Size, strength and allometry of joints in the articulated coralline *Calliarthron*

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Summary

Articulated coralline algae (Corallinales, Rhodophyta) dominate low-intertidal, wave-exposed habitats around the world, yet the mechanics of this diverse group of organisms has been almost completely unexplored. In contrast to fleshy seaweeds, articulated corallines consist of calcified segments (intergenicula) separated by uncalcified joints (genicula). This jointed construction makes calcified fronds as flexible as fleshy seaweeds, allowing them to 'go with the flow' when struck by breaking waves. In addition to functioning as joints, genicula act as breakage points along articulated fronds. Here, I describe the allometric scaling of geniculum size, breaking force and tissue strength along articulated fronds in two species of *Calliarthron*. Genicular material is much stronger than tissue from fleshy macroalgae.

Moreover, as fronds grow, genicula get bigger and their tissue strengthens, two processes that help them resist breakage. Within individual fronds, larger branches, which presumably experience greater drag force, are supported by bigger, stronger genicula. However, frond growth greatly outpaces genicular strengthening. As a result, *Calliarthron* fronds most likely break at their bases when critically stressed by incoming waves. Shedding fronds probably reduces the drag force that threatens to dislodge coralline crusts and may constitute a reproductive strategy.

Key words: algae, allometry, biomechanics, breaking stress, *Calliarthron*, coralline algae, decalcification, drag force, geniculum, intertidal, material properties, risk.

Introduction

Organisms that live in wave-exposed, intertidal habitats must contend with remarkable mechanical stresses on a daily basis. Breaking waves can generate water velocities greater than 20 m s^{-1} (e.g. Denny et al., 2003; O'Donnell, 2005) and impose considerable forces on intertidal inhabitants (Helmuth and Denny, 2003). Moreover, sessile organisms, such as marine macroalgae, cannot seek shelter when environmental conditions worsen; they must endure wave impacts wherever they settle and grow. Thus, for intertidal seaweeds, the threats of breakage and dislodgement are ever-present.

Lessons from fleshy macroalgae

For decades, researchers have studied the mechanical properties and morphological adaptations that allow macroalgae to survive intertidal wave forces (e.g. Delf, 1932; Gerard and Mann, 1979; Koehl, 1986; Armstrong, 1987; Denny et al., 1989; Carrington, 1990; Gaylord et al., 1994; Carrington et al., 2001; Hale, 2001; Milligan and DeWreede, 2004). Collectively, these studies have revealed general patterns in the interactions between algal thalli and their fluid environment, material composition and physical morphology that help macroalgae resist mechanical failure. For instance, the predominant hydrodynamic force applied to intertidal macroalgae by breaking waves is drag (Denny and Gaylord, 2002), not hydrodynamic acceleration (Gaylord, 2000), although wave impingement forces have yet to be properly quantified (Gaylord, 2000). Thus, we can define a risk factor (R) that describes how prone an alga is to mechanical failure:

$$R = F_d / F_b , \qquad (1)$$

where F_d is the drag force applied to the algal thallus and F_b is the force with which the alga resists breakage. Note that this risk factor is the inverse of the engineer's safety factor (Alexander, 1981). Seaweeds that experience excessive drag force relative to their strength are at greatest risk of failure. By comparing drag force to breaking force, past studies have successfully predicted the wave-induced failure of macroalgae in the field (e.g. Carrington, 1990; Dudgeon and Johnson, 1992; Shaughnessy et al., 1996; Bell, 1999). An evaluation of the risk factor suggests that, to reduce their risk of failure and increase their chance of survival, algae can decrease the effective drag force on their thalli or increase their physical strength.

Drag force (F_d) can be described in terms of thallus and fluid characteristics:

$$F_d = \tfrac{1}{2}\rho U^2 S C_d , \qquad (2)$$

where ρ is the density of seawater, *U* is the water velocity, *S* is the planform area of the alga (approximately half the wetted surface area), and C_d is the drag coefficient, an index of thallus shape. To reduce drag force, an alga must reduce at least one of these components. For instance, many intertidal seaweeds stay relatively small (Denny et al., 1985; Gaylord et al., 1994; Denny, 1999), thereby limiting *S*. In addition, most macroalgal thalli are flexible. Flexible seaweeds that 'go with the flow' reconfigure into more streamline shapes (reducing C_d) and may find refuge from intense water velocities (*U*) by hugging the substratum (see Koehl, 1984; Koehl, 1986; Vogel, 1994; Denny and Gaylord, 2002). Furthermore, the time that flexible fronds spend reorienting and reconfiguring may exceed the duration of brief hydrodynamic loads, such as the wave impingement force, potentially allowing them to evade these maximal forces (Gaylord, 2000; Gaylord et al., 2001). Flexibility has its limitations, as particularly massive macroalgae sometimes develop momentum as they reorient (Gaylord and Denny, 1997; Denny et al., 1998) and, under some circumstances, experience a harmful whiplash effect (Friedland and Denny, 1995). However, in general, flexibility is thought to be beneficial to marine macroalgae and flexible reconfiguration has been described as a 'prerequisite for survival' in unstable flow conditions (Harder et al., 2004).

An increase in the force required to break algal thalli also decreases the risk factor. Breaking force is affected by both material composition and cross-sectional area. For example, a single steel thread resists more force than one made of cotton, but cotton threads woven into a sturdy rope are considerably stronger than the slim steel thread. Unlike materials from other wave-exposed organisms, such as barnacle tests and limpet shells, seaweed tissues are rather weak (see summaries in Koehl, 1986; Hale, 2001). Some macroalgae, such as kelps, grow large in cross-section to compensate for their weak material construction, but large size may deleteriously increase drag force as well (see Eqn 2). Instead, weak seaweed materials are compliant, allowing them to stretch and absorb considerable energy from impinging waves before they break (Koehl, 1986; Hale, 2001). The utility of being stretchy, however, is not entirely clearcut and depends upon the duration of an applied force and whether an alga is deformed in bending or in tension (Gaylord et al., 2001). In some circumstances, compliance may actually exacerbate the consequences of an applied load (Gaylord et al., 2001). Nevertheless, the mechanical success of macroalgae in the wave-swept intertidal zone can be attributed, at least in part, to their flexibility and their weak but extensible material composition.

Unfortunately, previous studies of algal biomechanics (except Gaylord et al., 2001; Hale, 2001) have focused exclusively on fleshy macroalgae and neglected an entire taxonomic order of organisms: the coralline algae (Corallinales, Rhodophyta). Unlike fleshy seaweeds, corallines reinforce their cell walls with calcite, a crystalline form of calcium carbonate ($CaCO_3$) (Borowitzka, 1977; Johansen,

1981). In other words, coralline algae are composed of cells which are essentially encased in limestone. At the cellular level, such rigidity appears to stand in stark contrast to the flexible body plan that helps fleshy algae survive – yet coralline algae are abundant in oceans worldwide, frequently dominating low-intertidal habitats, where wave forces are expected to be most severe. Thus, coralline algae represent a significant gap in our understanding of algal biomechanics and provide an opportunity to test generalizations about how macroalgae survive breaking waves. In this paper, I take the first steps in incorporating coralline algae into the paradigm of algal biomechanics.

