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Wounded kelps: patterns and susceptibility to breakage

Thibaut de Bettignies[1,*], Mads S. Thomsen[1,2,3], Thomas Wernberg[1,2,4]

[1]Centre for Marine Ecosystems Research, Edith Cowan University, Joondalup, Western Australia 6027, Australia
[2]UWA Oceans Institute and School of Plant Biology (M096), University of Western Australia, Crawley, Western Australia 6009, Australia
[3]Marine Ecology Research Group, School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand
[4]Australian Institute of Marine Science, 39 Fairway, Crawley, Western Australia 6009, Australia

ABSTRACT: Kelps are highly productive seaweeds predominantly found in wave-exposed environments. Physical and biological processes such as sand abrasion, whiplash and grazing can wound kelp tissue, potentially weakening its ability to withstand wave forces. Despite the ecological importance of kelp tissue loss, few studies have quantified wounding patterns in kelps or how wounding might affect the biomechanical properties of kelps. We quantified the prevalence of wounds on 360 *Ecklonia radiata* kelps collected across 3 different reef lines (levels of wave exposure) in April (autumn), June (early winter), August (winter) and October (early spring) (i.e. before, during and after peak wave activity). Small holes in the centre of laterals dominated the wounds. Wounding pattern did not differ between reef lines but changed over time, with most in early winter and least in early spring (from 285 to 71 wounds kelp^{-1}). This pattern suggests that wounds accumulate over summer and that highly wounded parts of the frond (but not the entire kelp) break off when encountering the first storms. Biomechanical break-force tests assessed the effect of experimental wounds on the forces required to break kelp tissue. These tests showed that holes or horizontal cuts to the edge of the kelp frond dramatically reduced the strength, extensibility, toughness and stiffness of the tissue. We conclude that wounds are common in *E. radiata* and that the resulting loss of tissue integrity, caused by even small damages, can dramatically increase the susceptibility to breakage. Our findings may have important ecological implications; the peak in wounds in early winter is likely to increase fragmentation of the kelp, thereby reducing its size and hydrodynamic drag, and, paradoxically, reducing the risk of fatal dislodgment during severe winter storms.

KEY WORDS: Seaweed biomechanics · *Ecklonia radiata* · Wounds · Biomass loss · Pruning · Survival · Western Australia

INTRODUCTION

Kelp forests are highly productive and ecologically important habitats along rocky coastlines in polar to warm temperate regions where they influence ecosystem dynamics (Mann 2000, Steneck et al. 2002). Kelps are common in wave-exposed environments, where they experience extreme forces (Denny 1994, Thomsen et al. 2004) that can cause loss of parts of the thalli (pruning) and loss of the entire thalli (dislodgement) (Seymour et al. 1989, Dayton et al. 1992, Thomsen & Wernberg 2005), resulting in canopy loss on reefs and accumulation of drift kelp in adjacent habitats (Wernberg et al. 2006) and on the shore (Ince et al. 2007). Canopy loss and accumulation of drift kelp are important ecological processes that underpin much of the community dynamics on reefs (Dayton et al. 1992, Wernberg & Connell 2008) and in

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*Email: t.debettignies@ecu.edu.au

adjacent habitats (Bustamante et al. 1995, Wernberg et al. 2006). It is therefore important to understand the factors that influence the rate of kelp pruning and dislodgement. Conceptually, the mechanical process whereby entire kelps are dislodged from reefs is well understood (Denny 1995), but much less is known about pruning. In particular, the range and exact nature of mechanisms that influence the susceptibility of kelps to pruning are unclear.

To cope with extreme hydrodynamic forces, kelps can adjust their morphological (Roberson & Coyer 2004, Fowler-Walker et al. 2006, Wernberg & Vanderklift 2010) and/or material properties (Denny et al. 1989, Harder et al. 2006). Kelps can be described as 'shock absorbers' that absorb energy through tissue extension before breaking (Johnson & Koehl 1994). Due to the absence of stiff structural tissue components such as lignin in higher plants, kelp tissues are relatively weak, with a low breaking stress (σ_{brk} = 1 to 5 MN m^{-2}). On the other hand, kelps are highly extensible, with a high breaking extension or breaking strain (ε_{brk} = 0.3 to 0.75) compared to, for example, trees (wood, ε_{brk} = 0.01) (Harder et al. 2006). For instance, the stipe of the kelp *Nereocystis luetkeana* can extend up to 40% without sustaining cellular damage (Koehl & Wainright 1977). Moreover, kelps have typically streamlined morphologies with long, flat fronds and long stipes (Gerard & Mann 1979, Wernberg & Thomsen 2005, Wernberg & Vanderklift 2010) making them flexible and able to dissipate wave energy by 'going with the flow' (Friedland & Denny 1995). It has been proposed that this combination of high extensibility and flexibility explains the paradoxical existence of some of the largest plants on earth in one of the most hydrodynamically challenging environments (Koehl 1984, Denny et al. 1989).

