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Phenological decoupling of mortality from wave forcing in kelp beds

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Abstract. Kelps often live in a harsh hydrodynamic environment where wave-driven dislodgement of individuals can alter the biodiversity and functioning of reef systems, and increase production in coastal ecosystems adjacent to reefs. The current paradigm is that winter storms tear kelps from reefs once hydrodynamic forces exceed attachment or tissue strength—a threshold response that implies a pulsed relationship between wave forces and dislodgement. Here, we challenge this understanding by showing how kelp phenology can decouple susceptibility to dislodgement from seasonal patterns in wave forces. We measured kelp dislodgement rates and hydrodynamic forces at nine subtidal reefs over two years ($n = 4320$ kelps tagged and monitored). Contrary to expectation, we found relatively low and constant dislodgement rates for all reefs (13% ± 6% [mean per season ± SD]) in spite of a strong temporal pattern in wave action and extreme water velocities (winter peaks up to 3–4 m/s). A biomechanical model, based on the balance between kelp attachment strength and hydrodynamic drag, demonstrated that severe reduction in individual kelp size toward winter (>50% decrease in biomass for all sites) minimized drag and made the kelps less susceptible to high water velocities, allowing individuals to survive storm velocities over 3–4 m/s. We conclude that the timing of reduced susceptibility to disturbance, through the seasonal reduction of individual kelp biomass that coincides with times of highest water velocities is critical to the dynamics of kelp dislodgement and survival. We propose that phenological processes maintain many kelp beds in a higher degree of population stability and equilibrium with hydrodynamic forces than previously believed.

Key words: biomechanical model; break force; dislodgement; drag; Ecklonia radiata; *foundation species; kelp bed; phenology; physical disturbance; survival; wave exposure.*

INTRODUCTION

Living in a moving fluid, air, or water, can be challenging for sessile organisms as they are subjected to severe physical forces without opportunity to escape (Koehl 1996). Nevertheless, a variety of sessile organisms are well adapted to survive in mechanically stressful environments, such as trees in storm winds (Spatz and Bruechert 2000) or large algae in storm waves (de Bettignies et al. 2013*a*), and this implies that they possess functional traits that minimize stress and increase survival (Johnson and Koehl 1994, Koehl 1999). For example, macroalgae growing on wave-exposed reefs have a wide range of strategies to withstand the hydrodynamic stress, such as drag reducing shapes (Blanchette 1997) or tissue flexibility (Denny 1998). Understanding the relation between the intensity of physical forcing, organism survivorship, and functional traits remains a great challenge for predicting performance and persistence.

Importantly, disturbances that affect foundation species will have cascading effects on ecosystem structure and function (Hughes 1994, Ellison et al. 2005, Halpern et al. 2007). Kelps are foundation species in temperate reef systems and loss of kelps generally lead to a shift in community structure (Byrnes et al. 2011, Moy and Christie 2012, Wernberg et al. 2013). Many kelps inhabit one of the most mechanically challenging environments on earth, where wave forces are severe and the risk of disturbance through dislodgement of individual kelps is great (Seymour et al. 1989, Graham et al. 1997, Thomsen et al. 2004). Direct observations and indirect inferences of kelp dislodgement have emphasized the dynamic nature of kelp forests, which are

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constantly being reshaped by disturbances (Dayton et al. 1992). In temperate regions, large waves associated with storms usually occur in winter and often tear off kelp from reefs, reducing their abundance (Graham et al. 1997, Filbee-Dexter and Scheibling 2012). This wave-driven dislodgement of kelps in winter has been directly observed for large kelp species such as *Macrocystis pyrifera* (Seymour et al. 1989, Dayton et al. 1992, Graham et al. 1997). Inferences about wave-driven kelp dislodgement include the occurrence of patches devoid of kelp at wave-exposed reefs (Wernberg and Connell 2008, Thomson et al. 2012) and the accumulation of drift kelps in adjacent habitats directly after winter storms (Colombini and Chelazzi 2003, Filbee-Dexter and Scheibling 2012). Collectively, these observations suggest that dislodgement occurs as a threshold response to wave energy that, by definition, is triggered when the force exceeds the capacity of the kelp to resist the perturbation (Romme et al. 1998, Turner and Dale 1998). Theoretically, the dislodgement of kelps, and the threshold response, can take one of several forms in response to the magnitude of perturbation. Dislodgement could occur as either (1) pulses of dislodgement determined by storm intensity (i.e., when water velocity and the resulting force exceeds the strength of kelp attachment or (2) a disproportionate pulse accounting for the majority of kelp dislodgement when the first significant storm of the season occurs (a "first-flush" scenario sensu Lee et al. [2004]). The first flush will occur when weakly attached individuals have accumulated during the summer period of benign conditions and are dislodged during the first major storm of the season, leaving only individuals that are firmly attached to the reef and which will resist subsequent storms. In temperate regions, both scenarios are hypothesized to happen in winter, a period of frequent severe storms (e.g., Lemm et al. 1999). Another scenario (3) implies that the strength of attachment of most kelps remains greater than drag generated by storms, and therefore kelp dislodgement stays low and constant throughout the year (i.e., a storm-independent response).

Dislodgement and survival of sessile organisms such as macroalgae can be investigated through a mechanistic approach (Johnson and Koehl 1994, Koehl 1999), in which the dislodgement process is a balance between the hydrodynamic forces experienced by the organism, and the force required to break the organism off (break force), which in turn is related to kelp tissue properties and attachment to the substrate (Gaylord et al. 1994, Denny and Gaylord 2002). The different hydrodynamic forces acting on a sessile organism are drag, lift and acceleration, but the only major force exerted on subtidal macroalgae is the hydrodynamic drag (Denny and Gaylord 2002), which represents their resistance to the fluid movement. However, variation in kelp individual biomass is also important to drag and the probability of dislodgement, particularly at peak velocities (de Bettignies et al. 2013*a*). Because kelps such as our study species, *Ecklonia radiata*, often follow seasonal changes in thallus biomass, seasonal patterns should be incorporated into efforts to understand the balance between biomass and dislodgement. More specifically, the seasonal growth-erosion dynamics and the resulting decrease in individual biomass in autumn-winter might offset the increase in water velocity during winter storms by reducing the hydrodynamic drag (de Bettignies et al. 2012, 2013*a*, *b*).

To investigate this possible mechanism, we examined in detail the relationship between wave-generated perturbation to kelp beds (*Ecklonia radiata*) and the nature of the ensuing disturbance. Specifically, we tested if the relationship between peak water velocity and magnitude of kelp dislodgement best resembled a pulsed, first flush or constant delivery scenario. To address this main objective, we first characterized maximum in situ water velocities using a wave model and wave gauges in each season during two years, and during the most severe storm over that period. We then measured kelp dislodgement at nine reefs over a gradient of wave exposures and related dislodgement to water velocities. Finally, we examined the causes of this relationship through a biomechanical model that estimated the monthly risk of kelp dislodgement (three sites across the wave exposure gradient for three years) where we incorporated the influence of thallus biomass variation to test its implication for kelp survival.

