

LIFE HISTORY PHASES AND THE BIOMECHANICAL PROPERTIES OF THE RED ALGA *CHONDRUS CRISPUS* (RHODOPHYTA)¹

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Chondrus crispus Stackhouse alternates between two isomorphic life history phases that differ in cell-wall phycocolloid composition. It has been long hypothesized that the gametophyte, with strong-gelling kappa-type carrageenans, is mechanically superior to the tetrasporophyte, with nongelling lambda-type carrageenans, which could contribute to the observed gametophytic dominance in many wave-swept environments. Standard mechanical tests were performed on distal tissues of *C. crispus* sampled from a range of environments in Narragansett Bay, Rhode Island, using a tensometer equipped with a video extensometer. Life history phase was by far the most important determinant of mechanical properties, whereas environmental factors had only modest influence (vertical distribution) or no effect (exposure); gametophytic distal tissues were 43% stronger, 21% more extensible, and 21% stiffer than tetrasporophytic distal tissues. However, the superior strength of gametophytic tissues was not evident at the stipe/holdfast junction (where breakage typically occurs), and the two phases were equally susceptible to dislodgment by a given force. The primary ecophysiological role of carrageenans in *C. crispus* may not be the provision of a structure to resist wave action.

Key index words: biomechanics; carrageenans; *Chondrus crispus*; material properties, Rhodophyta; strength, wave exposure; water motion

Abbreviations: MN, mega-Newton (= 10⁶ N); N, Newton

Like all members of the Gigartinales, the life history of *Chondrus crispus* Stackhouse alternates between two independent phases, gametophytic and tetrasporophytic. The theoretical stable ratio of gametophytes to tetrasporophytes in a population has been a recent topic of debate, with predicted ratios (based on various assumptions) ranging from 1:1 to 4:1 (Scrosati and DeWreede 1999). Such predicted ratios correspond to populations that are 50%–80% gametophytic, respectively.

In nature, life history ratios of *C. crispus* populations are often within the range predicted by theory (Craigie and Pringle 1978, Chopin 1986, McLachlan et al. 1988). Exceptions abound, however; many populations having been found to be overwhelmingly gametophytic (>80%; Wright 1981, Bhattacharya 1985, Chopin 1986, Dudgeon and Johnson 1992), although tetrasporophyte-dominated populations have been observed infrequently (Lazo et al. 1989). There is some evidence that tetrasporophytic abundance increases with depth (Mathieson and Burns 1975, Craigie and Pringle 1978, Chopin 1986).

Because of the widespread gametophytic dominance in populations of species of the Gigartinales (Scrosati and DeWreede 1999) and its apparent dependence on environmental conditions, it has been suggested that the two isomorphic life history phases of *C. crispus* are not ecologically similar. Although numerous speculations on the ecological superiority of gametophytes have been put forth (haploid vs. diploid advantages; Santelices 1990), none adequately explains the pattern of life history ratios observed in nature. One hypothesis that has not been fully explored, however, is that of potential biomechanical difference: if gametophytes were mechanically stronger than tetrasporophytes, they would be less susceptible to dislodgment by waves and would consequently dominate in wave-swept habitats, especially high on the shore where water motion is most severe (Denny 1988, Carrington 1990, Gutierrez and Fernandez 1992, Hurd 2000).

The biomechanical hypothesis is interesting not only because it may explain field observations of life history ratios, but also because it potentially has a biochemical basis. The life history phases of *C. crispus* differ strikingly in their phycocolloid biochemistry: gametophytes produce strong-gelling κ -type carrageenans, whereas tetrasporophytes produce nongelling λ -type carrageenans (McCandless et al. 1973, Chopin et al. 1999). In 1973, Yaphe was the first to speculate that *C. crispus* gametophytes should have a structural advantage, because “the gel gives the plant a structure to resist wave action and desiccation” (Harvey and McLachlan 1973). Our understanding of the chemistry of phycocolloids has advanced considerably in recent years, largely due to the economic importance of these

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compounds (Chopin et al. 1999). However, despite the fact that carrageenans can represent a major portion of the dry weight of a plant (up to 74.7%; Chopin et al. in press), relatively little is known about their ecophysiological role (Chopin 1986). Various studies have explored how carrageenan content and type vary with environmental conditions (Fuller and Mathieson 1972, Neish et al. 1977, Chopin et al. 1987, Chopin and Floc'h 1992, Chopin and Wagey 1999), but the role of carrageenans in determining macroalgal biomechanics has never been tested directly.