Articulated coralline algae

Most coralline species grow prostrate on the substratum, forming calcified crusts of varied morphology (see Woelkerling, 1988), but many extend upright into the water column, forming complex fronds. One might imagine that, without an ability to 'go with the flow,' upright, calcified fronds would be highly susceptible to breakage or dislodgement in the wave-swept intertidal zone. However, in contrast to their crustose relatives, most species of upright coralline algae have evolved an 'articulated' morphology that reduces the overall stiffness of their fronds. That is, specific regions of the calcified fronds remain uncalcified or actively decalcify to form discrete flexible joints (Fig. 1). This jointed architecture, which consists of an alternating sequence of calcified segments (intergenicula) and uncalcified joints (genicula), lends flexibility to otherwise rigid coralline fronds. Thus, despite their largely calcified thalli, articulated corallines fit the flexible generality proposed for fleshy macroalgae. But are they, too, structural weaklings?

Several researchers (Borowitzka and Vesk, 1978; Johansen, 1981; Hale, 2001) have hypothesized that genicula play a critical role in the mechanical success of articulated coralline algae; however, little has been published about genicula physical characteristics, mechanical ability or material
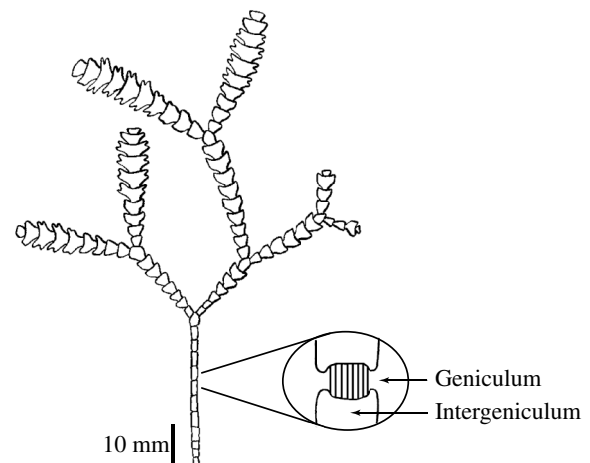

Fig. 1. Diagram of a representative frond from *Calliarthron cheilosporioides*.

composition. Johansen (Johansen, 1969; Johansen, 1974; Johansen, 1981) published the most comprehensive studies of articulated coralline algae, yet many questions about genicula remain.

Articulated corallines in the genus *Calliarthron* have genicula composed of a single tier of decalcified cells, which span the entire gap between adjacent intergenicula (Fig. 1). According to Johansen (Johansen, 1969), all cells in *Calliarthron* are calcified as they are initiated at the apical meristem, but certain medullary cells pre-destined to form a geniculum soon begin to decalcify and elongate. Shortly thereafter, the cortex surrounding the decalcified cells ruptures to reveal the mature geniculum. In *Calliarthron*, this decalcification process must strike a balance between providing flexibility and catastrophically weakening the fronds. Besides functioning as joints, genicula may, of necessity, act as weak breakage points along articulated fronds. The effect of decalcification on material strength is entirely unknown. Moreover, the material strength of this novel flexible tissue derived from calcified cells deserves further investigation.

Johansen reported (Johansen, 1969) that, as *Calliarthron* genicula develop, genicular cells lose most of their cytoplasm, and their nuclei disappear. This study suggests that mature genicula may consist of empty cell walls whose primary function is structural support, as wood provides support for terrestrial trees. However, without nuclei, genicular cells may be incapable of cell division, growth or repair, thereby imposing severe mechanical and growth limitations upon actively growing fronds. Are genicula static components within dynamically growing fronds?

Finally, the modular nature of articulated coralline algae provides a unique opportunity to quantify the scaling of material strength and mechanical ability along the length of algal thalli. Fleshy macroalgae have tapered homogenous fronds, which make it difficult to force breakage at pre-specified positions. By taking multiple measurements along articulated fronds, I can predict the position within coralline thalli most prone to mechanical failure in the field. The segmented body plan also facilitates comparisons among younger and older thalli, making it possible to estimate physical and material changes in specific genicula over time.

In this paper, I explore the mechanics, growth and allometric scaling of genicula in the wave-swept articulated corallines *Calliarthron cheilosporioides* Manza and *Calliarthron tuberculosum* (Postels and Ruprecht) Dawson. For the first time, I report the breaking strengths of individual genicula and compare them to the strengths of fleshy macroalgal materials. I describe the effects of decalcification on the strength of genicular tissue and provide results suggesting that genicula are not static entities, but change in size and strength as fronds grow. I measure the variation in genicula characteristics along articulated thalli and, by estimating drag force, predict at what positions thalli are likely to break when hydrodynamically stressed.

Materials and methods
Mechanical test overview

Because articulated coralline algae are composed of both calcified and uncalcified tissue, two separate mechanical tests were employed to measure their material strength (Fig. 2). When articulated fronds were pulled in tension, genicula behaved like other fleshy seaweeds (e.g. Hale, 2001), stretching until they broke. In contrast, intergenicula behaved more like other calcified materials, such as mollusc shell and coral skeleton, and rarely broke in tension. Furthermore, individual intergenicula were too small to grip in order to force tensile breakage. Thus, three-point bending tests were conducted on intergenicula (Fig. 2A) to measure their moduli of rupture (M_r), as has been done with other calcified biological materials (Currey, 1980; Vosburgh, 1982; Boller et al., 2002), while pull-to-break tests were conducted on genicula (Fig. 2B) to measure their tensile breaking stresses (σ).

Moduli of rupture and tensile breaking stresses are not directly comparable. Moduli of rupture are generally greater than tensile strength measurements because the localized breaks have a decreased likelihood of including pre-existing flaws (Currey and Taylor, 1974). Fortunately, data on both tensile breaking stress and modulus of rupture have been reported for mollusc shells (N=25: Currey, 1980) and coral skeleton (N=1: Vosburgh, 1982). A linear regression was fitted to these 26 data points extracted from the literature, and the breaking stress of intergenicula was estimated from the modulus of rupture.
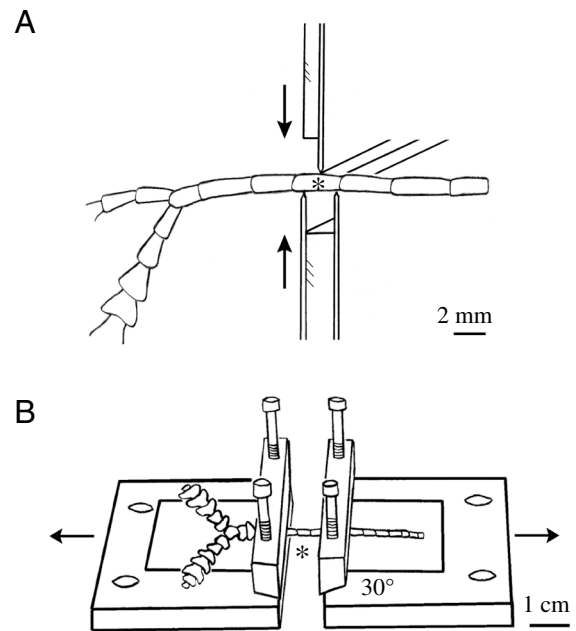

Fig. 2. Mechanical tests used to measure the strength of genicula and intergenicula. (A) Three-point bending test. Fronds were compressed between three razor blades until intergenicula snapped. (B) Pull-to-break test. Fronds were stretched until genicula broke. The asterisks indicate approximate break locations.