Kelps are under constant pressure from external stressors such as waves, abrading sediments, scouring fronds, grazers and pathogens. These physical and ecological stressors can wound and cause damage to the kelp through cuts, holes and scars in the kelp tissue (Dayton 1985, De Wreede et al. 1992, Krumhansl & Scheibling 2011b), likely affecting tissue properties such as strength and extensibility, and potentially making kelp tissue more prone to structural failure and crack propagation leading to tissue loss (Holbrook et al. 1991, Duggins et al. 2001). Depending on where on the plant the impact occurs, this might result in mortality (breakage of holdfast or stipe below the meristem = dislodgement) or lead to significant loss of biomass via pruning without necessarily killing the alga. Most previous studies have been concerned with processes that affect the survival of kelps only, and these studies have focused on, and simulated, stipe damage (Biedka et al. 1987, Denny et al. 1989, Duggins et al. 2001, Harder et al. 2006). However, it is also relevant to understand the susceptibility of kelps to non-fatal biomass loss to better understand detrital production and biomass export from kelp forests to adjacent habitats (Colombini & Chelazzi 2003, Vanderklift & Wernberg 2008, Kelly et al. 2012). Wounding processes can be particularly important if wounds weaken the tissue and increase rates of pruning and fragmentation of blades, thus affecting rates of export of kelp biomass from reefs to adjacent habitats. Indeed, it has been demonstrated that only 10% of kelp biomass is consumed directly by herbivores (Mann 2000), with the other 90% entering the coastal food web through the detrital component as particulate and dissolved organic matter (POM and DOM, respectively; Mann 1982, Duggins et al. 1989). This kelp-derived detritus can constitute the main source of carbon for detritivores in adjacent recipient habitat: in the supralittoral zone (Polis & Hurd 1996), intertidal zone (Bustamante et al. 1995, Bustamante & Branch 1996), seagrass meadows (Wernberg et al. 2006), distant reefs (Vanderklift & Wernberg 2008) and deeper habitats (Vetter 1994, Kelly et al. 2012).

Winter is a key period for kelp detrital production, when large waves associated with winter storms tear blades and plants off (Seymour et al. 1989, Graham et al. 1997, Reed et al. 2011). At the same time, tissue wounding is likely to be higher at more wave-exposed sites and in winter with increasing physical disturbance (i.e. scouring, whiplash). Therefore, this study aimed to, firstly, quantify spatio-temporal patterns around winter, in the prevalence of wounds in different kelp tissues, and secondly, test for effects of different types of wounds (simulated damage from cuts and holes at different positions on the tissue) on the strength, extensibility, stiffness and toughness of kelp tissues. We hypothesized (1) that wounds would be most prevalent in kelps from exposed reefs during winter months, when storm activity and sand abrasion peak (Lemm et al. 1999, Li et al. 2011), and (2) that wounds would influence tissue biomechanical properties dramatically.

MATERIALS AND METHODS

Study site

This study took place in Marmion Lagoon, Perth, Western Australia (32° S latitude). This region is strongly influenced by westerly and south-westerly wind and swell-generated waves (Searle & Semeniuk 1985, Lemm et al. 1999). Wave characteristics vary seasonally, but waves are largest in winter (June to August) when the average wave height is 1.5 to 2.5 m; storms (waves >4 m) occur ~30 times per year, with a peak frequency in winter (Lemm et al. 1999). A series of successive high-relief reef ridges (reef lines) run parallel to the shore, dissipating hydrodynamic forces by 50 to 75% as waves approach the coast, creating a gradient in exposure to wave forces (Phillips et al. 1997, Smale et al. 2011). Reefs throughout temperate Australia, including Marmion Lagoon, are dominated by the small kelp *Ecklonia radiata* (1 to 2 m) which has a terete basal stipe that bears a flattened blade (lamina) with ramified laterals (Wernberg et al. 2003) (see also Fig. 1A).

Experimental design

Kelps were sampled at 6 reefs (depth range from 8 to 10 m), with 2 reefs nested in 3 reef lines (protected midshore reefs, exposed midshore reefs and deep offshore reefs). Their respective wave exposures were measured as acceleration of the water flow (0.15 ± 0.02, 0.19 ± 0.04 and 0.16 ± 0.02 m s^{-2}) during 1 wk in winter (2 to 9 July 2010) with the 'H$_2$O Motion V1 design' (Evans & Abdo 2010). Kelps (n = 15) were collected from each reef in April (autumn), June (early winter), August (late winter) and October (spring). These sample times were targeted because wave-induced damage is most likely to occur late in the season when the kelp thalli (Wernberg & Goldberg 2008) and waves (Lemm et al. 1999) are largest.

Kelp wounds

We counted all macroscopic wounds (visible to the naked eye) on all stipes, laminae and subsamples of 3 laterals of similar surface area (5 to 7 cm × 15 to 20 cm) in the middle of the thallus from all 360 kelps. Wounds were classified as 'holes' (Fig. 1D–H), 'tears' (large piece of tissue torn off; Fig. 1A,G,I), and 'cuts and scars' (Fig. 1B,C). These wound types were quantified for different kelp tissues (stipe, lamina and laterals), and for laminae and laterals the 'positions' of wounds were recorded as either on the 'edge' or in the 'centre' of the tissue. Most wounds were circular holes (Fig. 1D,E,G), and these were categorised into 2

