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Grazing damage and encrustation by an invasive bryozoan reduce the ability of kelps to withstand breakage by waves

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ABSTRACT

Increased breakage of macroalgal fronds during large wave events can significantly reduce canopy cover and biomass. We examined the effects of encrustation by the invasive bryozoan *Membranipora membranacea* and damage by the snail *Lacuna vincta* on the ability of kelp blades (*Saccharina longicruris*, *Laminaria digitata*, and *Laminaria complanata*) to withstand wave forces. Using standard materials testing procedures, we documented significant reductions in the maximum stress before breakage, toughness, and extensibility of blade material following bryozoan encrustation. Histological sections of blade tissue indicated a significant degradation of the outer layers of cells following prolonged encrustation by *M. membranacea* as a likely cause of weakening. Full-thickness perforations and partial-thickness grazing scars also reduced blade strength, suggesting that grazing damage can initiate cracks that lead to blade breakage. Our findings provide a mechanistic link between the damaging effects of mesograzers and encrusting bryozoa on their algal hosts and the export of detrital material from subtidal kelp beds.

1. Introduction

The biomass of macroalgal beds is largely dependent on the balance of productivity and the rate at which thalli erode, fragment or dislodge from the substrate during periods of heavy wave action (Krumhansl and Scheibling, 2011; Seymore et al., 1989). Macroalgae in rocky intertidal and subtidal zones have developed morphological and material adaptations to withstand extreme wave conditions. Thalli are composed of highly flexible material that reconfigures and orients to flow to reduce drag (Boller and Carrington, 2006; Gaylord and Denny, 1997; Vogel, 1984), which is the primary force generating tension on blades. For many macroalgal species, the measured tensile strength of thalli exceeds the predicted force of drag in their natural habitats, suggesting that breakage or dislodgement is unlikely (Denny et al., 1997; Friedland and Denny, 1995; Utter and Denny, 1996). However, observational studies have shown that algal blades frequently fragment and dislodge (Krumhansl and Scheibling, 2011; Seymore et al., 1989), indicating that external factors limit the ability of macroalgae to withstand breakage by waves (Utter and Denny, 1996).

Fragmentation and dislodgement of large macroalgae, such as kelps, can occur through breakage at several points along the thallus. Failure at the holdfast and stipe is common, particularly at the junctions between stipe and holdfast, and stipe and blade (Duggins et al., 2001; Seymore et al., 1989; Utter and Denny, 1996). This type of breakage has been the focus of most studies because it causes mortality of individual thalli. Failure may also occur in the middle of blades, resulting in fragmentation. This process does not cause mortality unless breakage occurs below the meristem at the base of the blade. Fragmentation of blades, however, can result in significant losses of biomass from subtidal kelp beds (Krumhansl and Scheibling, 2011).

Breakage by wave action is often the result of previous damage to part of the thallus through grazing, abrasion with the substrate, or physiological stress (Biedka et al., 1987; Black, 1976). Grazing by herbivores may generate nicks, holes, and cuts that concentrate stress, leading to crack formation, propagation, and blade breakage at forces lower than the maximum recorded force-to-break undamaged macroalgal tissue. Cracks at the site of damage to a macroalgal blade can form during repetitive, low-force loading in wave-swept locations, propagating gradually until failure occurs (Mach, 2009). Alternatively, damage may cause stress concentration at high wave forces that leads to rapid crack formation and propagation. In particular, breakage at the stipe and holdfast has been linked to damage by herbivorous snails (Black, 1976; Duggins et al., 2001) and urchins (Biedka et al., 1987; Koel and Wainwright, 1977).

Seasonal variation in the rate of blade breakage of laminarian kelps along the Atlantic coast of Nova Scotia has been attributed to a combination of environmental and biological factors. Such factors include damage to blades caused by mesograzers (mainly the snail *Lacuna vincta*) and encrustation by the invasive bryozoan *Membranipora membranacea* (Krumhansl and Scheibling, 2011), although the direct effect of this damage on the material properties of blades has not been examined. *L. vincta* creates full perforations or partial-thickness grazing

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scars (excavations) on kelp blades, which may reduce the force to break blade tissue, increasing the incidence of blade breakage (Krumhansl and Scheibling, 2011). *M. membranacea* encrusts the surface of kelp blades, increasing rates of blade breakage (Krumhansl and Scheibling, 2011) leading to major canopy losses during periods of heavy wave action (Scheibling et al., 1999; Scheibling and Gagnon, 2006). It has been proposed that the mechanism by which the bryozoan renders the kelp prone to breakage is increased brittleness (Dixon et al., 1981), but this effect has not been tested explicitly.

