

Wounding, healing and survivorship in three kelp species

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ABSTRACT: *Pterygophora californica* Ruprecht, *Eisenia arborea* Areschoug and *Laminaria setchellii* Silva are 3 common kelps (Laminariales, Phaeophyta) found in the shallow subtidal of open coastal British Columbia, Canada. Earlier laboratory studies showed that *P. californica* stipes had a critical flaw length (CFL, the length of a flaw which, if exceeded, results in structural failure) of 0.2 mm. In this paper we report on studies to determine whether this CFL is valid *in situ*, whether all 3 species of kelp respond similarly to stipe damage and whether tissue that regrows in the site of a wound increases the mechanical strength of the stipe. We tested the effect of razor cuts less than the CFL and also razor cuts and cuts imposed by a triangular file that exceeded the CFL. Results were not as predicted. Neither razor cuts nor file cuts greater than the CFL significantly decreased the survivorship for *P. californica* over control thalli. *L. setchellii* had a significantly lower survivorship when cut by a triangular file but not when cut by a razor. Tissue regrowth does not significantly increase mean strength of the stipe. We hypothesize that the low survivorship of *L. setchellii* as a result of stipe damage is one factor responsible for preventing successful establishment of adults of this species in sites where sea urchins are common. In contrast, the comparatively higher survivorship of *P. californica* adult plants subjected to similar damage may be one factor enabling this species to survive in such sites.

INTRODUCTION

Three common species of kelp (Phaeophyta, Laminariales) in the shallow subtidal of open coastal British Columbia, Canada, are *Pterygophora californica* Ruprecht, *Eisenia arborea* Areschoug and *Laminaria setchellii* Silva. At Wizard Rocks in Barkley Sound, British Columbia, these 3 species are present in a predictable pattern, with *L. setchellii* occupying the highest subtidal and lowest intertidal and *P. californica* the lowest subtidal just above the urchin-coralline community. *E. arborea* is in sites between, and at times intermixed with, these 2 species. Based on our observations and work in progress we would classify the Wizard site as having intermediate wave exposure, being exposed to the full impact of some storms. Adults of all 3 species are thus subjected to wave impact and drag due to current, and the 2 deeper taxa to grazing by sea urchins. Events such as these, either alone or in combination with physical damage, can reduce the survivorship of kelps and other algae (Koehl & Wain-

wright 1977, Pearse & Hines 1979, Dean et al. 1984, Koehl 1984, Denny et al. 1989).

Biochemical studies (Biedka et al. 1987, Denny et al. 1989) have characterized stipes of some kelp species as being relatively stiff (i.e. with a higher modulus of elasticity, E) compared to other algae (e.g. capable of remaining upright when out of the water), but still flexible (i.e. capable of bending and returning to their original shape without being damaged). As an example of the latter we could bend intact stipes of *Pterygophora californica* in excess of 360° without breaking them. The stipes are also relatively brittle (with a low work of fracture). Results from the biomechanical study of Biedka et al. (1987) suggested a critical flaw length (CFL) of 0.2 mm for stipes of adult *P. californica*. In theory, if a cut exceeds the CFL then, regardless of stipe diameter, rapid extension of this flaw can occur with relatively little extra input of energy. The result is a catastrophic fracture of the stipe. Considering the high wave forces and subsequent abrasion on rocks and barnacles, as well as

urchin grazing, it seems likely that cuts and nicks greater than 0.2 mm are a common occurrence in kelp stipes. Similar cuts, when imposed on stipes of *Postelsia palmaeformis* (a kelp growing on very exposed headlands of the Pacific Northwest), resulted in complete breakage of all stipes within 24 h (Denny et al. 1989).

Kelps may alter the biomechanical effects of cuts by wound healing. Tissue regeneration can result in rounding off the angle of the cut so as to decrease the concentration of force (Denny et al. 1989) and in binding together the 2 sides of the cut so as to make its length less than the CFL. The process of wound healing has apparently not been examined for kelps with regard to either the tissues involved or its ecological significance. Fagerberg & Dawes (1976) described the healing process in *Sargassum filipendula* (a brown alga which is not a kelp) as consisting in part of a re-differentiation of sub-wound cells into mitotically active cells. A distinctive epidermal layer formed subsequently with lower cells forming an elongating and parenchymatous tissue. Fulcher & McCully (1969) suggested that (tissue) regeneration might be important '...in plants which are subjected to the rigors of a harsh environment...'.