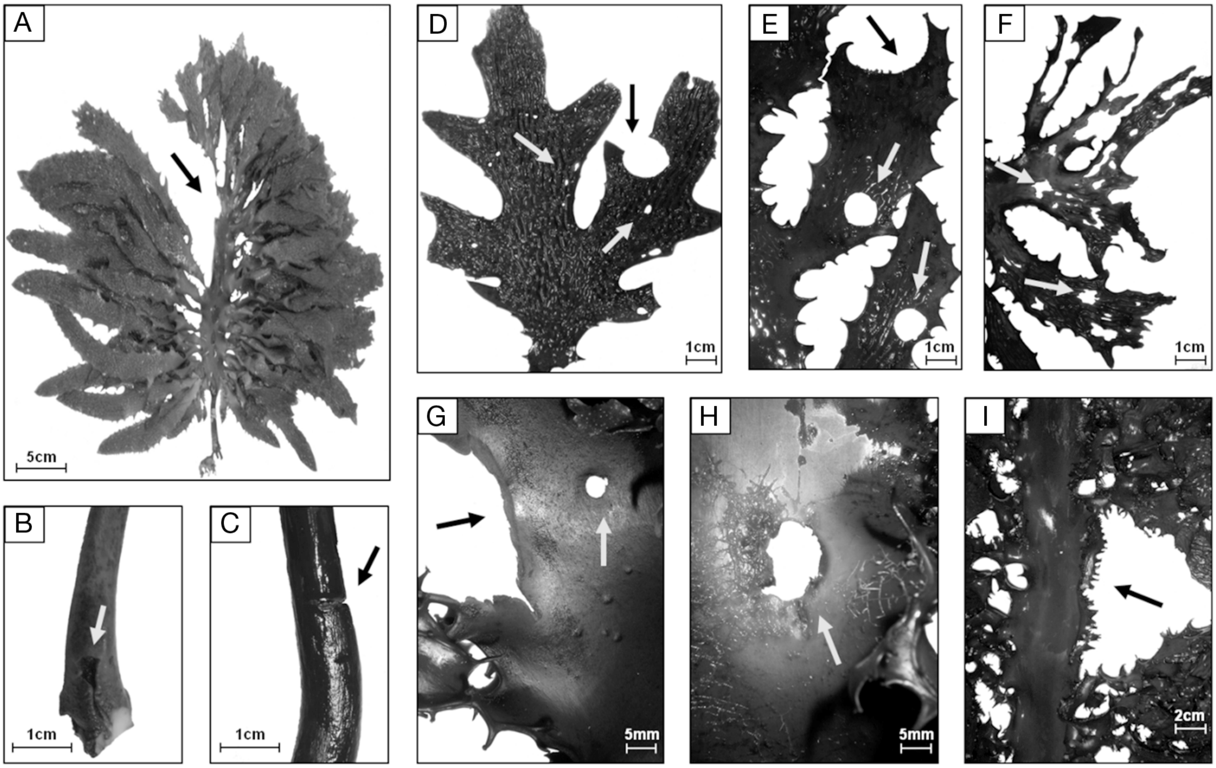

Fig. 1. *Ecklonia radiata*. Photographs of different types of damage recorded: (A) tear along the lamina; (B,C) stipe scars; (D,E,F) holes within and on the edge of the laterals; and (G,H,I) holes and tears within and on the edge of the lamina. Black and grey arrows indicate locations of damage

size groups: small and large holes (<10 and >10 mm diameter, respectively). In total, 9 wound variables were measured, representing observed combinations of wound type, tissue, position and size.

Biomechanical tests of effects of tissue wounding

Whole plants of *Ecklonia radiata* were collected from Marmion Lagoon and kept fresh until used for tensile tests within 24 h. Strips of healthy lamina tissue were cut into hourglass shapes, ca. 12 cm long and ca. 3 cm wide, narrowing to 3–8 mm width at the mid-section to facilitate controlled test-breakage at this tissue position (Fig. 2). Tensile tests were performed using mechanical force gauges (Shimpo) (±0.2% precision). One end of the tissue was fixed between a pair of neoprene-coated clamps to ensure that the tissue was firmly attached but did not break around the attachment point. This clamping device was attached to the force gauge. A standardized strain rate was applied by pulling the tissue by hand with a slowly increasing sweeping motion until the tissue broke (typically after 8 to 10 s). This strain rate aimed to mimic typical benthic surge created by waves (~5 to 12 s wave period; Lemm et al. 1999) and kelp frond reconfiguration (Wernberg 2005). The break extension was recorded by observing the exact point of tissue breakage against a background-ruler (Fig. 2). Tests in which breakage occurred near the attachment point of the clamp were discarded. Tensile tests of non-wounded controls (n = 52 successful tests) were compared to 3 types of artificially induced wounding (Fig. 2): 2 mm circles positioned centrally (n = 16), 2 mm half circles positioned along the edge (n = 15) and 2 mm linear cuts positioned along the edge (n = 17). These experimental wounds mimicked wounds seen *in situ*, likely reflecting grazing marks from mesograzers (holes, centre), fish (half circles, edge) or mechanic damage (cuts) (Fig. 2). Following breakage the tissue width and tissue depth at the exact break location was measured using callipers. From these data, strength (standard stress at breaking), extensibility (strain at breaking), stiffness (ratio of stress/strain at breaking) and toughness (work of fracture) were calculated (Harder et al. 2006). The standard stress (MN m^{-2}) was obtained by dividing the force at breaking by the cross-sectional area of tissue where it breaks. The strain at breaking was the ratio of the extension of the tissue at breaking to the initial tissue length (12 cm). Because the strain at breaking is dimensionless, the ratio of stress to strain (stiffness) has the dimension of stress (MN m^{-2}). The work of fracture was calculated as the area under the stress-strain curve (MJ m^{-3}).