Using a combination of materials testing and histological techniques, we have examined the effect of grazing damage by *L. vincta* or encrustation by *M. membranacea* on the material properties of laminarian kelps, including maximum stress (tensile strength) and strain (extensibility) before breakage, toughness, and stiffness. We predict that perforations and excavations generated by snail grazing and bryozoan encrustation will reduce the overall strength, extensibility, and amount of energy required to break kelp tissues. We also predict that *M. membranacea* will increase the stiffness of blades.

2. Methods

2.1. Sample collection

Samples of the kelps *Saccharina longicruris* and *Laminaria digitata* were collected offshore of a site (The Lodge, 44°33′32.98″N, 64°01′ 56.75″W) on the western shore of St. Margarets Bay, Nova Scotia, Canada. Undamaged thalli and those encrusted by *M. membranacea* (>25 cm blade length) were collected from 4 to 7 m depth on November 28, 2009 using SCUBA. Kelp thalli with grazing damage were selected from the same depths on December 15, 2009. For regional comparisons of the effect of grazing damage by *L. vincta* on material properties of kelps, samples of *Laminaria complanata* (>25 cm) were collected in the same depth range at a site (Shady Cove, 48°33′9″N, 123°3′ 43″E) on San Juan Island, Washington, USA on March 22, 2010. After collection, kelps were transported in enclosed bins for no more than 2 h to flow-through seawater tanks.

For kelps from Nova Scotia, the effect of encrustation by *M. membranacea* on material properties of blade tissues was examined at two levels of encrustation: fully encrusted or lesioned. Fully encrusted samples were completely covered on both sides by *M. membranacea* with no visible signs of tissue degradation. After prolonged encrustation, kelp tissue beneath a colony of *M. membranacea* may become highly degraded, resulting in perforation of the blade, termed a lesion. Lesioned samples were selected from highly degraded areas adjacent to such a perforation (Fig. 1). We expected that lesions would reduce the tensile strength, extensibility, and toughness of kelp blades to a greater degree than encrustations. Similarly, the effect of the mesograzer *L. vincta* was examined at two levels of grazing damage: excavations and full perforations of the blade (Fig. 1). Excavations spanned all or part (40 to 100%) of the sample width in the testing region, while perforations were always smaller in diameter (6 to 55%) than the width of the sample. We expected perforations would reduce the tensile strength, extensibility, and toughness of kelp blades to a greater degree than excavations. Results from these four sample condition groups were compared to undamaged and non-encrusted sections of each blade. For samples from Washington, only the effect of grazing was examined.

2.2. Mechanical testing

Standard pull-to-break uniaxial tensile tests were performed as per Carrington et al. (2001). In Nova Scotia, samples were tested using a computer-interfaced, 458-series MTS planar biaxial testing system. Extension was measured using video from a camera (Cohu CCD 4190) mounted above the sample, and interfaced with a Scion video capture board operating at 14.98 Hz. In Washington, samples were tested using a computer-interfaced tensometer (model 5565; Instron Corp., Canton, MA, USA) equipped with a non-contacting video extensometer (Model 2663, Instron Corp.). Both testing systems were equipped with load cells (100 N in Nova Scotia, 50 N in Washington). Samples of standard dimensions were excised from kelp using a "dog bone"-shaped template (ASTM/ISO D638-03, Fig. 1) in a longitudinal direction on blades. The distance of the sample from the base of the blade was recorded.