METHODS

Study site

The study was conducted in Marmion, 20 km north of Perth, southwestern Australia (Fig. 1). This region is strongly influenced by both swell- and wind-generated waves. In the austral summer (December–February), strong sea breezes generate moderate waves (up to 2 m) whereas in the austral winter (June–August), frequent storms generate large swell (up to 8–9 m; Searle and Semeniuk 1985, Lemm et al. 1999). The presence of successive lines of limestone reefs running parallel to the shore dissipates hydrodynamic forces with increasing proximity to the shore (Fig. 1A), resulting in a gradient of wave exposure (Thomson et al. 2012, de Bettignies et al. 2013*a*). Nine sites (depth range 8–10 m) were selected along this gradient of exposure (Fig. 1A, B).

Study species

The kelp studied, *Ecklonia radiata* (C. Agardh) J. Agardh, is a dominant habitat former on the temperate subtidal reefs of Australasia (Connell and Irving 2008). *E. radiata* is a perennial kelp that can reach a length up to 2 m and has a thallus with a terete basal stipe that bears a flattened blade with ramified lateral branches that often create a complex three-dimensional shape (Kirkman 1981, de Bettignies et al.

2013*a*; Appendix A: Fig. A1). The temporal growth dynamics of *E. radiata* leads to a minimum in individual biomass in autumn–winter, which might minimize the hydrodynamic drag during winter storms (de Bettignies et al. 2013*a*, *b*).

Peak water velocities

Wave model.—Water velocity at the seafloor was estimated using the SWAN model (simulating waves nearshore; Booij et al. 1999). Drawing on local bathymetry and oceanography the model simulates wave generation, propagation, and dissipation when forced at its western (seaward) boundary by daily averaged wave height, period, and direction obtained from an oceanic wave buoy (located 20 km southwest of the study area; Department of Transport of Western Australia, data *available online*).[6] The SWAN-predicted significant wave heights were in high agreement with daily averaged significant wave heights measured by an AWAC instrument (acoustic wave and current profiles) located in Marmion during 2007–2008 ($r^2 = 0.80$; see Appendix B: Fig. B1). The SWAN model was run for the period from September 2008 to September 2011, over an 18 km (north–south) by 11 km (east–west) grid encompassing all of Marmion, with grid cells of 30×30 m. The model produced wave parameters for each of the grid cells for each day (Fig. 1A). We extracted the orbital water velocity at the bottom (U_{bot}, m/s) calculated from the significant wave height, period and wavelength (Holthuijsen 1997) and obtained the maximum daily averaged U_{bot} for each reef × season combination ($U_{\mathrm{bot}}^{\max}$, $n = 72$), and estimated maximum individual water velocity as $U_{\max} = 2 \times U_{\mathrm{bot}}^{\max}$ (Holthuijsen 1997).

In situ wave gauges.—Within the kelp bed at each reef, a 3 m diameter area was cleared of all macroalgae for the deployment of an array of hydrodynamic recorders consisting of dynamometers and gravitational accelerometers with inbuilt data loggers (HOBO Pendant G; Onset Computer Corporation, Bourne, Massachusetts, USA). Three dynamometers and two accelerometers were deployed in each array for one week in winter (July 2010), a period that encompassed a substantial storm event (wave rider buoy, 6–7 m averaged wave height at 10–14 s period, offshore of Marmion, Fig. 4A). The dynamometers measured maximum drag through drag in a practice golf ball, which was converted to maximum water velocity using the calibration curves of Bell and Denny (1994). To continuously measure horizontal acceleration, the gravitational accelerometers loggers were mounted on a flexible bar with blades on the distal end (Evans and Abdo 2010, de Bettignies et al. 2013*a*). Acceleration was converted to water velocity from a previous calibration against an acoustic Doppler velocimeter (ADV; de Bettignies et al. 2013*a*).

Dislodgement rate

At each of the nine reefs, four circular plots (2 m diameter) were established and, within each plot, 15 adult kelps (stage 3; Kirkman 1981) with distinct holdfasts (no fused holdfasts; Wernberg 2005) were tagged around the stipe with cable ties inserted into fluorescent latex surgical tubing ($n = 540$ kelps; see Plate 1). At four of the reefs (along the gradient of wave exposure: WAT1, L1, H1, and DH1) half of the kelps (two out of four plots at each reef, $n = 120$ kelps) were double tagged to test for tag loss. After three months, 100% of the recovered kelps still had both tags, indicating that tag loss was negligible. Every three months during two years, four new, randomly located plots ($n = 60$ kelps per reef) were set up on each reef ($n = 4320$ kelps in total). For each plot, the tagged kelps were relocated and counted; dislodgement was inferred from an inability to relocate a tagged individual, which implied a breakage at the holdfast–reef junction, along the stipe, or at the stipe–lamina junction. Each plot was searched and counted three times to ensure all surviving kelps were located and avoid any overestimation of dislodgement. For each season, the kelp dislodgement rate from a plot was defined as the percentage of tagged kelps lost (from the 15 kelps tagged) after three months. Dislodgement rate of the nine reefs was also measured during the most severe storm of the study period (8–11 July 2010) after counting the tags in the three-month standard plots before and after the storm.

Biomechanical dislodgement model

A biomechanical dislodgement model, based on the balance between the hydrodynamic force exerted on a kelp thallus (drag; F_{drag}) and the force required to break the thallus (strength of the tissue and/or attachment to the reef; break force; F_{break}), was used to evaluate the risk of dislodgement at different water velocities. According to this biomechanical relationship, dislodgement occurs when F_{drag} is greater than F_{break}.

