

Mechanical Design and Hydrodynamics of Blade-like Algae: *Chondracanthus exasperatus*

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Abstract

Although many flexible macroalgae are passively reconfigured by ambient water flow into compact, streamlined shapes, some remain spread out as they are bent over by moving water. This study focused on how the thallus shape and material properties of blade-like red algae, *Chondracanthus exasperatus*, affect the shape changes they undergo and their danger of breakage in tidal currents. The flow microhabitats of *C. exasperatus* were characterized by fluctuating unidirectional flow of about 0.1 m/s, (much slower than freestream currents). The shape of a *C. exasperatus* thallus and its low tissue stiffness permit the alga to easily be twisted about its stipe and bent over parallel to the flow while its thick, undulate blade remains spread out. Such bending over close to the bottom can reduce the total drag on a thallus by 14 to 90%, resulting in a safety factor of ~11. The extensible tissue of the thallus acts as a shock absorber whose deformation during transient high forces protects the stipe from high stresses.

Introduction

Benthic marine macroalgae depend on ambient water flow for transport of nutrients, gases, gametes, and spores, and yet they also risk being dislodged or broken by hydrodynamic forces (e.g. Koehl, 1984; 1986; 1999; Koehl and Alberte, 1988; Stewart, 1999). Most macroalgae are flexible and are passively reconfigured by ambient water currents into more streamlined shapes as flow velocity increases. Although thallus shape can affect the hydrodynamic forces algae experience (e.g. Koehl and Alberte, 1988; Armstrong, 1989; Dudgeon and Johnson, 1992; Johnson and Koehl, 1994), Carrington (1990) found that a variety of very flexible blade-like, branching, and bushy seaweeds had similar drag coefficients (Eqn. 1) when subjected to rapid flow in which they all were compacted into streamlined bundles. In contrast, other

sessile organisms, like the blade-like red alga *Chondracanthus exasperatus* (Harvey and Bailey) Hughey, remain spread out in rapidly-flowing water, although they are bent over parallel to the flow. *C. exasperatus* occurs in rocky subtidal habitats to depths of 20 m, from Baja, Mexico, to British Columbia, Canada (Abbott and Hollenberg, 1976). The blade-like thallus (Fig. 1) of a male, female, or tetrasporophyte is undulate (ruffled), bears papillae, and is attached to the rock by a small stipe and discoidal holdfast. The purpose of this study was to use *C. exasperatus* to investigate how the flow microhabitat, body shape, and material properties of flexible organisms that remain spread out in flowing water affect the shape changes they undergo and their danger of breakage in unidirectional ambient currents.

Materials and Methods

Field sites and water velocity measurements: *C. exasperatus* were collected by SCUBA divers from two shallow, rocky subtidal sites near Friday Harbor, WA., USA: Minnesota Reef and Point George. Both sites are subjected to tidal currents, but not to surf. Water velocities were measured during ebbing tidal currents under non-storm conditions in August at Minnesota Reef with a two-axis electromagnetic flow meter (Cushing Engineering 600 Velmeter with miniature probe; time response 0.1s) as described in Koehl (1977) and Koehl and Alberte (1988).

The algae were kept in tanks of running seawater at Friday Harbor Laboratories, and were used for drag measurements or materials testing within 24 h of the time of collection. The life cycle of *C. exasperatus* includes sexual (gametangial) and asexual (tetrasporangial) stages that are similar in size and shape (Abbott and Hollenberg, 1976). The stage of each algal thallus was identified after collection; about half of the individuals were tetrasporophytes and half were female gametophytes. There was no significant difference between these stages in the morphometric, hydrodynamic, or mechanical properties measured (Student's t , $p > 0.05$), so data for all stages were pooled.

Drag Measurements: The peak drag (hydrodynamic force pushing a body downstream) on each alga was measured to the nearest 0.01 N using an Ohaus 8011 force transducer. The stipe of each alga was tied to the transducer. The alga was towed through the water by a boat at 0.15, 0.31, and 0.46 m/s; water velocity relative to the alga was measured using the Cushing Velmeter placed 2 cm upstream from the alga (the velmeter was removed from this position just before a drag measurement was taken). Thus, the water flow relative to each alga was an average current due to the movement of the boat plus the small velocity fluctuations due to the natural turbulence in the water column. Since flexible benthic algae can be bent over close to the substratum by moving water, drag was measured on each alga when it was attached to the force transducer mounted in the middle of a plywood substratum (1.6 m long x 1 m wide) that was attached to the side of the boat. To determine the effect on drag of the substratum, it was removed from the boat

and the drag on each alga was also measured while it was towed from an arm extending 1.0 m from the side of the boat.