Three-point bending test

Fourteen *Calliarthron cheilosporioides* fronds were collected from tidepools above a moderately wave-exposed surge channel at Hopkins Marine Station in Pacific Grove, California (36°36′N, 121°53′W). Presumably, the fronds had been broken off the substratum in the surge channel and recently cast ashore. Fronds exhibited healthy pigmentation, no decomposition, and no extensive grazer damage or epiphytism; aside from their dislodgement, all fronds appeared perfectly healthy. Specimens were kept in a flow-through, seawater table for a maximum of 48 h before testing. Prior to each experiment, fronds were removed from the seawater, briefly patted dry, and tested immediately while still damp.

To measure the force required to break the calcified intergenicula, three-point bending tests were performed using a custom-made tensometer. The tensometer used a linearly variable differential transformer (LVDT; model 100HR, Schaevitz Engineering, Pennsauken, NJ, USA) to measure the force applied to algal tissue between two clamps. The tensometer did not measure tissue strain. In this experiment, one clamp was outfitted with two dulled razor blades (2.25 mm apart) and the other clamp was outfitted with a single dulled razor blade aligned halfway between the other two. Each frond was positioned so that a single, cylindrical intergeniculum was held between the three razor blades (Fig. 2A). The razor blades were driven together along the tensometer track at 1 mm s^{-1} until the intergeniculum broke, and the applied force was recorded on a chart recorder. The dulled razor blades did not introduce cuts or flaws into the calcified tissue, and most intergenicula broke cleanly in half. The lengths of the major and minor axes of the broken intergenicula were measured, and the following equation was used to calculate the modulus of rupture (M_r):

$$M_r = F_b L r / 4I, \qquad (3)$$

where F_b is the breaking force, L is the length of the stressed tissue (i.e. the distance between the outer two razor blades), r is the intergeniculum radius parallel to the applied force, and I is the second moment of area, defined for an elliptical cross-section (Roark and Young, 1975).

Two intergenicula were broken per frond, and the modulus of rupture of each frond was calculated by averaging these two measurements. Mean intergeniculum modulus of rupture was calculated by averaging the moduli of the fourteen fronds. As explained above, the tensile breaking stress of intergenicula was estimated from the mean modulus of rupture using the linear regression calculated from previously published data (Currey, 1980; Vosburgh, 1982).

Pull-to-break tests

Twenty-nine *Calliarthron* fronds were collected from a single study site (approx. 1 m^2) within the surge channel mentioned above. The site was at mean lower low water (MLLW) near the landward end of the channel. Articulated coralline fronds comprising two size classes were collected: small fronds (*N*=16; length=38.8 mm±8.1, mean ± s.d.) and large fronds (*N*=13; mean length=101.4±24.8 mm). Large fronds had at least one dichotomy and proliferous lateral branching, while most small fronds were short, unbranched sprouts. The large fronds were composed of both *Calliarthron tuberculosum* (*N*=6) and *Calliarthron cheilosporioides* (*N*=7). The small fronds were generally unidentifiable to the species level, but were assumed to include both *Calliarthron* species. All fronds were completely intact with healthy meristems (i.e. small fronds did not appear to be remains of broken large fronds), and therefore, small fronds were assumed to represent a younger phase in the life of *Calliarthron*. A knife was used to separate each frond from its crustose holdfast at the first geniculum. Extra care was taken to ensure that each frond was removed from a different holdfast, so that the fronds were presumably representative of 29 distinct individuals. Fronds were kept in a flow-through seawater table, and all thalli were tested within 48 h to avoid tissue degradation. Prior to each experiment, fronds were removed from the seawater, briefly patted dry, and promptly tested while still damp. Fronds were re-submerged in seawater between trials.

The forces required to break individual genicula were determined by conducting pull-to-break tests using the same tensometer from the three-point bending tests. In this experiment, algal tissue was stretched between two aluminum wedge clamps, designed specifically for this purpose (Fig. 2B). In each clamp, fronds were held between a flat plat and a 30° wedge, both lined with 2 mm thick rubber pads. The clamps effectively gripped the coralline fronds without crushing the calcified intergenicula.

The clamps were secured along articulated fronds so that 2–4 intergenicula were left 'floating' between them. The wedge clamps were driven apart along the tensometer track at 1 mm s^{-1}, and the floating series of intergenicula and genicula was stretched until one geniculum broke. The force applied to the geniculum was recorded on a chart recorder. Breaks that occurred at an intergeniculum or at a clamp interface were noted, but not included in this analysis. After each break, the broken segment was set aside, the clamps were shifted down the frond, and the pull-to-break test was repeated. Broken genicula were numbered according to their relative position within a frond (Fig. 3A). Between two and four genicula were broken in each small frond and between five and eleven genicula were broken in each large frond, for a total of 157 genicula measurements. Broken segments were organized and taped to a sheet of paper for planform area analysis and archived collection (as depicted in Fig. 3A).

Cross-section measurements

For every genicular break, broken segments were turned up on end and the boundary between the calcified, intergenicular tissue and the decalcified, genicular tissue was identified (Fig. 3B). The dimensions of the genicular boundary and adjacent intergeniculum were measured using an ocular dial-micrometer. These values were used to calculate the cross-sectional area (*A*) of the broken geniculum and to estimate the cross-sectional area of the adjacent intergeniculum, assuming
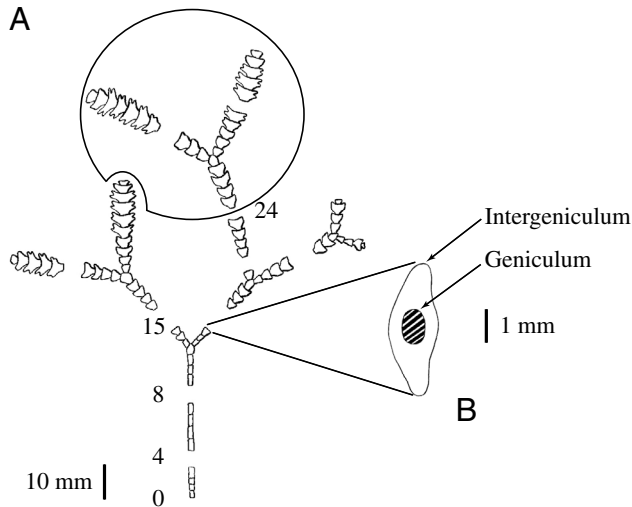
Fig. 3. Diagram of a *Calliarthron* frond after it has been broken. (A) Broken genicula were numbered according to their original position in the frond. Data from each broken geniculum was paired with the planform area of the frond that it would have supported in flow (e.g. encircled segments would be paired with geniculum no. 24). (B) Transverse view of a broken frond segment.

both were elliptical. Measurement error was estimated by repeatedly measuring the dimensions of five representative genicula. On average, repeated area measurements deviated from the mean by 5%. Cross-sectional areas of genicula and intergenicula from the large size class were plotted against geniculum position to summarize the relative variation in these values within an average frond and among *Calliarthron* species. The effect of geniculum position (covariate) and species (fixed factor) on geniculum cross-sectional area (response 1) and intergeniculum cross-sectional area (response 2) were analyzed using two separate analyses of covariance (ANCOVA).