F_{drag} (Newtons) can be derived from the standard empirical drag equation (Vogel 1984, Denny 1995)

$$F_{\mathrm{drag}} = \frac{1}{2}\rho \times U^2 \times C_{\mathrm{drag}} \times A \tag{1}$$

where ρ is the density of seawater (1026 kg/m^3), U is the water velocity (m/s), C_{drag} the drag coefficient (dimensionless), and A the surface area of the thallus (m^2). Drag can be predicted from A, the total area of the thallus and C_{drag} modeled as a function of water velocity ($C_{\mathrm{drag}} = 0.041[\text{water velocity}]^{-0.634}$) for *Ecklonia radiata* (de Bettignies et al. 2013*a*). The total area was obtained from the biomass (wet mass, WM) by applying a WM : A relationship derived for adult kelps (de Bettignies et al. 2013*a*). F_{break} was measured in situ by pulling

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[6] http://www.transport.wa.gov.au/imarine/historical-tide-and-wave-data.asp

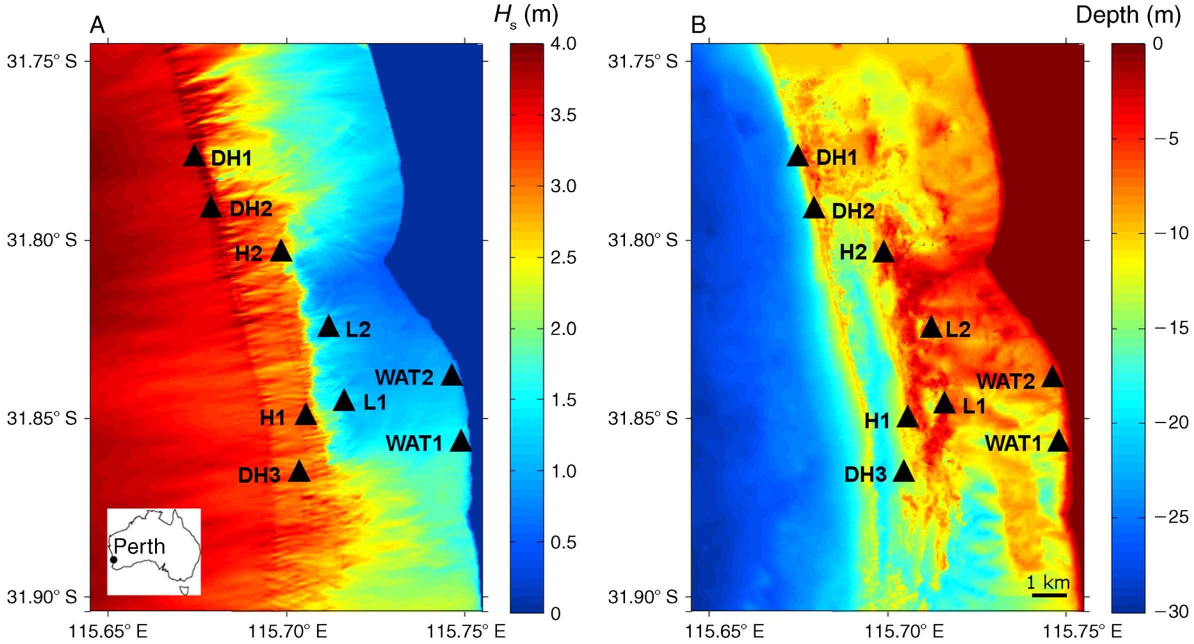

FIG. 1. SWAN model outputs across the Marmion region. (A) Maximum significant wave height (maximum H_s) for the period 1 September 2009–30 September 2011; the dark blue color was used to identify the land. (B) Bathymetry. WAT1, WAT2, L1, L2, H1, H2, DH1, DH2, and DH3 are the study sites. Inset shows location of Marmion, Perth in Australia.

kelps off the reef with a *Pesola* dynamometer (Thomsen et al. 2004). These biomechanical break tests were performed on 60 kelps per reef: 30 in early winter (early June 2010) and 30 at the end of winter (early August 2010), from a subset of four reefs of different wave exposure (WAT1, L2, H2, and DH1).

Drag was predicted from a combination of thallus biomass and water velocity. Thallus biomasses were obtained from a three-year data set (2009, 2010, and 2011) of monthly individual kelp biomass (M. Vanderklift, T. de Bettignies, and T. Wernberg, *unpublished data*; $n = 749$) and seasonal maximum water velocities ($U_{\max}$) from the SWAN model for three sites across the exposure gradient with enough biomass and break force data available (i.e., L2, H2, and DH1). For each predicted drag (each kelp thallus), a break force value was randomly generated from the normal distribution of break forces at each site, repeated three times (obtained with R version 2.15.2).

Subsequently, the dislodgement risk factor (DRF), a measure of the vulnerability of adult kelp to dislodgement, was calculated as

$$\mathrm{DRF} = 1 - F_{\mathrm{break}}/F_{\mathrm{drag}}. \tag{2}$$

When DRF ≥ 0, the kelp is dislodged from the reef. Furthermore, the significant erosion rate in autumn leads to a severe reduction of individual kelp biomass for *Ecklonia radiata* (∼50% decrease in biomass; Wernberg and Vanderklift 2010, de Bettignies et al. 2013*b*). A second scenario was then run with the maximum biomass maintained throughout the year, to look at the effect of this biomass loss on the dislodgement susceptibility of kelp. The month with the maximum averaged biomass was applied to the other months and DRF was calculated the same way as the original scenario.

In order to account for the possibility of important sources of variation and error reduction when calculating the drag, we determined a prediction error (Θ) based on the difference between modelled and measured drag values using data of de Bettignies et al. (2013*a*; Appendix C: Fig. C1). The prediction error was calculated as the mean of the absolute difference between modelled and measured drag ($\Theta = 9.63$ N). This value was then added to the previous drag values and the seasonal change in DRF was modeled again.

Statistical analysis

To test for spatiotemporal differences in kelp dislodgement, the dislodgement data collected from the nine reefs were analyzed by permutational analyses of variances (PERMANOVA) following two experimental designs. The first design focused on difference among seasons and reefs and included three factors: year (random factor with two levels), season (fixed factor with four levels, crossed with year) and reef (random factor with nine levels, crossed with year and season). The second design focused on dislodgement during the severe storm event and included only one factor: reef (random factor with nine levels). Shapiro-Wilk tests were applied to verify the normal distribution of break forces data.

