



LESS THAN THE SUM OF ITS PARTS: BLADE CLUSTERING REDUCES DRAG IN THE BULL KELP, *NEREOCYSTIS LUETKEANA* (PHAEOPHYCEAE)¹

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Nereocystis luetkeana is a large, canopy-forming kelp that is commonly found in nearshore waters between Alaska and California. Despite regularly reaching lengths in excess of 30 m, this alga demonstrates a remarkable ability to endure hydrodynamically stressful environments without being dislodged by waves or currents. While morphological aspects of this kelp, including its long flexible stipe, have been shown to reduce drag, blade clustering has never been directly tested. In this study, we examined how the distinctive multi-bladed morphology of *Nereocystis* thalli limits drag in flow. We measured drag on whole kelps in a large recirculating flume and quantified how drag was affected by serial removal of blades. We then compared measured drag with predictions of “additive drag”, which we defined as the sum of the drag that each blade experiences in isolation. We found that, on average, intact thalli experience only 37% of the predicted additive drag when subjected to a flow rate of 0.40–0.50 m · s⁻¹. Our results indicate that the subdivision of the photosynthetic area into multiple blades has a drag-reducing effect on *Nereocystis* thalli. We found drag increases less than proportionally with the cumulative area, meaning the contribution of individual blades to overall drag decreases with increasing blade number. That is, as thalli develop, each additional blade incurs a reduced hydrodynamic cost, perhaps lending insight into how thalli can grow so large.

Key index words: Biomechanics; drag coefficient; hydrodynamics; macroalgae; seaweed

The relationship between marine macrophytes and water motion is complex. While moderate water motion can benefit aquatic plants and macroalgae by promoting the transport of nutrients and gases across diffusive boundary layers and increasing rates of primary production (Conover 1966, Wheeler 1980, Gerard 1982, Stewart and Carpenter 2003), high levels of water motion place these organisms at risk of mortality due to breakage or dislodgement from the substratum (see Koehl 1984, Denny et al. 1985, Gaylord et al. 1994, Denny and Gaylord 2002). Moving water imposes a force on marine macrophytes, that is, predominantly oriented in the direction of flow and is therefore usually modeled as drag (Vogel 1984, Gaylord 2000).

To survive in highly wave- and current-swept environments, seaweeds must either tolerate large hydrodynamic stresses by developing robust support and attachment structures (Milligan and DeWreede 2000, Martone 2007, Starko et al. 2014, Starko and Martone 2016) or reduce the drag that they experience by adopting streamlined morphologies (Koehl and Alberte 1988, Armstrong 1989, Albayrak et al. 2012, Starko and Martone 2016) and reconfiguring in flow (Vogel 1984, Boller and Carrington 2006, Martone et al. 2012). Moreover, most current- and wave-swept organisms remain small at maturity (Denny et al. 1985, Wolcott 2007, Martone and Denny 2008), as drag is directly proportional to planform area. Thus, the ability of kelps (Phaeophyceae, Laminariales) to achieve large sizes in hydrodynamically stressful environments has long been a focus of researchers on biomechanics (Charters et al. 1969, Koehl and Wainwright 1977, Friedland and Denny 1995, Denny et al. 1997, de Bettignies et al. 2013). Importantly, while many researchers have studied how flexibility permits seaweed to reconfigure in flow to limit drag (Vogel 1984, Carrington 1990, Friedland and Denny 1995, Harder et al. 2004, Boller and

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Carrington 2006, Gaylord et al. 2008, Martone et al. 2012), we know very little about how the subdivision of the area into multiple blades affects drag.

The bull kelp, *Nereocystis luetkeana*, is commonly found in nearshore waters between Alaska and California. This species has a unique morphology that consists of a long, narrow stipe that may exceed 36 m in length, connecting a robust holdfast to a single large gas-filled pneumatocyst, which provides buoyancy for as many as 100 blades, each up to 4 m long (Abbott and Hollenberg 1976, Graham et al. 2017; refer to Fig. 1 for general morphology). Given that *Nereocystis* is one of the largest of all kelp species (Abbott and Hollenberg 1976), researchers have often wondered how *Nereocystis* populations can survive in areas with sustained current speeds as high as 3 m s^{-1} (Canadian Hydrographic Service 2019).

Past research has uncovered two biomechanical strategies employed by *Nereocystis* to survive high flow. Firstly, *Nereocystis* stipes are highly flexible and extensible (Koehl and Wainwright 1977, Denny et al. 1997, Denny and Hale 2003), allowing them to “go with the flow” as waves roll back and forth, and stipes that are sufficiently long can usually avoid the inertial forces imposed by waves if they do not reach the end of their range of motion before the next wave approaches (Koehl 1984, Denny et al. 1997). *Nereocystis* blades are also morphologically plastic, reducing the amount of drag they experience in flow while optimizing rates of photosynthesis: in low-flow environments, blades are broad and undulate in shape to promote flapping and mass transfer, whereas in high-flow environments, blades are narrow and flat to reduce drag (Koehl and Alberte 1988, Koehl et al. 2008).

One unexplored factor that may also contribute to the hydrodynamic performance of *Nereocystis* is the subdivision of the photosynthetic area into multiple blades. Many of the largest seaweeds have multiple blades (e.g., *Macrocystis pyrifera*, *Durvillaea* spp.) or dissect their blades into multiple pieces, either through normal development (e.g., *Nereocystis luetkeana*; Nicholson 1970) or wave action (e.g., *Laminaria setchellii*, *Hedophyllum sessile*; Armstrong 1989,

Milligan and DeWreede 2004), suggesting that subdividing photosynthetic area may help these species achieve their large size. Seaweeds growing in close proximity to each other can shield each other from ambient flow, limiting the drag experienced by individuals located in the middle of the bed (Johnson 2001). Similarly, epiphytic algae experience less drag when growing on a host seaweed than when living in isolation, as hosts likely shield epiphytes from flow in a manner comparable to neighboring epilithic seaweeds (Anderson and Martone 2014). Bundling blades tightly together could also serve to reduce flow-induced flapping, which has been observed to increase drag in *Nereocystis* (Koehl and Alberte 1988), as well as in man-made structures like flags (Taneda 1968). Subdividing its photosynthetic area into blades that can form a cluster may permit *Nereocystis* to produce more photosynthetic area than it could otherwise support in high-flow conditions, perhaps even permitting the kelp to develop additional blades at relatively little hydrodynamic cost. In fact, there is some evidence that *Nereocystis* thalli in high-flow environments have more blades than thalli in low-flow environments (Koehl and Alberte 1988). Although clustering has been shown to vary with blade morphology and to reduce light interception (Koehl and Alberte 1988), the effect of blade clustering on drag has not been quantified.