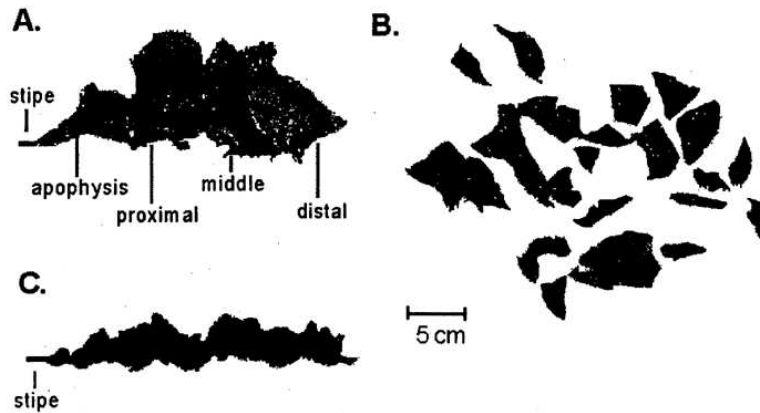


Fig. 1. A. Planform view of a *C. exasperatus*. Images such as this were used to measure the "plan area" of each alga. The small discoidal holdfast is not shown. B. The individual shown in "A" has been cut into pieces that lie flat. Images such as this were used to measure the "real area" of each alga. C. Side view of a *C. exasperatus*, illustrating the undulate (i.e. ruffled) shape of the blade.

Drag coefficient (C_D) is an index of how drag-inducing the shape of a body is. For large objects in rapidly-flowing water, C_D is given by:

$$C_D = 2 D / (\rho U^2 S) \quad (1)$$

where D is drag, ρ is the density of the fluid (1026 kg/m³ for seawater at 10°C), U is the water velocity relative to the body, and S is a relevant plan area of the body (the convention for macroalgae is the maximum plan area of the thallus, Fig. 1, A; Koehl, 1986; Vogel, 1989; Carrington, 1990; Gaylord, *et al.*, 1994; Friedland and Denny, 1995; Gaylord and Denny, 1997). Vogel (1984) proposed an index, the "figure of merit" (B), to describe the relative reduction in drag experienced by flexible structures as they reconfigure as flow velocity increases. B is the slope of a log-log plot of speed-specific drag (D/U^2) as a function of velocity; the greater the absolute value of the negative slope, the greater the relative drag reduction experienced with an increase in velocity. We determined B for each individual kelp by calculating the slope of a linear regression of a plot of $\log(D/U^2)$ versus $\log U$.

Morphometrics: Each alga was photographed and its plan area (Fig. 1, A) was measured to the nearest 0.0001 m² (Koehl and Alberte, 1988), and blade width at the midpoint between the stipe and the blade tip was also measured to the nearest 0.001m. The real area of an undulate thallus is greater than its plan area. Thus, after an intact thallus was photographed, it was cut it into pieces that would lie flat (Fig. 1, B), and was photographed again; the total area of all the pieces was measured as the "real area" of the thallus (Koehl and Alberte, 1988). Stipe diameter was measured to the nearest 0.0001 m using vernier calipers.

Material Properties: Mechanical properties of tissues from each alga were measured by conducting tensile stress-extension tests on a Houndsfield Ten-

someter, Model W (details in Koehl and Wainwright, 1977; Johnson and Koehl, 1994). Strips of tissue were pulled until they broke, while their extension and the force with which they resisted being stretched were recorded. Tests were done on strips of tissue 0.023m in width (w). The thickness (T) of each specimen was measured (between papillae) to the nearest 0.0001m using vernier calipers, and cross-sectional area ($A_0 = Tw$) was calculated. The pre-test length between the grips of each specimen (L_0) was measured to the nearest 0.001m with vernier calipers. Material properties were only determined for specimens that did not slip or break at the grips. Strain rates ($(\Delta L/L_0) / t$, where ΔL = the increase in length of the specimen as it was pulled, and t is the time interval over which ΔL occurred) of $0.003s^{-1}$ and $0.03s^{-1}$ were tested in preliminary trials and found to have no significant effect (Student's t , $p > 0.05$) on any of the material properties measured, hence strain rates of 0.02 to $0.03s^{-1}$ were used in this study.

The material properties we calculated are illustrated in Fig. 2. Extension ratio (λ) of the specimen is given by

$$\lambda = (\Delta L + L_0) / L_0 \quad (2)$$

and the stress (σ) is given by

$$\sigma = F / A_0 \quad (3)$$

where F is the force with which the specimen resisted that extension. The slope (E) of a plot of stress versus extension ratio of the tissue is its modulus, a measure of the stiffness of the material. The stress at which a specimen broke (σ_{brk}) is a measure of the strength of the tissue, and the extension ratio at which it broke (λ_{brk}) is a measure of its extensibility. The area under a plot of σ as a function of λ for a specimen pulled until it broke is the work per volume $[W/V]_{brk}$ required to break that specimen, an estimate of its "toughness" that includes not only the work of fracture (work required to make new surfaces in a material as a crack propagates), but also the energy lost as heat when the structure was stretched and the energy released during the elastic recoil of the breaking specimen.