Statistical analyses

The 9 wound variables were square root transformed to down-play the importance of small abundant wounds over large and less frequent wounds and to reduce potential differences in the dispersion of the data. Euclidian distances were calculated between each reef–time combination. Permutation-based multivariate analysis of variance (PERMANOVA; Anderson et al. 2008) was used to partition variation between sampling 'Times' (fixed factor = April, June, August, October), 'Reef line' (fixed factor = protected midshore reefs, exposed midshore reefs

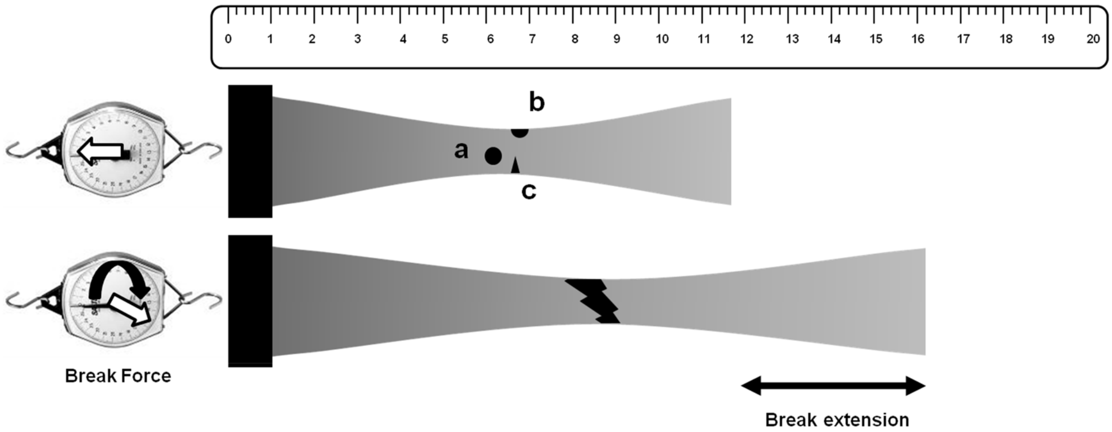

Fig. 2. *Ecklonia radiata*. Schematic view of the tensile test before and after the pull test. A strip of tissue (12 cm long) was clamped to a mechanical gauge and pulled manually until breakage. The letters a, b and c represent the 3 types of artificially induced wounding, i.e. hole in the middle, and hole or cut at the edge of kelp tissue. Each type of damage was made on different test pieces

and deep offshore reefs) and 'Reefs' nested within reef lines (random factor, n = 2). Subsequently, pairwise comparisons were performed for the significant factors. The key results of wounding pattern were visualised by constrained analysis of principal coordinates (CAP; Anderson et al. 2008), and vectors for strongly correlated variables ($r > 0.5$) were overlaid to identify the wound variables potentially driving the patterns. The PERMANOVA and CAP analyses revealed that, by far, the most multivariate data variability was explained by Time on 3 of the 9 wound variables (see 'Results'). We therefore proceeded with 1-way ANOVAs on the Time tests factor (on square root-transformed data) followed by a post hoc test (Tukey) on these 3 wound variables. We also used 1-way ANOVAs to test for effects of simulated wounding on kelp tissue biomechanical properties. When homogeneity of variance could not be met even after transformation (square root), significance was interpreted conservatively at $p < 0.01$ (Underwood 1997).

RESULTS

Field survey of wounds

The majority of the thalli analysed had wounds in their tissue (93 to 100% for each of 24 combinations of reefs and times). There was a high variability in wounding at different times and reef lines as suggested by the highly significant Time × Reefs nested in Reef lines ($p = 0.009$; Table 1). However, as the 2-way interaction between Time and Reef lines was marginally non-significant ($p = 0.074$) and accounted for very little variation relative to time (MSs of 108.3 vs. 18.5; Table 1), we proceeded to analyse the single-factor effects of Time and Reef lines. There was strong temporal variation in wounding pattern ($p = 0.001$), but no difference with reef lines ($p = 0.407$; Table 1). The wounding patterns were similar in April and June ($p = 0.287$), but different between all the other months ($p < 0.05$; Table 1). Three distinct groups for the factor Time were also seen from the CAP analysis (Fig. 3), with April and June grouped together and August and October separated. Three wound variables were strongly correlated with the multivariate wounding patterns ($r > 0.5$; Fig. 3): >10 mm holes in the centre of laminae, and <10 mm holes and >10 mm holes in the centre of laterals. There was strong temporal variation in the severity of wounding for these 3 variables ($p < 0.003$; Table 2, Fig. 4) and differences in wounds between the 4 mo (Fig. 4). In general, there was a significant decrease in number of wounds at the different times, with a minimum in October (Fig. 4). Interestingly, the highest number of wounds was not observed in August when wave energy peaks, but in April and June (Fig. 4). We subsequently used our wounding data to