In this study, we examine the putative drag-reducing effect of blade clustering in *Nereocystis* thalli. Specifically, we address two questions. First, we check if any drag-reducing benefit exists by comparing the total drag experienced by intact thalli to the sum of the drag experienced by each of their blades in isolation (so-called “additive drag”). If clustering blades together have no influence on the hydrodynamic forces they experience, then the drag on an intact thallus should equal additive drag; if blade clustering conveys a hydrodynamic benefit, we expect the drag on a cluster to be less than additive drag; if blade clustering increases drag, the drag on an intact thallus should be greater than additive drag (Fig. 1).

Second, we test if the drag-reducing benefit depends on the number of blades in a cluster. If the benefit is independent of the number of blades in a cluster (and perhaps a property of clustering arrangement generally), then the drag on any cluster would increase proportionally with the area of each successive blade (Fig. 2, triangles). Alternatively, if the benefit increases with the number of blades, then the drag on any cluster would increase at a diminishing rate with each successive blade (Fig. 2, circles). Clusters with more blades would be less drag-prone per unit area than clusters with fewer blades because of interactions between their blades. Finally, we considered the possibility that blade clustering could exacerbate drag as has been demonstrated in dichotomously branched seaweeds (Starko et al. 2014). In this case, clusters with more

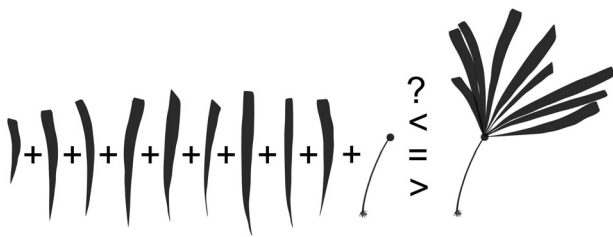


FIG. 1. A visual representation of the additive null hypothesis and alternative hypotheses. To the left of the (in)equalities signs are each blade and the stipe and pneumatocyst in isolation. To the right of the (in)equalities signs are an intact *Nereocystis luetkeana* thallus with blades, pneumatocyst, and stipe.

blades would be relatively more drag-prone per unit area than smaller clusters and the drag on any cluster would increase at an increasing rate with each successive blade (Fig. 2, squares). Clarifying the effect of blade clustering on drag will provide further insight into the ability of *Nereocystis* and other large seaweeds to thrive in hydrodynamically stressful environments.

MATERIALS AND METHODS

Characterizing ruffle index and drag of single blades. One hundred blades from 12 different mature

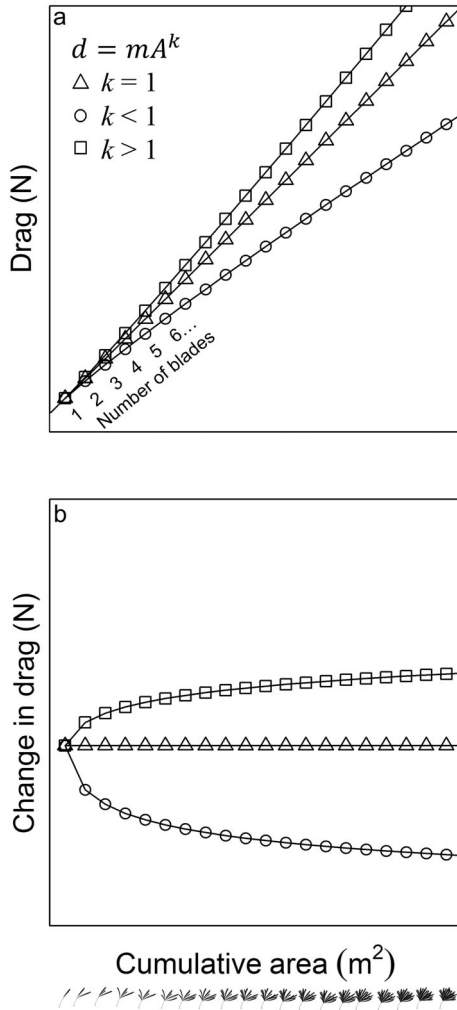


FIG. 2. Hypothetical trends in (a) drag and (b) change in drag as functions of the cumulative area. Each successive point (left to right) represents the addition of one blade. For simplicity, blades are assumed to be identical and experience the same amount of drag in isolation. In each case, drag is proportional to cumulative area (A) to some exponent k , that is, Drag (N) = $d = mA^k$. The triangles represent the case where $k = 1$, and drag increases proportionally with the cumulative area. The squares represent the case where $k > 1$ and additional blades contribute relatively more drag than previous blades. The circles represent the case where $k < 1$ and drag increase less than proportionately with the cumulative area.