The purpose of this study is to compare the mechanical properties of *C. crispus* life history phases that are isomorphic yet differ in carrageenan types. The comparison of gametophyte and tetrasporophyte biomechanics is made under a range of environmental conditions that vary in vertical distribution (intertidal vs. subtidal) and wave exposure (exposed vs. sheltered).

MATERIALS AND METHODS

Whole plants of *C. crispus* were collected July 6–24, 2000 from the shores of Ft. Wetherill State Park, Rhode Island (41.5°N, 71.4°W) and maintained in flowing seawater for no more than 48 h before mechanical testing. Over 300 plants were sampled haphazardly from each of four sites (two vertical distributions \times two exposures); intertidal and subtidal (-3.0 m below mean lower low water) plants were collected from each of an exposed headland and a sheltered cove. Of these sampled plants, only a small subset (<10%) were selected for biomechanical analysis in the laboratory, as described below.

The initial qualitative designation of a site as "exposed" or "sheltered" was confirmed by deploying three replicate maximum velocity meters (Bell and Denny 1994) at each intertidal site August 7–12, 2000. Each meter was read and reset daily. A two-way repeated measures analysis of variance (ANOVA) was used to evaluate the effect of site and date on the water velocity recordings.

In the laboratory, plants were designated as tetrasporophytic or gametophytic via a visual screening (gametophytes are iridescent; Craigie et al. 1992), followed by a resorcinol assay (Garbary and DeWreede 1988). In this manner, a three-factor (life history phase, vertical distribution, and exposure) fixed-effect orthogonal design was used to examine the mechanical properties of *C. crispus*.

Standard tensile tests were conducted using a computer-interfaced tensometer equipped with a 50-N load cell (model 5565, Instron Corp., Canton, MA). A sample approximately 2 cm long was isolated from the distal region of each plant that was 1) a "healthy" deep red color, 2) free of obvious flaws (i.e. grazing marks or reproductive tissue), and 3) contained a natural "neck," or region of reduced cross-sectional area, where breakage was likely to occur when tension was applied. The sample was held at each end by a pneumatic grip ($4 \text{ kg}\cdot\text{cm}^{-2}$) lined with fine sandpaper to provide additional friction. Two silver paint stripes, approximately 5 mm apart, were applied within the neck of the sample to define the test region. Because a minimum of 5 mm of tissue was placed in the grip, the test region was near, but never included, apical tissue. Stipe material was not used in these laboratory tests because its tapered geometry did not meet the third criterion (failure would always occur at the grips).

The distance between the two stripes, or extension (l), was detected by a noncontacting video extensometer (± 0.005 mm; model 2663, Instron Corp.). The sample was wetted with seawater before testing at a crosshead extension rate of $10 \text{ mm}\cdot\text{min}^{-1}$ until failure occurred. Thickness and width of the test region were measured to the nearest 0.02 mm using dial calipers. Force measurements were converted to stress (σ , in $\text{N}\cdot\text{m}^{-2}$) by

dividing by the cross-sectional area of the test region. Extension was converted to strain (ϵ) using the formula $(l - l_0)/l_0$, where l_0 is the initial unstressed length of the test region.

Three mechanical properties were calculated for each sample. Modulus (or material stiffness, E , in $\text{N}\cdot\text{m}^{-2}$) was calculated as the slope of a regression line through the steepest linear portion of the stress-strain curve. Ultimate stress (or material strength, σ_u) and ultimate strain (or material extensibility, ϵ_u) were reported only for those samples where failure occurred in the test region (not due to damage by the grips). Occasionally, the test region realigned out of view of the extensometer during a test; calculations involving strain measurements were omitted in these instances. Thus, sample size was variable for each category, ranging from 4 to 20. A three-way ANOVA was used to evaluate the effects of life history phase, tidal height, and exposure on the mechanical properties of *C. crispus*.