In this paper we address the following questions: (1) Is the prediction of a critical flaw length of 0.2 mm for *Pterygophora californica* supported by field experimental evidence? (2) Do the 3 species of kelps, *P. californica*, *Eisenia arborea*, and *Laminaria setchellii*, react similarly to imposed stipe damage? (3) Does the regeneration of tissue in a damaged stipe increase the strength of that plant over a freshly wounded plant?

METHODS AND MATERIALS

Site characterization. The study area is a 200 m subtidal stretch at Wizard Rocks ($125^{\circ} 10' N$, $48^{\circ} 51' W$), in Barkley Sound, British Columbia, Canada. A transect line spanning the 3 kelp zones was placed in 8 random locations within the study area, and four 0.5×0.5 m quadrats were placed in random locations along the line. In each quadrat individuals of the 3 kelp species and sea urchins (predominantly *Strongylocentrotus franciscanus* Agassiz) were enumerated and depth below chart datum determined. Species were enumerated on all transects in August and December (1988) and in May (1989). All 3 species were collected from additional quadrats and their age was determined by counting rings from sections (DeWreede 1986, Klinger & DeWreede 1988).

Expt 1 (wounding and survivorship of 3 kelps). Within 7 sites, plants of *Pterygophora californica*, *Eisenia arborea*, and *Laminaria setchellii* were ran-

domly designated as either controls (no treatment) or treatment; treatments consisted of a razor cut of either 0.11 mm (i.e. < 0.2 mm) or 1.5 mm (i.e. > 0.2 mm) or a cut imposed by a triangular file to a depth of 2.0 to 2.5 mm. All 3 cuts passed through the meristoderm and into the cortex. The choice of damage treatments was based on previous laboratory biomechanical studies on *P. californica* (Biedka et al. 1987). Although the file treatment approximates a small bite by an urchin, our visual observations in the field suggest that all treatments in this study probably inflicted smaller wounds than those caused by urchins *in situ* in Barkley Sound. Plants chosen for this study were adults (4 yr old or older), and plants that had an abnormal appearance (e.g. tumors, split stipes or missing apices) were rejected. Due to the variation in species composition at different sites, the experiment began with a total of 220 *P. californica*, 240 *E. arborea* and 280 *L. setchellii* (Table 1). Since individuals of these species are oriented with the flatter side of the stipe parallel to the shore, all cuts were made on the shoreward side of the stipe. We did not test, nor is it reported in the literature, whether plants would react differently to cuts on the shoreward vs seaward side of the stipe. Cuts were located ca 5 cm above the holdfast and both treatment and controls were tagged at the base with plastic tie-straps and colored wire to distinguish treatments. This experiment began in July 1988 and was terminated in August 1989. Each treatment group was monitored 7 times at approximately 2 mo intervals to obtain data on survivorship.

Expt 2 (effect of a deeper cut on *Pterygophora californica*). Based on results from Expt 1 a second experiment was done with a deeper file cut (2.5 to 3.0 mm) on *Pterygophora californica*. Five groups of 20 randomly chosen plants were filed and labeled as in Expt 1; controls were the same individuals as in Expt 1. Survivorship was monitored 3 times from June 1989 to May 1990.