Nereocystis thalli (approximately 8–10 blades per thallus) were collected in June 2017 from an inland site southeast of Brockton Point lighthouse at Stanley Park in Vancouver, British Columbia (49.2986 N, 123.1166 W). Kelps within 2 m of the edge of the bed were sampled haphazardly at low tides and then transported to a laboratory at the University of British Columbia, where they were stored in a sea table at 12°C for 1–4 d. All blades were removed from each kelp's pneumatocyst and their morphologies were characterized; blade measurements included total length, projected length measured along the midline and margins, planform area, width, and ruffle index. Total length was measured by laying a string along each margin of the blade, following all contours and undulations, whereas projected length was measured as the straight-line length of the two blade margins, as viewed from above; see Fig. 3). Planform area was estimated by analyzing photographs of each blade lying flat with the software ImageJ (Rasband 2021). The width was estimated by dividing the planform area by blade length. Ruffle index (U), a measure of undulation, was calculated as:

$$U = \frac{\sum L_t}{\sum L_p} \quad (1)$$

where L_t = total edge length and L_p = projected edge length. A perfectly flat blade will yield $U = 1$, whereas more undulate blades will yield $U > 1$ (see also Koehl et al. 2008, Coleman and Martone 2020).

Each blade was secured to a force transducer (World Precision Instruments, FORT5000) in a recirculating flume filled with freshwater (see the setup in Martone et al. 2012, Starko et al. 2014) and drag was measured for each individual blade at $0.50 \text{ m} \cdot \text{s}^{-1}$, a moderate flow speed fairly typical of tidal currents in most *Nereocystis* habitats (Koehl and Alberte 1988, Koehl et al. 2008). Blades were submerged in freshwater for <1 min before drag was measured and blades showed no signs of osmotic damage or changes in morphology. This flow speed was $0.09 \text{ m} \cdot \text{s}^{-1}$ higher than the flow speed used in the larger flume (used for measuring drag on whole kelps in the next experiment) and was selected to ensure that predictions of drag coefficient (and predicted additive drag) at $0.41 \text{ m} \cdot \text{s}^{-1}$ would be slightly underestimated. Therefore, conclusions about the drag-reducing benefits of clustering would be conservative. Drag on a single blade was modeled according to the drag equation:

$$d = \frac{1}{2} \rho A u^2 C_D \quad (2)$$

where d = the force of drag (N), ρ = fluid density, A = planform area (m^2), u = water velocity ($m \cdot s^{-1}$), and C_D = drag coefficient, a dimensionless

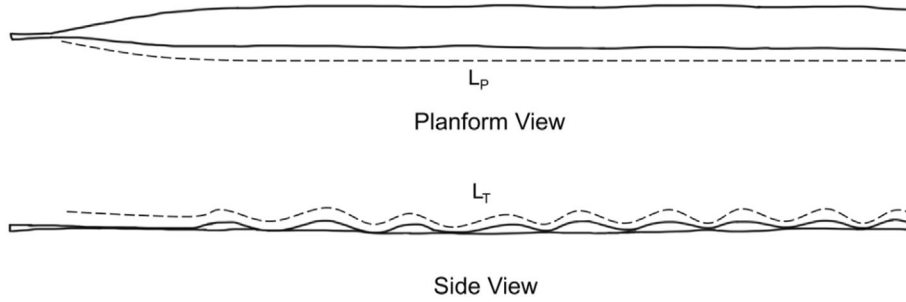


FIG. 3. Measurements of projected lengths (L_p) and total lengths (L_r) of the margins of *Nereocystis* blades.

index associated with shape (Boller and Carrington 2006, Martone et al. 2012). After measuring planform area (A), drag coefficients (C_D) were calculated for each blade:

$$C_D = \frac{2d}{\rho A u^2} \quad (3)$$

Maximum likelihood mixed effects models were created, predicting the drag coefficients of single blades from their morphological characteristics (all possible additive combinations of ruffle index, width, and length). Kelp of origin was included as a random factor to account for multiple blades harvested from individual thalli. The best predictive model of blade drag coefficient was chosen using AIC (Table 1). The final model was fitted using restricted maximum likelihood. The measured drag coefficient was plotted against the predicted drag coefficient for all blades to visually assess model accuracy (Fig. S1 in the Supporting Information). These analyses were done in R (R Core Team 2021).

Measuring drag on whole kelps and blade clusters. Seventeen whole, mature *Nereocystis* thalli (approximately 3–5 m in length) were collected from two surge channels in Bamfield, British Columbia—one in Mathers Bay (48.4957 N, 125.8059 W) and one at Aguilar Point (48.8373 N, 125.1439 W) in July 2017. Kelps were sampled haphazardly within 2 meters of the edge of the channel. The

experimental kelps were returned to the Bamfield Marine Sciences Centre (BMSC) and stored in a flow-through sea table for 1–3 d.

For 13 intact kelps, the stipe was attached to a force transducer (World Precision Instruments, FORT5000) and placed in a large recirculating flume (12 m long) filled with seawater at BMSC (See details in Starko and Martone 2016). We measured drag at $0.41 \text{ m} \cdot \text{s}^{-1}$ —the maximum flow speed of the large flume—and then proceeded to remove blades haphazardly from the pneumatocyst one at a time, continuously measuring drag to quantify the contribution of each blade to overall drag. Blade morphological characters (ruffle index, length, and width) described above were measured for each blade as it was removed. This process continued until all blades were removed, and the entire procedure was repeated for 13 of 17 experimental kelps.

The drag contributed by the stipe and pneumatocyst of each kelp was subtracted from all drag measurements during serial blade removal, leaving only measurements of drag that could be attributed to blades. The single-blade drag coefficient model (described under “Characterizing ruffle index and drag of single blades”) was used to predict the drag coefficient of each blade, allowing us to predict the drag that each blade would experience in isolation. We assumed that drag coefficients did not vary between salt water and freshwater because the density difference is minimal ($\sim 2\%$), and biomechanics studies routinely apply drag coefficient predictions across the two media (Denny et al. 1985, Carrington 1990, Denny 1995, Boller and Carrington 2006, Martone and Denny 2008, Martone et al. 2012).

The sum of drag that all blades were predicted to experience in isolation—hereafter referred to as “predicted additive drag”—was calculated for intact kelps, as well as for dissected kelps after each blade removal using the single-blade drag coefficient model.