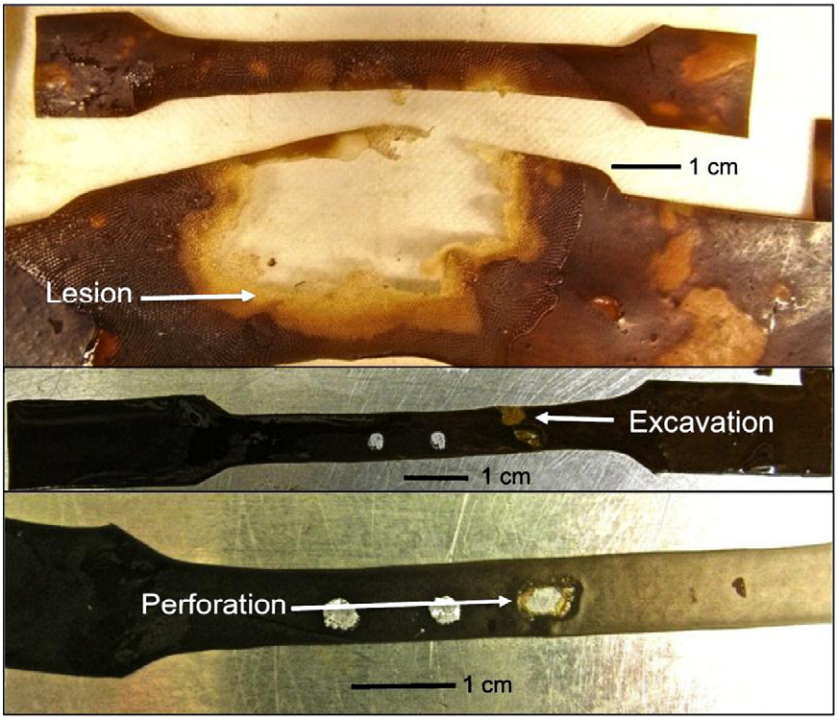

Fig. 1. Photographs of lesioned, excavated, and perforated samples used to examine the effect of encrustation by *M. membranacea* and grazing damage on the material properties of kelps. Samples were excised from blade tissue in standard dimensions using a "dog bone" template.

Thickness (0.01-mm precision) was measured in three locations on each sample using a non-rotating thickness gauge prior to testing. In Nova Scotia, samples were held in manually tightened grips lined with neoprene and fine sandpaper. Two white candy confection balls were placed 3–4 cm apart on the surface of the sample, defining the testing region. In Washington, samples were held in pneumatic grips lined with fine sandpaper at a pressure of 20 psi. Two silver dots were painted with solvent-based paint approximately 10 mm apart on the surface of the sample to define the testing region. Samples from this experiment were never observed to break at the silver dots, which was consistent with previous studies that used the same marking material on macroalgal samples (Boller and Carrington, 2007; Carrington et al., 2001). Therefore it was assumed that samples were unaffected by the paint. Samples were photographed before testing, and sample width was measured in the testing region using image analysis (ImageJ). The sample was extended at a rate of 50 mm min^{-1} until breakage occurred. Samples were tested in open air at room temperature, and periodically wetted with seawater to prevent desiccation.

Applied force (N) was captured during extension for each sample. Stress (σ) was then calculated as:

$$\alpha = F / A$$

where F is force (N) and A is the initial cross-sectional area of the sample (mm^2). In Nova Scotia, extension at grips was measured during testing, and grip-to-grip strain (ε) was calculated as:

$$\varepsilon = \Delta l / l_o$$

where Δl is extension between the markers (mm) and l_o is the initial length of the testing region defined by the markers (mm). Strain in the testing region was calculated from grip-to-grip strain using a correction technique that related grip-to-grip extension to extension in the testing region. To generate this correction, the distance between dots was measured in still images (ImageJ, 0.01-mm precision) taken from the captured video at 10 evenly spaced increments by time throughout the course of the test, and divided by grip extension at the same time points. This ratio was then plotted against video frame number and a logarithmic function was fitted to the points ($R^2 > 0.90$). This function was then used to convert the grip-to-grip extension to extension in the testing region and these data were then synchronized to the captured load data. In Washington, a video extensometer measured extension of the testing region by tracking the movement of the silver dots throughout the course of the video (0.005-mm precision) and strain was calculated as described. A tangent modulus of material stiffness (MPa) was calculated as the steepest slope of the stress–strain curve and toughness was calculated as the area under the stress–strain curve (MJ m^{-3}).