Expt 3 (wounding and tissue regeneration). Three sets of 30 individuals each of *Pterygophora californica*,

Table 1. Number of treatment groups (each group consisted of 20 individuals) by treatment and species. Control: no treatment; <: razor cut of < 0.2 mm (0.11 mm); >: razor cut of > 0.2 mm (1.5 mm); file: cut of 2.0 mm imposed by a triangular file

Treatment	<i>Pterygophora californica</i>	<i>Eisenia arborea</i>	<i>Laminaria setchellii</i>
Control	4	3	4
<	3	3	4
>	2	3	4
File	3	3	2

Eisenia arborea and *Laminaria setchellii* were filed to a depth of 2.0 mm and labeled to measure the time course of tissue regeneration after wounding and to investigate biomechanical strength as a function of tissue regeneration. The experiment was initiated in May 1990 and 9 individuals of each species were randomly harvested during June, August and November 1990. Individuals were stored in 5% formalin in seawater and controls were similarly stored to check for tissue shrinkage. Individuals obtained from the November collection were kept in running and aerated seawater for 1 wk while biomechanical tests were done.

Tissue regeneration. Per cent regrowth was calculated by measuring the volume of new tissue using calipers and a dissecting microscope. Sections of the stipe with the original and regenerated tissue were mounted on a slide and examined under a compound microscope to compare tissue types. This material was photographed using a Wild MPS-45 camera system with Kodak EPY-50 film.

Biomechanical tests. A specially designed cutting block was used to excise sections (ca 5 cm long, 1 cm wide, and 3.5 to 4.0 mm thick) from kelp stipes for tensile tests. Sections were trimmed with a razor blade and a semicircular notch was made opposite the cuts (Fig. 1) to ensure that the break would occur in the desired place. Two samples were cut longitudinally from the basal portion of each stipe as illustrated in Fig. 1; the third sample was cut from immediately above one of the other 2 sections. Each section consisted of meristoderm and cortical tissue. Two different treatments and one control were tested (Fig. 1): Treatment 1 contained the regenerated tissue; Treatment 2 contained a fresh cut the same size as the original (unhealed) cut in Treatment 1; the control had only the semicircular notch. Sections were subjected to tensile tests by clamping their ends in pneumatic grips at a pressure of 20 psi using an Instron Model 1122 Tensile Testing machine. Sections were stretched at a rate of 5 mm min⁻¹. Results were recorded in units of stress (σ) [force (F) per unit area (A), measured in Pascals; Newtons per m² (N m⁻²)]. Tensile stresses were recorded at the breaking point of the section and the cross-sectional area of the original stipe tissue was measured with calipers. Since the regenerated tissue was not included in the calculation of the cross-sectional area in Treatment 1, any difference in biomechanical properties between control and treatments with regrown tissue was attributable to the regenerated tissue.

Results from the field and laboratory experiments were compared using 1-way ANOVAs (after testing for homogeneity of variance and transforming the data as required), with Tukey's HSD test used to identify significant (0.05 level) differences among treatments.

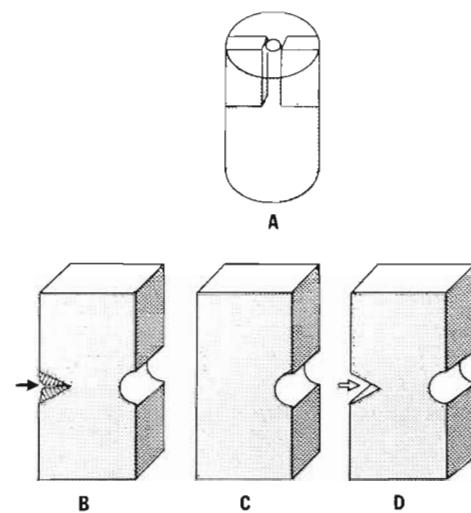


Fig. 1. Kelp stipe sections and treatments of sections used for biomechanical tests (not to scale). (A) Orientation of sections obtained from the stipe; central circle denotes core of medullary tissue; (B) Treatment 1, showing regenerated tissue (arrow), and cut made to ensure tissue would break at designated point; (C) Treatment 2, control; (D) Treatment 3, showing new cut (arrow)

Data were re-transformed to the original values for tables and figures. All tests were done using SYSTAT (Wilkinson 1989).

