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Strength, drag, and dislodgment of two competing intertidal algae from two wave exposures and four seasons

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Abstract

Intertidal macroalgae often experience greater risk of dislodgment with increasing size because of underscaling of breaking force of their stipes relative to drag on their thalli. This ratio (breaking force/drag) indicates safety from breakage at a given flow speed, with values greater than one indicating safety from breakage and values lower than one indicating danger of breakage. We examined this force ratio for the largest thalli of two species of co-dominant, red algae, *Chondrus crispus* Stackhouse and *Mastocarpus stellatus* Stack. In With. (Guiry), in four seasons at two wave exposures. During fall and winter, the largest thalli in both populations were dislodged resulting in a decrease in mass of the largest thalli found. This decrease was greater for *Chondrus* than for *Mastocarpus*, but their mass-specific force ratios (at 0.55 m s^{-1}) were equal indicating similar size-specific risk of dislodgment. The equality of force ratios was underlain by two similarities: (1) breaking force was independent of mass and not different between species; (2) mass-specific drag was not different between species. These similarities were underlain by dissimilar causes: (i) similarity in breaking force (the product of cross-sectional area and material strength) occurred because greater material strength of *Mastocarpus* compensated for greater mass-specific cross-sectional area of *Chondrus*; (ii) similarity in mass-specific drag (a function of planform area and the coefficient of drag) occurred because greater drag coefficients for *Mastocarpus* compensated for greater mass-specific planform areas of *Chondrus*. The similarity in force ratio, if it held at season- and site-relevant flow speeds, would suggest that during seasons of minimal growth and high wave exposure, the mass of the largest thalli of both species should be the same. *Chondrus*, however, had a greater mass at both sites in all seasons. *Chondrus* experienced greater decreases in mass probably because it grew larger and larger thalli are less safe. Extrapolation of a site-relevant force ratio for *Chondrus* in the fall revealed (1) that the site-relevant force ratio did not differ between exposures

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even though the mass-specific force ratio was greater at the protected site, and (2) a paradoxical result that all *Chondrus* thalli studied ought to have dislodged, but had not. This paradox may be resolved by consideration of the protection conferred by canopies of *Chondrus*: a canopy may effectively raise its site-relevant force ratio. Perhaps differences in protection conferred by different canopies explain why larger *Chondrus* persist with *Mastocarpus* even given a similarity in mass-specific force ratio. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Dislodgment; Drag; Intertidal macroalgae; Safety factor; Seasons

1. Introduction

1.1. Context and mechanical background

Dense algal canopies carpet the intertidal and shallow subtidal along rocky coastlines. These canopies, which dominate primary space and provide secondary habitat for diverse encrusting organisms, are comprised of individual thalli whose persistence is crucial to the maintenance of that canopy. Persistence in the exposed rocky intertidal, however, is challenged by the extreme wave forces experienced there (Denny et al., 1985; Denny, 1995).

Forces from waves dislodge intertidal organisms and have been invoked as an explanation for their small size relative to terrestrial or wave-protected marine organisms (Denny et al., 1985). Drag has become the primary candidate as a size-limiting force for algae (Denny, 1999; Gaylord, 2000), yet the relationship between maximum size and drag remains tangled. This is because although organisms generally experience increasing drag with increasing size, their risk of dislodgment will depend on how drag scales relative to their ability to remain unbroken and attached. Size-dependent risk of dislodgment has been examined in studies on several species of macroalgae (Koehl and Wainwright, 1977; Carrington, 1990; Dudgeon and Johnson, 1992; Gaylord et al., 1994; Johnson and Koehl, 1994; Blanchette, 1997; Gaylord and Denny, 1997; Bell, 1999; Gaylord, 2000; Shaughnessy and DeWreede, 2001). The effects of size on dislodgment are important because large size can confer a competitive and reproductive advantage (Denny et al., 1985; Gaylord et al., 1994; Dudgeon et al., 1999).

Size limits on macroalgae may be enforced either by breakage at the stipe, thus removing the entire thallus but leaving a holdfast (Carrington, 1990; Gaylord et al., 1994; Bell, 1999; Denny, 1999; Gaylord, 2000), or by tattering of the fronds (Armstrong, 1987, 1989; Blanchette, 1997; Dudgeon et al., 1999; Milligan and DeWreede, 2000; Shaughnessy and DeWreede, 2001). For thalli that break at the stipe, size may be limited by the ratio of the force at which a stipe breaks (F_{break}) to the force experienced by the stipe due to the maximum drag acting on the thallus ($F_{\text{maximum drag}}$) (Johnson and Koehl, 1994; Denny, 1999; Gaylord, 2000; Koehl, 2000).

This safety factor has been called an Environmental Stress Factor (ESF, sensu Johnson and Koehl, 1994) when calculated over a specific time period (e.g., a season) or a life-history stage rather than over a lifetime. In this paper, we call the drag used in the calculation of ESF the site-relevant drag ($F_{\text{site-relevant drag}}$). High values of ESF imply

relative safety whereas low values of ESF imply higher risk of dislodgment. This relationship is the inverse of the index of risk (R , Denny, 1999). Each of the two forces comprising this safety factor is influenced by differences in algal shape and size.

Breaking force (F_{break}), which is the product of stipe cross-sectional area and stipe material strength, often underscales with the size of intertidal algae (Carrington, 1990; Dudgeon and Johnson, 1992; Gaylord et al., 1994). For stipes that are loaded in tension, underscaling means that when breaking force is plotted as an exponential function of mass, the exponent is less than $2/3$. Such underscaling can occur either because the cross-sectional areas of stipes underscale with increasing size of the thalli (Peterson et al., 1982; Carrington, 1990; Dudgeon and Johnson, 1992; Gaylord et al., 1994; Johnson and Koehl, 1994) or because material strength of the stipe decreases with increasing stipe cross-sectional area (Dudgeon and Johnson, 1992). For algae that experience underscaling, there is typically a maximum size that a thallus can reach for a given flow speed before it becomes dislodged by drag (but for an exception, see Johnson and Koehl, 1994).

Drag at a given flow speed (F_{drag}) is a function of planform area and shape (typically quantified as the coefficient of drag) of the thallus. Some species of macroalgae, such as large kelps, alter their shape in response to changes in flow regime. For example, the subtidal kelp *Nereocystis luetkeana* produces smooth, narrow blades in faster flow habitats and wider, ruffled blades in slower flow habitats (Koehl and Alberte, 1988). Similarly, the kelp *Laminaria saccharina* produced narrower blades when grown with constant longitudinal tension (Gerard, 1987). For *N. luetkeana*, this difference in shape, and hence difference in coefficient of drag, results in maintenance of their risk of dislodgment (i.e., their ESF) between flow habitats, although not between seasons (Johnson and Koehl, 1994; Koehl, 1999). In contrast, the coefficient of drag tended to be very similar for seven species of intertidal macroalgae that compact into streamlined bundles at high flow speeds (Carrington, 1990). Changes in drag as a result of seasonal and site-specific differences in shape and planform area, however, have not been investigated in intertidal red algae.

In this study, we quantify seasonal and site-specific changes in size, morphology, and mechanical behavior that underlie changes in $F_{\text{break}}/F_{\text{drag}}$ for two spatially dominant, competing species of intertidal macroalgae, *Chondrus crispus* and *Mastocarpus stellatus*.

1.2. Biological background

C. crispus and *M. stellatus* are ecologically, morphologically, and physiologically similar species that are thought to compete intensely for space in the rocky intertidal (see, for example, Dudgeon et al., 1999). These species, both of which are in the Order Gigartinales, consist of a bifurcated thallus atop a narrow stipe that is attached to a persistent encrusting holdfast. *Chondrus*, however, gets much larger and bushier than does *Mastocarpus*. Although the green sea urchin *Strongylocentrotus droebachiensis* can graze subtidal *Chondrus* down to its holdfast (personal observation), neither species is readily consumed by herbivores in the intertidal (Lubchenco, 1978; Green, 1983; Dudgeon et al., 1999). Together they dominate the lower intertidal on many wave-swept rocky shores on both sides of the North Atlantic (Mathieson and Burns, 1971; Burns and Mathieson, 1972; Dudgeon et al., 1989, 1995, 1999; Dudgeon and Johnson, 1992). While *Chondrus* occurs

to ~ 15 m depth in the Gulf of Maine (Mathieson and Burns, 1971), the intertidal zone formed by these two species extends from ~ 1–3 m below mean low water (MLW) to ~ 1–2 m above MLW where these two species occupy nearly 70% of available space (Mathieson and Burns, 1971; Mathieson and Prince, 1973; Lubchenco, 1980; Dudgeon et al., 1989). Once established, genets of both species are able to maintain their hold on primary rock substrata, even after periods of seasonal dislodgment, because new thalli regenerate from persistent encrusting holdfasts.

Three distinct sub-zones have been recognized within the *Chondrus/Mastocarpus* zone: *Chondrus* (lowest), mixed *Chondrus* and *Mastocarpus* (mid), and *Mastocarpus* (highest) (Mathieson and Burns, 1971; Dudgeon et al., 1989). *Mastocarpus* coexists with *Chondrus* higher in the intertidal, in part, because of *Chondrus*' lower physiological tolerance to exposure to air and freezing (Mathieson and Burns, 1971; Davison et al., 1989; Dudgeon et al., 1989, 1990, 1999). *Chondrus*, which is the dominant competitor on low intertidal rock substrata in New England (Lubchenco, 1980), slows the growth and reproductive output of upright thalli of *Mastocarpus* in the lower intertidal and shallow subtidal (Dudgeon et al., 1999). It is able to outcompete *Mastocarpus*, partly because it grows faster and larger (Burns and Mathieson, 1972; Dudgeon and Johnson, 1992; Dudgeon et al., 1999). Despite its greater competitive ability, *Chondrus* experiences more winter dislodgment than does *Mastocarpus*. The reduction in canopy cover quantified for *Chondrus* is up to ~ 30% and for *Mastocarpus* is up to ~ 10% (Dudgeon and Johnson, 1992); the reduction in total mass quantified for *Chondrus* is up to ~ 50% and for *Mastocarpus* is up to ~ 40% (Dudgeon et al., 1999).

1.3. Goals

If *Chondrus* and *Mastocarpus* have a different size-specific risk of dislodgment then, after seasons of minimum growth and maximum wave exposure, the one with the greater size-specific risk of dislodgment should have a smaller maximum thallus size. In this study, we assess firstly the factors that contribute to F_{break} and F_{drag} (quantified at 0.55 m s^{-1}), and secondly the contributions of these two forces to understanding relative mass of the largest thalli in these two populations, via the force ratio $F_{\text{break}}/F_{\text{drag}@0.55}$ and, for *Chondrus* in the fall, via the *ESF* ($F_{\text{break}}/F_{\text{site-relevant drag}}$). Examination of seasonal and site-specific changes in the size, morphology, and mechanical characteristics of the largest individuals in these populations may help us to understand the extent to which mechanics and morphology determine limits to size.

