post hoc* comparisons. To verify the ability of model macroalgae to mimic real macroalgae in flow, projected areas and drag measurements were used to calculate drag coefficients for model macroalgae using the methodology described in Martone *et al.* (2012).

Trends in dislodgement

We defined dislodgement force as the tensile force required to detach an alga perpendicular to the substratum, by either holdfast dislodgement or stipe breakage. Dislodgement force data and frond planform areas of various algal species were recorded with spring scales in the field and supplemented with data from previous studies (Supporting Information, Table S1). Data were collected from macroalgae at Wreck Beach in Vancouver, British Columbia (BC), and from Saltspring Island, BC, Barkley Sound, BC, and Whiffin Spit, Sooke, BC (see Table S1). Additional data for wave-swept macroalgae were compiled from Martone *et al.* (2012) and from several independent studies reported by Thomsen & Wernberg (2005) (see Table S1); previous data on wave-protected macroalgae or macroalgae attached to soft substrata were not included. Macroalgae were assigned to one of two morphological categories: 'unbranched' (U) or 'branched' (B). Morphologies that did not fit into either category were included as 'ambiguous' (A). In order to prevent overrepresentation of certain well-studied macroalgal genera (e.g. *Mazzaela*, *Mastocarpus*, *Saccharina*), data were averaged for each genus. Dislodgement force and frond planform area data were log-transformed and an ANCOVA was used to determine the effect of branching (fixed factor, two levels) on the relationship between frond area (covariate) and dislodgement force. Phylogenetic analyses were not possible because of a lack of molecular data and the vast evolutionary distance between macroalgal divisions. However, to demonstrate that trends in dislodgement were not driven by differences between the macroalgal divisions, ANCOVAs were also performed on red (Rhodophyta) and brown (Heterokontophyta) algae separately.

Results

Reconfiguration

Model macroalgae began to flap and flutter at 0.25 m s^{-1} and branched shapes began to reconfigure at 1 m s^{-1}. At this velocity, primary dichotomies (DB = 1) tended to fold over lengthwise to resemble an unbranched frond. Often these fronds would fold incompletely, forming a fork at the apical end. However, with increasing velocity, most primary dichotomies were completely folded by 3.5 m s^{-1}. At 2 and 3.5 m s^{-1}, secondary (DB = 2) and tertiary (DB = 3) fronds bent and folded their branches and minimized their lateral spread. At low velocities, unbranched fronds did not change shape but experienced undulated flapping; above 2 m s^{-1} many unbranched fronds folded into tight, stable tubes or cones, but continued to flap and flutter, which tended to increase projected area (see later).

Effect of shape on drag

At all test velocities, drag differed among fronds with different degrees of branching (0.25 m s^{-1}, ANOVA, $F=6.59$, $P<0.01$; 1.0 m s^{-1}, ANOVA, $F=10.63$, $P<0.001$; 2.0 m s^{-1}, ANOVA $F=12.98$, $P<0.001$; 3.5 m s^{-1}, ANOVA, $F=114.99$, $P<0.001$; Fig. 2). Secondarily and tertiarily branched fronds consistently experienced significantly more drag than unbranched fronds (Tukey's honestly significant difference (HSD), $P<0.05$ at all velocities; Fig. 2). However, there was no significant difference in drag experienced by primary branched and unbranched fronds (Tukey's HSD, $P>0.05$ at all velocities; Fig. 2). As velocity increased, drag increased on all shapes, but not at the same rate (Fig. S1, ANCOVA, shape × velocity, $P<0.001$). As velocity increased, drag increased most quickly on secondarily and tertiarily branched fronds and most slowly on unbranched fronds (Fig. S1). Drag coefficients calculated for model macroalgae were comparable to drag coefficients reported for real macroalgae (Fig. S2).

Correlation between projected area and drag

There was a significant correlation between drag and projected area at 0.25 m s^{-1} ($P<0.05$; Fig. 3). However, there was no significant correlation between drag and projected area at higher velocities ($P>0.05$ at 1, 2, and 3.5 m s^{-1}; Fig. 3). Unbranched shapes had lower projected areas than all branched shapes at 0.25 and 1.0 m s^{-1} (Tukey's HSD, $P<0.05$; Fig. 3). However, at 2.0 and 3.5 m s^{-1}, projected areas of unbranched and tertiary branched shapes were not significantly different (Tukey's HSD, $P<0.05$; Fig. 3). Projected area decreased with velocity for branched models; however, in unbranched shapes, projected area increased with velocity as a result of flapping, flagging and undulating (Fig. 3).