RESULTS

Site characterization

The 3 kelp species were distributed as illustrated in Fig. 2. The mean age and standard error (SE) was 7.1 yr (SE = 0.36, n = 42) for *Pterygophora californica*, 5.7 yr (SE = 0.29, n = 23) for *Eisenia arborea*, and 5.9 yr (SE = 0.19, n = 61) for *Laminaria setchellii*. Sea urchins were relatively common at the lower boundary of

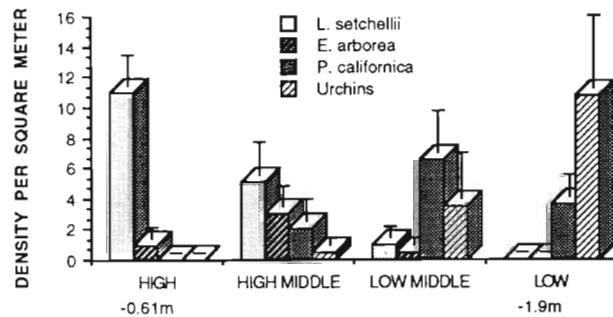


Fig. 2. *Laminaria setchellii*, *Eisenia arborea*, *Pterygophora californica*. Density of kelp species and sea urchins as a function of elevation (depth below chart datum) in the subtidal zone; error bars indicate 1 standard error

the algal zone where *P. californica* predominates and absent from the upper *L. setchellii* zone.

Expt 1

Laminaria setchellii had a lower mean survivorship than either *Eisenia arborea* or *Pterygophora californica* (Fig. 3). *L. setchellii* was more affected than *P. californica* by the file treatment. Analysis of data for differences in survivorship due to treatment within a species for the first sampling date after treatment (Day 42,

August 1988) showed that only the file treatment on *L. setchellii* resulted in survivorship significantly lower ($F = 36$, $p = 0.00$) than the control and other treatments. Likewise (again based on the original number of individuals of each species), the file treatment produced the only significantly lower per cent survivorship when differences between species were analyzed on the first sampling date after initiation of the experiment. While these differences were highly significant ($F = 9.15$, $p = 0.02$), data could not be transformed to have homogeneity of variance and thus results should be interpreted with caution. These survivorship differences occur between *P. californica* and the other 2 species but not between *E. arborea* and *L. setchellii*.

Based on per cent mortality between enumerations (Fig. 4), the only significant difference ($F = 35.5$, $p < 0.01$) again was between the field and the control and cut thalli of *Laminaria setchellii*; this was true only for the first interval between enumerations. *Eisenia arborea* had the highest mean loss due to file treatment immediately after the treatments were imposed, but this was not significantly different from other treatments and control groups.