The resilience (ability to store strain energy for elastic recoil) of strips of *C. exasperatus* tissue was measured in tensile free-vibration tests, as described by Nielsen (1962). The top end of a specimen (0.023 m wide, 0.09 m long between the grips) was held stationary, and the free bottom end was attached to the core of a LVDT (Schaevitz Engineering, Model 200 HRDC). An extension ratio of <1.1 was imposed on a specimen and released, allowing the tissue to rebound while the displacement of the free end was recorded as a function of time. The greater the resilience of a tissue, the more slowly the oscillations of the free end are damped out. Because the E of *C. exasperatus* tissue is nearly independent of extension ratio (Fig. 2) and strain rate, an estimate of resilience (R) is given by

$$\ln(100 / R) = \Delta \quad (4)$$

where Δ is the logarithmic decrement in amplitude of the deformation of the specimen from one cycle of oscillation to the next ($\Delta = \ln [D_n / D_{n+1}]$, where

D_n is the amplitude of the displacement of the free end of the specimen during cycle n , and D_{n+1} is the amplitude during cycle $[n + 1]$ (Alexander, 1966; 1983; Wainwright, *et al.*, 1976).

Statistical Analyses: Parametric statistical tests were done using Excel 97 software, and nonparametric tests were done using Statview 5.0 software.

Results and Discussion

Hydrodynamic Habitat: *C. exasperatus* at our study sites encountered rapid tidal currents that flowed in one direction for several hours, slowed at slack tide, and then flowed rapidly in the opposite direction. Although the flow was unidirectional on a time scale of seconds to hours, it was turbulent and

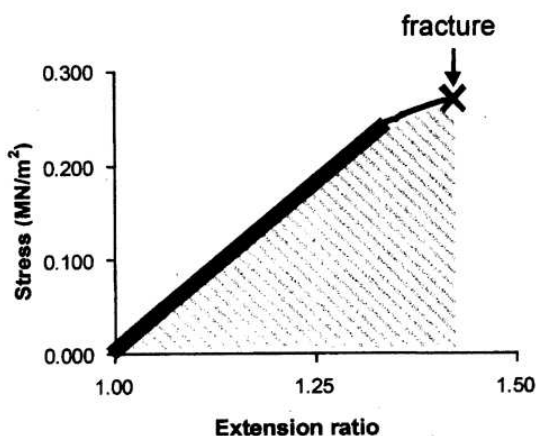


Fig. 2. Example of a typical plot of stress as a function of extension ratio for tissue from *C. exasperatus*. The slope (grey line) represents the elastic modulus (stiffness) of the tissue. The stress and extension ratio when the tissue fractures represent its strength and extensibility, respectively. The hatched area under the curve represents the work per volume of tissue required to break it.

velocity fluctuated rapidly (Fig. 3, A). *C. exasperatus* were bent over close to the substratum by the current, hence they encountered velocities lower than freestream (Fig. 3, B). Often *C. exasperatus* occurred in patches of seaweed; water velocities encountered by the individuals within such algal canopies were lower than those experienced by solitary *C. exasperatus* or by those at the upstream edge of the group (Fig. 3, B). Such flow reduction has also been measured in kelp canopies (e.g. Koehl, 1986; Koehl and Alberte, 1988; Eckman, *et al.*, 1989; Duggins, *et al.*, 1990).

Drag: When subjected to water currents, *C. exasperatus* are bent over parallel to the direction of water movement. The drag on macroscopic organisms is due to the pressure difference across the body that occurs when a wake forms behind the organism (form drag), and to the viscous resistance of the fluid along the surface of the body to being sheared (skin friction drag). Passive reorientation or reconfiguration of flexible organisms by flowing water, such as that exhibited by *C. exasperatus*, reduces the size of the wake downstream, thereby reducing form drag (e.g. Koehl, 1977; 1986; Vogel, 1984; 1989; Koehl and Alberte, 1988; Carrington, 1990). In addition, if the flexibility of a blade-like sessile organism permits it to be pushed down close to the substratum, the underside of the blade encounters slower flow than the

upper surface, thereby reducing the shear and thus the skin friction drag on that surface (Koehl, 1986). Comparison of the drag on thalli when near a substratum versus when not showed that this mechanism can reduce the total drag by 14 to 90% (Fig. 4). For *C. exasperatus*, the drag-reducing effect of proximity to the substratum was independent of flow velocity and of thallus size (real blade area) (ANOVA, $p > 0.05$).