The cross-sectional areas of the basal genicula (no. 0) were recorded for the small fronds ($N=10$) and large fronds ($N=11$) that were not chipped by the knife during collection. The cross-sectional areas of genicula nos 2, 4, 6, 8 and 10 were measured similarly. To avoid any effect of branching on geniculum size, only genicula below the first branching dichotomy were analyzed. Additional geniculum data collected from large fronds were incorporated into the interspecific ANCOVA described above. The effects of size class (fixed factor) and geniculum position (fixed factor) on cross-sectional area (response) were analyzed using a two-way analysis of variance (ANOVA), and the cross-sectional areas of genicula from the two size classes were compared at specific positions using *post hoc* planned comparisons.

Geniculum breaking forces (F_b) were plotted against cross-sectional areas (A) for all broken genicula within each size class. The effects of size class (fixed factor) and cross-sectional area (covariate) on breaking force (response) were initially analyzed with ANCOVA. However, size class regressions had significantly different slopes and were treated separately.

Breaking stress calculations

The breaking stress (σ) of each broken geniculum was calculated by dividing breaking force (F_b) by cross-sectional area (A) (Denny, 1988). Measurement error in cross-sectional area was propagated into calculation error in breaking stress; reported breaking stresses are assumed to be within 5% of the actual value.

The mean breaking stress of each frond was calculated by averaging together the breaking stresses of its broken genicula. Interspecific variation in the large size class was evaluated using a Student's *t*-test. *Calliarthron* species were not significantly different and breaking stress data from the large size class were pooled. The mean breaking stresses of fronds from each size class were compared using a Student's *t*-test. Mean breaking stresses of fronds from the large size class were nominally compared with the breaking stresses of flexible macroalgae.

Planform area measurements

Digital photographs were taken of the broken fronds once they were arranged and taped down. This organization of frond segments allowed each broken geniculum to be paired with all segments distal to it, as these segments comprise the portion of the frond the geniculum must support in flow (Fig. 3A). The planform areas (S) of the distal segments were measured using an image analysis routine written in LabView (version 6.0.2, National Instruments Corporation, Austin, TX, USA). Measurement error was estimated by repeatedly calculating the planform areas of seven frond segments. On average, repeated planform area measurements deviated from the mean by 4%. For each large frond, the breaking force (F_b), cross-sectional area (A), and breaking stress (σ) of each broken geniculum were correlated to the planform area of the frond (S) distal to and supported by that geniculum in flow. Data from each frond were tested separately using regression analyses. The effect of planform area (covariate) on geniculum breaking force (response) for all fronds from the large size class (fixed factor) was analyzed using ANCOVA.

Risk factor index

Ideally, to predict where articulated fronds will fail, the risk factor (R) at each geniculum would be calculated according to Eqn 1. However, it is difficult to measure the force of drag pulling on each geniculum in flow. Instead, assuming a constant drag coefficient (C_d) and water velocity (U), frond planform area (S) can be used as a proxy for drag force (F_d) (see Eqn 2). This assumption is supported by previous studies, which demonstrated that thallus area explains most of the variation in drag (e.g. Carrington, 1990; Milligan and DeWreede, 2004). All else being equal, genicula that support larger branches experience proportionately more drag force. Thus, instead of calculating risk factor (R), the planform area of the frond (S) distal to each geniculum was divided by its breaking force (F_b) to calculate the risk factor index (I_r):

$$I_r = S / F_b ,\qquad(4)$$

where risk factor index was assumed to be proportional to risk factor (R). Risk factor indices were calculated for all broken

genicula from the large frond size class. Data were log-transformed, and regression analysis was used to test the correlation between genicula risk factor indices and the planform areas of the branches they support. The trend was used to predict at what geniculum position an average frond would be most likely to break.

Statistics

JMPIN (version 3.2.1, SAS Institute Inc., Cary, NC, USA) was used to perform all statistical analyses.

Results
Intergeniculum tissue strength

The modulus of rupture of intergenicular tissue from *C. cheilosporioides* was 54.6±2.6 MN m^{-2}, mean ± s.e.m.

(Table 1). The linear regression fitted to data extracted from Currey (Currey, 1980) and Vosburgh (Vosburgh, 1982) showed a significant correlation (R^2=0.57, P<0.001) between the moduli of rupture (M_r) of calcified materials and their tensile breaking stresses (σ):

$$\sigma = 0.29M_r + 12.65 . \qquad (5)$$

Based on this regression, the mean intergeniculum breaking stress was estimated to be 28.5 MN m^{-2}.

Geniculum cross-sectional areas

Genicula sizes varied greatly (coefficient of variation CV=48%), spanning an order of magnitude difference (A_{min}=0.13 mm^2, A_{max}=1.30 mm^2, A_{mean}=0.52 mm^2). Overall, genicula near the bases of large fronds had significantly larger cross sections than genicula near the frond tips (Fig. 4;

Table 1. *Tissue strengths of calcified and uncalcified biological materials*

Division	Species	Tissue	σ (MN m^{-2})	M_r (MN m^{-2})	Reference
	Calcified				
	Gastropod (average)	Sh	50.1	130.0	(Currey, 1980)[†]
	Bivalve (average)	Sh	49.1	124.8	(Currey, 1980)[†]
	Plexaura kuna	Gor	–	75.0	(Boller et al., 2002)
Red	*Calliarthron cheilosporioides*	I	28.5*	54.6	This study
	Acropora reticulata	C	25.6	36.1	(Vosburgh, 1982)
	Uncalcified macroalgae				
Red	*Calliarthron cheilosporioides*	G	25.9		This study
Red		G	25.1		(Hale, 2001)
Red	*Calliarthron tuberculosum*	G	25.2		This study
Red	*Mastocarpus stellatus*	S	18.9		(Dudgeon and Johnson, 1992)
Red		S	11.1		(Pratt and Johnson, 2002)
Red	*Chondrus crispus*	S	10.5		(Dudgeon and Johnson, 1992)
Red		S	7.0		(Pratt and Johnson, 2002)
Red	*Endocladia muricata*	Br	8.1		(Hale, 2001)
Red	*Mazzaella splendens*	S	7.8		(Shaughnessy et al., 1996)
Red	*Prionitis lanceolata*	Br	7.3		(Hale, 2001)
Brown	*Pterygophora californica*	S	7.5		(Biedka et al., 1987)
Brown		S	6.6		(DeWreede et al., 1992)
Red	*Mastocarpus papillatus*	S	6.7		(Carrington, 1990)
Red		S	6.3		(Kitzes and Denny, 2005)
Brown	*Eisenia arborea*	S	6.0		(DeWreede et al., 1992)
Brown	*Egregia menziesii*	S	5.1		(Hale, 2001)
Brown	*Fucus gardneri*	S	4.3		(Hale, 2001)
Brown	*Nereocystis luetkeana*	S	3.6		(Koehl and Wainwright, 1977)
Brown	*Laminaria setchellii*	B	2.3		(Hale, 2001)
Brown	*Postelsia palmaeformis*	S	2.1		(Hale, 2001)
Brown	*Hedophyllum sessile*	B	1.5		(Armstrong, 1987)
Brown	*Lessonia nigrescens*	S	1.2		(Koehl, 1986)
Brown	*Durvillaea antarctica*	S	0.7		(Koehl, 1986)
Green	*Enteromorpha intestinalis*	B	0.7		(Hale, 2001)
Green	*Codium fragile*	Br	0.2		(Hale, 2001)