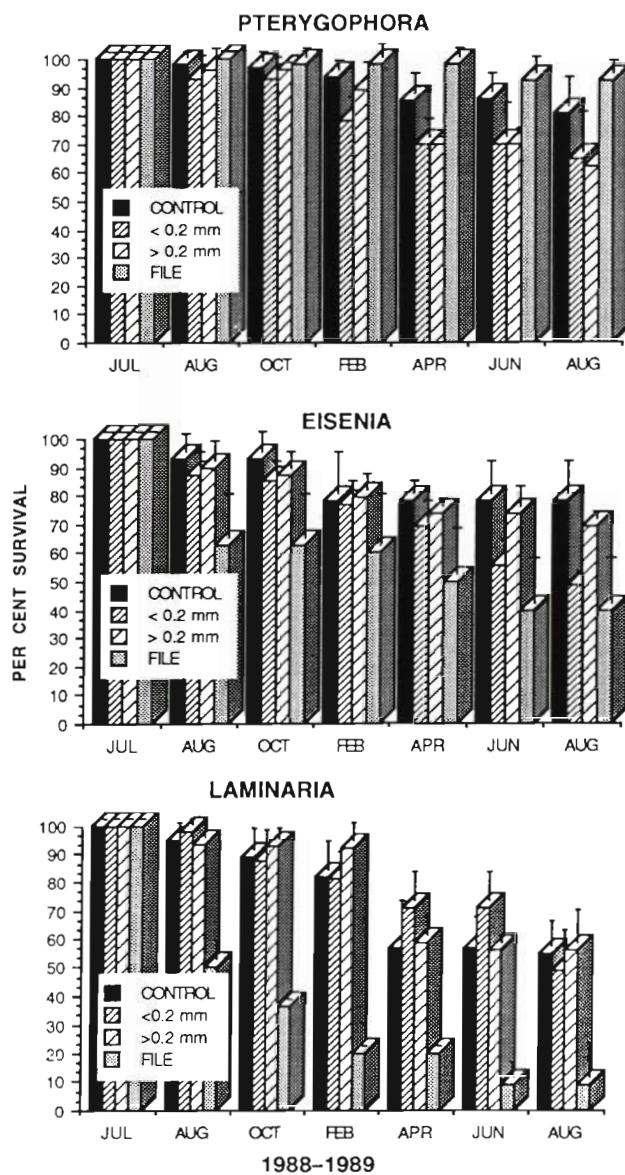


Fig. 3. *Pterygophora californica*, *Eisenia arborea*, *Laminaria setchellii*. Per cent survivorship over time as a function of treatment (< 0.2 mm = a cut of 0.11 mm; > 0.2 mm = a cut of 2.0 mm); error bars indicate 1 standard error

Expt 2

The effect of a deeper file cut (2.5 to 3.0 mm) on *Pterygophora californica* was to increase attrition compared to both the control and treatment (2.0 mm file cut) imposed in Expt 1. When daily attrition was calculated, the loss due to the deeper file cut was significantly ($F = 32$, $p < 0.01$) higher than both controls and shallow file cut only for the first sampling date (Day 55, Fig. 5; $F = 20.5$, $p < 0.01$); once again, the highest mortality occurred during the time immediately after file cuts were imposed.

Expt 3

The volume of tissue regrown in filed stipes of all 3 species increased over time. *Eisenia arborea* had significantly more regrowth than the other 2 species by August (Table 2), but only more than *Pterygophora californica* by November.

Laminaria setchellii and *Pterygophora californica* regenerated tissue in a similar fashion. New tissue formed from the surface of the wound site and grew outward so the 2 surfaces left by the triangular file cut approached each other. Cells of the regenerating tissue were smaller and grew toward the center of the cut. In contrast, larger cells of the original stipe tissue grew radially inward from the stipe surface (Fig. 6). The gap between the 2 approaching sides was still pre-