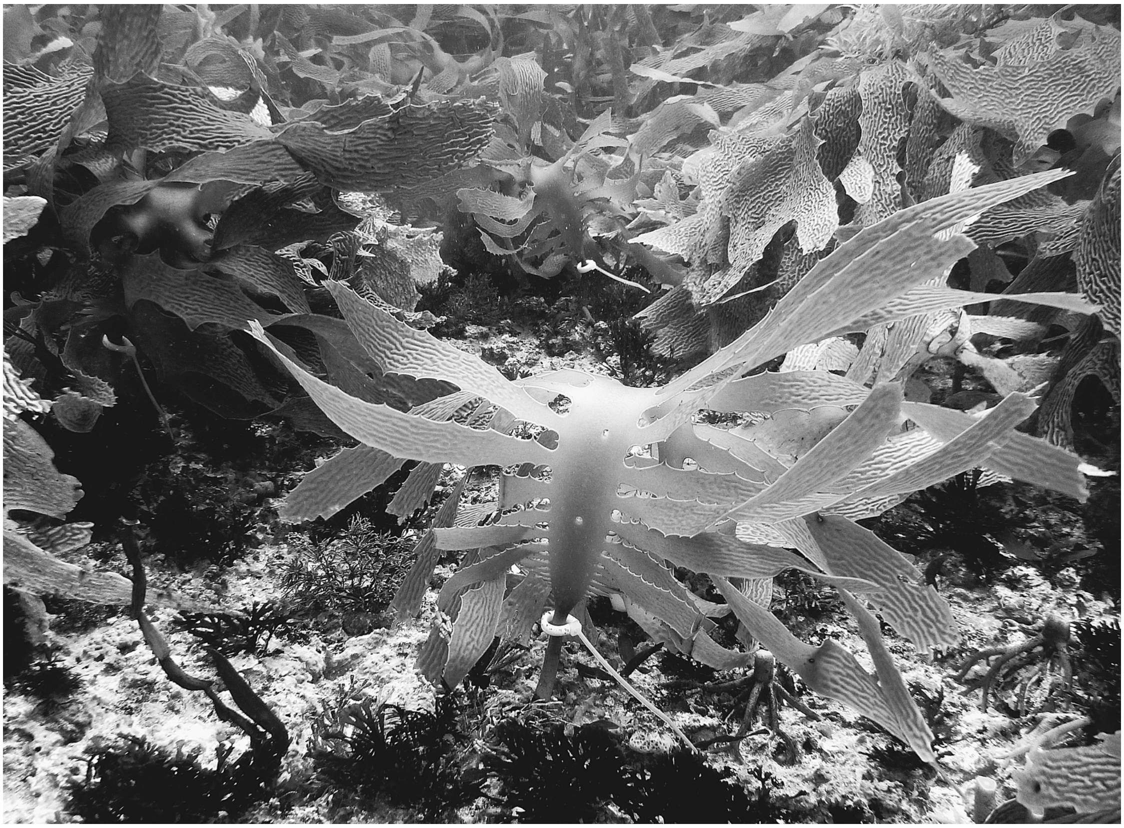

Plate 1. *Ecklonia radiata* kelp bed off southwestern Western Australia with tagged adult kelp in the foreground (tag around the stipe). Photo credit: T. Wernberg.

Results

Kelp dislodgement vs. water velocity—season

Variation in model-generated $U_{\mathrm{bot}}^{\max}$ (Fig. 2) reflected the offshore-onshore gradient in significant wave height (combined with the wave period) and bathymetry; particularly in winter, when the two most offshore reef lines were relatively exposed (Fig. 2). Maximum bottom velocities at the nine reefs highlighted the strong seasonality in wave exposure from spring 2009 to winter 2011 with peak velocities in winter except for the most protected reefs (Figs. 2, 3A). $U_{\max}$ was highest offshore but there were no major differences in maximum values between the mid-shore outer reefs and the deep offshore reefs (Fig. 3A). In contrast to the strong seasonality in water velocities (Fig. 3A), the kelp dislodgement rate did not increase in winter, nor was it greater at the most wave-exposed reefs (Fig. 3B). Instead, winter 2010 had relatively low and similar kelp dislodgement rates for the nine reefs (10% ± 2.3% per season, Fig. 3B) and winter 2011 did not show any major differences from the other seasons. In general, kelp dislodgement occurred at the reef–holdfast junction (100%) and the rate varied from nearly 0% up to 30%, with an average of 13.4% ± 6.5% ($n = 69$) kelps dislodged per season (Fig. 3B).

There was no relationship between maximum water velocity and kelp dislodgement rate when considering all combinations of reef × season ($r^2 < 0.001$, $P = 0.954$, $n = 69$; Fig. 3C), and there was no peak in dislodgement rate in winter, the time of highest water velocities (Fig. 3A, B, C). The three-way PERMANOVA confirmed that the differences among reefs, seasons and years were negligible ($P = 0.710$, 0.839, and 0.278, respectively) but indicated that seasonal patterns in dislodgement were not the same in each year (year × season, $P = 0.012$). Kelp dislodgement was significantly ($P < 0.05$) higher in spring vs. autumn and winter in 2009–2010 and lower in summer vs. autumn in 2010–2011.

Kelp dislodgement vs. water velocity during a storm

The storm monitored in July 2010 was the most severe during the two-year study period (November 2009 to September 2011) with offshore waves up to 7 m high (averaged per hour, nondirectional wave data from the Rottnest wave buoy; Fig. 4A). Due to the limited memory capacity of the HOBO G-loggers, the sampling period of the accelerometer did not encompass the entire storm (Fig. 4B). The values from the dynamometers (black dots, Fig. 4B) were however the averaged maximum velocities (±SD) recorded for the entire storm period. No results are presented for site DH3 because