Measured drag on intact kelps was plotted as a function of predicted additive drag and the correlation was tested using a linear regression. Predicted additive drag was also compared to measured drag

TABLE 1. AIC scores of candidate drag coefficient models. Every model had kelp of origin included as a random effect.

| Model | Fixed effect(s) | AIC |
|-------|-----------------------------|--------|
| 1 | Ruffle index, length, width | −646.1 |
| 2 | Ruffle index, width | −638.1 |
| 3 | Ruffle index, length | −623.0 |
| 4 | Ruffle index | −612.6 |
| 5 | Length | −604.4 |
| 6 | Length, width | −602.8 |
| 7 | Width | −595.1 |

through the calculation of drag ratio (R):

$$R = \text{Measured drag} / \text{Predicted additive drag} \quad (4)$$

Drag ratio (R) was calculated for 13 kelps after each blade removal, and for four additional kelps, only after all blades had been removed. If $R < 1$, then the cluster of blades experienced less drag than the sum of the predicted drag for each blade in isolation. The drag ratio (R) of intact kelps was plotted as a function of the total blade number (n) and the correlation was tested using a linear regression. All calculations and analyses thus far were done in R (R Core Team 2021).

Fitting curves to drag versus cumulative area. We modeled drag as a simple function of the cumulative planform area of blades:

$$d = mA^k \quad (5)$$

where d is drag (N), A is cumulative planform area (m^2), $k > 0$, and $m > 0$ (Fig. 2). Therefore, the slope of this function:

$$\frac{dd}{dA} = kmA^{k-1} \quad (6)$$

reveals the rate of increase in drag associated with each additional blade, depending on the current size of the blade cluster. If the exponent $k < 1$, then $\frac{dd}{dA}$ is decreasing, meaning each successive blade contributes less drag to the overall cluster than previous blades, and drag per unit area decreases with the size of the cluster (Fig. 2, circles). Conversely, if $k > 1$, then $\frac{dd}{dA}$ is increasing, meaning each successive blade contributes more drag to the overall cluster than previous blades and larger clusters are more drag-prone than smaller clusters (Fig. 2, squares).

If drag increases proportionally with planform area as predicted in the drag equation (Eq. 2), then $k = 1$. In this case, $\frac{dd}{dA} = kmA^{k-1} = kmA^0 = km$ and the drag contributed by each blade would depend only on the planform area, not on how many blades are already in the cluster (Fig. 2, triangles). Clusters of many or few blades would be similarly drag-prone and drag would increase predictably with planform area.

For 13 kelps, we plotted drag as a function of cumulative area, calculated as the sum of the remaining blade planform area after each blade removal. We fitted curves of the form $d = mA^k$ to drag versus cumulative area data sets in order to estimate values of m and k for each kelp (Table-Curve 2D, version 5.0.1). In R (R Core Team 2021). We used a one-sample, two-sided t -test to infer whether the mean value of k was significantly different than 1. We used linear regressions to test whether estimates of k or m depended on blade number.

Cluster characterization. To further investigate how the drag-reducing property of a cluster varied with increasing blade number, we created 95% confidence intervals of mean drag ratio at each blade number for 13 kelps. We characterized the shape of this generalized curve and used the upper limit of these confidence intervals to infer when measured drag dropped below 75% and 50% of predicted additive drag, and at which blade number the drag ratio stabilized. For further reference, measured drag, predicted additive drag, and predicted drag from the fitted curves ($\hat{d} = mA^k$) were also plotted as functions of the cumulative area.

RESULTS

Drag coefficient model. Morphology of *Nereocystis* blades was highly variable at both Stanley Park and Bamfield. Blade lengths were 58.0–187.5 cm (mean \pm SD = 92.0 ± 24.0 cm) at Stanley Park and 7.0–225.5 cm (mean = 86.0 ± 34.0 cm) at Bamfield. Blade widths were 2.4 cm - 15.8 cm (mean = 7.5 ± 2.5 cm) at Stanley Park and 0.1–18.9 cm (mean = 4.3 ± 2.5 cm) at Bamfield. Ruffle index was 1.00–1.37 for blades at both sites (Stanley Park mean = 1.10 ± 0.06 ; Bamfield mean = 1.04 ± 0.04). The best model for predicting the drag coefficient of single blades from Stanley Park included ruffle index, width, and length as fixed factors, and kelp identity as a random factor (Table 1; Fig. S1). As expected, the ruffle index increased the drag coefficient of single blades ($P < 0.001$), and width and length both had small negative but significant ($P < 0.001$) effects on the drag coefficient. This model was used to predict drag coefficients of single blades from Bamfield throughout this analysis.

Drag on intact kelps. The stipe and pneumatocyst contributed 0.29 ± 0.14 N of drag to thalli (mean \pm SD), which was $13.0 \pm 5.3\%$ of the average total drag. Drag on clusters of blades differed from the sum of drag on individual blades. Measured drag was just 37.4% of predicted additive drag according to the slope of the regression of measured drag on predicted additive drag ($R^2 = 0.98$, $F_{1,16} = 640.9$, $P < 0.001$; Fig. 4). Drag ratio (R) did not vary significantly with blade number for intact kelps ($R^2 < 0.001$, $F_{1,15} = 0.01$, $P = 0.93$; Fig. 5) or with the total cumulative area of a kelp ($R^2 = 0.03$, $F_{1,15} = 0.51$, $P = 0.49$; Fig. S2 in the Supporting Information). These data demonstrated the drag-reducing benefit of blade-clustering in *Nereocystis* thalli.