2.3. Statistical analysis

Analysis of covariance (ANCOVA) was used to identify covariates common to all sample conditions that affect material properties for each species. Potential covariates were independently included in ANCOVA with condition as the main factor, and each material property (maximum stress before breakage, strain at fracture, modulus, and toughness) as the dependent variable. Linear regression was then used to determine the direction of the relationship between significant covariates and material properties. Linear regression was also used to examine the relationship between material properties and relevant independent variables within two levels of grazer damage (excavation and perforation width) for each kelp species. The effect of condition on material properties was examined using Multivariate Analysis of Covariance (MANCOVA) using statistically significant covariates for each kelp species where present, or MANOVA where no significant covariates were detected. 1-way ANCOVA or ANOVA followed by Tukey's HSD test were then used to compare sample condition groups for each material property. Data were square-root transformed where necessary to meet the assumptions of homogeneity of variance (Bartlett's test, $p<0.05$) and normality (Shapiro–Wilk test, $p<0.05$). Plots of the residuals versus predicted values were examined to test the assumption of linearity where linear regressions were used.

2.4. Histology

Histological techniques were used to examine the effect of *M. membranacea* on blade tissues of *S. longicruris* and *L. digitata* collected from The Lodge (4 to 7 m depth) on 18 November 2009. Kelps were transported and held as above, and processed within 24 h of collection. Samples $<1\ cm^2$ were excised from undamaged, encrusted, and lesioned sections (defined as above) and fixed in 7% formalin in seawater for 24 h. Samples were then washed twice in 70% ethanol in preparation for dehydration, clearing, and paraffin wax infiltration using the ASP300 Leica Tissue Processor. Specimens were embedded in paraffin and cut into 5 μm-transverse sections using a Reichert–Jung rotary microtome and mounted onto superfrost plus slides (Fisherbrand). Slides were then oven dried at 37 °C overnight before staining. Slides were de-paraffinized through xylene and graded alcohols and stained in 0.1% Saffranin for 6 min. Slides were then dehydrated in graded alcohols and mounted to cover slips with Cytoseal (Richard-Allan Scientific). The blade tissue sections were then examined using light microscopy (Nikon Eclipse E600 microscope) and photographed using a Nikon DXM1200F digital camera.

3. Results

Stress–strain curves of *S. longicruris*, *L. digitata*, and *L. complanata* were typically characterized by an initial linear or j-shaped portion where the sample deformed until the limit of extension was reached, defined as the location where the curve changed shape (~0.1 strain for *S. longicruris* and *L. complanata*, ~0.5–2.0 for *L. digitata*) (Fig. 2). The sample then entered a second phase in which plastic deformation likely occurred, resulting in a curve that was concave downward until failure. Some curves from grazed condition groups never reached this second phase, failing within the linear or j-shaped region (Fig. 2). The shapes of the curves for *S. longicruris* and *L. complanata* were more uniform across sample conditions than were the curves of *L. digitata* (Fig. 2).

ANCOVA showed that distance of the sample (for all conditions pooled) from the base of the blade had a significant effect on maximum stress before breakage in *S. longicruris* ($p = 0.044$) and on strain at fracture in *L. complanata* ($p = 0.047$). In both cases the material property decreased with distance (linear regression, *S. longicruris*: $b = -7.05 \times 10^3$, *L. complanata*: $b = -0.01$). There was no detectable effect of blade thickness on material properties in any of the three species of kelp, and no effect of distance from the base of the blade on material properties in *L. digitata* ($p > 0.05$). Therefore, distance from the base of the blade was included as a covariate in MANCOVA for *L. complanata* and *S. longicruris*, and no covariates were used in MANOVA for *L. digitata*.

The material properties of kelp blades were significantly altered by encrustation and lesioning by *M. membranacea* (*S. longicruris*: MANCOVA, $df = 4, 24$, $\Lambda = 0.155$, $F = 2.768$, $p = 0.003$, *L. digitata*: MANOVA, $df = 4, 28$, $\Lambda = 0.124$, $F = 5.10$, $p < 0.001$). Encrusted and lesioned samples were significantly less tough, had a lower maximum stress before breakage, and a lower strain at fracture than undamaged controls from both kelp species (Table 1, Fig. 3). Lesions had a greater effect on toughness, strain at fracture, and maximum stress before breakage than did encrustation for samples from both kelp species, but this relationship was only significant for samples from *L. digitata*. Encrustations and lesions did not alter the modulus of material stiffness relative to undamaged samples from either kelp species (Table 1, Fig. 3).