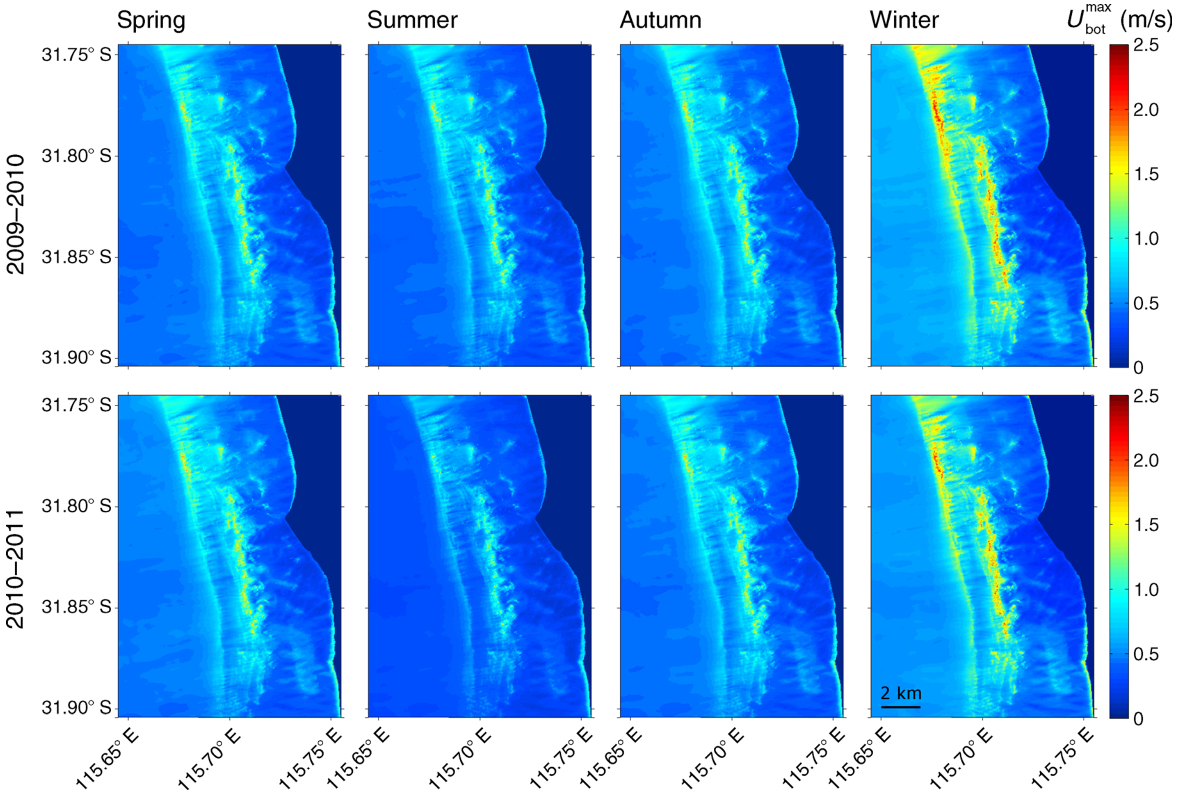

FIG. 2. Maps of maximum daily averaged water velocity for each reef × season combination (U_{bot}^{max}; see *Methods: Peak water velocities: Wave model*) generated by the SWAN model for the study period (spring 2009 to winter 2011). The summer months are December, January, and February; the spring months are September, October, and November; the autumn months are March, April, and May; and winter months are June, July, and August.

the hydrodynamic gauges were lost, and WAT2 was removed from the analysis because of unusual kelp mortality in summer 2010–2011 from unknown causes (either a sudden outbreak of overgrazing by arboreal sea urchins *Holopneustes* sp. or physiological stress because of high temperature and low light conditions during this period).

Maximum water velocities estimated from the SWAN wave model (Fig. 3A) and measurements in situ (Fig. 4B) were similar, up to 3–3.5 m/s for the most exposed sites (H1, H2, DH1, and DH2) with a few extreme peaks at 4 m/s for H1 and H2 (Fig. 4B). In contrast to the seasonal kelp dislodgement rate, we found a positive linear relationship between dislodgement rate and increasing water velocity during the largest storm ($r^2 = 0.52$, $P = 0.044$, Fig. 4C).

Biomechanical model

Break force tests.—Kelp break forces were measured in situ at WAT1, L2, H2, and DH1to build the biomechanical model of dislodgement. The four sites had similar tissue failure patterns with, on average, 60.8% breakage at the reef–holdfast junction, 4.6% at the stipe–holdfast junction, 6.8% along the stipe, and 27.8% above the meristem region. Breaking strengths were the lowest for the reef–holdfast location compared to the other breaking places. There was no change over time in the attachment and tissue strength of kelp before and after winter ($P = 0.22$). Break force differed between reefs ($P < 0.001$), driven by the difference between the most onshore site (WAT1) and the other three reefs (L2, H2, and DH1; pairwise tests, $P < 0.001$). Kelps at WAT1 had lower break force (126.8 ± 55.0 N [mean ± SD]) than L2, H2, and DH1 (162.5 ± 59.7 N, 173.5 ± 54.2 N, and 174.5 ± 50.5 N, respectively), and this was likely the consequence of more brittle limestone reef. In subsequent models, break force measurements from different times were pooled for each reef and their normality was tested (Shapiro-Wilk test). Break force data from the four sites (Appendix D: Fig. D1) were normally distributed (0.968, 0.975, 0.980, and 0.965 for WAT1, L2, H2, and DH1, respectively) and a value of break force was randomly generated from its normal distribution and allocated to each value of drag per individual and this was repeated three times.

Modeling of the dislodgement risk factor (DRF).—WAT1 was not included in the modeling of DRF because of lack of kelp individual biomass data throughout the year. The most sheltered reef, L2, did