Effect of branching on dislodgement

Larger macroalgae resisted greater dislodgement forces (ANCOVA, Size, $P<0.001$, $F=201.45$, Fig. 4). This increasing trend

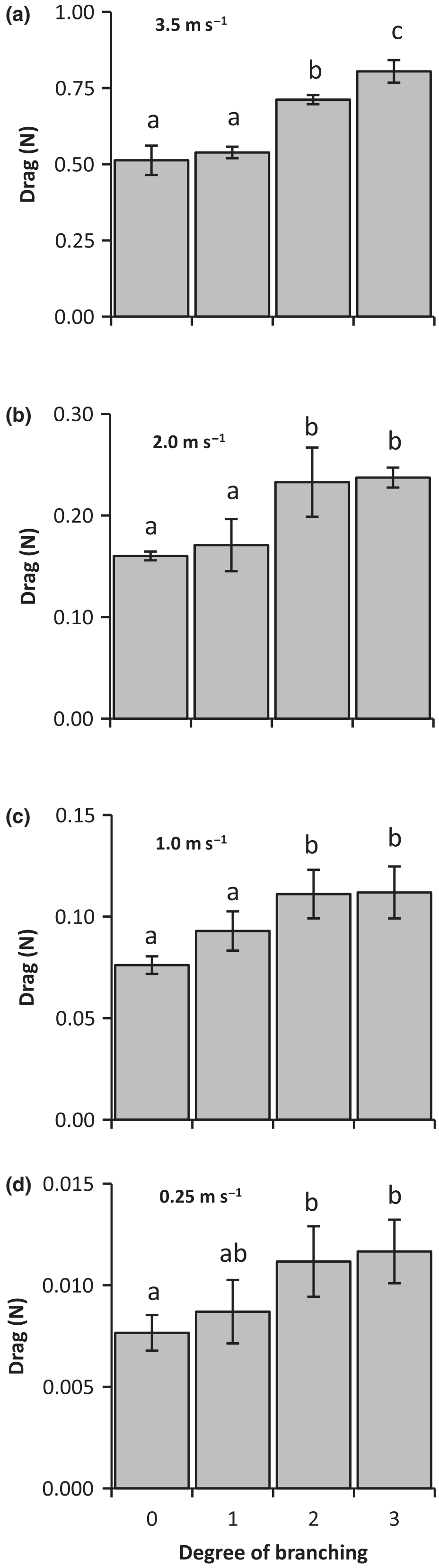

Fig. 2 Effect of branching on drag experienced by fronds at: (a) 3.5 m s^{-1}, (b) 2 m s^{-1}, (c) 1 m s^{-1}, and (d) 0.25 m s^{-1}. Error bars are 95% confidence intervals. Different letters represent significant differences (Tukey's honestly significant difference (HSD), $P < 0.05$).