Curve fitting results. For each of 13 kelps, drag increased less than proportionally with the cumulative area of blades (Fig. 6; Fig S3 in the Supporting Information; as predicted in Fig. 2, circles), and the mean value of k was significantly less than 1 ($t_{12} = -17.78$, $P < 0.001$). In fact, all 13 fitted values of k were less than 1 (mean = 0.69, SE = 0.02; Figs. 5, S2). The average fitted value for m was

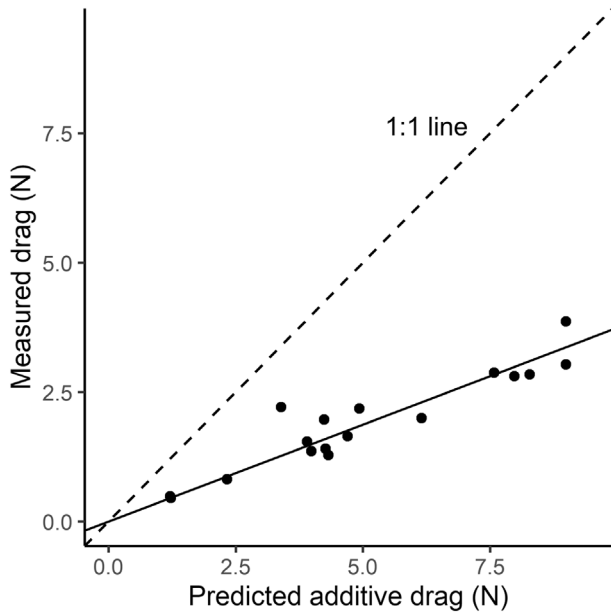


FIG. 4. Measured drag (N) as a function of predicted additive drag (N) for all experimental kelps prior to any blade removal. The dashed line represents a 1:1 relationship, whereas the solid line represents a linear regression of measured drag as a proportional function of predicted additive drag.

1.42 ± 0.07 (mean \pm SE). Values for neither k nor m depended on blade number (k : $R^2 < 0.001$, $F_{1,11} = 0.88$, $P = 0.77$; m : $R^2 = 0.06$, $F_{1,11} = 0.63$, $P = 0.44$; Fig. 5). Likewise, neither k nor m depended on the total cumulative area (k : $R^2 < 0.001$, $F_{1,11} < 0.001$, $P = 0.98$; m : $R^2 = 0.27$, $F_{1,11} = 4.0$, $P = 0.07$; Fig. S2). Thus, the drag-reducing

benefit of blade-clustering increased with the number of blades, and clusters with more blades experienced less drag per unit area than clusters with fewer blades.

DISCUSSION

Data suggest that *Nereocystis* can produce additional blades at a reduced hydrodynamic “cost.” Fitted values for k were all less than 1, indicating that drag increases less than proportionally with the cumulative area (Figs. 6, S3). Since $k < 1$ for all of our experimental kelps, the slope of drag versus cumulative area is decreasing. That is, drag increases by a decreasing amount as blades are added to an already large cluster, and successive blades add more drag to a smaller cluster than to a large cluster.

The drag-reducing benefits of clustering increase solely with the increasing number of blades (as seen in decreasing drag ratio, Fig. 7) and did not depend on blade size or cumulative area (see Figs. 5, S2). Although drag ratio (R) tends to be higher and more variable in clusters of fewer blades, it tends to decrease until approximately 36 blades, where it then remains steady. This eventual plateau indicates that the hydrodynamic cost of additional blades (i.e., drag per unit area) decreases at first, but eventually reaches some minimum. The pattern of variability seen in Figure 7—relatively high at first and steadily declining—is due to kelps approaching this plateau at different rates. Some reached this plateau with very few blades, whereas others required up to 36 blades to reach it. Even the smallest kelps must have reached this plateau at a low blade number,

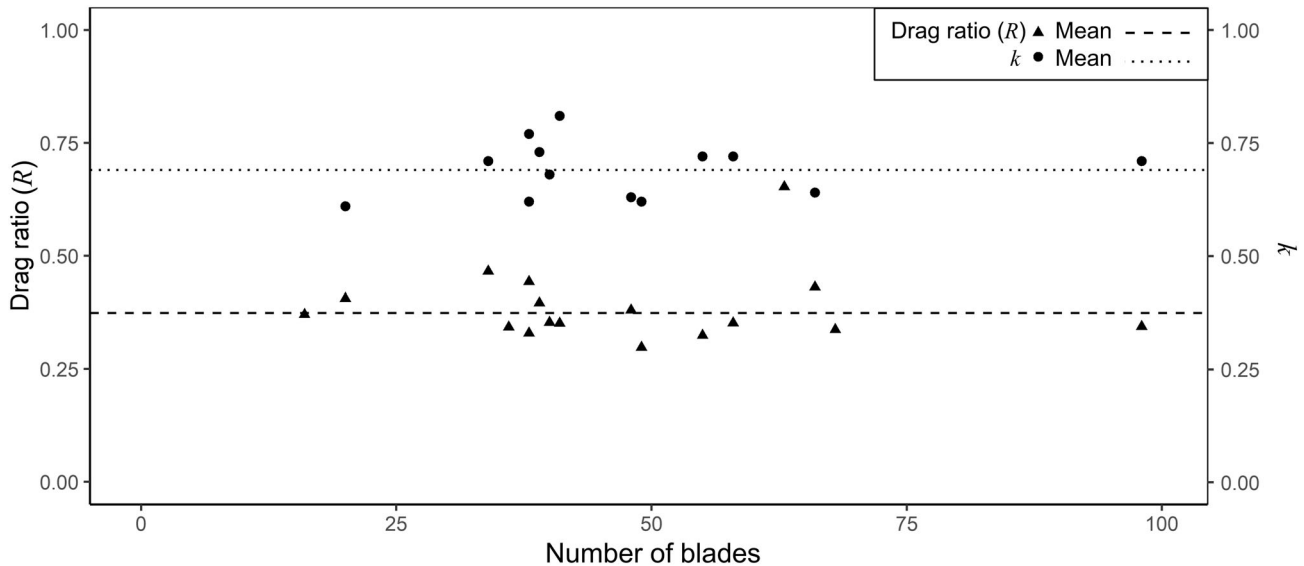


FIG. 5. Drag ratio (R) and estimates of the parameter k as a function of blade number for all kelps prior to blade removal. The dashed line on the figure corresponds to the predicted drag ratio of all kelps in our study (0.37, $n = 17$, triangles) and the dotted line corresponds to the average value for k for all kelps with complete data sets (0.69, $n = 13$, circles).