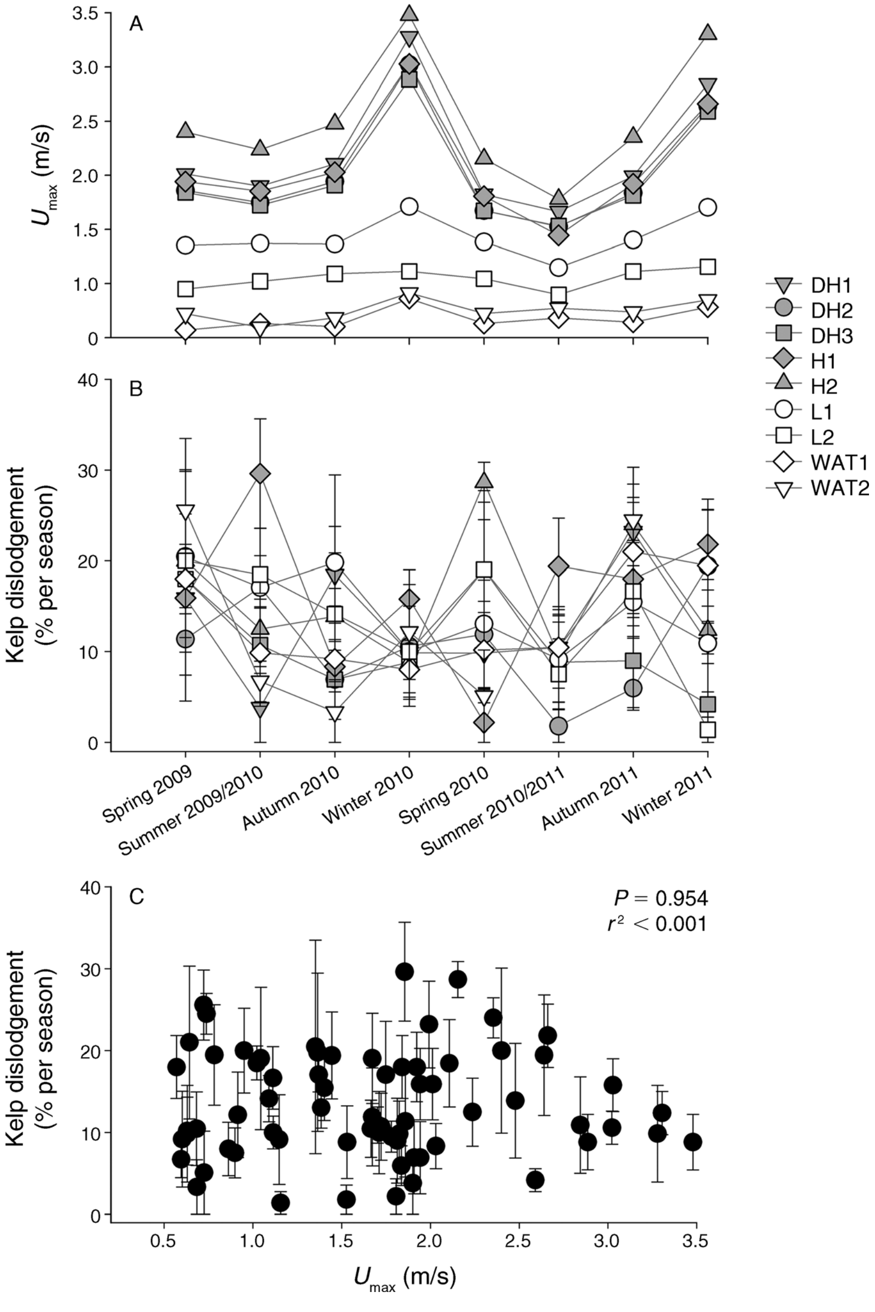

FIG. 3. Relationship between maximum individual water velocities (U_{max}; see *Methods: Peak water velocities: Wave model*) and kelp dislodgement rate. (A) Seasonal variation of maximum water velocities at the nine reefs, (B) seasonal variation of kelp dislodgement rate (mean and SE) at the nine reefs, and (C) response of kelp dislodgement rate (mean and SE) to increasing water velocity. Gray, white, and black filled symbols (A, B, C) represent the more exposed, more sheltered, and all sites, respectively.

not exhibit the same monthly variations in water velocities as the other sites (H2 and DH1) with values around 1 m/s all year-round and only a small increase in winter (Fig. 5A). For all three reefs, the changes in individual biomass were opposite to variation in water velocities, with a maximum in late spring and summer and minimum in autumn and winter (Fig. 5B). Because the break force remained the same over time and the drag is a function of water velocity and kelp biomass (or thallus area), the contrasting variation of both parameters resulted in a relatively constant negative DRF under −5 for H2 and DH1 during the year (Fig. 6A). Due to the combination of minimum individual biomass in winter and a relatively constant water velocity over the year, the reef L2 had a very low DRF (−20 to −30) during the year (Fig. 6A). Instead, all three reefs had some of the lowest DRF in winter when water velocity was the highest (≈−35, −10 and −6 for L2, H2 and DH1 respectively; Fig. 6A). When adjusting the calculation of drag with the prediction error, the DRF increased (3–5 units) but still remained very negative and did not reach the threshold for dislodgement (DRF = 0; Appendix E: Fig. E1). For the hypothetical scenario of no-biomass decrease in autumn–winter (the maximum, February, biomass was maintained in the model), the DRF was dramatically higher in winter (July–August) when the water velocities peaked, close to a value of 0, when kelp get dislodged, for the most exposed reefs (H2 and DH1, Fig. 6B). For the more sheltered reef L2, the DRF remained low even in winter (DRF ≈ −15, Fig. 6B). The same pattern was evident when calculating the prediction error although less difference was found between winter and the other seasons (Fig. E1).

Discussion

This study provides new insights into the relationship between peak water velocities and disturbance in kelp beds. Of the three scenarios of kelp dislodgement proposed in the introduction (pulsed, first flush, or constant) our data support a model of constant kelp dislodgement independent of wave-induced water velocities (13.4% ± 6.5% per season). This model does not exclude a threshold pulsed response when the disturbance is extreme as indicated by an increase in kelp dislodgement for the more exposed reefs (∼10% of kelp) during the most severe storm. However, the kelp dislodgement was not greater in winter (10% ± 2.3% and 13% ± 7.4% for winter 2010 and 2011, respectively) when storms were more frequent than other times of the year (Lemm et al. 1999). The biomechanical model resolved this apparent contradiction by showing how seasonal changes in individual kelp biomass (thallus area) result in a low and constant risk of dislodgement over the year (DRF very negative), allowing *E. radiata* to persist in an environment where wave-generated water velocities are high.

The biomechanical model highlighted the importance of seasonal variation in kelp individual biomass and provided a mechanistic explanation for the observed invariance in dislodgement among seasons and reefs. The model indicates that seasonal variation in individual kelp biomass resulted in lower susceptibility to dislodgement during periods that coincided with peak water velocities, which in turn allowed kelps to withstand storm velocities. This loss of biomass resulted from the combination of low kelp growth and high erosion of kelp tissue (de Bettignies et al. 2013*b*). Previous research in this region (Kirkman 1984, Wernberg and Vanderklift 2010, de Bettignies et al. 2013*b*) has found a period of low growth in autumn and a peak in distal tissue erosion in autumn–winter that leads to a decrease in the biomass of individual thalli from March to July (autumn–winter), from 800–