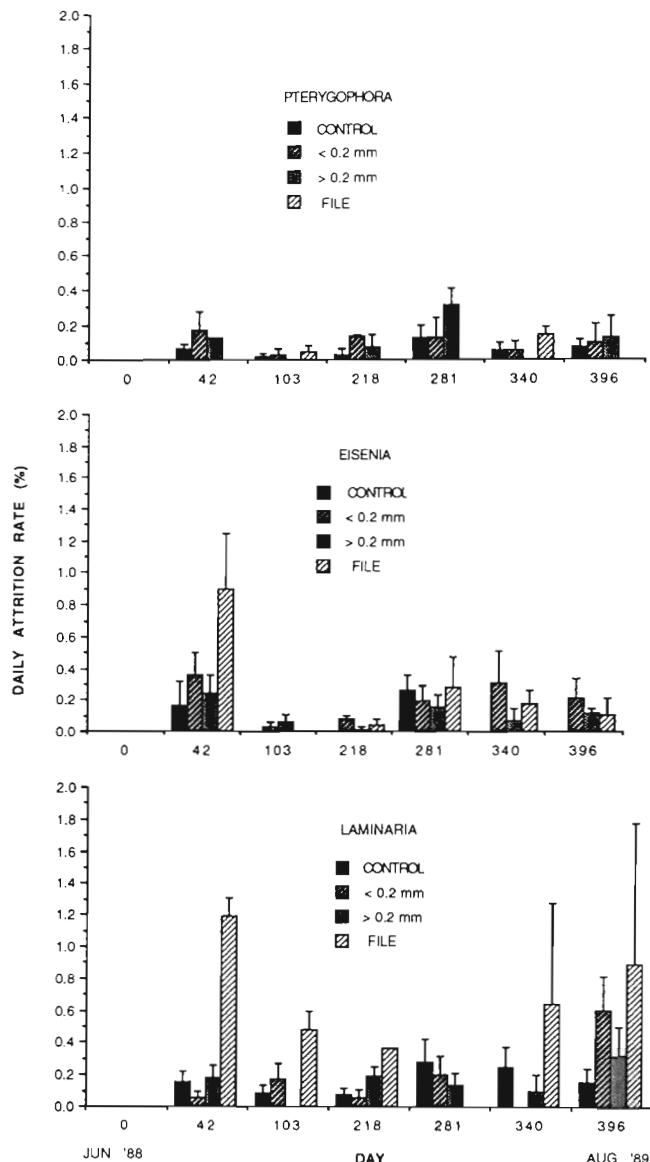


Fig. 4. *Pterygophora californica*, *Eisenia arborea*, *Laminaria setchellii*. Expt 1: Daily attrition rate for control thalli (no treatment) and 3 treatments (as in Fig. 3); error bars indicate 1 standard error

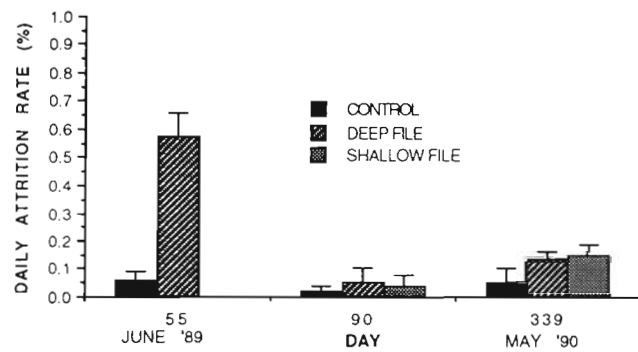


Fig. 5. *Pterygophora californica*. Expt 2: Daily attrition rate; error bars indicate 1 standard error

sent after 6 mo when observations were discontinued since all surviving plants were harvested for the biomechanical test. The angle of the wound also rounded off. Regenerated tissue of *Eisenia arborea* was slightly different from that of the other 2 species in that newly formed cells were more filamentous.

Biomechanical tests

Statistical analyses of tensile test results are given in Table 3; our mean values, along with those published by other investigators, are found in Table 4. When regenerated tissue was present the mean force required to break the stipe tended to increase (Table 4), particularly in the case of *Pterygophora californica*. However, these apparent increases were not statistically significant between species, within a treatment or between treatments within a species (Table 3).

DISCUSSION

Cuts and nicks in kelp stipes can result from herbivory (e.g. sea urchins and limpets) and from scrapes by being swept against nearby rocks and large barnacles. Cracks seem unlikely to arise from bending

Table 2. *Pterygophora californica*, *Eisenia arborea*, *Laminaria setchellii*. Results of a 1-way ANOVA testing for differences in tissue regrowth between species within time, and of a Tukey HSD test. Data are % regrowth values; those underlined with a solid line are significantly different from each other at a p-value of < 0.01, those with a dashed underline at < 0.05

Time	<i>F</i>	p	<i>P. californica</i>		<i>E. arborea</i>		<i>L. setchellii</i>	
			\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Jun	1.4	0.270	19	2.9	28	4.1	23	4.4
Aug	7.6	0.003	32	5.2	66	8.6	41	5.1
Nov	4.3	0.027	53	5.8	74	4.2	62	5.8