2. Materials and methods

2.1. Study sites and collection

Two sites of differing wave exposure located at Giant Steps, Bailey Island, Maine (43°43' N 69°59' W) were used for this study. The exposed site is a massive rock outcropping protruding toward the open ocean; the protected site is in a nearby cobbled area, about 200-m distance, in the lee of the outcropping. Three spring-scale maximum

flow meters (modified from Bell and Denny, 1994) were set out in the mixed *C. crispus*/*M. stellatus* zone in early September at each site to measure maximum flow speed. Meters were checked on October 25, at which time two of the meters at the exposed site had been dislodged by wave action. All remaining flow meters were subsequently dislodged before the next survey done on February 11.

At each site, 1-gal-buckets of thalli of *Chondrus* and *Mastocarpus* were collected haphazardly near the end of each season (spring: May 19; summer: August 3; fall: October 25; winter: February 11) during tides that were -0.03 m or lower. Only the upright thalli (with the complete stipe) were collected; the encrusting holdfast of both species remained attached to the substratum (and will regenerate new thalli). From the buckets, we subsampled thalli by selecting the largest thalli of each species that showed no evidence of grazing or epiphytes. Specimens were stored in a seawater tank at 10°C and, within 3–4 days of collection, either the 15 (spring) or the 20 (all other seasons) largest thalli of each species from each site were measured and tested as described below.

2.2. Drag

Drag on thalli ($F_{\text{drag}@0.55}$) was measured in a recirculating flow tank (0.2-m wide, 0.3-m deep, 2-m long, modified from Vogel and LaBarbera, 1978), at $0.55 \pm 0.02 \text{ m s}^{-1}$, by attaching each thallus to a sting mounted to a strain gauge beam. The sting projected 4 cm into the water in the working section of the tank; drag on the sting alone ($0.083 \text{ N} \pm 0.0013 \text{ S.E.}$) was subtracted from all subsequent drag measurements on each thallus. Although force was measured with a bias $< \pm 0.0001 \text{ N}$, imprecision of the drag measurement on the sting caused an inaccuracy (bias plus imprecision) in the drag measurement on the thalli of $\pm 10\%$ for those thalli with the lowest drag and $< \pm 1\%$ for those thalli with the highest drag.

The coefficient of drag (C_D) was calculated from the measured drag ($F_{\text{drag}@0.55}$) using the standard empirical drag equation:

$$C_D = \frac{F_{\text{drag}@0.55}}{0.5\rho U^2 S_p} \quad (1)$$

where ρ = fluid density, U = flow speed (0.55 m s^{-1}), and S_p = maximum planform area of the thallus. The convention for S_p for macroalgae has been the maximum planform area of the thallus (Koehl, 1986; Vogel, 1989; Carrington, 1990; Dudgeon and Johnson, 1992; Gaylord et al., 1994; Gaylord and Denny, 1997; Gaylord, 2000). Our measurements of planform area (described below) are equivalent to the “actual planform area” or “real area” quantified by Johnson and Koehl (1994) and Koehl (2000), respectively.

2.3. Morphology

We measured maximum planform area (S_p), mass (M), and stipe base cross-sectional area (S_{cs}) of each thallus. To measure the planform area, each thallus was dissected (so that it would lie flat), pressed between two plates of glass, and photographed. The negatives of the photographs were scanned into a computer, and the areas were digitized. The mass of

each thallus was determined by weighing (± 0.01 g). Cross-sectional areas of the circular to elliptical stipe bases were calculated (using the equation for the area of an ellipse) from measurements (± 0.01 mm; measured with calipers while viewed under a dissecting microscope) of their major and minor axes.

2.4. Mechanical characteristics

The force to break each stipe (± 0.001 N) was measured by loading each stipe into the two grips of an InstronTM materials testing machine, and pulling at a constant rate (2.1×10^{-4} m s⁻¹) until they broke. The cross-sectional area of the stipe at the place where it broke (which was always just proximal to the base of the stipe because the stipe base was itself clamped in the grips) was measured in the same manner as the stipe base cross-sectional area. Stipe material strength (σ_{break}) was quantified by dividing the stipe breaking force by the stipe cross-sectional area at the breaking point. Stipe breaking force was normalized to the cross-sectional area of the base of the stipe (S_{cs}), where stipes usually break in the field (98% of the time in field breaking tests, personal observation), by multiplying S_{cs} by σ_{break} . We call this force the inferred field breaking force (F_{break}).

To test whether material strength measured in this way differed from strength measured in field breaking tests, we determined stipe material strength for 21 thalli of each species first by using field breaking tests (described in Dudgeon and Johnson, 1992; similar to those used by Carrington et al., 2001) and then by using the laboratory breaking tests described above. There were no significant differences in the mean strength obtained by these two methods for either *Chondrus* (*t*-test, $p=0.10$) or *Mastocarpus* (*t*-test, $p=0.76$).

2.5. Scaling of thalli

Shape and material properties can be related to size to determine whether an organism scales isometrically. In general,

$$A = kM^b, \quad (2)$$

where A is the dependent variable (e.g., stipe base cross-sectional area), M is the independent variable (e.g., thallus mass), and k and b (coefficient and exponent, respectively) are calculated from the intercept and slope of standard least squares linear regressions of log–log plots of these two variables. For the example of the stipe cross-sectional area, at constant density, if $b=2/3$, isometric scaling is inferred, since area is proportional to length squared and mass is proportional to length cubed (for a review of scaling, see Brown et al., 2000). If $b < 2/3$, then the stipe base cross-sectional area does not increase isometrically with mass but instead underscales allometrically (e.g., becomes relatively, not absolutely, skinnier as the algae increase in size).

2.6. Risk of dislodgment

A ratio of the force that a stipe can resist (F_{break}) to the maximum force that a stipe experienced ($F_{\text{site-relevant drag}}$) was used to assess the possibility that a *Chondrus* thallus

in the fall population would dislodge. We calculated this ratio only for the fall season, for which we have measurements of maximum flow speed (one measurement at the exposed site and three measurements at the protected site), and only for *Chondrus*, for which we have estimates of Vogel's (1984) E -value (Johnson, 2001; described below). This ratio is the Environmental Stress Factor (ESF, sensu Johnson and Koehl, 1994), where

$$\text{ESF} = \frac{F_{\text{break}}}{F_{\text{site-relevant drag}}}. \quad (3)$$

To calculate ESF, the site- and season-relevant maximum drag on thalli in the field ($F_{\text{site-relevant drag}}$) was estimated for the fall populations of *Chondrus* as follows. For this estimate, we took into account the decrease in C_D with increase in velocity by use of E ,

$$\frac{F_{\text{drag}}}{U^2} = k_E U^E, \quad (4)$$

where F_{drag} is drag at a particular flow speed, U .

A value for E and k_E are determined using a linear regression of $\log(F_{\text{drag}}/U^2)$ vs. $\log U$ for regions of this graph without inflection points; E is the slope and k_E is the antilog of the intercept of this line. For bluff bodies of the approximate size of the experimental thalli, at the flow speeds considered by this study, the magnitude of E is zero. In contrast, a streamlined object may show a negative E of as much as -0.5 (Hoerner, 1965). For algae that can reconfigure in flow, a steeper negative slope (i.e., more negative E), indicates greater relative drag reduction experienced with an increase in velocity. This relative drag reduction is likely partially or mostly a consequence of reconfiguration. It can be seen by comparison of Eq. (1) to Eq. (4) that E can be interpreted as a change in C_D with increasing velocity (Vogel, 1984).

Eq. (4) can be rearranged as follows:

$$F_{\text{drag}} = k_E U^\beta, \quad (5)$$

where $\beta = 2 + E$. Vogel's E , as determined for *Chondrus* from a previous study (mean $E = -0.64 \pm 0.06$ S.E., measured at flow speeds up to 0.21 m s^{-1} ; Johnson, 2001) was independent of mass (linear regression analysis on log-transformed data: $p_{1,7} = 0.35$), but k_E was dependent on mass (linear regression analysis on log-transformed data, $p_{1,7} = 0.04$, $r^2 = 0.53$, for Eq. (8), below). The dependence of k_E on mass is expected, as can be seen from the following equation (modified from Denny, 1999):

$$F_{\text{drag}} = k_1 M^\alpha U^\beta \quad (6)$$

where M is thallus mass, and k_1 is a constant that depends on fluid density and algal shape.

Comparison of Eq. (5) to Eq. (6) reveals that:

$$k_E = k_1 M^\alpha. \quad (7)$$

The relationship between k_E and M was determined from a linear regression analysis of the log–log plot of k_E vs. M from the same data used to determine E , which gave:

$$k_E = 0.132M^{1.04}, \quad (8)$$

where the units for k_1 are $\text{kg}^{-0.04} \text{m}^{-0.36} \text{s}^{-0.64}$, the units for k_E are $\text{kg m}^{-0.36} \text{s}^{-0.64}$, and the standard error for the exponent α was 0.4.

From this relationship, we estimated the drag on the thalli of *Chondrus* during the fall using site-relevant flow speeds by using the following equation:

$$F_{\text{drag}} = 0.132M^{1.04}U^{1.36}. \quad (9)$$

Errors associated with the extrapolation of drag from laboratory flow tank measurements at relatively low flow speeds to maximum flow speeds in the field have been assessed for intertidal algae in the Family Gigartinaceae by Bell (1999). Our approach corresponds most closely to her model A, which predicts that the coefficient of drag continues to decrease with increasing flow speed. Most relevant to this paper is that this calculation is expected to represent an underestimate of the real $F_{\text{site-relevant drag}}$ since E generally becomes less negative with increasing flow speed (Carrington, 1990; Gaylord et al., 1994; Vogel, 1994; Bell, 1999).

2.7. Statistical analysis

Factorial analyses of variance (ANOVA) (StatView 4.0) were used to test for differences between species, between seasons, and between sites of different exposure. Factorial ANOVAs were also used on each species separately to test for species-specific differences between seasons. For variables for which there were no significant interactions, pairwise, a posteriori comparisons of means between seasons were conducted using Fisher's PLSD. For variables for which there were significant interactions between factors, multiple comparisons were conducted (Zar, 1996, p. 248) using Fisher's PLSD. Multiple comparisons were performed separately for each species to compare differences between exposures, separately for each exposure to compare differences between species, and, where there were significant differences between exposures, separately for each species at a given exposure to compare differences between seasons.

Analyses of covariance (ANCOVA) (performed using a Mathematica™ program written by Ellers, using formulas from Zar, 1996, pp. 363–368) were used to test whether standard least squares linear regression lines for the classified variables were parallel (i.e. do the variables covary at the same rate); if significant differences among slopes were not found then lines were tested to seek differences in elevations. Where there were significant differences (significance level $p \leq 0.05$), a posteriori pairwise comparisons of slopes and intercepts were assessed using Tukey's q -test (significance level $p \leq 0.05$; see Zar, 1996, pp. 367–368). When slopes were parallel, the common slope was used to plot the least squares regression lines shown in figures. When there were no differences in either slopes or intercepts, the common slope and common intercept were used to plot the least squares regression lines shown in figures.

To test whether the slope of a regression line was significantly different from an expected slope, the following t -test was performed:

$$t = \frac{b - \beta_0}{S_b} \quad (10)$$

where b is the slope of the calculated regression line, β_0 is the expected slope, and S_b is the standard error of the slope of the regression line (Zar, 1996, pp. 329–330).