The breaking force, or force to dislodge intertidal *C. crispus* gametophytes and tetrasporophytes, was measured *in situ* May–July 2000 at the exposed Ft. Wetherill site and at a similarly wave-exposed site at Beavertail State Park (approximately 4 km to the southwest). Following the method of Carrington (1990), a string connected to a recording spring scale was looped around the distal portion of a haphazardly selected plant. The scale was gently pulled parallel to the substrate, causing dislodgment to occur within 1–2 s. Failure typically occurred at the stipe/holdfast junction (not at the location of the string loop), and the cross-sectional area of this circular region was calculated from stipe diameter measured with calipers to the nearest 0.01 mm. Breaking force was divided by stipe cross-sectional area to yield material strength in $\text{N}\cdot\text{m}^{-2}$. Life history phase of each sample was determined using the resorcinol assay. A Mann-Whitney rank sum was used to test for differences in stipe strength between the two life history phases. Note that life history was the only factor varied in the field determination of breaking force because the laboratory tests indicated the factors vertical distribution and exposure to be relatively unimportant (see Results).

SigmaStat software (version 2.03, SPSS Inc., Chicago, IL) was used for all statistical analyses, except for the three-way ANOVA, where Systat was used (version 8.0, SPSS Inc.).

RESULTS

Daily measurements of maximal water velocity confirmed the designation of the headland and cove sites as exposed and sheltered, respectively. Maximal water velocities ranged from 1.7 to $3.3 \text{ m}\cdot\text{s}^{-1}$ at the sheltered intertidal site, whereas concurrent velocities at the exposed intertidal site ranged from 3.3 to over $6.3 \text{ m}\cdot\text{s}^{-1}$ (Table 1). Note that the upper limit for the recorders used in this study, $6.3 \text{ m}\cdot\text{s}^{-1}$, was reached at the exposed site on 2 of the 6 days; water velocity was therefore underestimated at the exposed site on these days. Nonetheless, a repeated measures two-way ANOVA indicated a significant difference between sites ($P <$

TABLE 1. Summary of daily maximal water velocities ($\text{m}\cdot\text{s}^{-1}$) recorded at two intertidal sites, August 7–12, 2000.

Date	Sheltered cove	Exposed headland
7 August	2.3 ± 0.3	4.3 ± 0.5
8 August	1.9 ± 0.2	3.7 ± 0.4
9 August	2.7 ± 0.5	5.5 ± 0.3
10 August	2.5 ± 0.6	6.1 ± 0.1
11 August	2.4 ± 0.5	$>6.3^a$
12 August	2.7 ± 0.5	$>6.3^a$

Values are means \pm SD for three replicates.

^a Velocities exceeded maximum limit of recorders; values are therefore underestimates.

0.001), with velocities at the exposed site, on average, exceeding those measured at the sheltered site by a factor of 2. Maximal velocity also varied significantly from day to day ($P < 0.001$), as did the magnitude of the difference between sites (site \times day interaction, $P < 0.001$).

A collection of over 300 plants from the sheltered intertidal site failed to yield any tetrasporophytic plants. This treatment combination was therefore missing from the orthogonal design, and the number of interactions evaluated by the three-way ANOVA was consequently reduced. Nonetheless, differences between the mechanical properties of life history phases were evident (Table 2) and are illustrated by the representative stress-strain curves shown in Figure 1. Specifically, ultimate stress, ultimate strain, and modulus differed significantly between life history phases ($P < 0.001$, 0.016, and 0.003, respectively; Table 3). When averaged across vertical distribution and exposure treatments, gametophytes were 43% stronger, 21% more extensible, and 21% stiffer than tetrasporophytes (Table 2).

No significant effect of exposure was observed in any of the mechanical properties ($P = 0.129$ – 0.333 ; Table 3). Vertical distribution had no significant effect on ultimate strain or modulus ($P = 0.578$ and 0.650 , respectively; Table 3) but did influence ultimate stress ($P = 0.039$; Table 3). However, this latter effect was modest; when averaged across life history and exposure treatments, subtidal plants were only 2% stronger (mean \pm SEM was 5.04 ± 0.21 [$n = 46$] and 5.15 ± 0.22 [$n = 45$] $\text{MN}\cdot\text{m}^{-2}$ for intertidal and subtidal samples, respectively). None of the interactions was significant for any of the mechanical properties measured (Table 3).