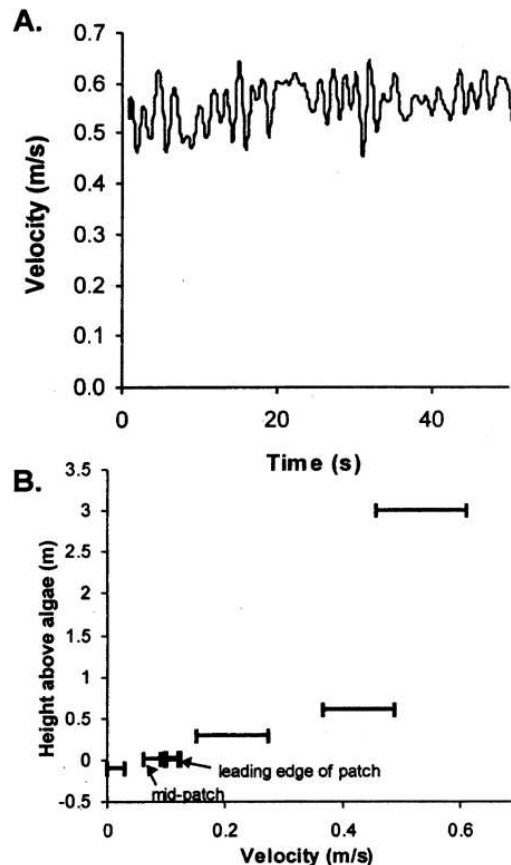


Fig. 3. A. Freestream water velocity recorded during peak ebbing tidal current above *C. exasperatus* habitat, plotted as a function of time. B. Range of water velocities (x-axis) measured at different heights (y-axis) relative to the top of a canopy of red algae, including *C. exasperatus*. Black bars represent velocity ranges recorded at the middle of the patch of algae, and the grey bar represents the velocity range recorded at the upstream edge of the patch.

Although *C. exasperatus* blades did not fold into compact streamlined shapes in rapid flow, their C_D 's (mean = 0.08, S.D. = 0.06, $n = 7$) were comparable to those of other flexible macroalgae (Table 1). At each velocity tested, C_D was independent of thallus size (real blade area) and of the degree of blade undulation (i.e. ruffiness, [real area] / [plan area]) (Kendall Tau, $p > 0.05$) (Fig. 5, A, B). The mean C_D of *C. exasperatus* did not differ significantly at different water flow velocities because of high variation between individuals (ANOVA, $p > 0.05$) (Fig. 5, C). Nonetheless, the figure of merit (B) for *C. exasperatus* (mean = -0.5, S.D. = 0.3, $n = 7$), which describes the relative drag reduction experienced by a flexible individual as flow velocity increases, was similar to the B's of other algae (Table 1). For *C. exasperatus*, B was independent of thallus size and of the degree of blade undulation (Kendall Tau, $p > 0.05$).

Material Properties: The tissues of a *C. exasperatus* thallus are usually isotropic and relatively uniform in material properties. For all but one thallus

Errata: The following figures were omitted when the book was printed.
They should have appeared between page 300 and page 301.

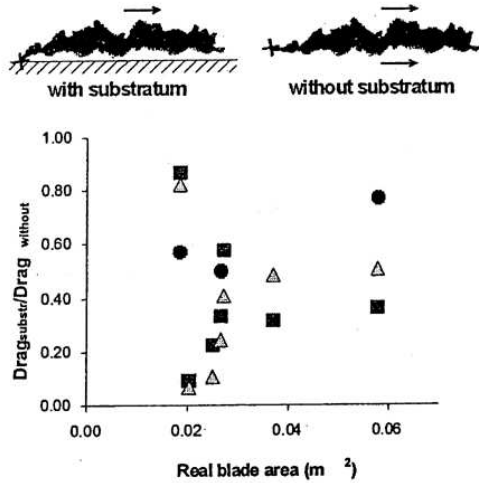


Fig. 4 Ratio of the drag measured on *C. exasperatus* next to a substratum to the drag measured on the same alga when not near a substratum, plotted as a function of thallus size (real area). Each point represents the ratio of the mean of 5 replicates for an individual alga next to the substratum to the mean of 5 replicates for that same alga not near a substratum. Symbols denote water velocity relative to the alga: ● = 0.15 m/s, ■ = 0.31 m/s, △ = 0.46 m/s. In the diagrams above the graph, the arrows indicate the direction of water flow relative to the alga, and the + indicates the point of attachment to the force transducer.