3. Results

3.1. Flow speed

During the fall, the exposed site experienced a higher maximum flow speed (9.2 m s^{-1} , $n = 1$) than did the protected site ($5.8 \text{ m s}^{-1} \pm 0.3 \text{ S.E.}$, $n = 3$). These flow speeds are similar to the ‘exposed’ ($10\text{--}20 \text{ m s}^{-1}$) and ‘moderately protected’ (5 m s^{-1}) flow categories used

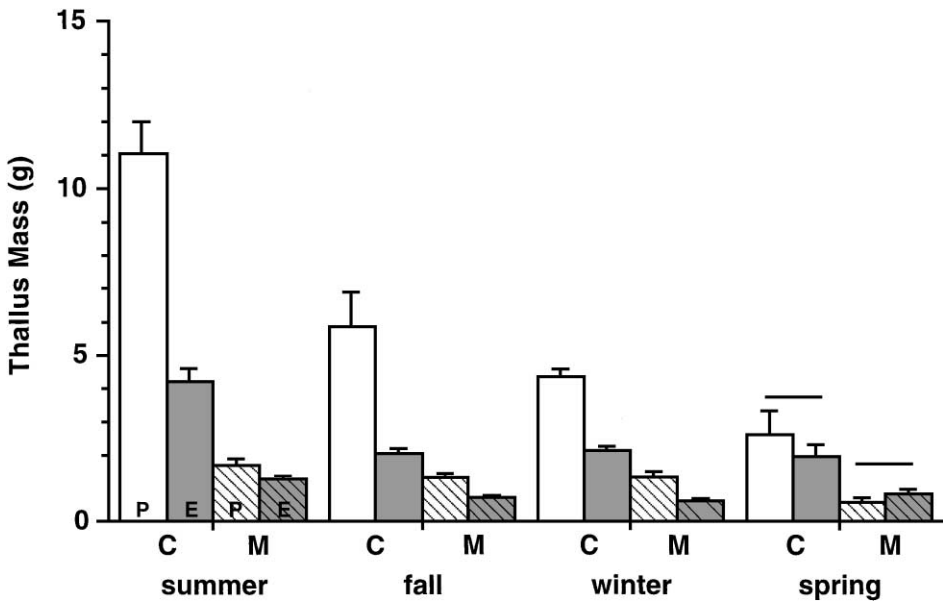


Fig. 1. Thallus mass (M) as a function of season for *C. crispus* (solid bars, C), and *M. stellatus* (hatched bars, M) at a protected site (white bars, P) and an exposed site (gray bars, E). Error bars indicate one standard error; $n = 14$ for *Mastocarpus* at the protected site in the spring, $n = 15$ for all other means from the spring, and $n = 20$ for all other means. A horizontal line over bars in a given season indicates no significant difference between exposures (each a posteriori $p \geq 0.2$). All other comparisons between exposures are significantly different (each a posteriori $p < 0.02$). See Section 3.2 and Tables 1 and 2 for other comparisons of means between seasons and between species.

by Bell (1999). Casual observations also indicate that the exposed site typically experiences higher flow speeds. At times in the fall and winter waves were so high that the exposed site could not be visited safely, but the protected site could always be visited.

3.2. Seasonal changes in mass

Comparisons between species revealed that the mean mass of the 15–20 largest thalli of *Chondrus* was significantly greater than that of the 15–20 largest thalli of *Mastocarpus* in all seasons at both sites (Fig. 1, Table 1; each a posteriori $p \leq 0.0003$ that both species at a given site in a given season have the same mean mass, except at the protected site in the spring, where $p = 0.03$). Comparisons between exposures revealed that the mean mass of the 15–20 largest thalli was significantly greater at the protected site relative to the exposed site (Table 1) for both species in all seasons except for both species in the spring (Fig. 1; a posteriori statistics given in the figure legend). The most noticeable seasonal effect was that for both species, the mean mass of the 15–20 largest thalli was significantly greater during the most benign season (summer) relative to all other seasons, especially at the more protected site for *Chondrus* (Fig. 1; Tables 1 and 2). There were no other significant differences between seasons at the exposed site. At the protected site, mean mass of the 15–20 largest thalli was also significantly greater in fall than in spring for both species and, for *Mastocarpus*, also greater in winter than in spring (Table 2).

The seasonal decline in mass from summer through spring differed between sites. For both species, the percentage decrease in mass in the spring relative to the summer was greater at the more protected site (76% and 65% for *Chondrus* and *Mastocarpus*, respectively) than at the more exposed site (54% and 35%, for *Chondrus* and *Mastocarpus*, respectively). As there was no significant difference in mass in the spring between

Table 1
Summary of significant probabilities from factorial ANOVA analyses

Source (<i>df</i>)	Variable symbol (residual <i>df</i>)					
	Mass, M_4 (283)	Breaking force, F_{break} (282)	Cross-sectional area, S_{cs} (283)	Strength, σ_{break} (282)	Planform area, S_p (277)	Coefficient of drag, C_D (277)
Species (1)	**** (C>M)	–	**** (C>M)	**** (M>C)	**** (C>M)	**** (M>C)
Exposure (1)	**** (P>E)	–	–	–	**** (P>E)	** (P>E)
Season (3)	****	**	****	***	****	****
Species × exposure (1)	****	–	**	–	****	****
Species × season (3)	****	–	–	–	****	***
Exposure × season (3)	****	–	**	–	**	****
Species × exposure × season (3)	****	–	–	–	*	–

Numbers in parentheses are the degrees of freedom. 'C' = *Chondrus*; 'M' = *Mastocarpus*; 'P' = protected; 'E' = exposed; '–' = not significant, i.e., $p > 0.05$. Asterisks indicate significant differences, where * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; **** $p < 0.0001$. See Table 2 for statistical comparisons between seasons.

Table 2

Pairwise a posteriori probabilities for seasonal differences for the factorial ANOVA analyses summarized in Table 1

Season	Variable symbol	Mass, M	Breaking force, F_{break}	Cross-section area, S_{cs}	Strength, σ_{break}	Planform area, S_{p}	Coefficient of drag, C_{D}
Sp, Su	Su**** (C, M)	–	–	Su*** (CP, M)	Sp** (C, M)	Su** (all)	–
Sp, Fa	Fa** (CP; MP)	–	–	Fa** (C, M)	Sp*** (C)	Fa*** (C; MP)	Sp*** (C)
Sp, Wi	Wi** (MP)	–	–	Wi*** (C, M)	–	Wi* (C; MP)	Sp*** (CE)
Su, Fa	Su**** (C; ME)	–	–	–	–	Su** (C; ME)	Su*** (C, M)
Su, Wi	Su**** (C; ME)	–	–	–	Wi* (C, M)	Su** (C; ME)	Su* (C, M)
Fa, Wi	–	–	–	–	Wi* (C, M)	–	Wi* (CP)

‘Sp’=spring; ‘Su’=summer; ‘Fa’=fall; ‘Wi’=winter; ‘C’=*Chondrus*; ‘M’=*Mastocarpus*; ‘P’=protected; ‘E’=exposed; ‘–’=not significant, i.e., $p > 0.05$. For significant differences, the season with the larger value is indicated (e.g., mass was greater in the summer than in the spring for both species at both exposures). Asterisks indicate probabilities, where * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; **** $p < 0.0001$. These probabilities are from a posteriori comparisons from the overall ANOVA in Table 1 when there were no significant interactions between factors in that table. When there were significant interactions indicated in Table 1, asterisks represent the largest probability from multiple comparison tests.

exposures, the greater decrease in mass at the more protected site was due to the greater mass in the summer at this site. At both exposures, seasonal loss of mass was greater for *Chondrus* than it was for *Mastocarpus*.

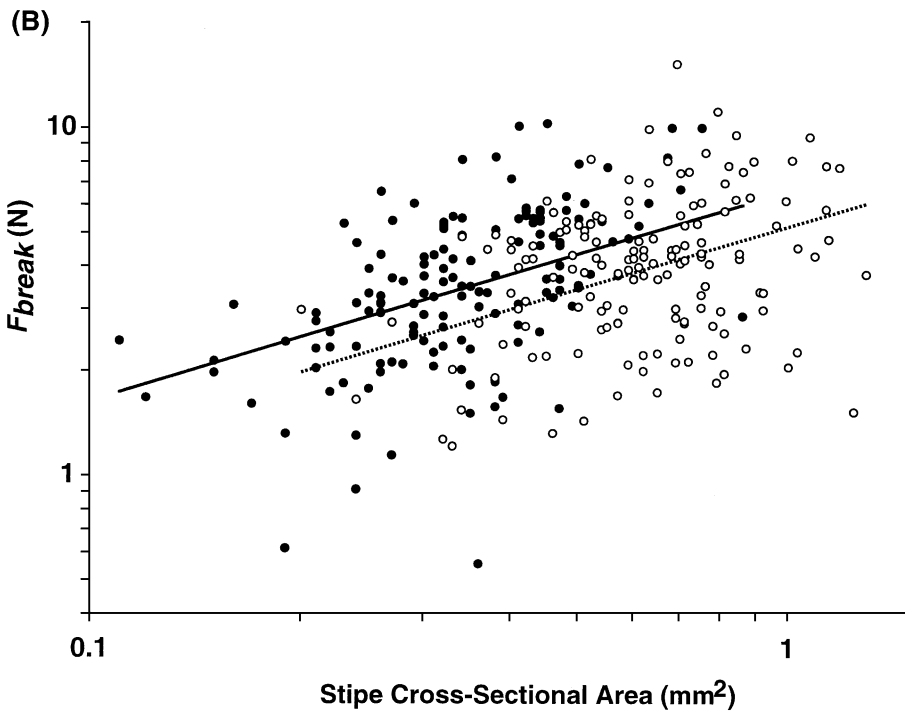
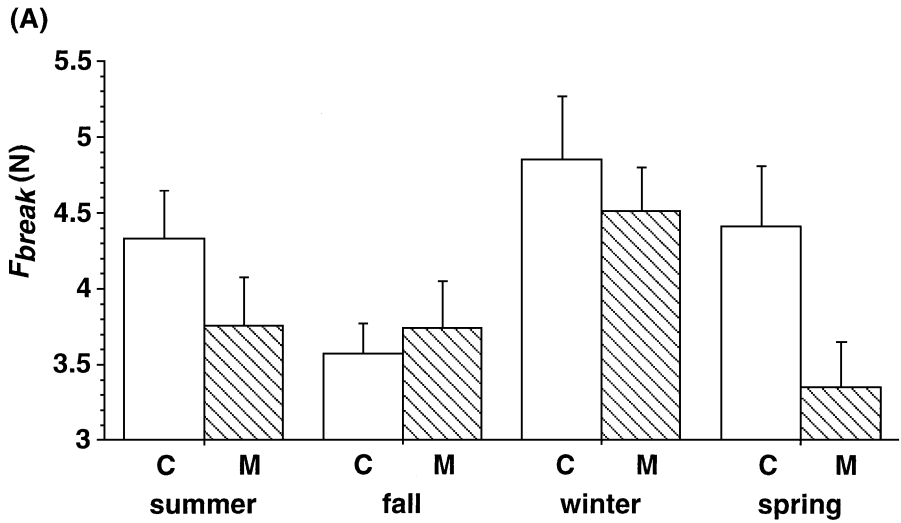
Thus, for both species there was a seasonal decline in mass from summer through spring that was more pronounced at the protected site than at the exposed site. Neither of these species is readily consumed by herbivores (Lubchenco, 1978; Green, 1983; Dudgeon et al., 1999), and forces due to acceleration should be negligible on algae of this size (Gaylord, 2000). Thus, decreases in mass reflect removal of thalli via drag or senescence.