Species are listed in decreasing order of tissue strength.
σ, breaking stress; M_r, modulus of rupture.
Macroalgae divisions: Red, Rhodophyta; Brown, Ochrophyta, Phaeophyceae; Green, Chlorophyta.
B, blade; Br, branch; C, coral; Gor, gorgonian; G, geniculum; I, intergeniculum; S, stipe; Sh, shell.
*Tensile breaking stress of *Calliarthron* intergeniculum was estimated from its modulus of rupture using Eqn 5.
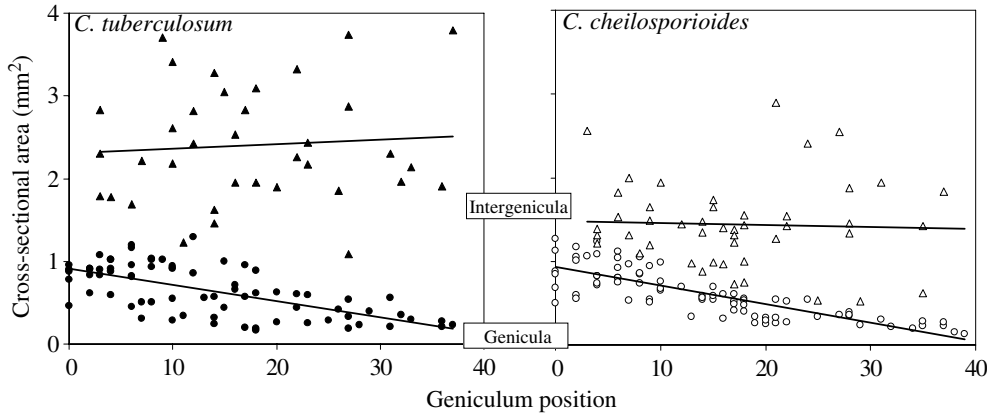[†]Only average values (Currey, 1980) are reported here.

Fig. 4. Cross-sectional areas of genicula (circles) and intergenicula (triangles) from *C. tuberculosum* (black symbols) and *C. cheilosporioides* (white symbols) from the large size class as functions of geniculum position. Lines represent linear regressions fitted to each data set. ANCOVA; for F and P values, see text.

ANCOVA $F_{1,151}=176.98$, $P<0.001$). Linear regressions fitted to genicula data from the two *Calliarthron* species had similar slopes (ANCOVA $F_{1,151}=0.88$, $P=0.35$) and revealed no significant interspecific differences (Fig. 4; ANCOVA $F_{1,151}=0.22$, $P=0.63$). At any given geniculum position, intergenicula from *C. cheilosporioides* (mean $A=1.44\pm0.51$ mm^2, mean ± s.d.) and from *C. tuberculosum* (mean $A=2.40\pm0.70$ mm^2, mean ± s.d.) were larger than adjacent genicula; this difference was barely measurable near frond bases, but substantial near frond tips (Fig. 4). Cross-sectional areas of intergenicula from the two species followed similar patterns (ANCOVA $F_{1,78}=0.30$, $P=0.58$), but did not vary predictably with geniculum position (Fig. 4; ANCOVA $F_{1,78}=0.05$, $P=0.82$). Intergenicula from *C. tuberculosum* were significantly thicker in cross-section than intergenicula from *C. cheilosporioides* (Fig. 4; ANCOVA $F_{1,78}=8.09$, $P<0.01$).

Cross-sectional areas of genicula from the two size classes followed similar patterns over comparable geniculum positions (Fig. 5; ANOVA $F_{5,133}=0.39$, $P=0.85$). The effect of geniculum position on cross-sectional area was insignificant in the first ten positions (ANOVA $F_{5,133}=0.34$, $P=0.89$). Overall, genicula from large fronds had significantly larger cross-sections than genicula from small fronds (Fig. 5; ANOVA $F_{1,133}=41.83$, $P<0.001$). *Post hoc* planned comparisons revealed that the cross-sectional areas of genicula from large and small fronds were more different at geniculum positions 4–10 (all $P<0.01$) than at geniculum position 2 ($P<0.05$) or at geniculum position 0 ($P=0.13$), where differences between genicula from large and small fronds were not detectable (Fig. 5). Variances were not significantly different among large and small fronds at any geniculum position (Levene test: minimum $P=0.10$).

Geniculum breaking forces

Geniculum breaking forces spanned nearly an order of magnitude: the weakest geniculum resisted 2.9 N before breaking, and the strongest geniculum resisted 24.5 N before breaking (Fig. 6). In general, bigger genicula required more force to break than smaller genicula (Fig. 6). Linear regressions fitted to genicula data from the two size classes had significantly different slopes (ANCOVA $F_{1,153}=5.01$, $P<0.05$) and were analyzed separately. Regressions fitted to both large frond ($R^2=0.76$, $P<0.001$) and small frond ($R^2=0.72$, $P<0.001$) datasets were significant. For genicula from large fronds
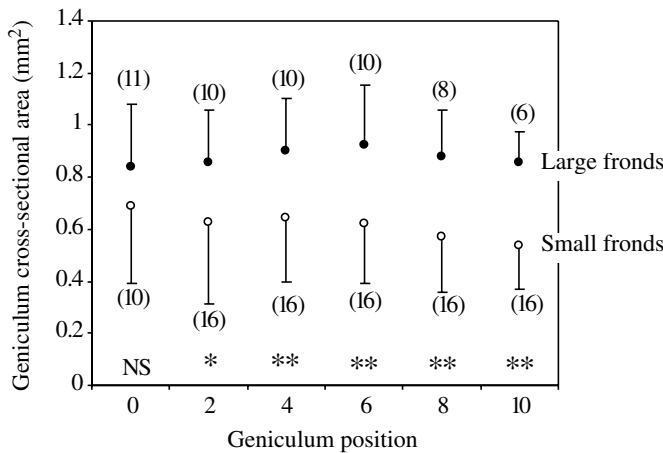

Fig. 5. Comparison of mean cross-sectional areas (A, mean ± s.d.) of genicula from small fronds (white circles) and large fronds (black circles). Central error bars were omitted to clarify the graph. The numbers of genicular measurements are given in parentheses. NS, not significantly different; *$P<0.05$, **$P<0.01$.
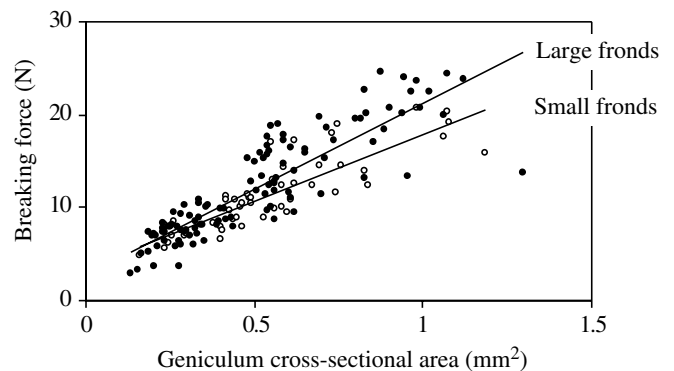

Fig. 6. Breaking forces of genicula from large fronds (black circles; $N=107$) and small fronds (white circles; $N=50$) as functions of their cross-sectional areas. For regression equations, see text.
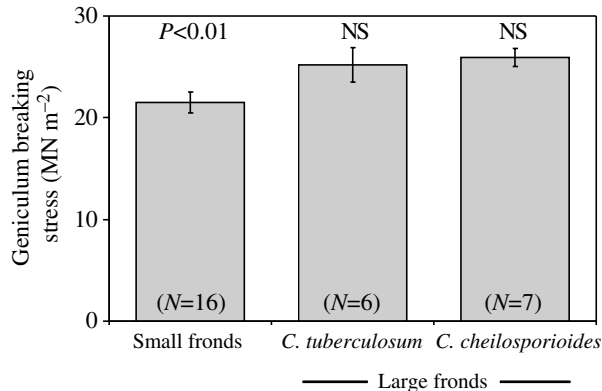
Fig. 7. Comparison of the mean breaking stress (σ; mean ± s.e.m.) of large and small *Calliarthron* fronds.