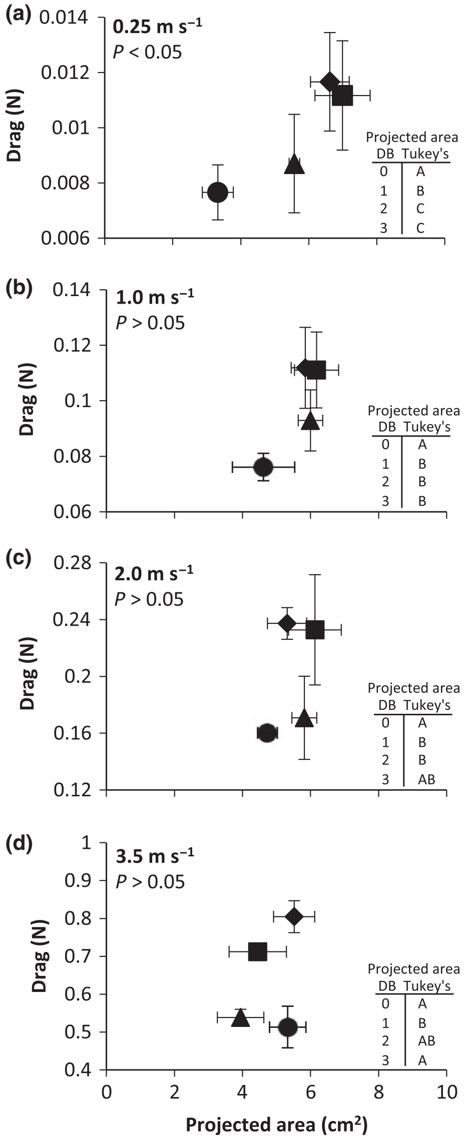

Fig. 3 Effect of projected area on drag experienced by fronds at: (a) 0.25 m s^{-1}, (b) 1.0 m s^{-1}, (c) 2.0 m s^{-1}, and (d) 3.5 m s^{-1}. Error bars are ± SD. Shapes represent different branching types: circles, (degree of branching) DB = 0; triangles, DB = 1; squares, DB = 2; diamonds, DB = 3. Different letters within inset tables indicate significant differences (Tukey's honestly significant difference (HSD), $P < 0.05$) in project areas of shapes with different DBs.

was similar for both branched and unbranched macroalgae (ANCOVA, size × branching, $P = 0.14$, $F = 2.27$) and documented over four orders of magnitude of macroalgal size (Fig. 4). For any given frond size, branched macroalgae resisted greater dislodgement forces than unbranched macroalgae (ANCOVA, branching, $P < 0.001$, $F = 15.57$, Fig. 4). This same trend was also documented for each macroalgal division separately (Rhodophyta – ANCOVA, size, $P < 0.001$, $F = 34.02$; ANCOVA, branching, $P < 0.05$, $F = 7.87$; branching × size, $P = 0.22$, $F = 1.65$; Heterokontophyta – ANCOVA, size, $P < 0.001$, $F = 93.25$; ANCOVA, branching, $P < 0.05$, $F = 5.76$; branching × size, $P = 0.16$, $F = 2.29$; Fig. S3).

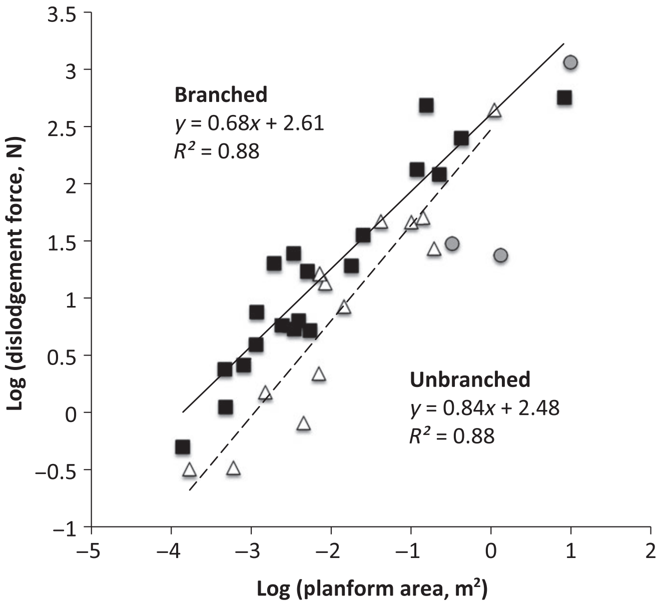

Fig. 4 Correlation between planform area and dislodgement force for macroalgal genera with branched (squares) and unbranched (triangles) morphologies. Macroalgae with ambiguous morphologies are also plotted for comparison (circles). Each datapoint represents average data for a single genus. Raw data and species names are included in Table S1.

Discussion

Branched algae experience more drag

Previous studies have investigated the effects of morphology on drag. However, because of species-specific natural variation in size, shape, and material properties, direct conclusions about the effect of morphology on drag have remained elusive. In this study, we found that branching alone had a significant effect on drag: unbranched shapes experienced the least drag, and fronds with the greatest degrees of branching consistently experienced the most drag at all water velocities. Differences between branched and unbranched shapes became more pronounced with increasing velocity and were largely independent of projected area.