3.3. Resistance of drag by the stipe: size vs. strength

Ultimately, drag is transmitted to the stipe and it is the force required to break the stipe at its narrowest point (where it attaches to the holdfast) that determines whether the thalli of *Chondrus* or *Mastocarpus* will dislodge. Overall, the inferred field breaking force (F_{break}) did not differ significantly between either species or exposures (Fig. 2A, Table 1; mean $F_{\text{break}} = 4.1 \text{ N} \pm 0.1 \text{ S.E.}$). Although there was an overall effect of season (Table 1), the only significant seasonal effect was that the F_{break} tended to be greater in the winter (Table 2).

F_{break} increased with increasing stipe cross-sectional area and, for a given cross-sectional area, was greater for *Mastocarpus* than for *Chondrus* (Fig. 2B; regression statistics are in the figure legend). Linear regression analyses of the log-transformed data showed that F_{break} was, however, independent of mass for both species with neither slopes ($p_{2,294} = 0.63$) nor intercepts ($p_{2,294} = 0.31$) being significantly different between species (common equation: $F_{\text{break}} = 3.4 \text{ mass}^{0.04}$, $r^2 = 0.02$, $p_{2,295} = 0.75$ that the common slope is zero).

Stipe cross-sectional area (S_{cs}) was significantly greater for *Chondrus* in all seasons at both sites (Fig. 3A, Table 1; each a posteriori $p \leq 0.0003$ that both species at a given site in a given season have the same mean stipe cross-sectional area) both because *Chondrus*



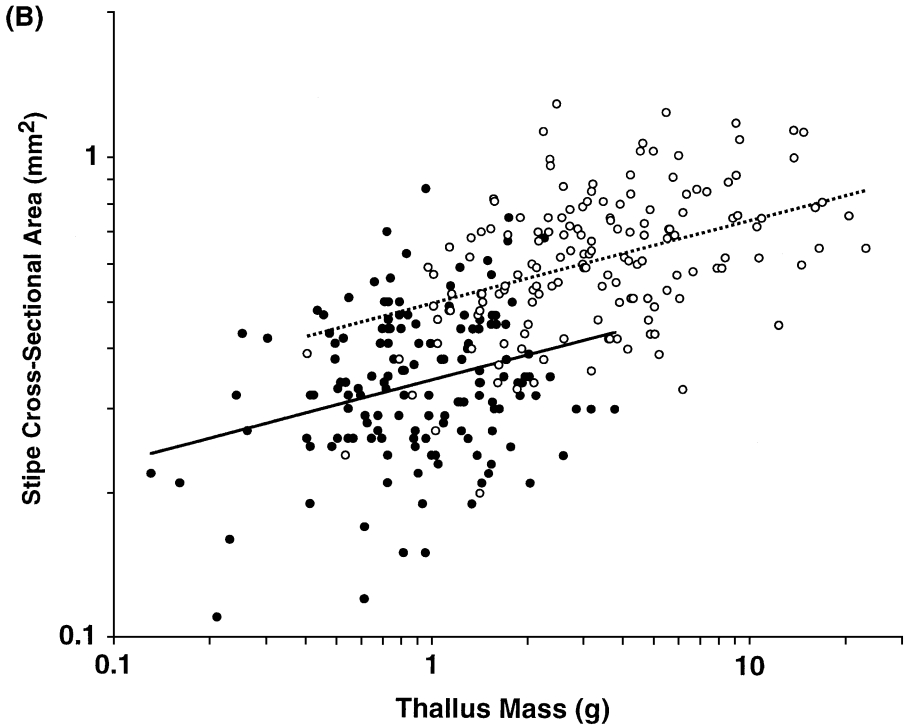
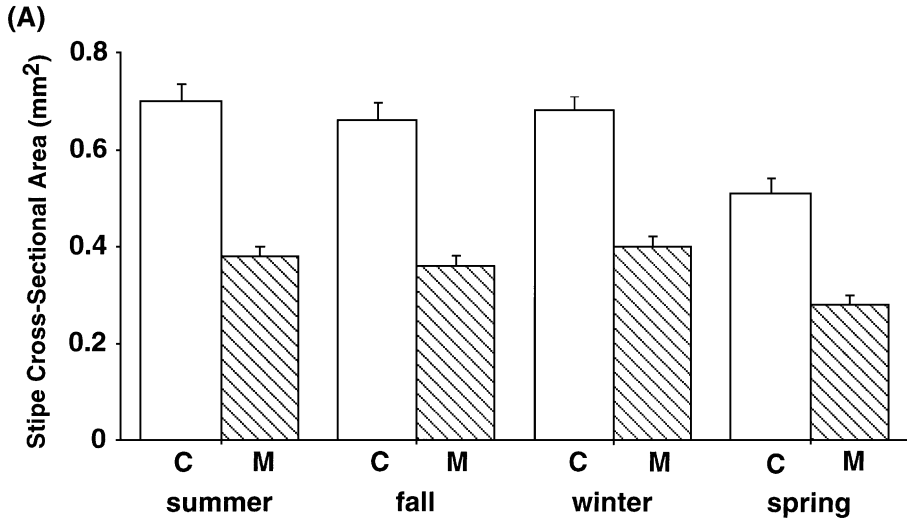
were larger and because *Chondrus* stipes had a greater cross-sectional area at a given mass than did *Mastocarpus* (Fig. 3B; regression statistics in the figure legend). As with F_{break} , overall stipe cross-sectional area did not differ significantly between exposures, although there was a significant interaction between exposure and both species and season (Table 1). These interactions resulted from a relatively greater stipe cross-sectional area for thalli of *Chondrus* in the summer at the protected site relative to the exposed site; that is, multiple comparisons tests revealed that there were no significant differences between exposures for a given species in a given season (each a posteriori $p > 0.1$) except for *Chondrus* in the summer (a posteriori $p < 0.001$). There was a seasonal effect on stipe cross-sectional area (Tables 1 and 2); for both species, stipe cross-sectional area tended to be least in the spring.

Given the greater cross-sectional area of *Chondrus*, the absence of differences in F_{break} between *Mastocarpus* and *Chondrus* is surprising, but less so when considered in the context of the scaling of the stipe cross-sectional area that resists the breaking load. For example, the scaling of stipe cross-sectional area with mass (exponent = 0.17) was much less than isometric (Fig. 3B; predicted exponent = 0.67, statistics are in the figure legend; see Eq. (2)), indicating that the greater size of *Chondrus* did not correspond to an isometrically larger stipe cross-sectional area relative to *Mastocarpus*. Furthermore, F_{break} for a given cross-sectional area (i.e., material strength) was greater for *Mastocarpus* (Figs. 2B and 4B; regression statistics are in the figure legends).

Thus, the effect of cross-sectional area on F_{break} was counterbalanced by the differences in the material strength (σ_{break}) of the stipes of these two species (Fig. 4). The stipes of *Mastocarpus* were significantly stronger (mean $\sigma_{\text{break}} = 11.1 \text{ MN m}^{-2} \pm 0.4 \text{ S.E.}$) than those of *Chondrus* (mean $\sigma_{\text{break}} = 7.0 \text{ MN m}^{-2} \pm 0.3 \text{ S.E.}$; Fig. 4, Table 1). As with F_{break} , stipe strength was independent of exposure (Fig. 4A, Table 1). There was a seasonal effect on strength (Table 1); for both species strength tended to be greater in the spring and winter than in the summer and fall (Table 2).

Increasing size further diminished the effect of a larger stipe cross-sectional area on larger thalli of *Chondrus* because for both species strength significantly decreased with increasing mass (exponent = -0.14; Fig. 4B; linear regressions statistics for the log-transformed data are in the figure legend).

Fig. 2. (A) Inferred field breaking force of the stipe (F_{break}) as a function of season for *C. crispus* (solid bars, C), and *M. stellatus* (hatched bars, M). Error bars indicate one standard error; $n = 29$ for *Mastocarpus* in the spring, $n = 30$ for *Chondrus* in the spring, $n = 39$ for *Mastocarpus* in the summer, $n = 40$ for all other means. Data were pooled between exposed and protected sites because F_{break} was independent of exposure (Table 1; ANOVA factorial, $p_{1,282} = 0.10$). See Section 3.3 and Table 2 for other statistical comparisons. (B) Log-log plot of inferred field breaking force of the stipe (F_{break}) as a function of stipe cross-sectional area (S_{cs}) for *C. crispus* (open circles, dashed line) and *M. stellatus* (closed circles, solid line). Slopes were not significantly different between species (ANCOVA, $p_{2,294} = 0.06$; common equation: $F_{\text{break}} = k_{F_{\text{break}}} S_{\text{cs}}^{0.60}$, $r^2 = 0.18$, $p_{2,295} \ll 0.001$ that the common slope is zero). There were significant differences in intercepts (ANCOVA, $p_{2,294} < 0.001$; *Chondrus*: $k_{F_{\text{break}}} = 5.2$, *Mastocarpus*: $k_{F_{\text{break}}} = 6.5$), such that *Mastocarpus* required a greater breaking force for a given stipe cross-sectional area than did *Chondrus* (i.e., *Mastocarpus* had greater material strength, see Fig. 4).



3.4. Drag

Drag is a function not only of size, typically quantified as planform area, but also of the coefficient of drag (C_D , Eq. (1)). The relative contribution of these two factors varied with exposure and season (Fig. 5, Table 1). Seasonal and site-specific trends in planform area were similar to those described above for mass, although with more pronounced differences in fall and winter relative to spring for *Chondrus* (Figs. 1 and 5; Tables 1 and 2).