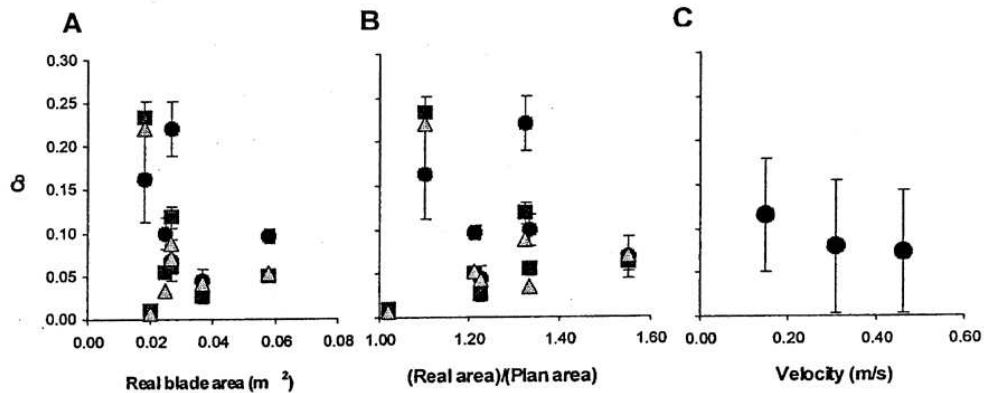


Fig. 5 A. Drag coefficient (C_D) of *C. exasperatus* next to a substratum plotted as a function of thallus size (real blade area). B. C_D plotted as a function of the degree of undulation of a thallus ($[\text{real area}]/[\text{plan area}]$). Each point in A and B represents the mean of 5 replicates for an individual alga. Symbols denote water velocity relative to the alga: ● = 0.15 m/s, ■ = 0.31 m/s, △ = 0.46 m/s. C. C_D plotted as a function of velocity. Each point represents the mean of the mean C_D 's of the algae ($n = 7$) measured at each velocity. Error bars in A, B, and C represent one standard deviation.

tested, there was no significant difference between the E , σ_{brk} , λ_{brk} , or $[W/V]_{brk}$, when tissues were pulled parallel to the long axis of the thallus versus when pulled perpendicular to the long axis, nor between tissues from the edges of the blade versus those from the center (Student's t , $p > 0.05$). Growth of red algae is chiefly apical (Abbott and Hollenberg, 1976), but material properties were similar along the length of *C. exasperatus* thalli (Fig. 6). Furthermore, for each of the regions of the thalli, there was no significant difference between the material properties of tissues from algae of different sizes (lengths) (ANOVA, $p > 0.05$).

The material properties of the tissues of *C. exasperatus* are compared with those of other algae in Table 2. As illustrated by the stress-extension curve in Fig. 2, *C. exasperatus* tissues are highly extensible, typically stretching by about 40% of resting length before breaking (mean of the means of $\lambda_{brk} = 1.4$, S.D. = 0.2, $n = 4$ algae, 4 to 12 replicates each). *C. exasperatus* has a low modulus of elasticity that changes little with extension ratio (Fig. 2) (mean of the means of $E = 2.4$ MN/m², S.D. = 1.0, $n = 4$ algae, 4 to 13 replicates each). In contrast, stipe tissues from some brown algae are stiffer at low λ than at high λ ; Holbrook, *et al.*, 1991; Johnson and Koehl, 1994) (Table 2). *C. exasperatus* tissues undergo brittle fracture at low breaking stress (mean of the means of $\sigma_{brk} = 0.78$, S.D. = 0.12, $n = 4$ algae, 4 to 12 replicates each), but because of their great extensibility, they require more work per volume to break (mean of the means of $[W/V]_{brk} = 0.15$ MJ/m², S.D. = 0.07, $n = 4$ algae, 4 to 11 replicates each) than much stronger biomaterials, such as bone or insect cuticle (Wainwright, *et al.* 1976; Vincent, 1990). The mean resilience (R) of *C. exasperatus* tissue measured in free-vibration tests was 52% (mean of the means for 3 individuals, 4 replicates each, S.D. = 16%). Although not as high as the R 's measured in free-vibration tests for rubbery animal proteins such as abductin ($R = 80$ to 91%, Alexander 1966; Vincent, 1990) or resilin ($R = 96\%$, Vincent, 1990), the R of *C. exasperatus* tissue is similar to that of the rubbery stipes of the giant kelp, *N. luetkeana* ($R = 43 - 55\%$, Koehl, unpublished data).

Thallus Design and the Performance of *C. exasperatus* in Tidal Currents: The deformation and breakage of an algal thallus depends on its size and shape as well as its material properties. Not only does thallus shape determine the magnitude of the hydrodynamic forces an alga experiences when exposed to ambient currents, but it also determines the distribution of stresses within the thallus when bearing those forces, while the material properties of the tissues determine the response of the alga to those stresses, i.e. its deformation and likelihood of breaking (Koehl, 1984; 1986).

Table 1. Hydrodynamic Characteristics of Algal Thalli.