$F_b=18.49A+2.81$, and from small fronds $F_b=14.42A+3.49$. The slope of the large frond regression was 28% steeper than the slope of the small frond regression.

Geniculum tissue strength

The mean breaking stresses of genicular tissue from *C. cheilosporioides* and *C. tuberculosum* were 25.9 ± 0.9 MN m^{-2} and 25.2 ± 1.7 MN m^{-2}, means ± s.e.m., respectively (Table 1). These genicular measurements were not significantly different (Fig. 7; Student's $t=0.42$, d.f.=11, $P=0.68$), and data from large fronds of both species were pooled. The mean breaking stress of genicula from small fronds, 21.5 ± 1.0 MN m^{-2}, was significantly weaker than the mean breaking stress of genicula from large fronds, 25.6 ± 0.9 MN m^{-2} (Fig. 7; Student's $t=2.98$, d.f.=27, $P<0.01$). Variances among the two size classes were not significantly different (Levene test: $P=0.56$).

Variation within fronds

Genicula at the bases of large fronds required more force to break than genicula near the tips (Fig. 8A). In general, genicula supporting large branches resisted more force than genicula supporting small branches, and thallus planform area distal to genicula explained most of the variation in breaking force (mean: $R^2=0.75$, $P<0.05$). Similarly, genicula at the bases of large fronds were bigger in cross-section than genicula near the tips (Fig. 8B). Large branches were supported by large genicula, small branches were supported by small genicula, and thallus planform area distal to geniculum explained most of the within-frond variation in cross-sectional area (mean: $R^2=0.72$, $P<0.05$). In contrast, breaking stresses of genicula within a given frond were similar regardless of location (Fig. 8C). Thallus planform area distal to geniculum explained little of the within-frond variation in breaking stress (mean: $R^2=0.17$, $P=0.45$).

When fronds from the large size class were all plotted on the same linear scale, the slopes of breaking force–planform area regressions were significantly different (Fig. 9A; ANCOVA $F_{12,81}=9.81$, $P<0.001$). Regressions of larger fronds had lower slopes than regressions of smaller fronds (Fig. 9A). On average, basal
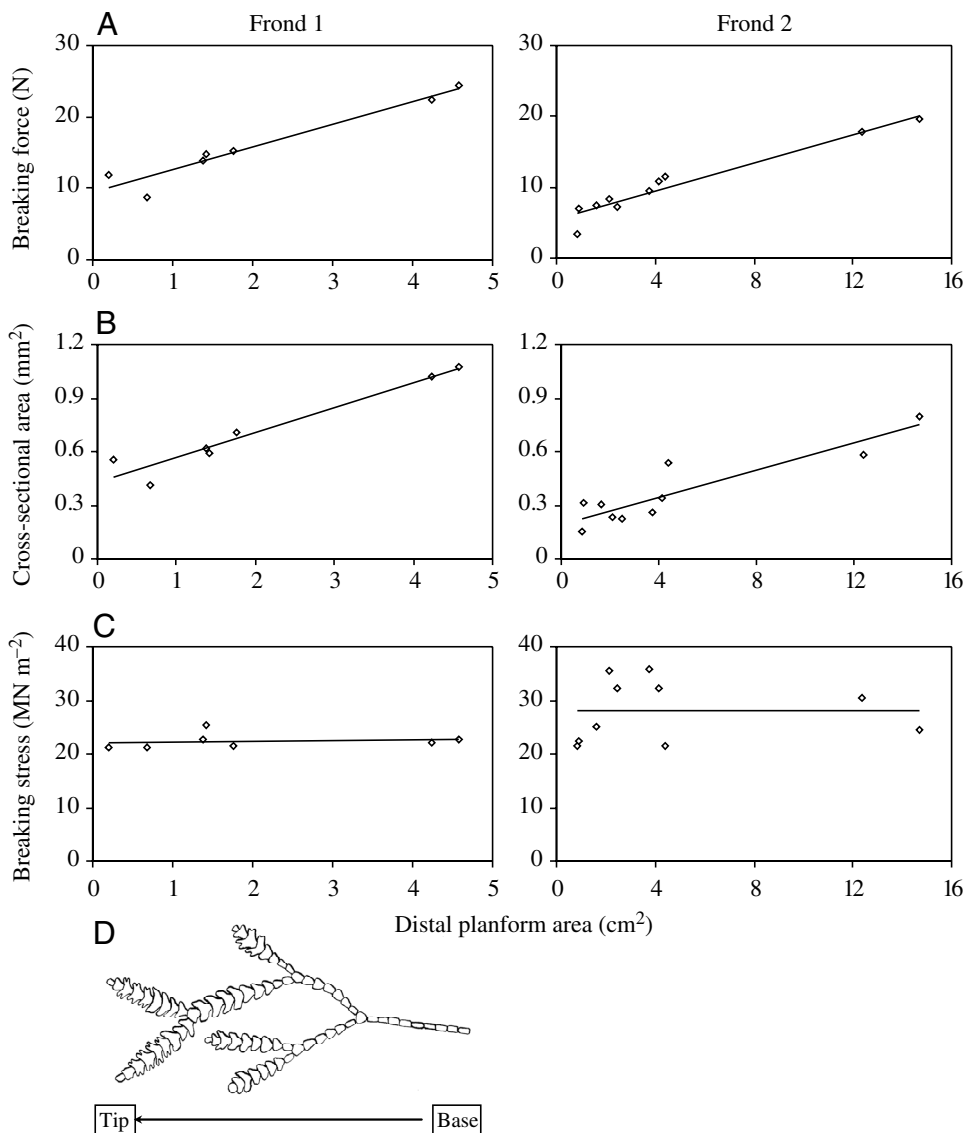