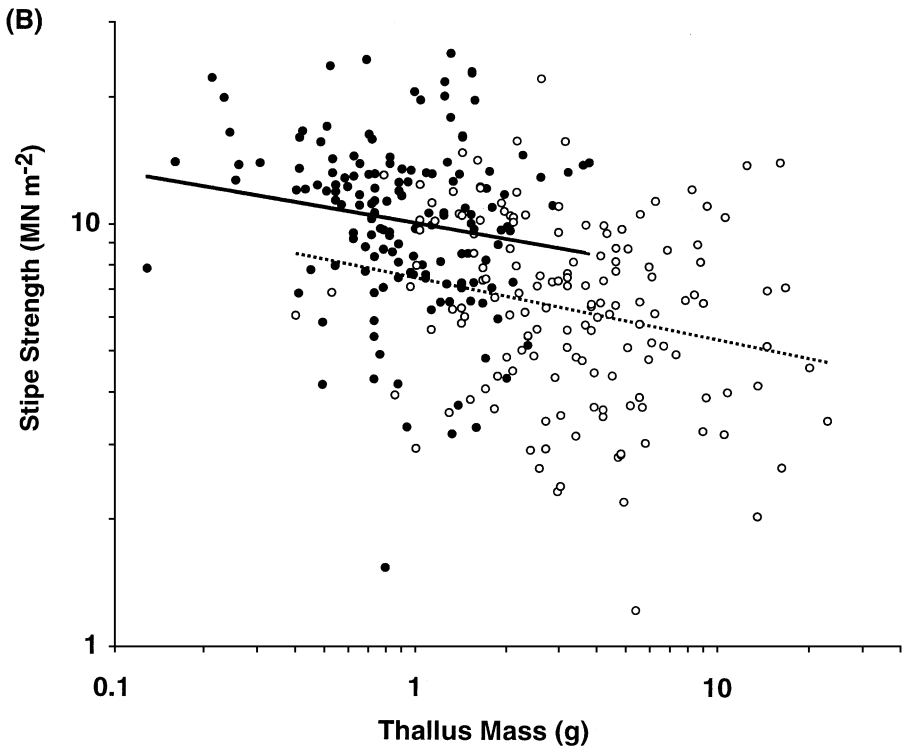
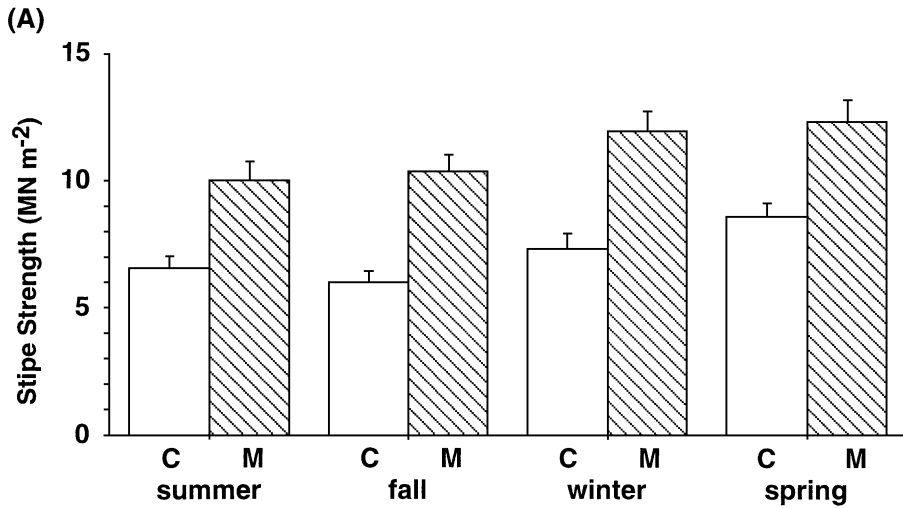
There were, however, differences in the magnitude of trends for drag and planform area that reflect the additional contribution of the C_D . For example, while there was an 83% difference in planform area between *Mastocarpus* and *Chondrus* at the exposed site in winter, there was only a 67% difference in drag, because the lower C_D for *Chondrus* relative to *Mastocarpus* partially compensated for its greater planform area (Fig. 5).

Overall, the C_D was greater for *Mastocarpus* than for *Chondrus* (Fig. 5, Table 1; each a posteriori $p < 0.05$), except at the protected site in summer and spring (Table 2; both a posteriori $p > 0.1$). For *Chondrus*, the C_D was greater at the protected site than at the exposed site in the summer and winter (each a posteriori $p < 0.0001$), but not in the spring and fall (each a posteriori $p > 0.1$), and was higher in the summer and spring and lower in the fall and winter (Table 2). For *Mastocarpus*, the coefficient of drag was higher in the summer than in the fall and winter (Table 2) but did not differ significantly between exposures (a posteriori $p > 0.05$).

Although the coefficient of drag tended to be greater for *Mastocarpus* (*Mastocarpus*: mean $C_D = 0.50 \pm 0.010$ S.E.; *Chondrus*: mean C_D protected = 0.46 ± 0.017 S.E., mean C_D exposed = 0.34 ± 0.017 S.E.), this does not necessarily mean that at a given mass *Mastocarpus* will experience a greater drag than *Chondrus*. When $F_{\text{drag}@0.55}$ was examined as a function of mass there were no significant differences in slope or intercept of this relationship between species and exposures (Fig. 6A; linear regression statistics for the log-transformed data are in the figure legend). This is because the lower C_D for *Chondrus* is coupled with a higher planform area per mass, especially at the more exposed site (Fig. 6B; linear regression statistics for the log-transformed data are in the figure legend). In fact, C_D increased with increasing mass at an indistinguishable rate between species ($p_{4,285} = 0.32$; common equation: $C_D = k_{C_D} M^{0.14}$, $r^2 = 0.27$, $p_{4,288} \ll 0.001$ that the common slope is zero). There were significant differences in intercepts ($p_{4,286} \ll 0.001$). A posteriori q -tests indicate that k_{C_D} for each species at each site (exposed *Chondrus*: $k_{C_D} = 0.28$, protected *Chondrus*: $k_{C_D} = 0.34$, exposed *Mastocarpus*: $k_{C_D} = 0.51$, and pro-

Fig. 3. (A) Stipe cross-sectional area (S_{cs}) as a function of season for *C. crispus* (solid bars, C), and *M. stellatus* (hatched bars, M). Error bars indicate one standard error; $n = 29$ for *Mastocarpus* in the spring, $n = 30$ for *Chondrus* in the spring, $n = 40$ for all other means. For simplicity of presentation, data were pooled between exposed and protected sites as there were only two significant differences between exposures. See Section 3.3 and Table 2 for statistical comparisons. (B) Log–log plot of stipe cross-sectional area (S_{cs}) as a function of thallus mass (M) for *C. crispus* (open circles, dashed line) and *M. stellatus* (closed circles, solid lines). Slopes were not significantly different between species (ANCOVA, $p_{2,295} = 0.22$; common equation: $S_{cs} = k_{S_{cs}} M^{0.17}$, $r^2 = 0.49$, $p_{2,296} \ll 0.0001$ that the common slope is zero; t -test: $p_{1,296} < 0.001$ that the common slope is isometric [$b = 0.67$]). Intercepts were significantly different (ANCOVA, $p_{2,295} \ll 0.0001$; *Chondrus*: $k_{S_{cs}} = 0.50$, *Mastocarpus*: $k_{S_{cs}} = 0.35$), such that *Mastocarpus* had a smaller stipe cross-sectional area for a given mass than did *Chondrus*.

tected *Mastocarpus*: $k_{C_D} = 0.46$) were all significantly different from one another (all $p_{4,286} < 0.025$), except for *Mastocarpus* between exposures ($p_{4,286} > 0.2$ that the mean C_D for *Mastocarpus* did not differ between exposures).



Thus, within the intertidal populations of *Chondrus* and *Mastocarpus* examined by this study, *Chondrus* experienced greater drag because their thalli had a greater mass. When drag is normalized by size, we found that thalli of a similar mass experienced a similar drag because the greater planform area per mass of *Chondrus* was balanced by a lower coefficient of drag.

3.5. Risk of breakage

Drag measured at 0.55 m s^{-1} ($F_{\text{drag}@0.55}$) suggests that the stipes of *Chondrus* are more likely to break in the field because their thalli had a greater mass and, for both species, thalli with a greater mass had a smaller force ratio (i.e., have a lower $F_{\text{break}}/F_{\text{drag}@0.55}$; Fig. 7A; *Chondrus*: mean $F_{\text{break}}/F_{\text{drag}@0.55} = 17.1 \pm 3.1$ S.E.; *Mastocarpus*: mean $F_{\text{break}}/F_{\text{drag}@0.55} = 53.2 \pm 3.1$ S.E.; $p_{1,297} < 0.001$ that the means are the same). However, there were no significant differences between species or exposures in slope or intercept of the least squares linear regression of $\log F_{\text{break}}/F_{\text{drag}@0.55}$ as a function of \log mass (Fig. 7A; linear regression statistics are reported in the figure legend). This similarity in force ratio, if it held at higher flow speeds, would suggest that thalli of a given mass of either species are equally likely to break.

When Eq. (9) was used to estimate the drag on *Chondrus* thalli at 0.55 m s^{-1} , then estimated drag scaled with measured drag with an exponent of 1.0 (± 0.03 S.E.):

$$F_{\text{drag estimated}@0.55} = 0.66 (F_{\text{drag measured}@0.55})^{1.0} \quad (11)$$

($p_{1,148} \ll 0.001$ that the exponent is zero, $r^2 = 0.89$), but underestimated the magnitude of the measured drag. When Eq. (9) was used to estimate the site-relevant drag ($F_{\text{site-relevant drag}}$) for *Chondrus* thalli from the fall population, then most of the 20 largest thalli found at these sites in the fall (90% from the more protected habitat, 80% from the more exposed habitat) are predicted to have a drag ($F_{\text{site-relevant drag}}$) greater than the maximum breaking force (F_{break}) for thalli from these habitats (i.e., their $\text{ESF} < 1$, Eq. (9), Fig. 7B; linear regression statistics for the log-transformed data are reported in the figure legend). The ESFs for these thalli were not significantly different between exposures (statistics reported in the figure legend for Fig. 7), indicating that these thalli would experience on average nearly twice the drag that they could withstand, implying that they should have broken. Thus, thalli that were found unbroken in the fall intertidal are predicted to have

Fig. 4. (A) Stipe material strength (σ_{break}) as a function of season for *C. crispus* (solid bars, C), and *M. stellatus* (hatched bars, M). Error bars indicate one standard error; $n=29$ for *Mastocarpus* in the spring, $n=30$ for *Chondrus* in the spring, $n=39$ for *Mastocarpus* in the summer, $n=40$ for all other means. Data were pooled between exposed and protected sites as there were no significant differences between exposures (Table 1; ANOVA factorial, $p_{1,282} = 0.14$). See Section 3.3 and Table 2 for other statistical comparisons. (B) Log–log plot of stipe material strength (σ_{break}) as a function of thallus mass (M) for *C. crispus* (open circles, dashed line) and *M. stellatus* (closed circles, solid line). There were no significant differences between slopes for each species (ANCOVA, $p_{2,295} = 0.80$; common equation: $\sigma_{\text{break}} = k_{\sigma_{\text{break}}} M^{-0.14}$, $r^2 = 0.24$, $p_{2,295} < 0.01$ that the common slope is zero). There were significant differences in intercepts between species (ANCOVA, $p_{2,295} \ll 0.001$; *Chondrus*: $k_{\sigma_{\text{break}}} = 7.4$, *Mastocarpus*: $k_{\sigma_{\text{break}}} = 10.0$), such that *Mastocarpus* stipes were stronger for a given stipe cross-sectional area than were those of *Chondrus*.