Species	shape	C_D	B
RHODOPHYTA			
<i>Chondracanthus exasperatus</i> *	blade	0.08	-0.5
<i>Chondrus crispus</i>	branches	0.48 ⁴	-
<i>Endocladia muricata</i> *	bush	0.05 to 0.13 ²	-0.48 ²
<i>Gigartina leptorhynchus</i> *	bush	0.08 to 0.16 ^{2,6}	-0.52 ²
<i>Iridaea flaccida</i> *	blade	0.04 to 0.07 ^{2,6}	-0.76 ²
<i>Mastocarpus jardinii</i> *	branches	0.10 to 0.36 ²	-0.28 ²
<i>Mastocarpus pappilatus</i> *	branches	0.02 to 0.27 ²	-0.38 ²
<i>Mastocarpus stellatus</i>	branches	0.19 ⁴	-
12 species (freshwater)	crust, blade, tuft, filament	-	-1.27 to -0.33 ⁹
PHAEOPHYTA			
<i>Egregia menziesii</i> *	long feathery strap	0.02 ⁵	-
<i>Eisenia arborea</i>	stipe and blades	0.04 ⁷	-
<i>Fucus distichus</i> *	branches	0.07 to 0.10 ²	-0.50 ²
<i>Hedophyllum sessile</i>	blades	-	-1.2 to -0.6 ¹
<i>Macrocystis pyrifera</i>	long stipes and blades	0.01 ⁵	-
<i>Nereocystis luetkeana</i>	long stipe and blades	0.02 to 0.40 ⁸	-1.20 to -0.75 ⁸
<i>Pelvetia fastigiata</i> *	branches	0.05 ²	-0.33 ²
<i>Pelvitiopsis limitata</i> *	branches	0.17 ⁶	-
<i>Pterogophora californica</i>	stipe and blades	0.04 ⁷	-
<i>Sargassum filipendula</i>	branches	-	-0.6 to -1.47 ¹⁰
CHLOROPHYTA			
<i>Udotea flabellum</i>	blade	0.02 to 0.2 ³	-
*Drag measured with thallus near a substratum.			
¹ Armstrong (1989); ² Carrington (1990); ³ Collado-Vides, <i>et al.</i> (1998); ⁴ Dudgeon and Johnson (1992); ⁵ Friedland and Denny (1995); ⁶ Gaylord, <i>et al.</i> (1994); ⁷ Gaylord and Denny (1997); ⁸ Johnson and Koehl (1994); ⁹ Sheath and Hambrook (1988); ¹⁰ Vogel (1984)			

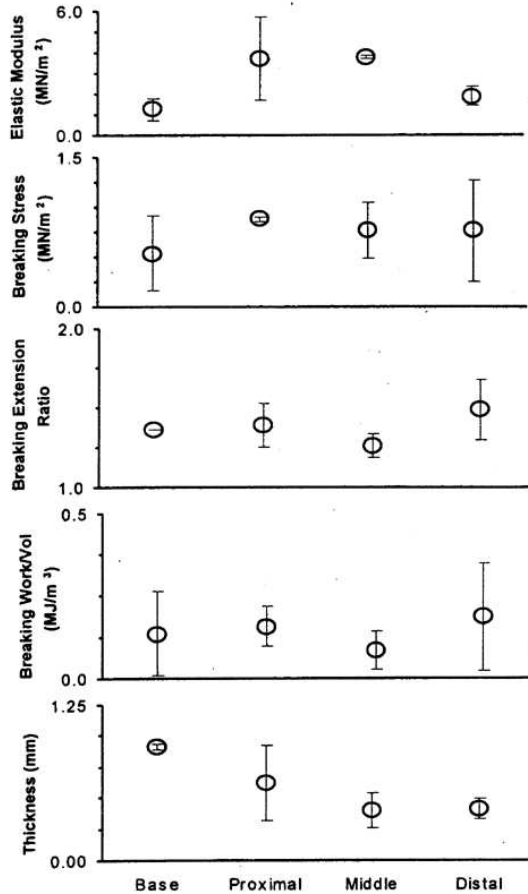


Fig. 6. Material properties (defined in Fig. 2) and thallus thickness measured for different regions (Fig. 1,A) of *C. exasperatus*. Symbols represent the mean of the mean values of replicates for each of the plants ($n = 4$) tested; error bars represent one standard deviation.