Table 1. PERMANOVA, testing for differences in wounding patterns between Time (April, June, August, October; fixed factor), Reef lines (1 to 3 from inshore to offshore; fixed factor) and 2 Reefs nested within each reef line (random factor)

Source of variation	df	MS	*F*	p
Time	3	108.32	12.12	0.001
Reef line	2	15.76	1.54	0.407
Reefs(RL)	3	10.18	2.10	0.041
T × RL	6	18.50	2.07	0.074
T × R(RL)	9	8.95	1.84	0.009
Residual	325	4.84		

Time (pairwise test)	*t*	p
April vs. June	1.22	0.287
April vs. August	2.96	0.038
April vs. October	3.96	0.020
June vs. August	2.97	0.042
June vs. October	4.60	0.017
August vs. October	3.13	0.021

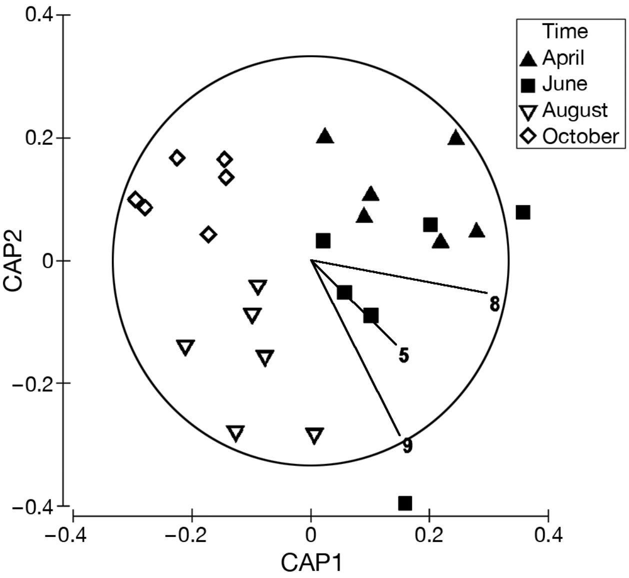

Fig. 3. *Ecklonia radiata*. Ordination (constrained analysis of principal coordinates; CAP) of kelps from Marmion Lagoon based on their wounding patterns constrained by sampling times and vector overlays with selection criterion at Pearson coefficient >0.5 (3 variables). Variables 5, 8 and 9 correspond, respectively, to >10 mm holes in the centre of lamina, and <10 mm holes and >10 mm holes in the centre of laterals. The squared correlation coefficient and result of leave-one-out allocation success were $\delta^2 = 0.78$ and LoA = 79.2%, respectively, using m = 6, where m is the number of axes

Table 2. One-way ANOVA results for the effect of Time (April, June, August and October) on the 3 wound variables found to correlate (r > 0.5) with wounding patterns. Homogeneity of variance could not be met even after transformation; significance was therefore interpreted conservatively as p < 0.01

Variables	df	MS	*F*	p
Lamina (centre), large holes	3	1.79	4.68	0.003
Residual	345	0.38		
Lateral (centre), small holes	3	5032.09	14.95	<0.001
Residual	345	336.59		
Lateral (centre), large holes	3	24.34	13.24	<0.001
Residual	345	1.83		

calculate the total number of wounds an 'average kelp' with 1 stipe, 1 lamina and ca. 40 laterals (Wernberg & Vanderklift 2010) is expected to have (Fig. 4D). For this average kelp, we observed almost the same pattern as for the small holes (<10 mm) at the centre of laterals (which dominated the number of wounds; see Fig. 4D). The total number of wounds on an average kelp was significantly higher in April (285 ± 47, mean ±SE) and June (256 ± 25) compared to August (123 ± 11) and October (71 ± 8) (Fig. 4D).