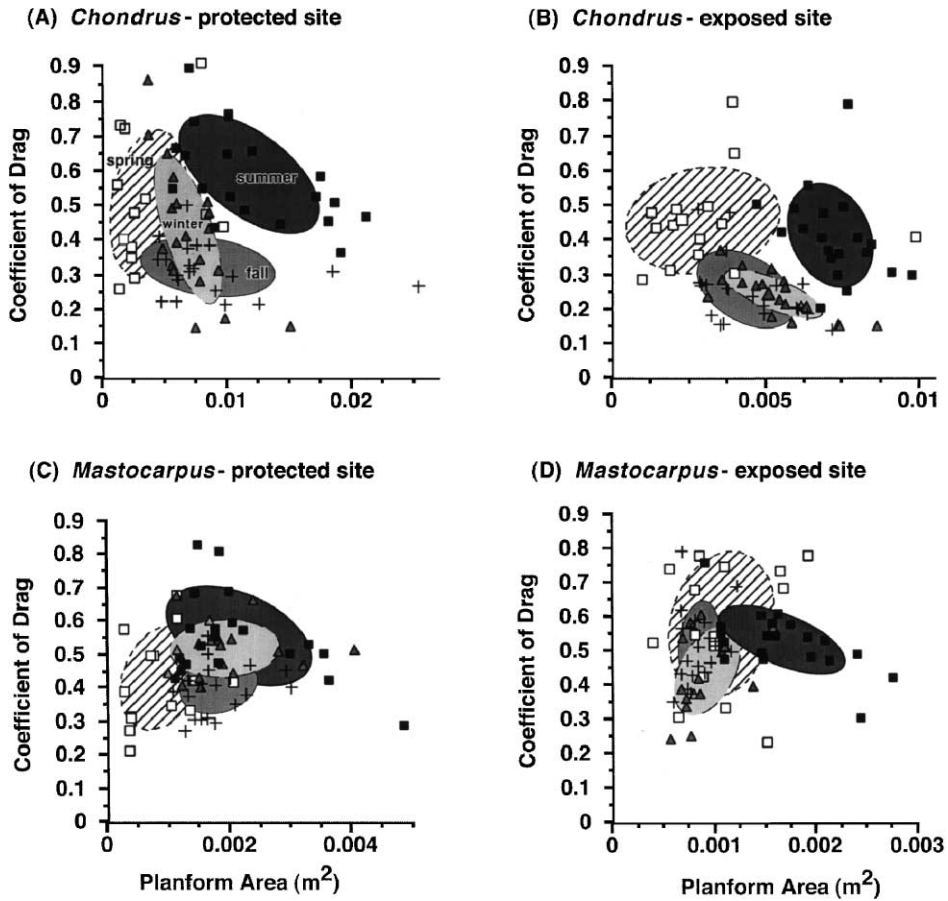


Fig. 5. Coefficient of drag (C_D) as a function of planform area (S_p) for *C. crispus* (A, B) and *M. stellatus* (C, D) from the protected site (A, C) and the exposed site (B, D). Bivariate normal ellipses ($p=0.50$) are used to illustrate seasonal trends in the data for summer (closed squares; thick, solid line, dark grey fill), fall (plus signs; thin, solid line, medium grey fill), winter (grey triangles; thin, dashed line, light grey fill), and spring (open squares; thick, dashed line, hatched fill).

been broken in the flows that were measured there. Thalli from the protected site had the same ESF as those from the exposed site, even though they had a greater mass-specific ESF, because ESF decreased with size and thalli from the protected site were larger.

There are two major types of error associated with the extrapolation of drag from laboratory flow tank measurements at relatively low flow speeds to maximum flow speeds in the field: (1) extrapolation of measured variance among individuals, and (2) the existence of unknown errors that result from mechanistically based changes in the parameters used in the extrapolation. A measure of the contribution of the first type of error to the likelihood that real forces were lower than predicted forces can be obtained by using the lower bounds of the standard errors for the exponents in Eq. (9), which gives $\alpha = 0.64$ and $\beta = 1.30$. Even using these lower bounds of the exponents, the mean ESF was

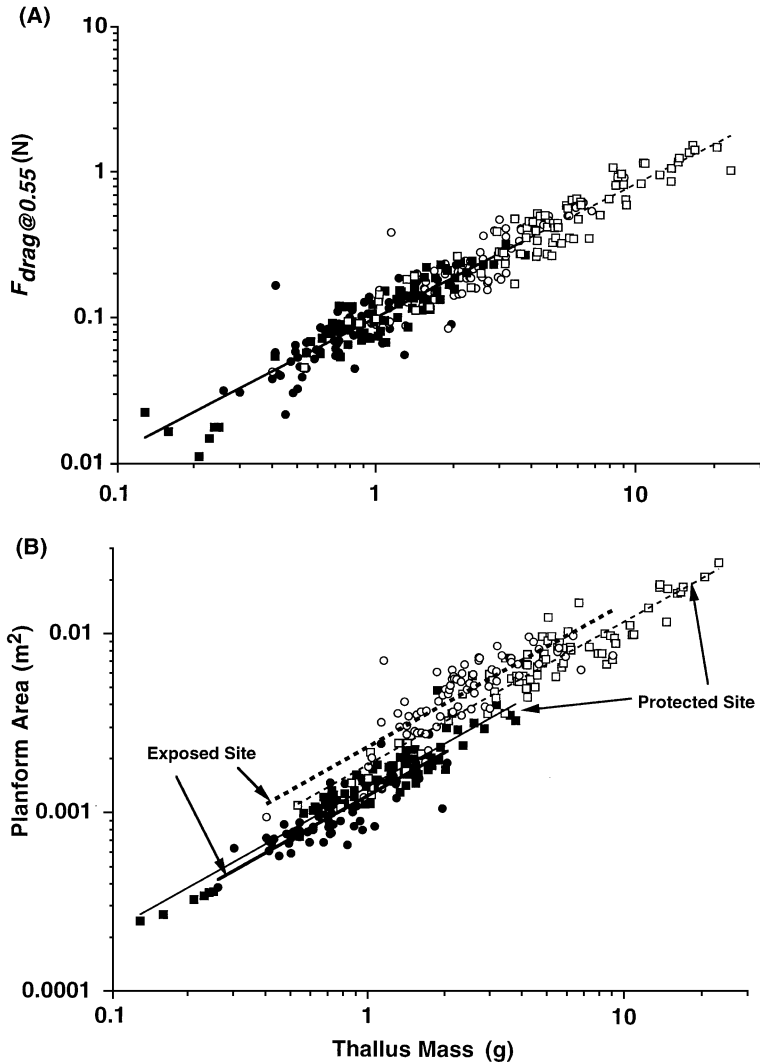


Fig. 6. Log–log plots of (A) drag ($F_{\text{drag}@0.55}$), and (B) planform area (S_p) as a function of thallus mass (M) for *C. crispus* (open points, dashed lines) and *M. stellatus* (closed points, solid lines) at the protected site (squares, thin lines) and exposed site (circles, thick lines). For (A), there were no significant differences in slopes ($p_{4,291}=0.57$) or intercepts ($p_{4,291}=0.98$) for each species at each exposure (common equation: $F_{\text{drag}@0.55}=0.1M^{0.94}$, $r^2=0.91$, $p_{4,294}\ll 0.001$ that the common slope is zero). For (B), there were no significant differences in slopes of least squares regression lines ($p_{4,286}=0.48$; common equation: $S_p=k_{S_p}M^{0.81}$, $r^2=0.94$, $p\ll 0.001$ that the common slope is zero), but there were significant differences in intercepts ($p_{4,286}\ll 0.001$). A posteriori q -tests indicate that k_{S_p} (from top to bottom: 0.0024, 0.0019, 0.0014, and 0.0013) were all significantly different from one another (all $p_{4,286}<0.025$).

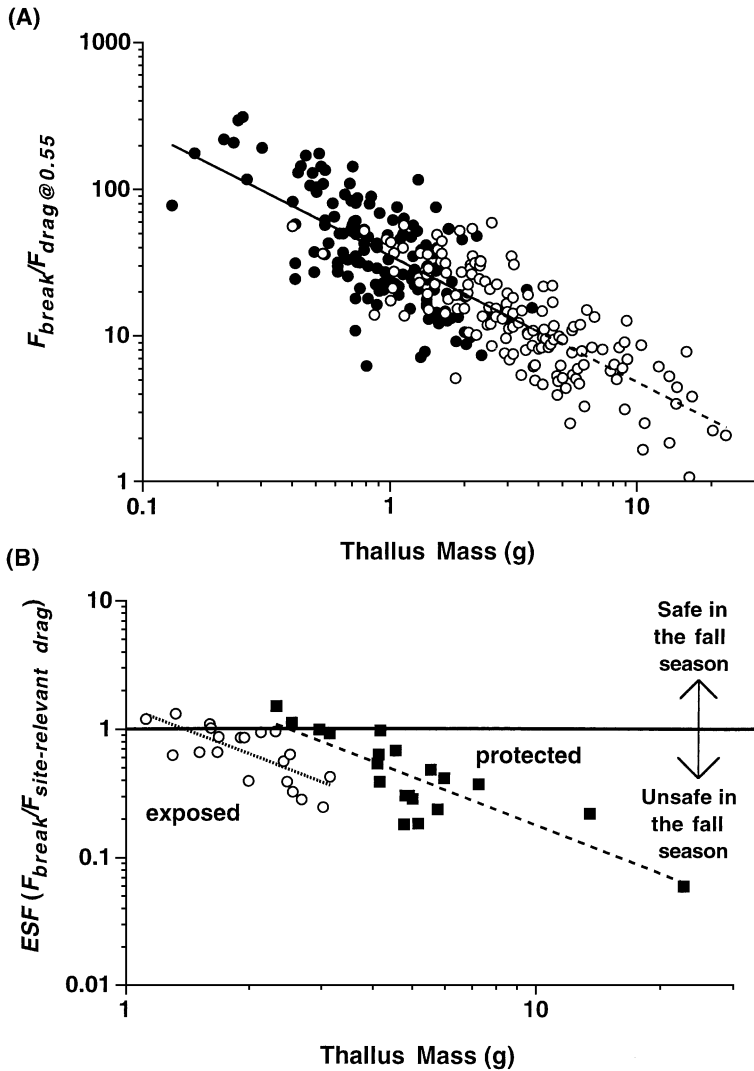


Fig. 7. (A) Log–log plot of the ratio of stipe inferred field breaking force (F_{break}) to the measured drag ($F_{drag@0.55}$) as a function of thallus mass (M) for *C. crispus* (open points, dashed lines) and *M. stellatus* (closed points, solid lines). There were no significant differences in slopes ($p_{2,294}=0.35$) or intercepts ($p_{2,295}=0.52$) between species (common equation: force ratio = $34.7M^{-0.90}$, $r^2=0.69$, $p_{2,295}\ll 0.001$ that the common slope is zero). (B) Log–log plot of the estimated ESF as a function of thallus mass (M) for the fall populations of *C. crispus* at the exposed site (open circles, tightly dashed line) and the protected site (closed squares, loosely dashed line). There was no significant difference in the slope (ANCOVA, $p_{2,36}=0.98$; common equation: $ESF = k_{ESF}M^{-1.24}$, $r^2=0.69$, $p_{2,37}\ll 0.001$ that the common slope is zero), but the intercepts were significantly different (ANCOVA, $p_{2,36}<0.001$; protected: $k_{ESF}=3.1$, exposed: $k_{ESF}=1.5$), such that thalli from protected sites had a greater ESF for a given mass than did thalli from exposed sites. The average ESF for each site, however, was not significantly different between sites (t -test: $p_{1,38}=0.12$; mean = 0.63 ± 0.06 S.E.).

still just one (mean ESF = 1.0 ± 0.08 S.E.), so that half the thalli would still be expected to have dislodged. The second type of error is expected to be, on balance, in the direction of higher real forces than estimated forces (e.g., Eq. (11)) because E -values measured for intertidal macroalgae become less negative with increasing flow speed (Carrington, 1990; Gaylord et al., 1994; Bell, 1999). Because the estimated drag is expected to be an underestimate, the ESF calculated above should underestimate the tendency to be dislodged.