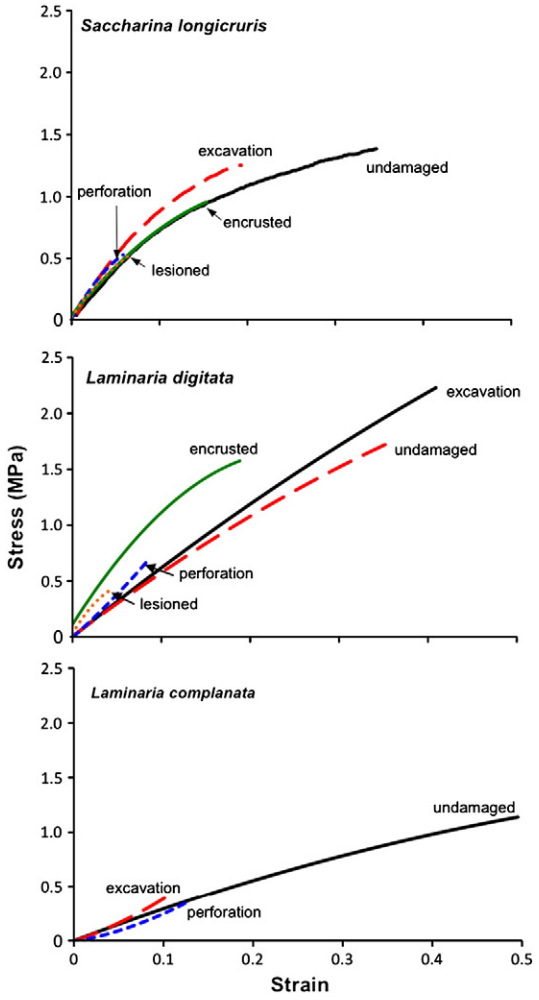

Fig. 2. Examples of stress–strain curves for undamaged, encrusted, lesioned, excavated, and perforated samples from *S. longicruris*, *L. digitata*, and *L. complanata*. Example curves in figures best represent the means of each sample condition group.

Grazing damage by *L. vincta* on kelp blades also had a significant effect on the material properties of *S. longicruris*, *L. digitata*, and *L. complanata* (MANCOVA, df = 2, 18, $\Lambda = 0.090$, $F = 2.35$, $p = 0.009$). Grazed perforations decreased the maximum stress before breakage, strain at fracture, and toughness relative to undamaged controls for samples from all three species (Table 1, Fig. 3), having the same effect as lesions created by *M. membranacea* on samples from *S. longicruris* and *L. digitata*. Grazed excavations did not affect material properties of samples from *L. digitata* relative to undamaged controls, but lowered the toughness of samples from *S. longicruris*. In contrast, the maximum stress, strain at fracture, and toughness of samples from *L. complanata* all were reduced by grazed excavations as compared to undamaged tissue. Neither grazed holes nor excavations affected the modulus of material stiffness for samples from *S. longicruris*, *L. digitata*, or *L. complanata* (Table 1, Fig. 3). There were no significant relationships between excavation and perforation widths and material properties for samples from any of the three kelp species.

Table 1
Results of ANOVA or ANCOVA (*distance from base of blade as a covariate) to examine differences between condition groups (undamaged, encrusted, lesioned, excavation, perforation) for each material property and kelp species.

Species	Material property	df	F	p
S. longicruris	Maximum stress*	4,20	7.43	<0.001
	Toughness	4,25	14.3	<0.001
	Modulus	4,25	1.35	0.278
	Strain	4,25	11.45	<0.001
L. digitata	Maximum stress	4,30	19.3	<0.001
	Toughness	4,30	18.4	<0.001
	Modulus	4,30	3.15	0.028
	Strain	4,30	9.61	<0.001
L. complanata	Maximum stress	2,19	19.2	<0.001
	Toughness	2,19	27.2	<0.001
	Modulus	2,19	0.21	0.814
	Strain*	2,16	3.86	0.043

Undamaged samples of *S. longicruris* and *L. digitata* consisted of three distinct cell layers (Fig. 4). The meristoderm is visible as several intact layers of small epidermal cells, with cells gradually increasing in size towards the cortex. The cortex consists of larger circular cells that are more elongate close to the central medulla. The medulla is a dense layer of elongate cells in the center of the tissue. The tissue structure of samples encrusted by *M. membranacea* (not adjacent to a lesion) was similar to the structure of undamaged tissue, and we found no evidence that the bryozoan penetrates the meristoderm. In contrast, samples that were lesioned were missing the meristodermal layer completely, and were often also missing the majority of cortical cells. This effect was similar for both kelp species.