When measured *in situ*, the breaking force of *C. crispus* did not depend on the cross-sectional area of the stipe/holdfast junction (Fig. 2; $P = 0.66$ and 0.54 for gametophyte and tetrasporophyte linear regression, respectively). Material strength of the stipe/holdfast junction did not differ between gametophytes and tetrasporophytes (Mann-Whitney rank sum test; $P = 0.31$), with a pooled mean value of $10.83 \pm 1.19 \text{ MN}\cdot\text{m}^{-2}$ ($n = 58$).

DISCUSSION

Of the factors considered in this study, life history phase was by far the most important determinant of

mechanical properties of *C. crispus*, whereas environmental factors had only modest influence (vertical distribution) or no effect (exposure). The most-cited biological roles of cell-wall polysaccharides of algae are mechanical, hydration, and electrochemical regulations (Kloareg and Quatrano 1988). The results of this study are consistent with the hypothesis that carrageenan types influence macroalgal mechanical properties: distal portions of gametophytes (which produce the strong-gelling $\kappa/\iota/\mu$ carrageenans) were significantly stronger, more extensible, and stiffer than distal portions of tetrasporophytes (which produce nongelling $\lambda/\theta/\alpha$ carrageenans). From a quantitative point of view within the same phase (the same carrageenan type), the mechanical and hydration regulating role of carrageenans is, however, questionable. Fuller and Mathieson (1972) showed no significant difference in carrageenan content between exposed and sheltered populations of *C. crispus* in New Hampshire. These authors, as well as Mathieson and Tveter (1975), showed that carrageenan content was lower in intertidal than in subtidal plants, whereas Chopin and Floc'h (1992) showed no correlation between vertical distribution and carrageenan content in *C. crispus* from Brittany, France.

It is important to note that an exclusively mechanical role for carrageenans remains at this point speculative. Carrageenans are only one of many components of *C. crispus* cell walls, and it is possible that some other component(s) of the cell wall or intercellular matrix could also be a primary load-bearing structure(s) in the plant (as has been suggested for *Egregia menziesii* [Turner] Areschoug; Kraemer and Chapman 1991). Indeed, life history phases of *C. crispus* also differ in cuticle ultrastructure (Craigie et al. 1992), but the mechanical contribution of the cuticle is not known.

Regardless of whether it is due to carrageenan type or some other aspect(s) of their ultrastructure, gametophytes appear to have distal tissues that are mechanically superior (stronger, stiffer, more extensible) to those of tetrasporophytes. Does this translate to a mechanical "advantage" for gametophytes? The answer is not so clear. As reviewed by Bell (1999), plant failure (breakage) occurs whenever the hydrodynamic stress

TABLE 2. Mechanical properties of *Chondrus crispus*.

	Ultimate stress, σ_u ($\text{MN}\cdot\text{m}^{-2}$)	Ultimate strain, ϵ_u	Modulus, E ($\text{MN}\cdot\text{m}^{-2}$)
Gametophytes			
Subtidal exposed	5.48 ± 0.33 (12)	0.47 ± 0.04 (7)	14.55 ± 0.68 (8)
Subtidal sheltered	5.68 ± 0.33 (18)	0.45 ± 0.03 (15)	16.22 ± 1.09 (18)
Intertidal exposed	5.76 ± 0.28 (16)	0.51 ± 0.04 (12)	16.13 ± 1.06 (13)
Intertidal sheltered	5.30 ± 0.29 (20)	0.44 ± 0.03 (18)	15.71 ± 0.94 (17)
Tetrasporophytes			
Subtidal exposed	4.44 ± 0.49 (10)	0.40 ± 0.04 (8)	14.35 ± 1.19 (9)
Subtidal sheltered	3.87 ± 0.59 (5)	0.38 ± 0.09 (4)	10.88 ± 1.22 (6)
Intertidal exposed	3.36 ± 0.27 (10)	0.36 ± 0.01 (6)	13.82 ± 1.27 (9)
Intertidal sheltered	N/A	N/A	N/A
All gametophytes	5.55 ± 0.15 (66)	0.46 ± 0.02 (52)	15.82 ± 0.53 (58)
All tetrasporophytes	3.89 ± 0.26 (25)	0.38 ± 0.02 (18)	13.28 ± 0.75 (24)

Values are means \pm SEM (n).