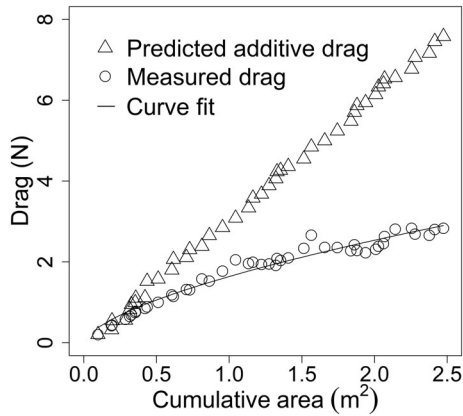


FIG. 6. Predicted additive drag (N) and measured drag (N) plotted against cumulative area (m^2) for one representative kelp. The curve fit of measured drag is also plotted for reference (curve fit parameters: $m = 1.64$, $k = 0.63$). Plots for all 13 kelps can be found in Figure S2.

since blade number did not affect the drag ratio of intact kelps (see Fig. 5). Variation in the rate of decline in drag ratio may reflect characteristics that vary across kelp blades, such as blade width and ruffle index. This is consistent with previous work demonstrating that additional narrow and flat

blades cluster together more efficiently than additional wide and ruffly blades (Koehl and Alberte 1988).

The drag-reducing strategy identified in this study is likely important during *Nereocystis* development, as sporophytes begin with one blade that splits lengthwise as they grow. Our results suggest that a cluster of even 2 blades will likely experience less drag per unit area than a single blade and further splits will provide an increasing and significant hydrodynamic benefit (Fig. 7). A growing sporophyte that splits its original blade into multiple blades may, therefore, grow larger relative to its attachment strength. This may explain why several kelp genera have adopted multi-bladed morphologies, and why some single-bladed kelp species subdivide their blades in exposed environments (Fritsch 1923, Armstrong 1989). For example, *Hedophyllum sessile* is able to grow along highly exposed coastlines, but as wave-exposure increases, this species subdivides its blade such that its morphology resembles a multi-bladed cluster (Armstrong 1989). Perhaps kelps with single blades, such as *Neogagarum fimbriatum*, are generally restricted to laying prostrate against the substratum where water velocity is limited, whereas large multi-bladed kelps such as *Nereocystis luetkeana* and *Macrocystis pyrifera* can grow upright in the water

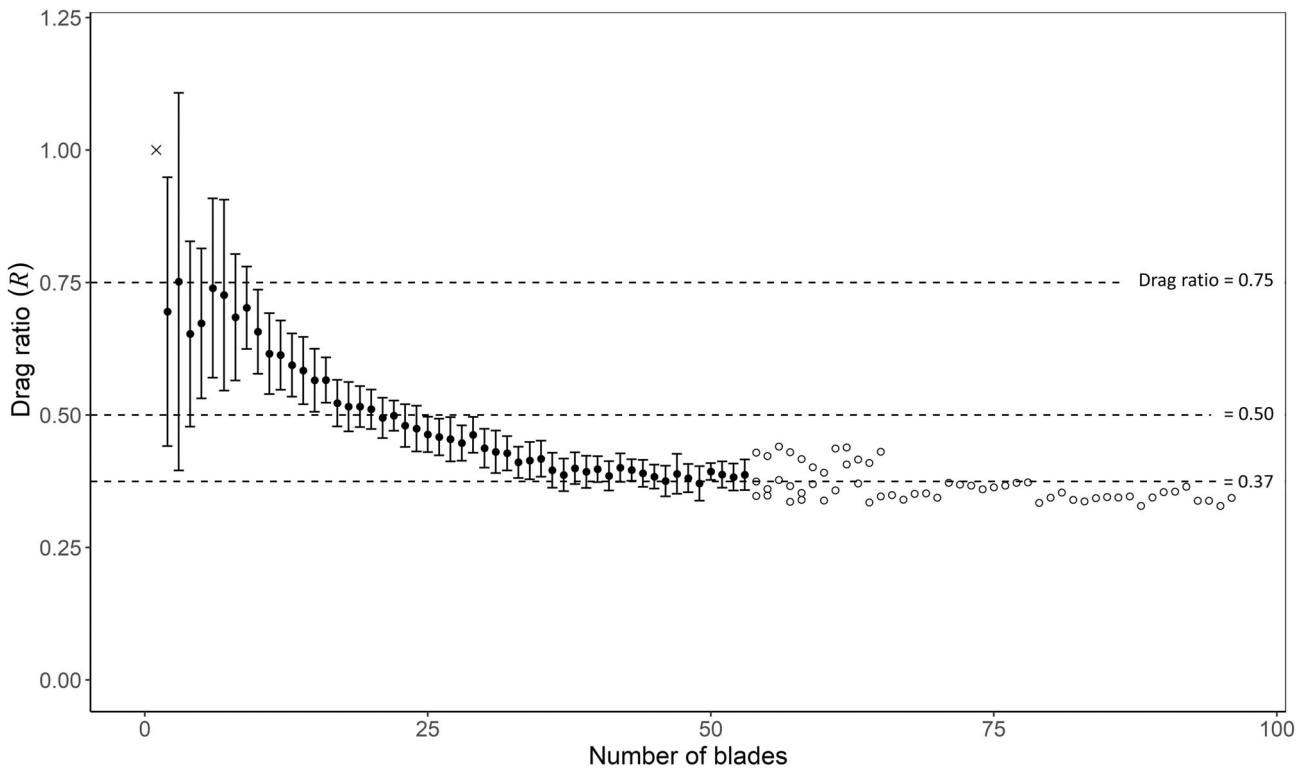


FIG. 7. 95% confidence intervals of mean drag ratio (R) at each blade number for 13 experimental kelps. The top two horizontal dotted lines represent drag ratios of 0.50 and 0.75. The lowest horizontal dotted line represents the predicted drag ratio for intact kelps (0.37). Open dots are plotted individually if there are fewer than four points per blade number. The 'x' indicates that clusters of one blade will always have a drag ratio of one.

column because they experience reduced drag per unit area. Furthermore, shorter multi-bladed kelps such as *Postelsia palmaeformis* and *Lessoniopsis littoralis* thrive in highly exposed environments where single-bladed kelps are conspicuously absent.