C. exasperatus exposed to tidal currents are bent over in the direction of flow, but the blade remains spread out; such behavior should enhance interception of sunlight by the blade. The resistance of a structure to bending is its flexural stiffness, EI , where E is the modulus of the tissue and I is the second moment of area of the cross-section of the structure, a measure of the distribution of tissue around the axis of bending (e.g. Wainwright *et al.*, 1976; Alexander, 1983; Vogel, 1995). Similarly, the resistance of a structure to twisting is its torsional stiffness, GJ , where G is the shear modulus of the tissue and J is the polar second moment of area of the cross-section. For cylindrical structures such as the stipe of *C. exasperatus*, I and J are given by

$$I = \pi r^4 / 4 \quad \text{and} \quad J = \pi r^4 / 2 \quad (5)$$

where R is the stipe radius. For flat blades, I and J are given by

$$I = 4 w t^3 / 3 \quad \text{and} \quad J = a b^3 [5.33 - 3.36 \{b/a\} \{1 - (b^4 / 12 a^4)\}] \quad (6)$$

where w is blade width, t is thickness, a is $w/2$, and b is $t/2$ (Roark and Young, 1975). *C. exasperatus* stipes have very low flexural stiffness (mean $EI = 3.1 \times 10^{-11} \text{ MN}\cdot\text{m}^2$, S.D. = 1.2, $n = 7$), and thus permit the thallus to easily bend over. If the apophysis and blade of a *C. exasperatus* were flat, they also would offer very little resistance to bending (mean apophysis $EI = 0.9 \times 10^{-11} \text{ MN}\cdot\text{m}^2$, S.D. = 0.2, $n = 7$; mean blade $EI = 3.7 \times 10^{-11} \text{ MN}\cdot\text{m}^2$, S.D. = 0.8, $n = 7$). The apophysis is much narrower than the blade, but it is thicker (Fig. 6) and hence has an EI only slightly lower than that of the blade

(since $I \propto t^3$, a small increase in thickness can lead to a large increase in resistance to bending). Although values for G for *C. exasperatus* are not available, these algae have very low J 's (26.8×10^{-12} , 0.9×10^{-12} , and $3.9 \times 10^{-12} \text{ m}^4$ for stipe, apophysis, and blade, respectively) and should offer little resistance to twisting. However, the blade is undulate, not flat (Fig. 1, C). If a sheet is curved or corrugated, its I , and hence its resistance to bending, can be increased substantially (Francis, 1985). Thus, the undulate shape of *C. exasperatus* blades (which are thick compared with blades of the other red algae that do fold up laterally into compact shapes in rapid flow; Carrington, 1990) no doubt contributes to their ability to remain spread out in rapid currents. Undulate blade shapes have also been shown to reduce self-shading in multi-bladed species, and to induce flow separation around blades, increasing drag but not necessarily enhancing uptake of dissolved materials (Koehl and Alberte, 1988; Hurd, *et al.*, 1996; 1997). Thus, the shape of a *C. exasperatus* thallus, coupled with its low E , permit the alga to be twisted about its stipe so that its width is perpendicular to the flow, and to be bent at the stipe so that it is pushed over parallel to the flow while its thick, undulate blade remains spread out.

When *C. exasperatus* are pulled from the substratum, they usually break at the base of the stipe, as has also been observed for a variety of other species of macroalgae (Koehl and Wainwright, 1977; Carrington, 1990; Hawes and Smith, 1995; Shaughnessy, *et al.*, 1996). One index of the ability of *C. exasperatus* to resist being washed away by ambient water flow is its "safety factor", the ratio of its tissue strength (σ_{brk}) to the maximum stress it experiences during its lifetime due to hydrodynamic forces. However, since ambient forces on and material properties of algae can vary with age and season, an "environmental stress factor" can be calculated that relates the ability of organisms at their particular stages in ontogeny to resist breakage relative to the maximum loads that they experience in nature at those stages (Johnson and Koehl, 1994; Koehl, 1999). Even though *C. exasperatus* tissues have low σ_{brk} and their stipes are small, the environmental stress factor calculated for these algae in August at Minnesota Reef were very high (mean = 432; S.D. = 254, $n = 6$), suggesting that they are in little danger of being washed away. By assuming that σ_{brk} does not change with season for these perennial (Abbott and Hollenberger, 1976) algae, and by assuming that C_D is independent of velocity, an estimate of the safety factor of *C. exasperatus* can be calculated by assuming they are exposed to a water velocity of 1.24 m/s, which is the 99th percentile current speed measured during storms at 0.20 m above the substratum at Reid Rock, a site near Point George (Duggins, Eckman, Siddon, and Klinger, pers. com.). The mean estimated safety factor for *C. exasperatus* is 11 (S.D. = 13, $n = 7$), which is comparable to those estimated for other macroalgae (Koehl and Wainwright, 1977; Friedland and Denny, 1995). The safety factors calculated for blades of *C. exasperatus* (mean = 210, S. D. = 281, $n = 7$) are much higher than those of the stipes, hence it is not surprising that thalli most often break at the stipe. Both the August environmental stress factor and the safety factor are independent of thallus size (Kendall Tau, $p > 0.05$).

Table 2. Material Properties of Algal Tissues.