Fig. 8. Data collected from broken genicula in two representative fronds. (A) Breaking forces, (B) cross-sectional areas and (C) breaking stresses of genicula as functions of the planform areas of distal frond segments supported in flow. (D) Diagram of a representative frond oriented as in A–C.
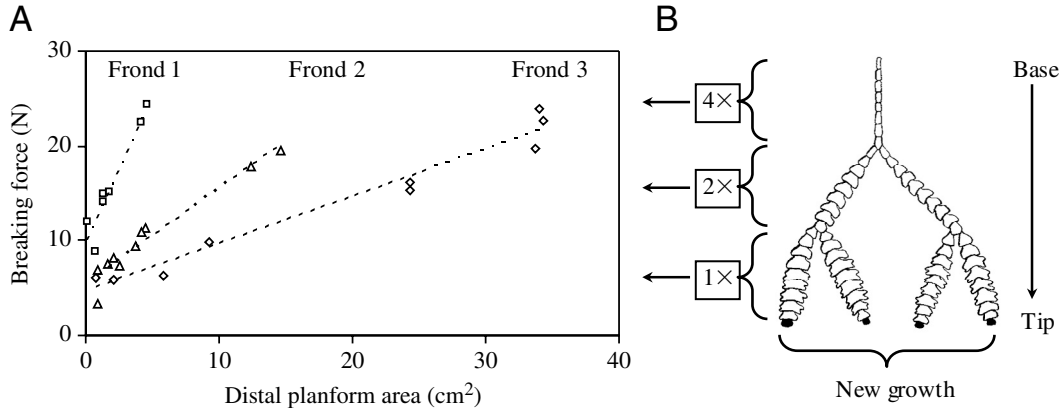
Fig. 9. (A) Breaking forces of genicula from three representative fronds as functions of the planform areas of distal frond segments supported in flow. (B) Diagram of hypothetical *Calliarthron* frond, explaining the pattern of decreasing slope with increasing frond size. $1\times$, $2\times$ and $4\times$ refer to the number of new growth units distal to genicula in the specified regions. See text for details.

genicula from the large size class supported 30-times more thallus planform area than basal genicula from the small size class.

Risk factor index

Risk factor index increased significantly with distal planform area (Fig. 10; $R^2=0.88$, $P<0.001$). Genicula which support the largest branches have the greatest risk of breaking (Fig. 10).

Discussion

Effect of decalcification

The modulus of rupture of calcified intergenicular tissue is greater than that of coral skeleton, less than that of gorgonian skeleton and about half that of mollusc shell (Table 1). However, based on Eqn 5, the tensile strength of *Calliarthron* intergenicula is estimated to be quite similar to that of coral skeleton, suggesting a material commonality among coral and coralline tissues, at least when stressed in tension. Furthermore, *Calliarthron* intergenicula and genicula are estimated to have similar tensile strengths (Table 1). This suggests that as calcified coralline tissue decalcifies to form genicula, material strength may not be affected. The decalcification process that removes the calcium carbonate from coralline cell walls may leave the other cell wall constituents unchanged.

However, decalcification produces genicula that are smaller in cross section than the nearest intergenicula (Fig. 4) and, because of that simple morphological difference, fronds almost always fail at genicula. For example, an average-sized *C. cheilosporioides* intergeniculum is predicted to resist approximately 41 N in tension before breaking, but an average-sized *C. cheilosporioides* geniculum snaps at 13 N. Over the course of conducting pull-to-break tests on 157 genicula, intergenicula broke before genicula only 10 times. Many of these incidental breaks occurred at geniculum/intergeniculum interfaces or near the frond tips where reproductive

conceptacles form, suggesting that tissue decalcification in these areas may have compromised the intergenicular material in unpredictable ways. Thus, genicula function as pre-defined breakage points along articulated fronds, not because of their weaker material strength, but because of their smaller cross-sectional area.

Geniculum strength

Tissue from *Calliarthron* genicula is more than an order of magnitude stronger than many brown and green algal materials, several times stronger than other red algal materials, and even 35% stronger than *Mastocarpus stellatus*, the previous record-holder (Table 1). Moreover, genicular tissue is as strong as coral skeleton with the added benefit of flexibility. Although seaweed materials are weaker than several other biological materials (see Gordon, 1978; Koehl, 1986), the dissimilarity of *Calliarthron* tissues compared to most other macroalgal tissues casts some doubt on the broad generalization that seaweeds are all 'weaklings.' Rather,
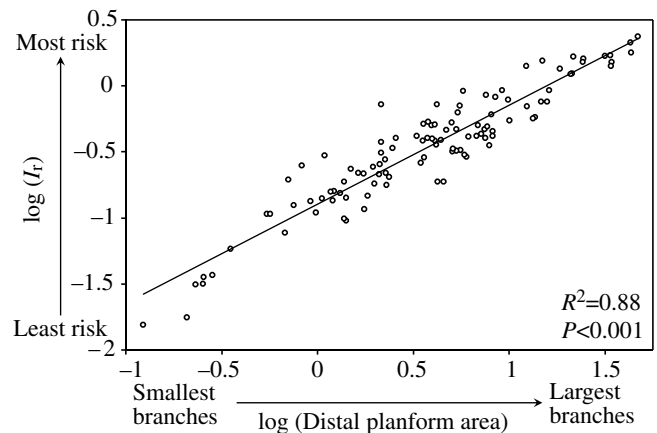

Fig. 10. Risk factor indices (I_r) of genicula from the large size class as a function of the planform areas of distal frond segments supported in flow.

macroalgal materials encompass a wide range of tissue strengths (e.g. Table 1).

From this widening strength distribution, two patterns are starting to emerge. First, in general, red algal materials are stronger than most brown algal materials which, in turn, are stronger than most green algal materials (Table 1). Second, algae with large cross-sectional areas, such as *Durvillaea*, are composed of some of the weakest materials, while skinnier algae, such as *Calliarthron*, possess the strongest materials (Table 1). To what degree these two patterns interact is unclear, but the continuum of fat-but-weak and skinny-but-strong is intriguing and merits further study. Strong materials and large cross-sectional area both contribute equally to algal breaking force and, as such, comprise two distinct strategies of mechanical design. By being ten-times stronger, *Calliarthron* can resist the same breaking force as a typical brown alga with ten-times the cross-sectional area.

Data presented here suggest that, as *Calliarthron* grows, genicula increase in both cross-sectional area and material strength, employing both strengthening strategies. On average, genicula from large fronds were composed of a material that was 20% stronger than tissue from small fronds (Fig. 7) – a conclusion that is generally supported by the 28% difference in large and small frond regression slopes (depicted in Fig. 6). Thus, for a given cross-sectional area, genicula from large fronds resist 20–28% more force than genicula from small fronds. Furthermore, genicula from large fronds were as much as 60% bigger, on average, than genicula from small fronds (Fig. 5; see geniculum position 10). These two processes work together to help genicula avoid breaking when stressed by intertidal waves. According to these patterns, an average geniculum that grows larger and strengthens its material composition could almost double its ability to resist breakage (i.e. $1.20\sigma \times 1.60A = 1.92F_b$).

Geniculum growth

Although correlative, data from the two size classes strongly support hypotheses of genicular growth and activity, calling into question Johansen's note that mature genicula do not have nuclei (Johansen, 1969). Data presented here are probably not the result of a selective process, where only the small fronds with big genicula composed of strong materials survive to become large fronds. If that had been the case, data from large fronds would have comprised a small subset of measurements from small fronds, resulting in differing variances between the two datasets. However, material strength and cross-sectional area data from large fronds do not represent a subset of small frond measurements, as seen in variances that were not significantly different. Correlative data, such as these, may have to suffice for now, as breaking stress and cross-sectional area measurements require destructive sampling, precluding repeated testing of individual genicula through time.

Previous studies have hinted that genicular cells may change their material properties through time. Johansen noted that genicular cell walls change in staining properties as they age (Johansen, 1974), and Borowitzka and Vesk found, in their study of a closely related articulated coralline, that the amount of fibrillar material in the genicular cell walls increases with age (Borowitzka and Vesk, 1978). Both of these observations support a shift in material properties and, potentially, strengthening of genicular tissue through time. The present study takes the first steps toward quantifying and proposing the functional effects of such a change.