4. Discussion

An understanding of the dislodgment of intertidal organisms by flow requires information not just from one site and one season (typically summer) but also from different wave exposures and in different seasons. At more exposed rocky intertidal sites, the maximum size of individuals of a given species is typically smaller than at less exposed sites (reviewed in Denny et al., 1985; Gaylord et al., 1994; Blanchette, 1997). Similarly, for some intertidal macroalgae the maximum size is smaller in more wave-exposed seasons (Armstrong, 1989; Dudgeon and Johnson, 1992; Blanchette, 1997; Dudgeon et al., 1999; Milligan and DeWreede, 2000). For intertidal macroalgae, the environmental variation that is associated with differences in wave exposure (e.g., wave, temperature, and desiccation stresses, fluctuations in dynamic light supply) can influence not only dislodgment but also productivity (Greene and Gerard, 1990; Bell, 1993; Wing and Patterson, 1993; Dudgeon et al., 1995; Kübler and Dudgeon, 1996; Kübler and Raven, 1996; see Hurd, 2000 for a review).

Thus, during the growing season size differences between different wave exposures could be due to site-specific differences in both mechanical limits and growth, at least for species such as *Chondrus* and *Mastocarpus* that are not readily consumed by herbivores (Lubchenco, 1978; Green, 1983; Dudgeon et al., 1999). During other seasons, when growth is minimal, changes in maximum size of thalli presumably occur as a result of dislodgment of the largest thalli. It is during those seasons that inter-species differences in size-specific dislodgment risk should become apparent. During those seasons, species with a greater size-specific risk of dislodgment should have a smaller maximum thallus size than would those with a smaller size-specific risk of dislodgment. We found, however, that despite their similarity in size-specific force ratio (Fig. 7), *Mastocarpus* had a smaller maximum mass of thalli than did *Chondrus* in all seasons at both exposures (Fig. 1). In the following sections, we discuss firstly the factors that contribute to the breaking force of the stipes and drag on the thalli of these two species; and secondly, the contributions of these two forces to understanding the relative safety of these two species in the New England rocky intertidal.

4.1. Breaking force

4.1.1. Similarities underlain by differences

As did Dudgeon and Johnson (1992), we found that although *Chondrus* had a greater stipe cross-sectional area for a given mass than did *Mastocarpus* (Fig. 3), this was balanced by the greater material strength of *Mastocarpus* (Figs. 2 and 4), resulting in the

statistical equality of mass-specific breaking force (Section 3.3). Even though breaking force in both species increased with increasing stipe cross-sectional area (Fig. 2B), underscaling of the stipe cross-sectional area with increasing mass (exponent=0.17 for both species, Fig. 3B) combined with decreasing strength of stipes of increasing mass (exponent=−0.14 for both species, Fig. 4B) to result in a breaking force that was statistically independent of mass.

4.1.2. Material strength

The material strengths we measured in this study (*C. crispus*, $7.0 \text{ MN m}^{-2} \pm 0.3 \text{ S.E.}$; *M. stellatus*, $11.1 \text{ MN m}^{-2} \pm 0.4 \text{ S.E.}$) were similar to those measured for several other species of intertidal red macroalgae (*M. papillatus*, 6.7 MN m^{-2} , Carrington, 1990; three species of *Mazzaella*, $\sim 4\text{--}9 \text{ MN m}^{-2}$, Shaughnessy et al., 1996) and one subtidal macroalgae (*Pterygophora californica*, 9 MN m^{-2} , Biedka et al., 1987), and greater than the strength of three brown algae (*Hedophyllum sessile*, $0.7\text{--}2.6 \text{ MN m}^{-2}$, Armstrong, 1987; *Postelsia palmaeformis*, $1.1\text{--}1.3 \text{ MN m}^{-2}$, Holbrook et al., 1991; *N. luetkeana*, $2.7\text{--}5.0 \text{ MN m}^{-2}$, Johnson and Koehl, 1994) and the subtidal red alga *Chondracanthus exasperatus*, 0.78 MN m^{-2} (Koehl, 2000). (See Koehl, 2000, for a more extensive summary of algal material strengths.)

The material strengths of stipes of *C. crispus* and *M. stellatus* measured in the present study were lower than those measured for these species by Dudgeon and Johnson (1992) (mean strength= $10.5 \text{ MN m}^{-2} \pm 0.9 \text{ S.E.}$ and $18.9 \text{ MN m}^{-2} \pm 1.2 \text{ S.E.}$, respectively) and that measured for *C. crispus* by Carrington et al. (2001) (mean strength= $10.8 \text{ MN m}^{-2} \pm 1.2 \text{ S.E.}$). The differences in strength measured in these studies are unlikely to be due to differences in methodology since the strengths we obtained from the Instron tests in the present study were indistinguishable from those we measured using the field methods of Dudgeon and Johnson (1992). The absence of site-specific differences in strength in the present study would suggest that wave exposure does not account for the difference between studies. The more southern populations of these species may represent different, stronger subpopulations of these species. Alternatively, our sampling of the largest, and therefore, weakest thalli in the population might account for their lower mean material strengths.

4.1.3. Strength and wave exposure

The absence of differences in material strength between flow habitats was somewhat surprising because the wear and tear of being battered by waves might be expected to either weaken stipes via accumulation of small cracks (Armstrong, 1987; Biedka et al., 1987; Denny et al., 1989) or to cause environmentally induced strengthening of the tissue, which has been demonstrated for some species of brown algae (Kraemer and Chapman, 1991; Lowell et al., 1991). But our findings are consistent with Carrington et al. (2001), who also found no effect of differences in wave exposure on material properties of *C. crispus*. While differences in material properties in different flow habitats have been demonstrated for some species of brown algae (Charters et al., 1969; Armstrong, 1987; McEacheron and Thomas, 1987; Johnson and Koehl, 1994; Milligan and DeWreede, 2000), it has not been demonstrated for intertidal red algae.

4.1.4. Seasonal changes in strength and breaking force

Although it is not clear why the material strength of stipes of *Chondrus* and *Mastocarpus* was greatest in the spring and winter (Fig. 4A), it may have to do with which thalli survived winter storms (perhaps the strongest) and with the mean size of stipes in the spring (the thinnest and, therefore, strongest). Conversely, thalli presumably have the lowest material strength in the summer and fall because the stipes are relatively “fat” (and “fat” stipes are relatively weak; Fig. 3A). In addition, mechanical wear and tear on the stipes during fall storms may be an added cause of the low material strength of stipes during that season. This latter explanation seems less likely given the absence of differences in strength between wave exposures.

Seasonal effects on breaking force are explicable given seasonal effects on the factors underlying breaking force. Breaking force was greatest in the winter (Fig. 2A) when material strength was highest (Fig. 4A). Although stipe strength was also high in the spring, breaking force was not significantly greater in the spring because the cross-sectional area of the stipes was at a minimum in that season (Fig. 3A).

4.2. Drag

4.2.1. Similarities underlain by differences

The similarity in mass-specific drag ($F_{\text{drag}@0.55}$) between species arose from differences in the underlying variables (C_D , S_p ; see Eq. (1), Fig. 5) that influence the variability in drag at a given flow speed. As did Dudgeon and Johnson (1992), we found that *Chondrus* had a greater planform area for a given mass than did *Mastocarpus* (Fig. 6B), especially at the exposed site. Despite these differences, the greater planform area of *Chondrus* was offset by a lower C_D , especially at the exposed site (Section 3.4), resulting in the statistical equality of mass-specific drag (Fig. 6A).

4.2.2. Coefficient of drag

Given its relatively bushy morphology, it is not surprising that for *Chondrus*, the coefficients of drag that we measured (mean C_D protected = 0.46 ± 0.017 S.E.; mean C_D exposed = 0.34 ± 0.017 S.E.) were relatively high for a small intertidal red macroalgae ($C_D = 0.02$ – 0.36 for five species, Carrington, 1990; Gaylord et al., 1994; see Koehl, 2000 for a summary). Given its more flattened, less bifurcated morphology, it is more surprising that the C_D was even greater for *Mastocarpus* (mean $C_D = 0.50 \pm 0.010$ S.E.). The flow speed at which we measured C_D s for both *Chondrus* and *Mastocarpus* (0.55 m s^{-1}) was slower than that used by Carrington (1990) and Gaylord et al. (1994), which will partly account for the higher C_D s we measured (since E is usually negative and thus affects C_D).

Overall, the C_D s we measured for *Chondrus* were comparable to those measured by Dudgeon and Johnson (1992) (mean $C_D = 0.48$). However, the mean C_D we measured for *Mastocarpus* is more than twice as large as that measured by Dudgeon and Johnson (1992) (mean summer $C_D = 0.19$). The differences in C_D s are not likely due to differences in method since our set-up was nearly identical to theirs except that their flow speed was slower (0.21 m s^{-1}). Differences in wave exposure and season are also unlikely to account for the differences between studies because, for *Mastocarpus*, C_D did not differ

between exposures and the mean C_D measured in the summer (mean $C_D = 0.54 \pm 0.017$ S.E.) in the present study did not significantly differ from the mean C_D averaged over all seasons. The more southern population of *Mastocarpus* might represent a subgroup with differing morphology. Alternatively, as with strength, differences in the portion of the population sampled (largest thalli vs. size range of thalli) may contribute, especially given that C_D increased with increasing mass (Section 3.4).

4.2.3. Season and site-specific differences in drag coefficient

For *Chondrus*, seasonal shifts in the drag coefficient (C_D ; Fig. 5), which reflect changes in shape and possibly thallus stiffness, are similar to differences in shape between exposure: the C_D is greatest at the most protected site and in the most benign season (summer). The causes of these differences may differ depending upon site and season. The decrease in C_D that occurred between summer and fall for both *Mastocarpus* and *Chondrus* at both sites was presumably the result of dislodgment of the thalli with higher drag morphologies during seasonal storms.

In contrast, during seasons of fast growth, differences in C_D between exposures may also be influenced by temperature- and site-dependent growth responses. For example, morphological variability in intertidal *Chondrus* (e.g., fewer dichotomies per unit length at more exposed intertidal sites) is associated with differences in both flow habitat (Gutierrez and Fernandez, 1992) and water temperature (e.g., more branches per unit length produced at higher temperatures; Kübler and Dudgeon, 1996). The increased photosynthetic area associated with greater branching is likely to increase productivity of those thalli (Kübler and Dudgeon, 1996). However, increased complexity would also be expected to increase drag by increasing both planform area and C_D . For example, the increase in C_D of *Chondrus* thalli in the spring is probably associated with new growth.

The plasticity in growth response of *Chondrus* suggests that shape differences in this species can be the result of both differential dislodgment and plastic responses to environmental cues. Conversely, the absence of shape differences in *Mastocarpus* between exposures and in the spring relative to other seasons (Fig. 5, Table 2) may indicate that the shape differences between the summer, fall, and winter seasons were primarily the result of differential dislodgment of thalli with higher C_D s.

The site- and season-specific differences in C_D that we found for *Chondrus* are in contrast to those of Carrington (1990) who found that differences in C_D could be ignored in assessments of the contributors to drag. The differing conclusions are not surprising since large *Chondrus* thalli did not compact into streamlined shapes up to the flow speeds used in the present study (personal observation). Several other studies have also found that differences in thallus shape do affect differences in drag (Armstrong, 1989; Koehl and Alberte, 1988; Sheath and Hambrook, 1988; Johnson and Koehl, 1994; Koehl, 1999). That *Chondrus* is less streamlined is visually apparent when it is emersed at low tide where, unlike the majority of intertidal seaweeds, large *Chondrus* thalli do not lay flattened on the substratum, but instead are supported by the three-dimensional branches of their thalli. For *Mastocarpus*, its less bushy morphology along with the lack of site-specific differences in C_D and the greater subtlety of seasonal differences in C_D all suggest that at high flow speeds *Mastocarpus*

behaves less like *Chondrus* and more like the intertidal algae studied by Carrington (1990).