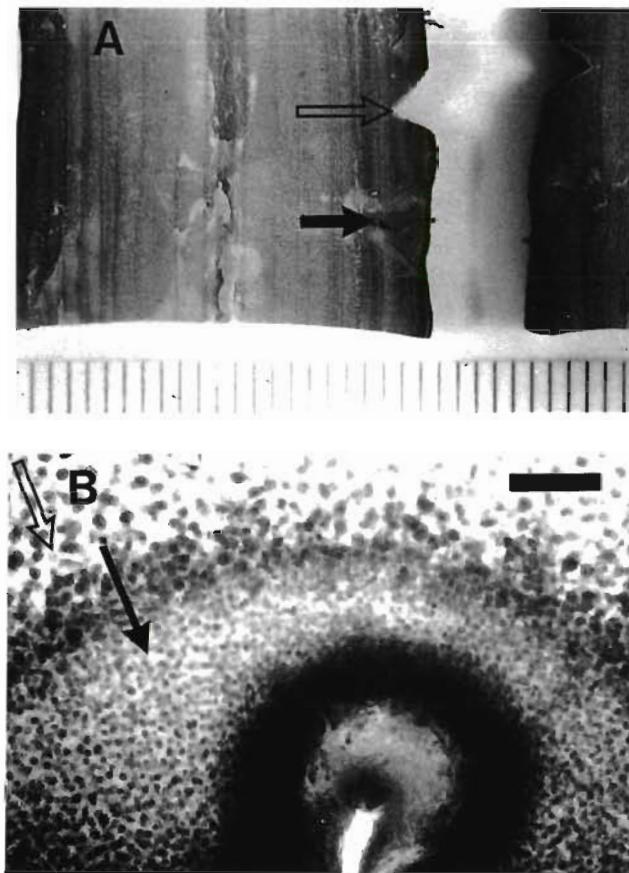


Fig. 6. Regrowth in *Pterygophora californica* and *Laminaria setchellii*. (A) Sections of *P. californica* stipes showing tissue (closed arrow) regrown after 1 yr, and a new cut (open arrow); scale divisions = 1 mm. (B) Microscopic section of *L. setchellii* showing newly formed tissue (closed arrow) adjacent to original tissue (open arrow); note also the incompletely healed central portion of the cut after 6 mo; scale bar = 0.2 mm

stresses since stipes are extremely flexible (Koehl 1984, Biedka et al. 1987, Denny et al. 1989).

The prediction derived from laboratory studies that 0.2 mm is the CFL for *Pterygophora californica* is not supported by our experiments on this species in its natural habitat. Based on the daily mortality rate, none of the treatments of *P. californica* in Expt 1 differed significantly from each other or from controls.

The absence of catastrophic failure by *Pterygophora californica* stipes in response to cuts 1 order of magnitude larger than calculated as critical is surprising. One reason why stipes did not crack completely may be that drag forces encountered by the plants were insufficient to enlarge cuts. However, this seems unlikely since Expt 1 lasted over a year and numerous storms occurred during this time.

Results of Expts 2 and 3 are consistent with another hypothesis, namely that stipes healed rapidly and hence

Table 3. *Pterygophora californica*, *Eisenia arborea*, *Laminaria setchellii*. Results of a 1-way ANOVA testing for tensile strength differences between species within treatments (left portion of table) and within species between treatments (right portion of table)

Treatment	F	p	Species	F	p
Healed	1.15	0.35	<i>P. californica</i>	3.57	0.06
Control	1.47	0.27	<i>E. arborea</i>	1.31	0.31
New cut	0.68	0.53	<i>L. setchellii</i>	—	—

Table 4. Summary of tensile test results on kelp tissue reported in this study and others taken from the literature; values (in 10^6 Pa) indicate force required to tear the tissue; standard error ($n = 5$) given in parentheses

Species	Healed	Uncut	New cut
<i>Pterygophora californica</i> ^a	10.9 (2.0)	6.6 (0.5)	7.0 (0.8)
<i>Eisenia arborea</i> ^d	7.8 (1.4)	6.0 (0.4)	5.9 (0.9)
<i>Laminaria setchellii</i> ^a	8.7 (0.9)	7.1 (0.5)	—
<i>Pterygophora californica</i> ^a	—	5.70	—
<i>Eisenia arborea</i> ^b	—	12.50	—
<i>Nereocystis leutkeana</i> ^c	—	3.64	—
<i>Hedophyllum sessile</i> ^d	—	1.95	—
<i>Egregia menziesii</i> ^e	—	0.23	—

^aBiedka et al. (1987); ^bDenny et al. (1989); ^cKoehl & Wainwright (1977); ^dArmstrong (1987); ^eKraemer & Chapman (1991)

sufficiently deep cuts were only present for a short time. Results from Expt 2, in which deeper cuts were imposed on *Pterygophora californica* leading to significantly higher mortality, are consistent with this hypothesis. If wound healing does play a role in reducing mortality then it follows that, since larger cuts take longer to heal, there will be a longer period when stipes are vulnerable to catastrophic failure. Also consistent with this hypothesis are the daily attrition rate data. If wound healing strengthens the stipe, then any effect of a flaw would be most pronounced immediately after the flaw is made. Our data show that the only statistically significant increases in mortality due to stipe cuts occurred during the time between the start of the experiment and the first enumeration for survivorship.