That measured drag is 37.4% of the predicted additive drag for kelp in this study likely depending on flow speed. At higher speeds ($>0.50 \text{ m} \cdot \text{s}^{-1}$), we speculate that the hydrodynamic benefit of blade clusters may be even greater because flow would compress the blades into a tighter cluster, more effectively sheltering neighboring blades. Furthermore, as speed increases, individual blades might be expected to flap irregularly, exacerbating drag (Taneda 1968, Vogel 1989), whereas blade clustering likely reduces flapping to further mitigate drag (Koehl and Alberte 1988). At slower speeds ($<0.50 \text{ m} \cdot \text{s}^{-1}$), we speculate that the drag ratio would be greater (i.e., measured drag would be more similar to predicted additive drag) due to the reduced density of the cluster. However, slow flow speeds are unlikely to damage or dislodge *Nereocystis* and so are perhaps less important to consider for drag reduction. Because drag coefficients of seaweeds vary with flow speed (Boller and Carrington 2006, Martone et al. 2012) and are notoriously difficult to predict (Martone et al. 2012), the drag-mitigating effect of blade clustering at higher speeds is not easy to quantify. Additional data would need to be collected at higher flow speeds to adequately update the drag model for single blades, allowing future researchers to investigate additional correlations between measured drag and predicted additive drag.

In summary, we demonstrate that producing separate blades that can interact as a cluster is a drag-reducing strategy in *Nereocystis*. Clusters of blades experience significantly less drag than the sum of the drag experienced by individual blades alone: at $0.40\text{--}0.50 \text{ m} \cdot \text{s}^{-1}$, drag on the blades of *Nereocystis* is about 37% of predicted additive drag. This growth strategy likely contributes to the ability of kelps like *Nereocystis* to grow larger than they otherwise would with a single blade of comparable size. Moreover, because our estimates of additive drag were derived from single-blade measurements at a slightly higher speed, our conclusions about the benefits of blade clustering are conservative. Since drag coefficients are generally higher at lower flow speeds (Martone et al. 2012), actual drag coefficients of single blades at $0.41 \text{ m} \cdot \text{s}^{-1}$ could have been slightly higher than those measured at $0.50 \text{ m} \cdot \text{s}^{-1}$, increasing additive drag estimates and therefore magnifying the drag-reducing benefits of blade clustering beyond that reported here.

Finally, we note that the benefit of blade clustering in *Nereocystis* likely depends upon the attachment of blades at a single point, which allows them to collapse and form a drag-reducing cluster. *Nereocystis* may receive an even greater benefit from blade

subdivision than other kelps because of this morphological characteristic. This feature also likely explains the hydrodynamic difference between blade clusters in *Nereocystis*, which ameliorate drag, and dichotomous branching in other seaweeds, which increase drag (Starko et al. 2014). Perhaps, as a consequence, the attachment strength of *Nereocystis* thalli to the substratum is less than that predicted by scaling relationships for typical branched seaweeds (Starko et al. 2014), suggesting that blade-clustering in *Nereocystis* may relieve some of the burden of attachment by limiting drag.

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AUTHOR CONTRIBUTIONS

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- Abbott, I. A. & Hollenberg, G. J. 1976. *Marine algae of California*. Stanford University Press, Stanford, 827 p.
- Albayrak, I., Nikora, V., Miler, O. & O'Hare, M. 2012. Flow-plant interactions at a leaf scale: effects of leaf shape, serration, roughness and flexural rigidity. *Aquat. Sci.* 74:267–86.
- Anderson, L. M. & Martone, P. T. 2014. Biomechanical consequences of epiphytism in intertidal macroalgae. *J. Exp. Biol.* 217:1167–74.
- Armstrong, S. L. 1989. The behavior in flow of the morphologically variable seaweed *Hedophyllum sessile* (C. Ag.) Setchell. *Hydrobiologia* 183:115–22.
- Boller, M. L. & Carrington, E. 2006. The hydrodynamic effects of shape and size change during reconfiguration of a flexible macroalga. *J. Exp. Biol.* 209:1894–903.