4. Discussion

Our study is the first to quantify a decrease in the tensile strength, extensibility, and toughness of kelp blades associated with encrustation by the invasive bryozoan *M. membranacea*. Lesions that formed after prolonged encrustation caused a greater weakening of blades than did encrustation alone, suggesting that tissue strength decreases with increasing duration of bryozoan coverage. Histological preparations showed that encrustation by *M. membranacea* causes degradation of the meristoderm and eventually of the cortex, likely through shading (Oswald et al., 1984) and reductions in nutrient uptake (Hurd et al., 1994) and tissue pigment content (Hepburn et al., 2006). Such damage to the meristoderm may concentrate stress when the blade is experiencing drag-induced tension, leading to crack formation and propagation at lower force applications than required to break undamaged tissue (Mach, 2009). While macroalgal tissue is highly flexible and extensible, less energy is required to propagate cracks once initiated by fatigue or damage (Denny et al., 1989; Mach, 2009), suggesting that macroalgal blades are particularly susceptible to failure following damage, such as through bryozoan encrustation.

Contrary to our predictions, encrustation by *M. membranacea* did not have an effect on the stiffness of kelp blade tissue when force was applied in tension. Stress and hydrodynamic drag increase with stiffness in tension (Boller and Carrington, 2007; Gaylord and Denny, 1997), such that stiffer blades are less able to withstand breakage by wave forces. The fact that we did not observe an effect of bryozoan encrustation on blade stiffness suggests that this factor may be less important than stress concentration at the point of cellular degradation of encrusted blades in causing observed increased rates of breakage (Krumhansl and Scheibling, 2011) and canopy loss (Lambert et al., 1992; Scheibling et al., 1999; Scheibling and Gagnon, 2006). However, encrustation by *M. membranacea* could also increase stiffness in bending, which would reduce the flexibility of blades and contribute to blade breakage.

Full-thickness perforations created by the mesograzer *L. vincta* also reduced the strength, extensibility, and toughness of blade tissue from *S. longicruris, L. digitata*, and *L. complanata*. While partial-thickness excavations did not have a significant effect on the material properties of *L. digitata*, they had a similar effect as perforations for *L. complanata* and reduced the toughness of *S. longicruris*. Flaws introduced by grazer damage therefore likely also act as force concentrators, initiating cracks and breakage when in tension. We observed that sample failure always occurred at the site of a grazed perforation or excavation, and propagated in an across-blade direction perpendicular to the applied force. We note that cracks in kelp blades propagate more easily along the