We also tested whether the 3 kelp species reacted similarly to different kinds of stipe damage. While the critical flaw length is unknown for *Laminaria setchellii*, this species had significantly higher mortality from file cuts than the control. Based on mean values, *Eisenia arborea* may have had a higher mortality than *Pterygophora californica*, but any significant difference that may exist is obscured by the large variance in the data. The cause of this large variance was not studied. It is evident from these results that *L. setchellii* suffers more attrition from stipe damage than the other 2 species.

Our results may explain, in part, the observed distribution at our study site of these 3 species. *Laminaria setchellii* grows higher in the subtidal zone than *Pterygophora californica*. As documented for this site by Pace (1981), DeWreede (1984) and in this study, sea urchins are not seen above the *P. californica* zone and hence are unlikely to be a factor in causing stipe damage to *L. setchellii*. We have observed urchin damage on *P. californica* at the same height on the stipe as, and of greater magnitude than, our experimentally induced file cuts. We hypothesize that *P. californica* adults are capable of surviving in sites subjected to some sea urchin grazing as mimicked in our experiment by the shallow file cuts, while *L. setchellii* are not. When *P. californica* experiences more severe grazing (our deeper file cuts) higher mortality occurs; if this were to occur commonly, it is unlikely the species could persist.

This response to stipe damage may be one factor in limiting the lower distribution of both species. This conclusion is born out by results of earlier experiments at this same site by Pace (1981). Pace constructed a fence which extended seaward from the *Pterygophora californica* zone 20 m into the lower urchin zone. Both *P. californica* and *Laminaria setchellii* were common in the fenced area within 1 yr of excluding urchins. *Eisenia arborea* was not reported from within the enclosure. This shows that while *L. setchellii* is physiologically capable of growing in deeper sites, it may not do so because its susceptibility to stipe damage ensures a high mortality rate.

The process by which wounds in kelp stipes are healed appears to be similar to that described by Fagerberg & Dawes (1976) for *Sargassum filipendula*. The layer of cells that forms on the cut surface is continuous with the old meristoderm and seems to function as a new meristoderm. New cells beneath the new meristoderm push it out and fill in the damaged area. The growth of new tissue also has the effect of rounding off the angle of the original cut, which reduces the concentration of force lines there (Denny et al. 1989).

We conclude that cuts slightly in excess of 0.2 mm do not result in significantly higher mortality (as compared to controls) for *Pterygophora californica*. File cuts of 2.0 to 2.5 mm also do not cause higher mortality in *P. californica* but do so in *Laminaria setchellii*. Thus, we also conclude that the 3 species tested respond differently to stipe damage (as measured by *in situ* mortality and tissue regrowth) and that this response may function to limit the extension of *L. setchellii* into the lower subtidal zone. Although all 3 species showed tissue regeneration, this process did not result in a significant increase in stipe strength as measured by a tensile test. However, there was a trend for mean tissue strength to increase over controls, and newly cut stipes of *P. californica* exhibited a nearly significant ($p = 0.06$) increase in strength of 65 %.

This field investigation has shown that a laboratory-predicted critical flaw length has little predictive value due to wound healing that occurred in the field during this study. Since our field experiments were started in summer it is possible that cuts imposed in winter (when storm-induced waves are larger) might result in higher mortality. Earlier work (DeWreede 1984) has shown highest growth rates from April to June; thus healing would also be slower in winter months. However, urchin densities around *Pterygophora californica* are reduced in winter. These 3 kelp species are able to heal damaged tissues, and the species-specific healing capacity may be one factor affecting their distribution. Observations such as these help in rationalizing the relationships between laboratory-determined biomechanical features and the results of field experiments.

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