Species	E (MN/m ²)	σ_{BRK} (MN/m ²)	λ_{BRK}	[W/V] _{BRK} (MJ/m ³)
RHODOPHYTA				
<i>Chondracanthus exasperatus</i> (b)	2.4	0.78	1.4	0.15
<i>Chondrus crispus</i> (s)	18 ⁶	10.5 ⁶	-	-
<i>Mastocarpus stellatus</i> (s)	26 ⁶	18.9 ⁶	-	-
<i>Mastocarpus papillatus</i> (s)	-	6.7 ²	-	-
<i>Mazzaella linearis</i> (b)	-	4.2 ¹⁶	-	-
<i>Mazzaella splendens</i> (b)	-	6.2 to 9.0 ¹⁶	-	-
<i>Porphyra lanciniata</i> (s)	-	-	1.23 ⁴	-
<i>Sarcophyllis edulis</i> (s)	-	-	1.29 ⁴	-
12 species (freshwater) (f)	-	0.012 to 1.4 ¹⁷	1.1 to 1.3 ¹⁶	-
PHAEOPHYTA				
<i>Ascophyllum nodosum</i> (s)	-	1.5 ⁴ , 2 to 5 ¹⁵	1.1 to 1.5 ¹⁵	1.1 to 1.5 ¹⁵
<i>Durvillaea antarctica</i> (s)	-	0.7 ¹¹	1.17 ¹²	0.004 ¹¹
<i>Eisenia arborea</i> (s)	-	12.5 to 24.1 ³	-	-
<i>Egregia menziesii</i> (s)	12 ⁷	4.4 ⁷	-	-
<i>Fucus serratus</i> (s)	-	4.2 ⁴	-	-
<i>Fucus vesiculosus</i> (s)	-	5.1 ⁴	-	-
<i>Hedophyllum sessile</i> (b)	4.0 to 9.7 ¹	0.7 to 2.6 ¹	1.2 to 1.5 ¹	0.07 to 0.32 ¹
<i>Laminaria dentigera</i> (b)	-	10 ⁵	-	-
<i>Laminaria digitata</i> (b/s)	-	1.5 ¹⁸ /0.9 ⁴	-	-
<i>Laminaria saccharina</i> (s)	-	-	1.23 ⁴	-
<i>Lessonia nigrescens</i> (s)	-	1.2 ¹¹	1.05 ¹²	0.004 ¹¹
<i>Nereocystis luetkeana</i> (s)	E ₁ : 16.6 to 38.0 ¹⁰ E ₂ : 5.8 to 8.8 ¹⁰	2.7 to 5.0 ^{10,13,14}	1.3 to 1.4 ^{14,10}	0.46 to 1.11 ^{14,10}
<i>Postelsia palmaeformis</i> (s)	E ₁ : 9.5 to 6.4 ⁹ E ₂ : 4.4 to 5.2 ⁹	1.1 to 1.3 ⁹	1.2 ⁹	0.002 ⁹
CHLOROPHYTA				
<i>Ulva lactuca</i> (b)	-	0.34 ⁸	-	-
<i>Ulva sp.</i> (b)	-	2.6 ⁵	-	-
Tissue type: (b) blade; (s) stipe; (f) filament.				
¹ Armstrong (1987); ² Carrington (1990); ³ Charters <i>et al.</i> (1967); ⁴ Delf (1932); ⁵ Denny <i>et al.</i> (1989); ⁶ Dudgeon and Johnson (1992); ⁷ Friedland and Denny (1995); ⁸ Hawes and Smith (1995); ⁹ Holbrook <i>et al.</i> ; (1991); ¹⁰ Johnson and Koehl (1994); ¹¹ Koehl (1986); ¹² Koehl (1999); ¹³ Koehl and Alberte (1988); ¹⁴ Koehl and Wainwright (1977); ¹⁵ Lowell <i>et al.</i> (1991); ¹⁶ Shaughnessy <i>et al.</i> (1996); ¹⁷ Sheath and Hambrook (1988); ¹⁸ Vincent and Gavelli (1986).				

The stresses experienced by the stipes of *C. exasperatus* may be lower than estimated above. Because of the tidal currents to which these algae are exposed are turbulent, the highest hydrodynamic forces they experience occur during brief pulses of rapid flow (Fig. 2, A). The extensible, low-E tissue of the thallus of a *C. exasperatus* can act as a shock absorber whose deformation during transient high forces can protect the stipe from high stresses. This protective consequence of low tissue stiffness has been noted for other macroalgae as well (Koehl and Wainwright, 1977; Koehl, 1986; Armstrong, 1987; Gaylord and Denny, 1997; Koehl, 1998). Because *C. exasperatus* tissue is quite resilient, it can recoil before the next transient high load is likely to hit. Unfortunately, high resilience carries with it the danger of brittle fracture, especially in regions of a thallus with surface scratches and flaws, as has been noted for other resilient algae (Koehl and Wainwright, 1977; Vincent and Gravell, 1986; Denny, *et al.*, 1989; Holbrook, *et al.*, 1994).

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