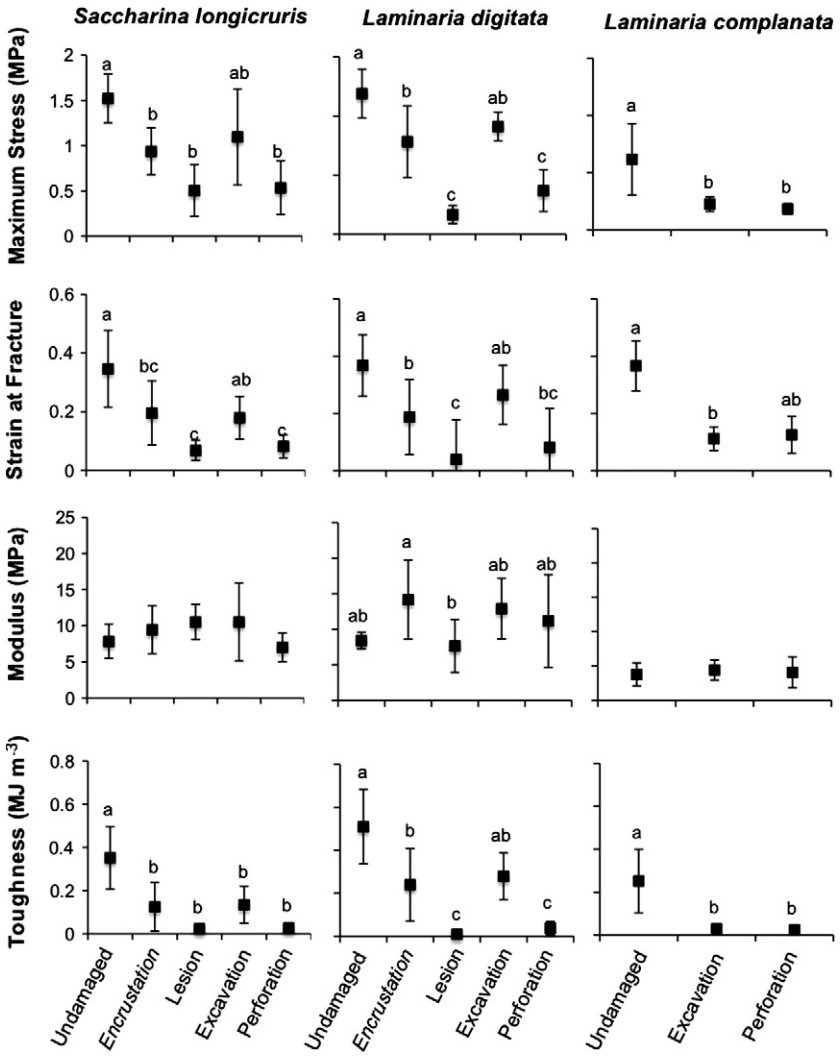

Fig. 3. Mean (±1 SD) maximum stress, strain at fracture, modulus, and toughness for undamaged, encrusted, lesioned, excavated, and perforated samples of *S. longicruris*, *L. digitata*, and *L. complanata* (n = 5–10). Letters denote statistically significant groupings.

blade than across the blade because of the orientation of central medulla fibers (Vincent and Gravell, 1986). This suggests that cracks initiated by grazer damage or encrustation would likely propagate along the blade at even lower force applications than we observed for across-blade propagation.

Force concentration is dependent on the shape of the flaw, with sharp-edged flaws concentrating force to a greater degree than more rounded flaws (Denny et al., 1989). We expected perforations to concentrate more force than excavations because they are sharp-edged and affect the entire blade thickness rather than a portion of it. This prediction was true for *L. digitata* but not for *L. complanata*. This suggests that the removal of meristoderm cells by partial-thickness grazing concentrates enough force to cause blade breakage in *L. complanata* at forces comparable to those causing breakage at perforations. We found some evidence that excavations reduce the ability of blades from *S. longicruris* to withstand breakage, although this species appears to be more resistant to partial-thickness damage than *L. complanata*. Our results indicate that *L. digitata* is the most resistant of the three kelp species to strength reductions caused by partial-thickness excavations. Interestingly, the magnitude of tissue strength reduction was not related to the size of the flaw for any of the three kelp species.

We observed significant decreases in the maximum stress before breakage and strain at fracture of blade tissue with increasing distance of the sample from the base of the blade for *S. longicruris* and *L. complanata*. Kelp blades are often tattered and degraded at the distal end, in part due to abrasion with other blades and the substratum. Our results suggest that this damage and degradation causes the material to become more susceptible to breakage, which is consistent with previous observations that kelps erode gradually from the distal end, even in relatively calm conditions (Krumhansl and Schiebling, 2011). This effect was not observed for samples from *L. digitata*, indicating that this species may be more resistant to damage at the distal end. *L. digitata* is often found shallower and in more exposed locations than *S. longcruris* in Nova Scotia (Mann, 1972), likely in part because it is less susceptible to damage-induced breakage by wave action. The material properties of blade tissue of *L. digitata* differed in many respects from those of the two other kelp species. This can also be seen in the shapes of the stress–strain curves for the three kelp species considered, which differed more widely between sample conditions for *L. digitata* than for *S. longicruris* and *L. complanata*. This indicates that, while the overall effect of damage to kelp blades is similar across species, natural variation in material properties exists between species, even in similar environments (Hale, 2001).

Our results provide a mechanistic explanation for increased fragmentation of kelp blades (Krumhansl and Scheibling, 2011) leading to extensive canopy loss during periods of peak encrustation by *M. membranacea* in Nova Scotia (Saunders and Metaxas, 2008; Scheibling et al., 1999; Scheibling and Gagnon, 2006) and the Gulf of Maine (Lambert et al., 1992). We have shown that grazing damage by *L. vincta* also reduces breaking strength, likely leading to increased fragmentation during periods of high wave action (Krumhansl and Scheibling,