- Canadian Hydrographic Service 2019. *Juan de Fuca Strait and Strait of Georgia*. Fisheries and Oceans Canada, Ottawa, 141 p.
- Carrington, E. 1990. Drag and dislodgment of an intertidal macroalga: consequences of morphological variation in *Mastocarpus papillatus* Kützinger. *J. Exp. Mar. Biol. Ecol.* 139:185–200.
- Charters, A. C., Neushul, M. & Barilotti, D. C. 1969. The functional morphology of *Eisenia arborea*. *Proc. Int. Seaweed Symp.* 6:89–105.
- Coleman, L. J. M. & Martone, P. T. 2020. Morphological plasticity in the kelp *Nereocystis luetkeana* (Phaeophyceae) is sensitive to the magnitude, direction, and location of mechanical loading. *J. Phycol.* 56:1377–97.
- Conover, J. T. 1966. The importance of natural diffusion gradients and transport of substances related to benthic marine plant metabolism. *Bot. Mar.* 11:1–9.
- de Bettignies, T., Wernberg, T. & Lavery, P. 2013. Size, not morphology, determines hydrodynamic performance of a kelp during peak flow. *Mar. Biol.* 160:843–51.
- Denny, M. 1995. Predicting physical disturbance: mechanistic approaches to the study of survivorship on wave-swept shores. *Ecol. Monogr.* 65:371–418.
- Denny, M. W., Daniel, T. L. & Koehl, M. A. R. 1985. Mechanical limits to size in wave-swept organisms. *Ecol. Monogr.* 55:69–102.
- Denny, M. & Gaylord, B. 2002. The mechanics of wave-swept algae. *J. Exp. Biol.* 205:1355–62.
- Denny, M., Gaylord, B. & Cowen, B. 1997. Flow and flexibility. II. The roles of size and shape in determining wave forces on the bull kelp *Nereocystis luetkeana*. *J. Exp. Biol.* 200:3165–83.
- Denny, M. W. & Hale, B. B. 2003. Cyberkelp: an integrative approach to the modelling of flexible organisms. *Philos. Trans. Biol. Sci.* 358:1535–42.
- Friedland, M. T. & Denny, M. W. 1995. Surviving hydrodynamic forces in a wave-swept environment: consequences of morphology in the feather boa kelp, *Egria menziesii* (Turner). *J. Exp. Mar. Biol. Ecol.* 190:109–33.
- Fritsch, F. E. 1923. Order VI. Laminariales. In *The Structure and Reproduction of the Algae*. Cambridge University Press, Cambridge, 192–260pp.
- Gaylord, B. 2000. Biological implications of surf-zone flow complexity. *Limnol. Oceanogr.* 45:174–88.
- Gaylord, B., Blanchette, C. A. & Denny, M. W. 1994. Mechanical consequences of size in wave-swept algae. *Ecol. Monogr.* 64:287–313.
- Gaylord, B., Denny, M. W. & Koehl, M. A. R. 2008. Flow forces on seaweeds: Field evidence for roles of wave impingement and organism inertia. *Biol. Bull.* 215:295–308.
- Gerard, V. A. 1982. In situ water motion and nutrient uptake by the giant kelp *Macrocystis pyrifera*. *Mar. Biol.* 69:51–4.
- Graham, L. E., Graham, J. M., Wilcox, L. W. & Cook, M. E. 2017. *Algae*, 3rd edition. LJLM Press, Madison, WI, 688 p.
- Harder, D. L., Speck, O., Hurd, C. L. & Speck, T. 2004. Reconfiguration as a prerequisite for survival in highly unstable flow-dominated habitats. *J. Plant Growth Regul.* 23:98–107.
- Johnson, A. S. 2001. Drag, drafting, and mechanical interactions in canopies of the red alga *Chondrus crispus*. *Biol. Bull.* 201:126–35.
- Koehl, M. A. R. 1984. How do benthic organisms withstand moving water? *Am. Zool.* 24:57–70.
- Koehl, M. A. R. & Alberte, R. S. 1988. Flow, flapping, and photosynthesis of *Nereocystis luetkeana*: a functional comparison of undulate and flat blade morphologies. *Mar. Biol.* 99:435–44.
- Koehl, M. A. R., Silk, W. K., Liang, H. & Mahadevan, L. 2008. How kelp produce blade shapes suited to different flow regimes: A new wrinkle. *Integr. Comp. Biol.* 48:834–51.
- Koehl, M. A. R. & Wainwright, S. A. 1977. Mechanical adaptations of a giant kelp. *Limnol. Oceanogr.* 22:1067–71.
- Martone, P. T. 2007. Kelp versus coralline: cellular basis for mechanical strength in the wave-swept seaweed *Calliarthron* (Corallinales, Rhodophyta). *J. Phycol.* 43:882–91.
- Martone, P. T. & Denny, M. W. 2008. To break a coralline: mechanical constraints on the size and survival of a wave-swept seaweed. *J. Exp. Biol.* 211:3433–41.
- Martone, P. T., Kost, L. & Boller, M. 2012. Drag reduction in wave-swept macroalgae: alternative strategies and new predictions. *Am. J. Bot.* 99:806–15.
- Milligan, K. L. D. & DeWreede, R. E. 2000. Variations in holdfast attachment mechanics with developmental stage, substratum-type, season, and wave-exposure for the intertidal kelp species *Hedophyllum sessile* (C. Agardh) Setchell. *J. Exp. Mar. Biol. Ecol.* 254:189–209.
- Milligan, K. L. D. & DeWreede, R. E. 2004. Morphological variations do not effectively reduce drag forces at high wave-exposure for the macroalgal species, *Hedophyllum sessile* (Laminariales, Phaeophyta). *Phycologia* 43:236–44.
- Nicholson, N. L. 1970. Field studies on the giant kelp *Nereocystis*. *J. Phycol.* 6:177–82.
- Rasband, W. 2021. *ImageJ 1.53i*. U. S. National Institutes of Health, Bethesda.
- Starko, S., Claman, B. Z. & Martone, P. T. 2014. Biomechanical consequences of branching in flexible wave-swept macroalgae. *New Phytol.* 206:133–140. <https://doi.org/10.1111/nph.13182>
- Starko, S. & Martone, P. T. 2016. Evidence of an evolutionary-developmental trade-off between drag avoidance and tolerance strategies in wave-swept intertidal kelps (Laminariales, Phaeophyceae). *J. Phycol.* 52:54–63.
- Stewart, H. L. & Carpenter, R. C. 2003. The effects of morphology and water flow on photosynthesis of marine macroalgae. *Ecology* 84:2999–3012.
- Taneda, S. 1968. Waving motions of flags. *J. Physical Soc. Japan* 24:392–401.
- Vogel, S. 1984. Drag and flexibility in sessile organisms. *Am. Zool.* 24:37–44.
- Vogel, S. 1989. Drag and reconfiguration of broad leaves in high winds. *J. Exp. Bot.* 40:941–8.
- Wheeler, W. N. 1980. Effect of boundary layer transport on the fixation of carbon by the giant kelp *Macrocystis pyrifera*. *Mar. Biol.* 56:103–10.
- Wolcott, B. D. 2007. Mechanical size limitation and life-history strategy of an intertidal seaweed. *Mar. Ecol. Prog. Ser.* 338:1–10.

Supporting Information

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

Figure S1. Real drag coefficient as a function of predicted drag coefficient for 100 isolated *Nereocystis* blades in $50 \text{ cm} \cdot \text{s}^{-1}$ of flow.

Figure S2. Drag ratio (R) and estimates of the parameter k plotted against cumulative area prior to blade removal.

Figure S3. Drag versus cumulative area (m^2) for the 13 *Nereocystis* thalli at each blade removal interval.