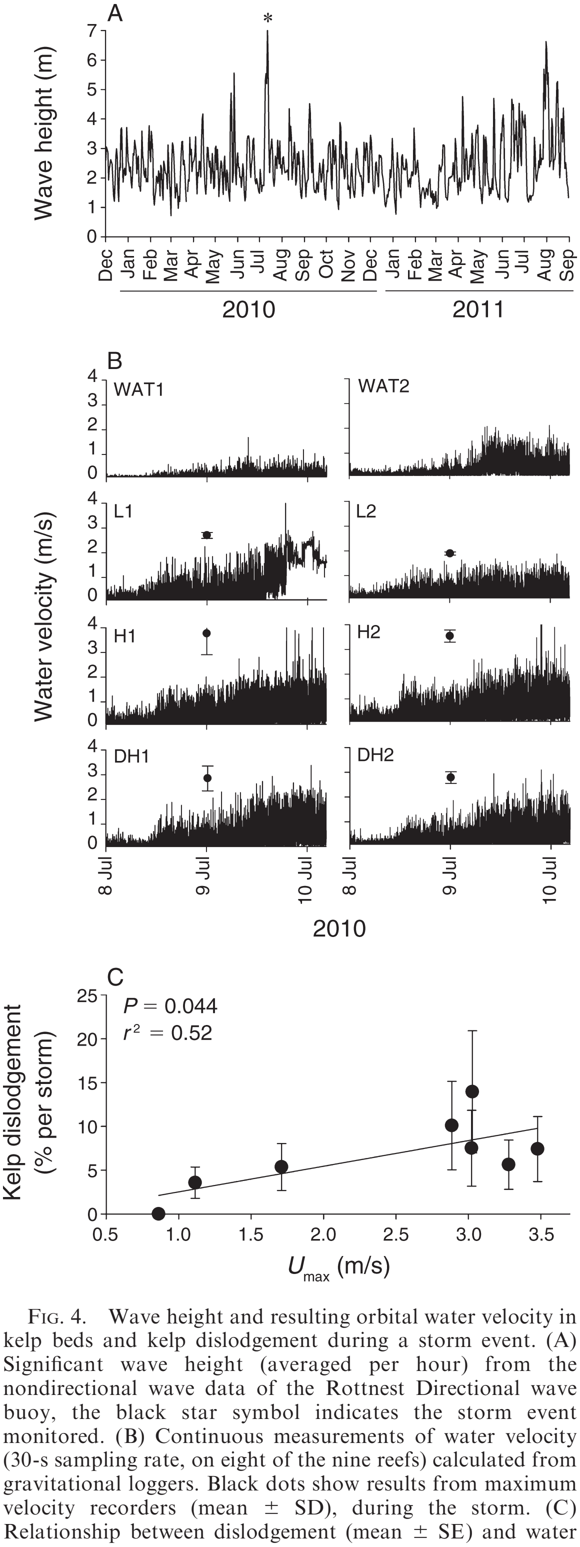

Fig. 4. Wave height and resulting orbital water velocity in kelp beds and kelp dislodgement during a storm event. (A) Significant wave height (averaged per hour) from the nondirectional wave data of the Rottnest Directional wave buoy, the black star symbol indicates the storm event monitored. (B) Continuous measurements of water velocity (30-s sampling rate, on eight of the nine reefs) calculated from gravitational loggers. Black dots show results from maximum velocity recorders (mean ± SD), during the storm. (C) Relationship between dislodgement (mean ± SE) and water velocity ($U_{\max}$) during the most severe storm in winter 2010 with P and r^2 from the linear regression. Water velocity is the maximum estimate from the SWAN model for the corresponding reef.

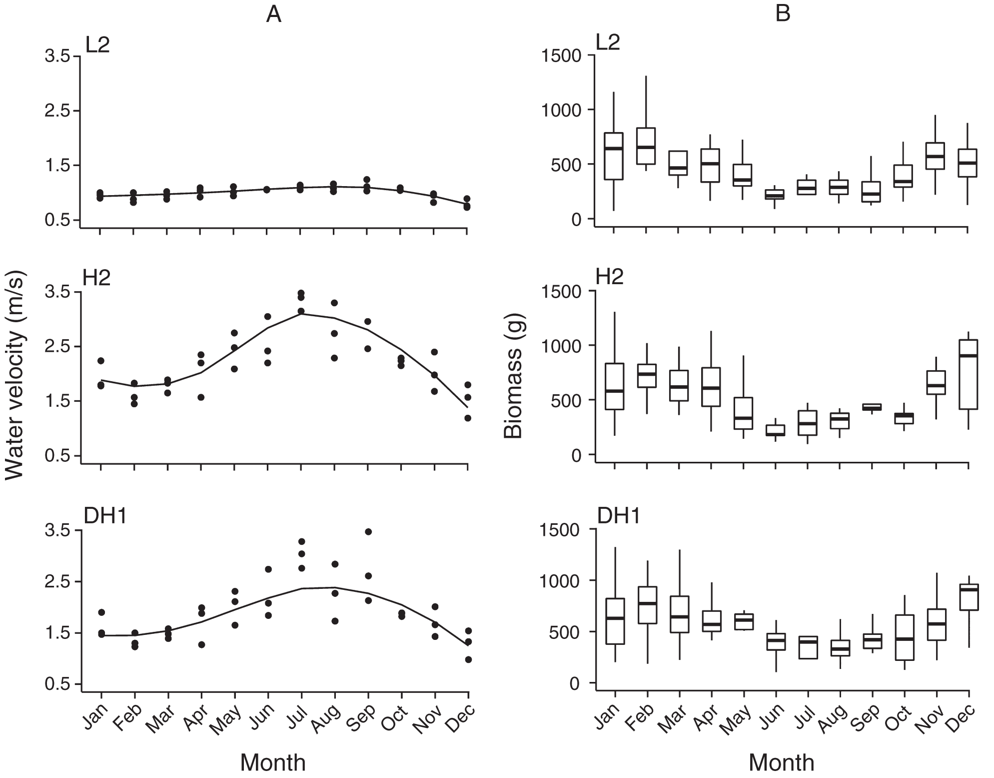

FIG. 5. Seasonal variations of water velocity and individual kelp biomass at three reefs across the hydrodynamic gradient. (A) Modeled monthly maximum water velocity for three years (2009 to 2011). (B) Monthly average of individual kelp biomass from the three years. Box plot components are middle line, median; box edges, first and third quartiles (the 25th and 75th percentiles); whiskers, extend from the edge to the highest and lowest value of 1.5 of the interquartile range (IQR); dots, outliers.

700 to 200–300 g fresh mass/individual. This peak in erosion coincides with spore production and severe tissue wounding and, as a result, weakening of the kelp tissue, which, combined with greater water motion, likely facilitates pruning and erosion in autumn–winter (de Bettignies et al. 2012, 2013*b*). This, in turn, reduces drag and increased survival is therefore predicted by the biomechanical model. Similar thallus erosion and increased survival has been shown for intertidal algae (Blanchette 1997, Demes et al. 2013). These findings are likely to be generalizable to other kelp systems because of the ecological and structural resemblance of *Ecklonia radiata* with other perennial subsurface kelps such as *Laminaria* spp. in Europe and northeastern North America (Jupp and Drew 1974, Brady-Campbell et al. 1984), *Ecklonia cava* in Japan (Haroun et al. 1989), and *Lessonia* spp. in South America (Tala and Edding 2005). All have similar growth–erosion dynamics with marked seasonality in individual biomass (minimum in winter).

The pattern and magnitude of dislodgement of *Ecklonia radiata* differs from that observed in some previous studies but can be explained by the intensity of wave disturbance. Previous observations of wave-driven algal mortality have been predominantly for intertidal algae (Dudgeon and Johnson 1992, Pratt and Johnson 2002) and giant, floating-canopy kelps such as *Macrocystis pyrifera* (Dayton and Tegner 1984, Seymour et al. 1989, Reed et al. 2008). Subsurface stipitate kelps such as *E. radiata* (see also *Ecklonia cava*, *Laminaria hyperborea*, *Laminaria pallida*, *Lessonia trabeculata*, or *Eisenia bicyclis*) do not experience breaking waves like algae inhabiting intertidal rocky shores or the full force of surface waves like floating-canopy kelps. Maximum velocities generated by breaking waves on the shore can reach up to 15–25 m/s, a force equivalent to a wind of more than 2000 km/h (Denny 1988, Denny and Gaylord 2002). In comparison, *E. radiata* at our study sites experienced maximum water velocities of only 1–4 m/s. Furthermore, some of the most significant wave-driven mortalities recorded (Dayton and Tegner 1984, Seymour et al. 1989, Filbee-Dexter and Scheibling 2012) have been associated with large (i.e., severe) infrequent disturbance episodes, referred to as LIDs (Romme et al. 1998). The response of kelp canopies to these events can differ quantitatively and qualitatively from responses to storm episodes of "normal" magnitude (Romme et al. 1998). Pioneering work on disturbances pointed out the importance of distinguishing between "catastrophe" (LIDs) and "disaster" (more frequent, less severe) when evaluating the