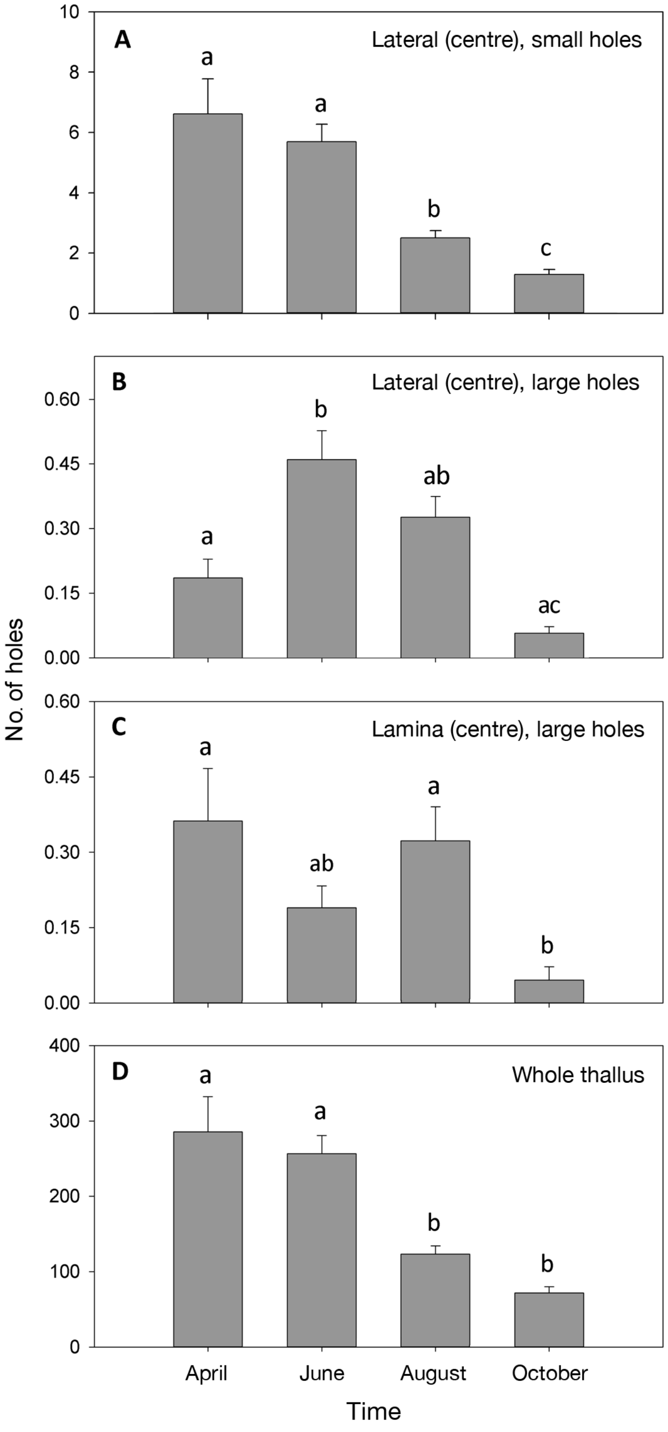

Fig. 4. *Ecklonia radiata*. Changes in wounds at different times (mean + SE) for (A) small holes in laterals, (B) large holes in laterals and (C) large holes in lamina. These 3 variables explained most of the multivariate wounding pattern for the 4 sampling times (April, n = 83; June, n = 90; August, n = 87; October, n = 89). (D) shows the total number of wounds extrapolated to an 'average-sized kelp', for each month (see 'Materials and methods'). Letters above bars indicate significantly different treatments (on square root-transformed data) from Tukey's post hoc tests (p < 0.01)

Biomechanical tissue tests of wounding effects

The tissue properties of intact strips of lamina had a relatively low standard stress at breaking (3.91 ± 1.11 MN m^{-2}, mean ± SD; Fig. 5A), but high extensibility (0.32 ± 0.08; Fig. 5B) and stiffness (12. 65 ± 3.96 MN m^{-2}; Fig. 5C) and therefore also a high toughness (0.65 ± 0.29 MN m^{-2}; Fig. 5D). We found that wounding significantly reduced these biomechanical properties (Table 3), showing a gradient in severity with centred holes and edge cuts having the least and most severe impacts, respectively (Fig. 5). For toughness, all wounding treatments differed from each other (p < 0.01, Tukey test; Fig. 5D). However, for extensibility, 'centred holes' did not differ from unwounded tissue (Fig. 5B). Similarly, for stiffness and strength at breaking, 'centred holes' did not differ from 'edge holes' (p > 0.01; Fig. 5A,C). Finally, centred holes, edge holes and edge cuts reduced the energy required to break healthy kelp tissue by 43, 75 and 92%, respectively (Fig. 5D). To summarize schematically how wounding influenced these key biomechanical properties (Fig. 5), we also plotted 'simplified standard stress-strain curves' (Fig. 6).