Given the similarity observed in projected area, increased drag on branched forms may be attributed to increased pressure drag or increased friction drag. Branching may prevent fronds from streamlining to delay flow separation and minimize wake and, consequently, larger wakes would lead to increased pressure drag (Vogel, 1994; Albayrak *et al.*, 2012). In addition, friction drag is probably higher on branched forms because blade surface area is always closer to a leading edge than blade surface area in an unbranched form, causing a steeper velocity gradient in the boundary layer. Boller & Carrington (2007) reported that branched morphologies tended to experience more drag because they were less 'compressible' than unbranched morphologies, that is, less able to reduce projected area in flow. In our study, however, unbranched and tertiary branched shapes had similar projected areas at 3.5 m s^{-1}, suggesting that branching does not necessarily have a predictable effect on projected area in high-speed flow. Furthermore, flapping caused an increase in projected area for unbranched shapes at higher velocities, whereas the projected area of branched shapes decreased with velocity. Nevertheless, tertiary branched shapes experienced more drag than unbranched shapes at all water velocities, suggesting that branching has a direct impact on drag independent of projected area.

Our results are consistent with previous studies on aquatic leaves (Albayrak *et al.*, 2012) and macroalgae (Boller & Carrington, 2007; Martone *et al.*, 2012), which demonstrated that unbranched species tend to experience the least drag in flow. In particular, our data support Martone *et al.* (2012), who demonstrated that unbranched species tend to be better at reducing drag than branched species through shape change and streamlining, rather than via reductions in projected area. Data presented here illustrate that deviations from a flat, blade-like morphology in only two dimensions increased drag; this hydrodynamic consequence of branching would probably be exacerbated if branching occurred in three dimensions, as observed in many real macroalgae. Three-dimensional branching could also cause an increase in volume, which could lead to an increased accelerational force (Gaylord, 2000). Future studies should address the possible effects of branching on other hydrodynamic forces imposed by acceleration and wave impingement, particularly in the rocky intertidal zone where crashing waves can generate water velocities of 25 m s^{-1} (Denny & Gaylord, 2002). Drag and other hydrodynamic forces experienced by macroalgae at such high velocities are notoriously difficult to estimate (Bell, 1999; Martone *et al.*, 2012). We assume that drag experienced by branched and unbranched morphologies would continue to diverge as water velocity increased (Fig. S1), but this assumption remains to be tested. Furthermore, future studies should explore how morphological characteristics of real macroalgae, such as bullations, perforations, and papillae, may further augment – or even ameliorate – increased drag on branched species.

Branched algae are also more strongly attached

If branched algae consistently experience more drag than unbranched algae, how do the two morphologies live side by side in hydrodynamically stressful habitats? Data presented here show that, for any given frond size, branched algae are more strongly attached to the substratum on average than unbranched algae. This striking pattern held true over four orders of magnitude in macroalgal size and over two completely distinct macroalgal division, Rhodophyta and Heterokontophyta (Phaeophyceae) (Fig. 4). For example, small unbranched macroalgae *Petalonia fascia* and *Cryptopleura* sp. (1.7–6.0 cm^2) have much lower attachment strengths (0.3 N) than small branched algae *Cryptosiphonia woodii*, *Pterosiphonia bipinnata*, *Mastocarpus papillatus*, and *Bossiella plumosa*, which are similar in size (1.4–8.1 cm^2) but attach much more strongly (0.5–2.6 N) (Table S1). Similarly, at a much larger size class, unbranched macroalgae, *Agarum fimbriatum* and *Saccharina japonica* (735–1558 cm^2), have lower attachment strengths (16.4–72.1 N) than branched macroalgae, *Ascophyllum nodosum* and *Fucus vesiculosus*, which can be similar in size (500–1177 cm^2) but attach more strongly (74.2–133.7 N) (Table S1). Thus, data presented here support previous work on the effects of physical stress on plant evolution, which found that redundant traits are often negatively correlated (Fineblum & Rausher, 1995; Baucom & Mauricio, 2008; Puijalon *et al.*, 2011). Our data suggest that branched algae either increase attachment strength to compensate for increased drag or inherently resist greater dislodgement forces, thereby permitting fronds to be more drag-prone. Unbranched algae attach less strongly but experience less drag. Thus, branched and unbranched macroalgae represent different morphological strategies along the theoretical avoidance–tolerance continuum (Puijalon *et al.*, 2005, 2011).