4.3. Larger thalli are more likely to break

Because F_{break} was independent of mass (Section 3.3) and $F_{\text{drag}@0.55}$ increased with increasing mass (Fig. 6A), relative safety (assessed as $F_{\text{break}}/F_{\text{drag}@0.55}$) decreased with increasing mass of the thallus for both species (Fig. 7A). This result is consistent with the findings of Dudgeon and Johnson (1992) for summer populations of *Chondrus* and *Mastocarpus*. For species such as these, there will be a maximum size that they can reach before they will be dislodged. If flow speed were always greatest at the most exposed site, then one would predict that the maximum size at the end of the high-wave, low-growth seasons should be smaller at the more exposed site. Although this was what we found for the fall and winter seasons, in the spring there was no difference in mean largest size between exposures for either species (Fig. 1). This result may indicate that the maximum flow speeds were similar between exposures in the spring.

Decreasing safety of thalli with increasing size has also been described for several other species of intertidal algae (Carrington, 1990; Gaylord et al., 1994), but is in contrast to what has been found for the giant kelp *N. luetkeana*. For *N. luetkeana*, at least during the summer, the maximum stresses on stipes and the Environmental Stress Factors (ESFs) of their thalli were similar for kelp of different sizes (Johnson and Koehl, 1994). For species, such as *N. luetkeana*, which do not regenerate from their holdfasts, the cost of failure (sensu Alexander, 1981, 1988) is probably high, although less so during the fall and winter after the bulk of spore production has occurred.

The highest risk of dislodgment is probably in the fall when both thalli and flow speeds are large, both of which tend to contribute to higher drag. Indeed, the greatest decreases in mass occurred between the summer and fall (Fig. 1). For *Chondrus* at both exposures, the largest thalli found on the shore in the fall had only 50% of the mass of the largest thalli found in the summer. For *Mastocarpus*, the largest thalli found on the shore in the fall were 11% and 44% of the mass of the largest thalli found in the summer at the protected and exposed sites, respectively. For species such as *Chondrus* and *Mastocarpus*, which do regenerate from their holdfasts, are there advantages to thallus dislodgment during the fall?

For both these species, dislodgment of thalli results in the dispersal of carpospores. During the fall, both species are highly reproductive with carposporic reproduction usually most intense in October for *Chondrus* (Prince and Kingsbury, 1973) and maximum carpospore release during decreasing temperatures from September to December for *Mastocarpus* (Burns and Mathieson, 1972). The largest thalli, which are most likely to be dislodged, are also most likely to have the greatest reproductive load (in general: Gaylord et al., 1994; for *Chondrus* and *Mastocarpus*, specifically: Dudgeon, personal communication).

Dislodgment of thalli could also remove older, compromised thalli that can be replaced with new thalli in the spring. For example, when *Chondrus* releases carpospores, it often leaves holes in the fronds. In addition, the epiphyte load is heaviest in the fall, which

seems likely to incur costs such as increased variation in drag (Johnson, unpublished data) and decreased photosynthesis.

4.4. Is there equality in dislodgment risk?

The force ratio ($F_{\text{break}}/F_{\text{drag}@0.55}$) decreased with size in the same way in both species (Fig. 7A). If extrapolation of the force ratio from the present study to higher, site-relevant flow speeds (i.e., the ESF) also did not differ between species, then there would be no difference in risk of breakage between these two species. If dislodgment risk is equal, then two predictions follow: (1) that *Chondrus*, because it is larger, would experience greater seasonal dislodgment, and (2) that by the end of high-wave, minimum-growth seasons the maximum size of thalli in each population should be approximately the same. Our data, which revealed greater seasonal mass loss of *Chondrus* relative to *Mastocarpus* (Fig. 1), and the data of others (Dudgeon and Johnson, 1992; Dudgeon et al., 1999), support the first prediction. The persistence of *Chondrus* that is larger than *Mastocarpus* at both sites and in all seasons (Fig. 1), however, suggests that *Chondrus* thalli are less vulnerable to dislodgment. Thus, although mass loss trends in the field are consistent with earlier predictions, data on maximum mass are more consistent with *Chondrus* having a higher ESF. This could happen if the decrease in coefficient of drag with increasing flow speed (Vogel, 1984; Carrington, 1990; Gaylord et al., 1994) was greater for *Chondrus* than for *Mastocarpus* (i.e., if the absolute value of E was greater for *Chondrus* than for *Mastocarpus*). This could also happen if the protection from flow afforded by being surrounded by a dense canopy of thalli (Johnson, 2001) provided greater protection for *Chondrus* thalli than for *Mastocarpus* thalli.

4.5. Assessing safety

A better assessment of safety is possible by using an estimate of the drag on thalli at site-relevant flow speeds to calculate ESF. We estimated ESF for *Chondrus* (using E) for the fall season (for which we measured site-relevant flow speeds). We found that ESF did not differ between exposures even though thalli from the protected site had a higher mass-specific ESF (Fig. 7). The equality in ESF occurred because thalli from the protected site were larger and larger thalli have a lower ESF. This similarity in ESF is reminiscent of the similarity in ESF of the kelp *N. luetkeana* from different flow habitats (Johnson and Koehl, 1994). For *N. luetkeana*, morphological plasticity of the thalli contributed to the equality of ESF between different flow habitats. Although *Chondrus* does exhibit differential growth forms (Gutierrez and Fernandez, 1992; Kübler and Dudgeon, 1996), the present study suggests that differential dislodgment of thalli with greater drag also contributes to the equality of ESF in this species.

The average ESF for *Chondrus* (0.63 ± 0.06 S.E.) was less than one; indicating that on average these thalli were at risk of experiencing nearly twice the drag that they could withstand before breakage. This estimate of the drag at site-relevant flows leads to the prediction that the maximum size of thalli in that fall population should have been smaller than those that we sampled. The C_{DS} of thalli at site- and season-relevant flow speeds might be lower than those predicted by this study; however, this seems unlikely as the

method used should represent an underestimate of the actual C_D (Eq. (11), Section 3.5; see also Bell, 1999). Instead, it may be that canopies of *Chondrus* confer some protection from flow forces.

Johnson (2001) found that canopies of *Chondrus* at a density typically found in intertidal populations of these algae (0.16 thalli per cm^2 , Dudgeon, personal communication) can reduce drag on an individual thallus by 82.6% ($\pm 0.4\%$ S.E.). When the site-relevant drag measured in the present study is reduced by that amount, then the average ESF for these populations shifts to a value greater than one (mean canopy-corrected $\text{ESF} = 3.7 \pm 0.3$ S.E.; Fig. 8). Taking into account this canopy effect, only one of the thalli from the more protected site would now have an ESF less than one. There are, of course, caveats to this estimate. Because the C_D used for this estimate will tend to be low, the original, uncorrected ESF will be lower. Further, the canopy effect used for this estimate was quantified at a flow speed of 0.45 m s^{-1} and, although Johnson (2001) found that the canopy effect increased with increasing flow speed, the specific drag-reduction that occurs in canopies at site-relevant velocities remains to be measured. Nonetheless, it seems likely that the presence of a surrounding canopy reduces the risk of breakage of constituent thalli. It also seems likely, given the less bushy morphology

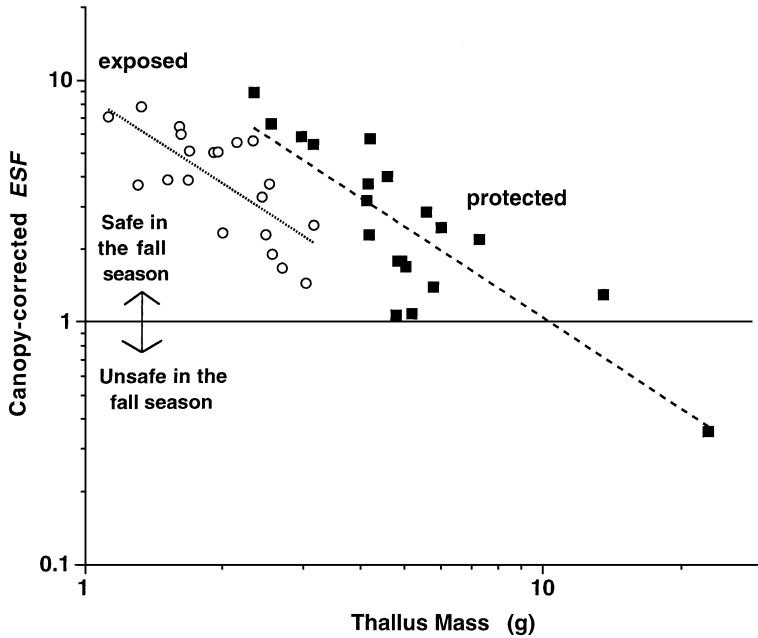


Fig. 8. Log–log plot of the canopy-corrected ESF ($\text{ESF}_{\text{corrected}}$) as a function of thallus mass (M) for the fall populations of *C. crispus* at the exposed site (open circles, tightly dashed line) and the protected site (closed squares, loosely dashed line). There was no significant difference in the slopes (ANCOVA, $p_{2,36} = 0.99$; common equation: $\text{ESF}_{\text{corrected}} = k_{\text{ESF}_{\text{corrected}}} M^{-1.24}$, $r^2 = 0.69$, $p_{2,37} \ll 0.001$ that the common slope is zero), but the intercepts were significantly different (ANCOVA, $p_{2,36} < 0.001$; protected: $k_{\text{ESF}_{\text{corrected}}} = 18.1$, exposed: $k_{\text{ESF}_{\text{corrected}}} = 8.7$).

of *Mastocarpus* that the protection from drag conferred by the canopy is likely to be less for *Mastocarpus* than it is for *Chondrus*. If so, it may be a difference in the protection conferred by the surrounding canopy that accounts for the consistently greater size of *Chondrus* in the exposed rocky intertidal.

4.6. Do mechanical limits to size differ in *Chondrus* and *Mastocarpus*?

The similarity in ESF for *Chondrus* from different flow habitats supports the hypothesis that mechanical forces do limit size in this species. Data on force ratios of isolated thalli of *Chondrus* and *Mastocarpus* at 0.55 m s^{-1} suggest that mechanical limits to size are indistinguishable between these two species. Field data on seasonal changes in mass of the largest thalli in a population suggest that at site- and seasonally relevant flows, mechanical limits to size constrain *Mastocarpus* to a smaller size than *Chondrus*. The apparent contradictions between these two sets of data are possibly due to differences in the way the mass-specific drag scales with flow speed between these two species and/or differential protection by canopies of each species. These mechanisms lead to a pair of testable predictions. If the former is more important, then one would predict that E would be more negative for *Chondrus* than for *Mastocarpus*. If the latter is more important, then one would predict that force-reduction by canopies of *Mastocarpus* is less than force-reduction by canopies of *Chondrus*.

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