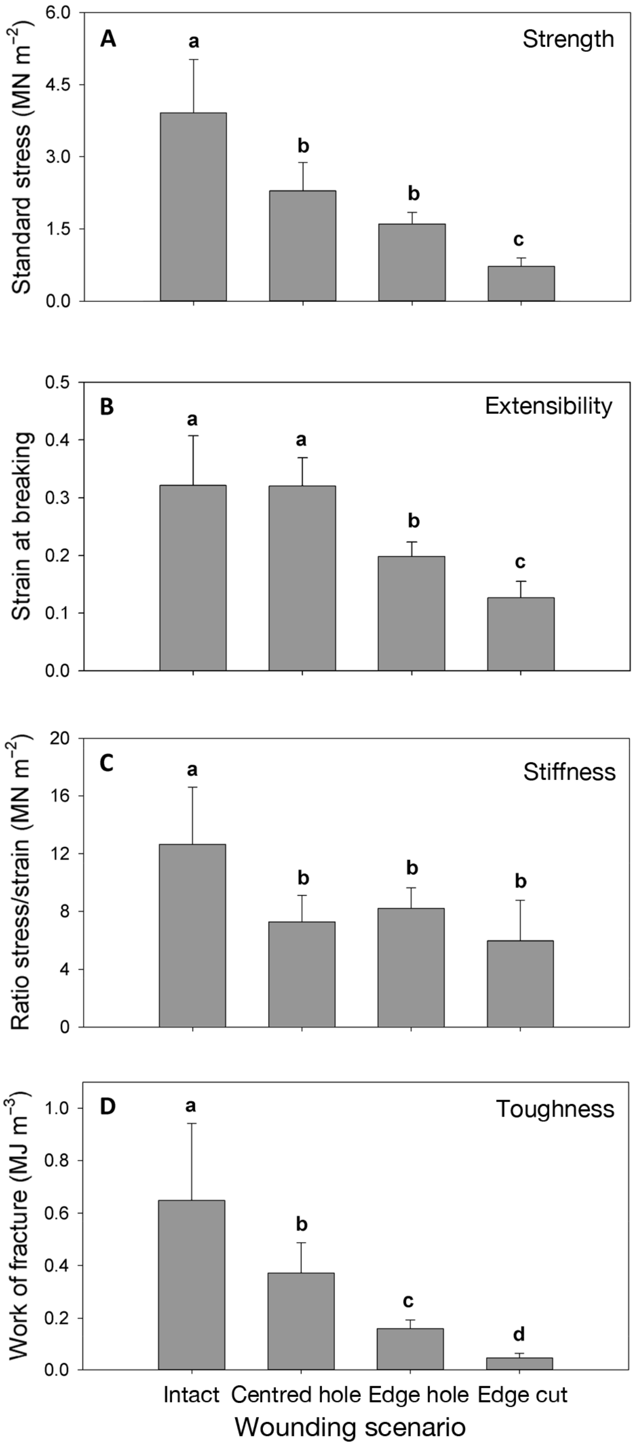

Fig. 5. *Ecklonia radiata*. Impact of simulated wounding on lamina tissue properties: (A) strength (=standard stress at breaking), (B) extensibility (=strain at breaking), (C) stiffness (=ratio stress/strain) and (D) toughness (=work of fracture); n = 52, 16, 15 and 17 for 'intact' 'centred hole', 'edge hole' and 'edge cut', respectively. Letters above bars indicate significantly different treatments (on square-root-transformed data) from Tukey's post hoc tests ($p < 0.01$)

Table 3. One-way ANOVA results for effect of different simulated wounds (no wounding, centred hole, edge hole and edge cut) on 4 biomechanical properties (strength at breaking, extensibility, stiffness and toughness) of lamina tissue

Variables	df	MS	*F*	p
Strength at breaking	3	6.12	116.02	<0.001
Residual	96	0.53		
Extensibility	3	0.17	61.65	<0.001
Residual	96	0.003		
Stiffness	3	6.97	31.39	<0.001
Residual	96	0.22		
Toughness	3	1.66	83.14	<0.001
Residual	96	0.20		

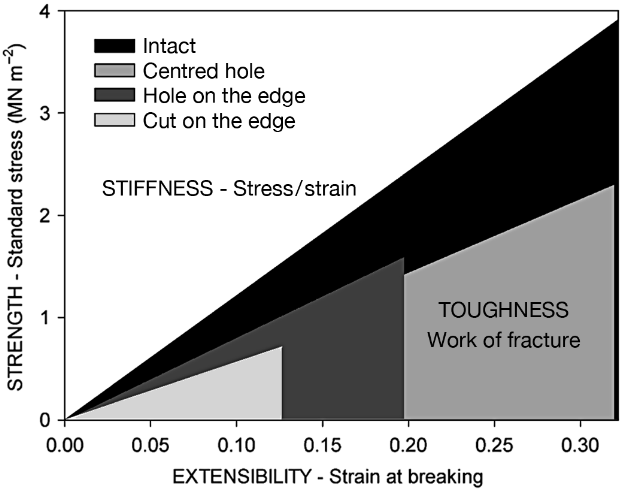

Fig. 6. *Ecklonia radiata*. Summary of changes in tissue properties after wounding. Strain and standard stress at breaking of wounded tissues are displayed on the figure; stiffness and toughness were obtained from stress-strain curves, respectively, as the slope of the stress-strain curves and the area under the curves

DISCUSSION

We found that average *Ecklonia radiata* kelps (i.e. with 1 stipe, 1 lamina and ca. 40 laterals; Wernberg & Vanderklift, 2010) can sustain from ~300 wounds thallus^{-1} in April to ~70 thallus^{-1} in October from relatively wave-exposed reefs. We are not aware of any studies to have reported whole-thallus wounding patterns, and we can therefore not evaluate if these numbers are representative for other species, regions, or habitats. In addition, we found that simulated wounds (holes or cuts) greatly affected the biomechanical properties of kelp tissue, reducing the energy required to break it by 45 to 82%. Overall, these findings indicate that wounds are very common on all kelps before winter and that wounds likely result in greatly increased kelp pruning rates for *E. radiata* beds. The high incidence of wounding implies that physical damage is a ubiquitous and constant pressure on kelps, which might, in turn, limit their size. Paradoxically, wounding may thereby increase kelp survival during storms, because drag and dislodgment is typically lower for small (pruned) than large (intact) kelps.