TABLE 3. Summary of three-way ANOVA of mechanical properties of *Chondrus crispus*.

Source	df	MS	F ratio	P value
Ultimate stress, σ_u				
Life history phase	1	42.418	26.647	<0.001 ^a
Vertical distribution	1	7.037	4.420	0.039 ^a
Exposure	1	2.586	1.624	0.206
Life history phase \times vertical distribution	1	5.419	3.404	0.069
Life history phase \times exposure	1	1.367	0.859	0.357
Vertical distribution \times exposure	1	1.750	1.099	0.297
error	84	1.592		
Ultimate strain, ϵ_u				
Life history phase	1	0.081	6.186	0.016 ^a
Vertical distribution	1	0.004	0.312	0.578
Exposure	1	0.012	0.954	0.333
Life history phase \times vertical distribution	1	0.010	0.758	0.387
Life history phase \times exposure	1	0.000	0.015	0.904
Vertical distribution \times exposure	1	0.004	0.300	0.586
error	63	0.013		
Modulus, E				
Life history phase	1	144.484	9.341	0.003 ^a
Vertical distribution	1	3.206	0.207	0.650
Exposure	1	36.476	2.358	0.129
Life history phase \times vertical distribution	1	10.495	0.679	0.413
Life history phase \times exposure	1	13.954	0.902	0.345
Vertical distribution \times exposure	1	58.292	3.769	0.056
error	84	15.467		

^a $P \leq 0.05$.

(force per area) on a given tissue exceeds its material strength. For a member of the Gigartinales like *C. crispus*, hydrodynamic drag typically causes failure at the stipe/holdfast junction, not at the distal branches. This study indicates the stipe/holdfast junctions of the two phases do not differ in breaking force or strength (force per area). Considering that the breaking stress of the stipe is approximately twice that of the distal region, it is possible that the stipe ultrastructure is modified to reduce any mechanical role of carrageenan, as has been suggested by Dudgeon and Johnson (1992). Thus, the large differences observed in the mechanical properties of the distal tissues are not manifested in the stipe/holdfast junction; gametophytes and tetrasporophytes are equally susceptible to dislodgment by a given force.

It is possible, however, that the mechanical properties of the distal region could influence the hydrodynamic loading of *C. crispus*. In general, less stiff plants are more flexible and can reduce drag by reorienting with flow (Vogel 1984, 1994, Carrington 1990, Koehl 1996, Bell 1999). However, flexibility is only one of many complex factors that determine hydrodynamic drag on a plant (Carrington 1990), and it is not clear whether a 21% increase in stiffness would effect an increase in drag (and dislodgment) of gametophytes that is biologically relevant.

On the other hand, decreased strength and extensibility of the distal region could render tetrasporophytes more susceptible to size reduction by waves or herbivores (Denny et al. 1989, Padilla 1989, 1993, Blanchette 1997). The advantage of size reduction ap-

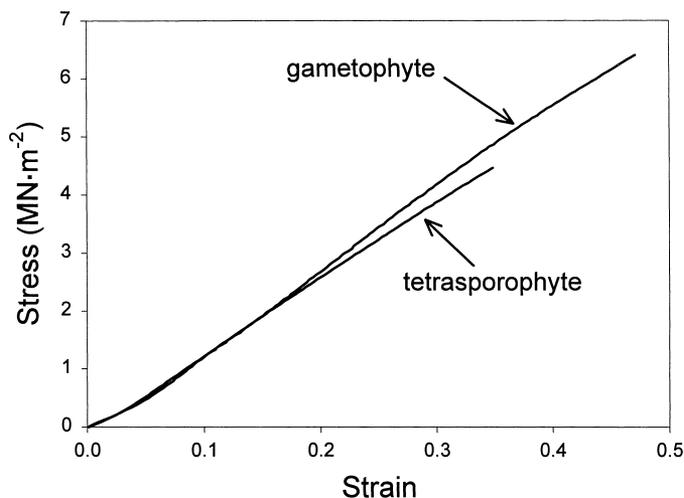


FIG. 1. Representative tensile tests of gametophytic and tetrasporophytic *Chondrus crispus* samples from a subtidal exposed site.

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