That genicula breaking stress increases as fronds grow is in sharp contrast to recent studies of size-dependent breaking stress in fleshy macroalgae. For instance, the stipe/holdfast junctions of long and short blades of the red alga *Mazzaella splendens* have similar tissue strengths (Shaughnessy et al., 1996). Furthermore, no correlation has been found between breaking stress and blade area (*Nereocystis luetkeana*: Johnson and Koehl, 1994), thallus size (*Mastocarpus stellatus* and *Chondrus crispus*: Dudgeon and Johnson, 1992), or thallus length (*Chondracanthus exasperatus*: Koehl, 2000). However, the specimens in these last three studies were approximately the same size, and only Shaughnessy et al. (Shaughnessy et al., 1996) explicitly compared young plants to mature, adult plants. Conversely, Delf (Delf, 1932) briefly noted that young *Laminaria digitata* had weaker breaking stresses than adult plants and, on this basis, discarded young plants from her analysis. Future work on size-dependent breaking stress in macroalgae would help resolve these patterns.

This is the first study to provide evidence of secondary growth in genicula after maturation (i.e. after they have been decalcified and revealed *via* cortex dissolution). Previous studies only reported growth in genicula cells prior to maturation (Johansen, 1969) or else simply reported ranges of genicula characteristics after maturation (Yendo, 1904; Johansen, 1969; Johansen, 1981). Because mature genicula supposedly lack nuclei (Johansen, 1969), evidence of growth is of particular interest. *Post hoc* comparisons indicate that the youngest genicula (position 10) compared among the two size classes were most different, while the oldest genicula (position 0) were not significantly different at all (Fig. 5). This pattern of decreasing differences through time suggests that, although genicula grow after maturation, this growth may cease only a short distance (as few as ten geniculum positions) behind the apical meristem. Experiments are currently in progress to clarify the mechanism of genicular growth (e.g. *via* increasing cell dimensions, thickening cell walls, or producing new genicular cells).

Geniculum allometry

Geniculum size and breaking force vary predictably along articulated fronds: the largest/strongest genicula are positioned at the bases of fronds, where they support the majority of the frond in flow, and the smallest/weakest genicula are positioned near the tips, where they support smaller branches (Fig. 8A,B). If larger branches experience greater drag force (see Eqn 2), then genicula of a given strength appear ideally situated to support branches of a given size. Ostensibly, such a correlation is consistent with the engineering theory of optimal design (also known as Maxwell's Lemma), which states that each unit

should be exactly as strong as it needs to be, without wasting energy or materials in its construction (see Wainwright et al., 1982; Niklas, 1992). Although natural selection is not an optimizing process, comparisons to such theoretical optima can be useful in exploring the adaptive significance of specific traits (Endler, 1986). If *Calliarthron* fronds were optimally designed to resist drag force, then all genicula within a given frond would be stressed equally in flow and risk factor indices (I_r) would necessarily be constant. In other words, all genicula would be predicted to fail simultaneously. In addition, all force–planform area regressions would need to be parallel, implying that, as fronds grow bigger and drag force increases, the force to break supporting genicula increases proportionately. That genicula increase their breaking force by growing bigger and increasing their material strength as fronds develop lends support to such a hypothesis. However, the force–planform area regressions are not parallel (Fig. 9A), and risk factor indices varied significantly within large fronds (Fig. 10).

Instead, the force to break individual genicula changes relatively little compared to the planform area of a growing frond. For example, genicula toward the bases of fronds 1 and 3 resisted a similar breaking force, but basal genicula from frond 3 supported seven times the distal planform area (Fig. 9A). Such a pattern of regressions may be explained by the largely dichotomous branching structure of *Calliarthron* fronds (Fig. 9B). If one new unit of growth is added to each of four apical meristems, basal genicula suddenly support four new drag elements, while genicula near the tips only support one. Thus, data from basal genicula move to the right in Fig. 9 four-times faster than data from apical genicula. As fronds transition from the small to the large size class, the average planform area of the fronds increases 30-fold, but the basal genicula that support those growing fronds may only double their ability to resist breakage. Therefore, genicula which support the largest branches have the greatest risk of breaking (Fig. 10) and, consequently, fronds are predicted to break near the base. Observations of entire fronds cast ashore in tidepools and on beaches lend credibility to this prediction. *Calliarthron* are clearly not optimally designed to resist drag force.

Nevertheless, genicula are fairly well-adapted to withstanding intertidal water velocities. Assuming a very conservative drag coefficient [C_d=0.1; estimated for *Mastocarpus papillatus* (Bell, 1999)], I estimate that a large intertidal frond (40 cm^2) with a strong basal geniculum (that breaks at 25 N) should be able to resist water velocities of 11 m s^{-1} (see Eqn 2). With such ability, articulated fronds would be able to survive in the wave-swept intertidal zone, where water velocities up to 10 m s^{-1} are common (O'Donnell, 2005), but would likely break when conditions worsen. Additional experiments are currently underway to resolve the true drag coefficient and mechanical limitations of *Calliarthron* at high water velocities.

Benefits of breakage

Data presented here suggest that *Calliarthron* fronds are not optimally designed to withstand drag force and, instead, break near the base when critically stressed. Although significantly different from optimal, could this mechanical design be adaptive? Like many red algae, *Calliarthron* have a perennial crustose base that maintains numerous upright fronds concurrently and replenishes those fronds over a lifetime (Johansen, 1969; Abbott and Hollenberg, 1976). As wave force increases, upright fronds may be designed to fail in order to reduce the drag force imposed on the crustose base and decrease the risk of dislodgement of the crust itself. Several other wave-swept red algae, including *Mastocarpus* spp. (Carrington, 1990; Dudgeon and Johnson, 1992; Pratt and Johnson, 2002), *Mazzaella* spp. (Shaughnessy et al., 1996), *Chondracanthus exasperatus* (Koehl, 2000) and *Chondrus crispus* (Dudgeon and Johnson, 1992; Carrington et al., 2001; Pratt and Johnson, 2002), employ a similar breakage strategy. Jettisoned fronds may also be favorably linked to the reproductive cycle of *Calliarthron*, just as fragmentation plays a critical role in coral reproduction (Highsmith, 1982). *Calliarthron* intergenicula are capable of re-attaching to hard substratum, forming new crustose bases, and eventually growing new upright fronds (Johansen, 1969). Moreover, *Calliarthron* fronds remain healthy and continue to grow for months after separation from their crustose base (P.T.M., personal observation). Thus, broken fronds may continue to release sexual material after breakage, assuming they do not get buried or cast ashore.

Conclusions

Despite their largely calcified thalli, articulated coralline algae have flexible joints, called genicula, which allow fronds to bend and reorient when struck by intertidal waves. Genicula are composed of a material that is considerably stronger than fleshy algal materials, but similar in strength to coral skeleton with the added benefit of flexibility. Genicula also function as discrete breakage points along articulated fronds because the decalcification process reduces the cross-sectional area of the thallus, not because it compromises material strength. Within individual fronds, larger branches are supported by stronger genicula and, as fronds grow, genicula get bigger and genicular material gets stronger. However, articulated fronds do not exhibit an optimal mechanical design and, when critically stressed by an incoming wave, fronds are predicted to break near the basal genicula. Breakage may relieve the drag force experienced by the coralline crust and may be favorably linked to the reproductive cycle of *Calliarthron*.

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