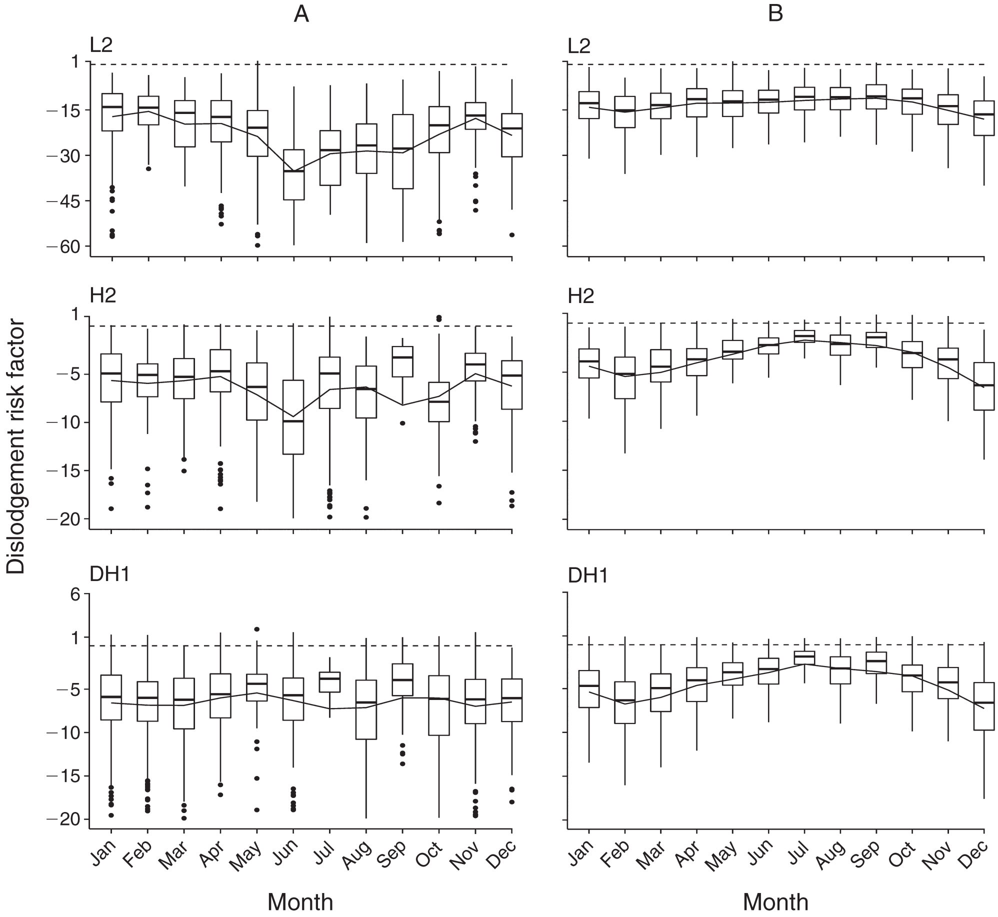

FIG. 6. Three-year modeling of the dislodgement risk factor (DRF; Eq. 2) for two scenarios (with and without biomass change) at three reefs across the hydrodynamic gradient. (A) Monthly DRF averaged across three years in natural conditions with Fig. 5A and Fig. 5B as inputs. (B) Monthly DRF with a hypothetical scenario of no seasonal change in kelp biomass and using maximum individual biomass (February, Fig. 5B) applied to each month. Box plot components are as in Fig. 5B.

organism–environment relationship (Harper 1977, Paine 1979). This implies that species might have evolved to cope with, or even depend on disasters but are incapable of an adaptive response to catastrophes, which lead to severe ecological impact. LIDs can have long-lasting consequences for ecosystems and can be a dominant structuring force of the ecosystem (Turner and Dale 1998).

The apparent discrepancy between some of the observed kelp dislodgement (up to 25–30% per season) and the model prediction of high kelp survival is most likely the consequence of both kelp holdfast fatigue and increased reef brittleness as kelps get older. Indeed, most of the observed dislodgement occurs at the holdfast-reef junction and indicates a failure of this attachment independent of wave exposure. We believe that kelp holdfasts become stiffer and weaker with age and are more susceptible to fatigue failure from nonlethal tissue strains (see Mach et al. 2007, 2011) likely combined with an increase in brittleness of the limestone reef from repetitive loading of large old kelps. Whereas dislodgement of other kelp populations can be strongly influenced by mesograzers and sea urchin activities on critical kelp tissue components (holdfast and/or stipe), this process remains marginal in *Ecklonia radiata* kelp beds in southwestern Australia (Vanderklift et al. 2009, de Bettignies et al. 2012).

In general, the dislodgement of *Ecklonia radiata* was independent of wave-induced water velocity, but did exhibit a pulsed response during the most severe storm. We conclude that the strong attachment strength to the reef and a seasonal cycle in individual kelp biomass maintain the kelp at a low and constant dislodgement risk, offsetting the seasonal increase in water velocity in winter and minimizing storm-generated drag on kelp thalli. This temporal biomechanical modification to water flow can be compared to the spatial variation in shape and material properties for other kelp species, such as *Nereocystis luetkeana*, which have evolved a plastic phenotype to maintain a similar low risk to enable them to inhabit wave-exposed environments (Johnson and Koehl

1994). Our findings also suggested that a decoupling of the antagonistic parameters, kelp biomass and peak water velocity, is critical for kelp survival. For example, the occurrence of severe storms in late spring and summer when kelp individual biomass is the greatest or an increase in storm intensity might affect kelp survival. For the last 23 years, the occurrence of extreme wave events (99th percentile significant wave height) has increased by ~1% per year along the southwestern Australian coastline (Young et al. 2011), and this is likely to have implication for the loss of kelp habitats if the trend continues, particularly in warmer latitudes where ecological performance of kelp recruits is reduced (Wernberg et al. 2010).

In conclusion, we showed that kelp phenology decouples susceptibility to dislodgement significantly from seasonal hydrodynamic forces. This mechanism maintains kelp beds in a higher degree of equilibrium with wave environment than previously believed and explain the ability of kelp to thrive under mechanical seasonally harsh conditions.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–E are available online: http://dx.doi.org/10.1890/13-2365.1.sm