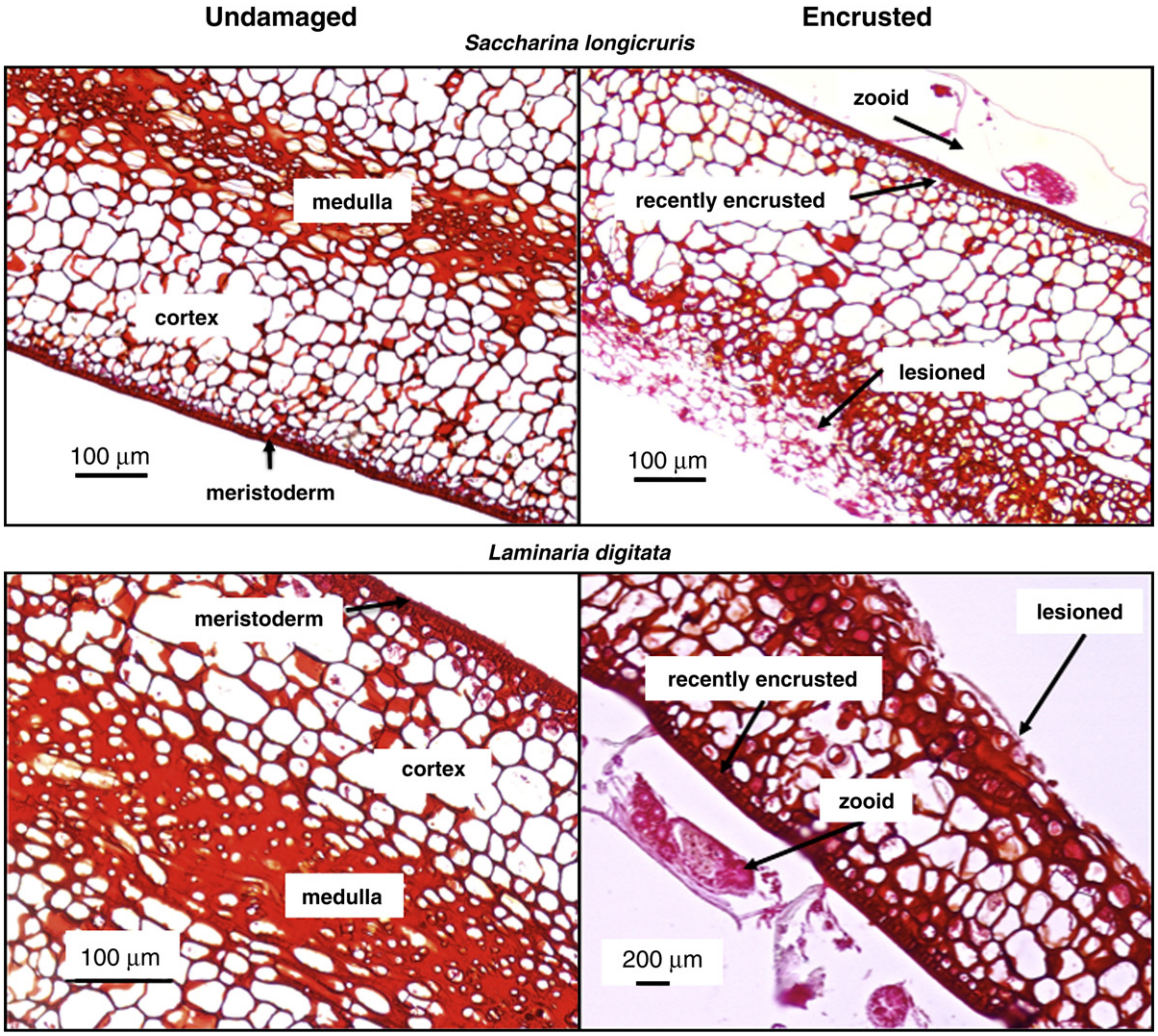

Fig. 4. Transverse sections of undamaged (left) and encrusted tissue (right) on *S. longicruris* and *L. digitata* prepared using histology techniques. Three distinct cell layers are visible in undamaged sections, while the meristoderm and cortex are highly reduced or absent on lesioned tissue Zooids of *M. membranacea* encrusting a kelp blade (on one side) are evident in panels on the right.

2011). Our findings support previous studies indicating that *L. vincta* and *M. membranacea* play major roles in the seasonal dynamics of detrital export from highly productive kelp beds to adjacent low-productivity habitats (Krumhansl and Scheibling, 2011).

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