If branched algae experience more drag and must invest additional energy into support structures or attachment, then why branch? Could there be some photosynthetic, ecological, or reproductive advantage to branching? As branched algae flap and reconfigure in flow, nutrient and gas exchange may increase as the diffusive boundary layer (DBL) is thinned (Koehl & Alberte, 1988; Hurd, 2000; Hurd & Pilditch, 2011). Unbranched macroalgae may not experience the same benefit, especially subtidally and in slow currents. In this way, deviations from a flat blade-like morphology might be tied to increased nutrient uptake and carbon fixation (Koehl & Alberte, 1988; Hurd & Pilditch, 2011). Furthermore, branching may increase the ratio of surface area to volume in real macroalgae, which may also increase net photosynthetic output in turbulent flow (Stewart & Carpenter, 2003). Branching helps to delay desiccation of intertidal macroalgae at low tide by trapping water when the tide recedes (Hay, 1981; Padilla, 1984) and has been shown to reduce the impact of herbivory in some algae (Padilla, 1984).

Assuming branching is beneficial to macroalgae in some way, our data may lend some insight into the early evolution of branched morphologies. The absence of significant hydrodynamic disadvantage between the unbranched and primary branched morphologies (Fig. 2) suggests that some branching may occur during macroalgal evolution without hydrodynamic cost. Subsequently, as some adaptive ecological benefit to branching was realized, branching may have increased with a concomitant increase in drag and, necessarily, attachment. For example, large marine kelps are thought to have evolved from simple unbranched ancestors, closely related to modern-day genera *Chorda* and *Pseudochorda* (Kawai & Kurogi, 1985; Kawai *et al.*, 2001; Bolton, 2010). Kelp morphologies are highly diverse, with branching forms probably evolving several times from unbranched forms (Lane *et al.*, 2006), perhaps suggesting some common selective benefit to branching and often leading to species that experience high drag forces and hold tight to the substratum (e.g. Biedka *et al.*, 1987; Johnson & Koehl, 1994; Friedland & Denny, 1995; Gaylord & Denny, 1997). For example, branched algae *Egregia menziesii* and *Eisenia arborea* have greater attachment strengths, on average, than several other unbranched species of similar size, such as *Costaria costata*, *A. fibriatum*, *Alaria marginata*, *S. japonica* and *S. latissima* (Table S1). Unfortunately, few data currently exist for many large kelps so this pattern cannot be completely resolved. Future research should focus on possible physiological and ecological advantages of branching, as realized benefits would have biomechanical consequences that may help to explain the morphological diversity of wave-swept marine macroalgae.

Conclusions

This study demonstrates that branched and unbranched macroalgae exhibit alternative biomechanical strategies for surviving adverse hydrodynamic forces. For a given size, unbranched macroalgae generally experience less drag than branched macroalgae. Branched macroalgae, on the other hand, experience more drag but compensate for their hydrodynamic disadvantage by increasing dislodgement force. These alternative strategies provide evidence for an avoidance–tolerance tradeoff in wave-swept macroalgae. This tradeoff could be driven by other ecological factors, such as photosynthesis, desiccation, or herbivore resistance, but performance differences between branched and unbranched algae have yet to be properly quantified. It is ultimately the additive effects of flexibility and increased investment in supportive tissues that allow for persistence of these less hydrodynamically favorable morphologies. This pattern was found irrespective of taxonomy and represents an interesting example of how physical stressors can generate common trends in plant evolution.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Drag as a continuous function of water velocity for each shape.

Fig. S2 Comparison of drag coefficients between model macroalgae and real macroalgae with increasing water velocity.

Fig. S3 Correlations between planform area and dislodgement force for macroalgal genera in the divisions Rhodophyta and Heterokontophyta, distinguishing between branched and unbranched morphologies.

Table S1 Average size and attachment strength of unbranched, branched, and ambiguously shaped seaweeds

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