Wounding patterns

Our study indicated that wounds occur in most kelp thalli (93 to 100%) and in all different kelp tissues (although rarely on stipes), where the vast majority of wounds were small holes located on laterals. Wounds were frequent, diverse and exhibited a complex temporal and spatial pattern around winter. Interestingly, we did not find support for the hypothesis that wounds would be most prevalent in kelps from exposed reefs during winter. Instead, we found no effects of wave exposure and a general peak in wounds in April to June (autumn to early winter), dropping off in August (mid-winter) and reaching a minimum in October (spring). This strong temporal pattern was mainly driven by small and large holes within the lateral tissue and, to a lesser extent, by large holes in the lamina. The only difference between June and April was a higher number of large holes in June, likely a result of 'wounding growth' of many small holes in April (abundant small holes in April propagating into larger holes in June). This overall high number of wounds in early winter could be the consequence of accumulation of wounds over time due to relatively low growth during this period (Kirkman 1984, 1989), increasing the exposure time of kelp tissue to damage. This accumulation of wounds has previously been shown to be associated with higher degradation of aged kelp tissue and a general decrease in toughness (Norderhaug et al. 2003, Molis et al. 2010). Wound accumulation could also constitute a natural seasonal senescence process in late austral autumn, when growth is inhibited by high temperature. Indeed, past research from south-western Western Australia has documented severe reduction in individual biomass in March to July (around 40 to 50% losses) (Kirkman 1984, 1989). Furthermore, grazing rates are generally very low in this system and decrease with increased wave action (Vanderklift et al. 2009); the seasonal pattern found here is, therefore, unlikely to be driven by grazers (we rarely found grazers associated with wounds). However, other studies have found herbivores such as sea urchins (Tegner et al. 1995), mesograzers (Duggins et al. 2001, Krumhansl & Scheibling 2011b), or fishes (Taylor & Schiel 2010) to be important wound generators. Our data suggest that wounds accumulate over time, that highly wounded individuals are likely to be 'weeded out' during storms and that wave exposure appears to be much less important than season in generating wounds.

Biomechanical tests

Our hypothesis that even small wounds would influence tissue biomechanical properties was supported. The tensile tests confirmed that tissue properties were significantly impacted with a loss of strength at breaking, extensibility, stiffness and toughness of up to 82, 57, 53 and 92%, respectively. Previous studies have demonstrated similar impacts of simulated wounds on kelp tissue (Biedka et al. 1987, Mach et al. 2007). Our tests showed that kelps like *Ecklonia radiata* are highly extensible and generally compliant with a low breaking strength and a low work of fracture, as documented for other macroalgae (Carrington et al. 2001, Denny & Gaylord 2002, Pratt & Johnson 2002). Because of these material properties, macroalgae are susceptible to propagation of small initial damages (Denny et al. 1989, Mach et al. 2007). Moreover, the type of wounding and its position had clear implications for the biomechanical properties. As expected, a cut on the edge resulted in the most dramatic effects. When kelps are wounded by cuts, crack propagation occurs easily and typically causes tissue breakage (Denny et al. 1989, Mach et al. 2007). Therefore, holes or cuts on the edge of the tissue are likely to cause the substantial loss of laterals associated with the part of lamina being torn off, as observed for some of the kelp sampled. Previous studies have shown that wounding can increase tissue loss and therefore decrease plant biomass (Toth & Pavia 2006, Krumhansl et al. 2011, Krumhansl & Scheibling 2011a) without affecting overall survival. However, the response might be slightly more complex, with several factors interacting. Indeed, our study did not take into consideration the repetitive loading characterizing hydrodynamic wave forces. Interestingly, Mach et al. (2007) found that repeated loading by sub-lethal force eventually caused complete failure of tissue by fatigue. However, it is also possible that fatigue can be countered by wound healing and induction of increased strength and toughness, as demonstrated for other kelp species (Lowell et al. 1991, De Wreede et al. 1992, Lüder &

Clayton 2004), whereby wounding ultimately minimizes the risk of breakage.

Overall, we found that kelps were highly wounded in April to June, before the peak of storm-generated waves in winter (July to August), with a high number of small holes within the lateral tissue. Additionally, we showed that simulating wounding significantly decreased tissue break forces and the extensibility of *Ecklonia radiata*. It has been shown that wave-swept algae, typically, are 'mechanically over-designed' (Denny 2006, Mach et al. 2007) and that they can cope with extreme drag forces. However, we demonstrated that even small individual occurrences of tissue damage can reduce kelp material properties dramatically and lead to breakage at much lower-than-expected hydrodynamic forcing. This could have severe consequences for the fitness and survival of kelps, making them more susceptible to wave force. However, wounds may also increase pruning rates, resulting in decreased total kelp biomass and thereby also decreased drag. Similarly, grazing damages and associated wounds have been found to increase kelp erosion and consequently decrease individual kelp biomass (Black 1976, Krumhansl & Scheibling 2011a). Black (1976) suggested this similar paradoxical beneficial function of reducing drag and increased survival for an intertidal kelp, *Egregia menziesii*. Previous research in the same region (Kirkman 1984, 1989, Wernberg & Vanderklift 2010) found a strong temporal growth pattern with a decrease in individual kelp biomass from March to July (autumn to winter). More specifically, Wernberg & Vanderklift (2010) investigated how seasonal growth influenced morphological variation in *E. radiata* and suggested that low growth and high erosion during the autumn to winter period leads to a minimum kelp individual biomass coinciding with the peak wave period. This reduction in biomass, via wounding-mediated erosion, reduces hydrodynamic drag forces and may also reduce dislodgement, resulting in increased survival during peak wave action. The net result of wounding-induced biomass pruning may thereby, paradoxically, lead to an increase in kelp survival during winter storms. Simultaneously, the resulting increase in detrital supply to adjacent habitats results in higher trophic connectivity within the coastal system during this period of peak wave action. Interestingly, climate-change modelling generally predicts an increase in storm frequency and intensity (Emanuel 2005), and the ecological implications of wounding, pruning, increased survival of pruned kelps and kelp detritus export could therefore become even more important in the future.

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