



Thallus pruning does not enhance survival or growth of a wave-swept kelp

Nicholas P. Burnett^{1,2} · M. A. R. Koehl¹

Received: 19 September 2019 / Accepted: 3 February 2020
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Abstract

Kelp are ecologically important in wave-swept habitats because their thalli provide food and habitat to many other organisms. Fronds of kelp thalli can be broken off by hydrodynamic forces that exceed frond strength, especially if the fronds are weakened by wounds inflicted by herbivores. Previous studies hypothesized that breaking benefits some kelp by reducing their size and the risk of dislodgement by large hydrodynamic forces, but we know little about the long-term effects of breaking on kelp growth and survival. Here, we used the intertidal kelp *Egregia menziesii* to study the relationship between the breaking of the kelp's fronds ("pruning") and the kelp's growth and survival. By surveying kelp pruning and herbivore wounds on fronds for 24 months at intertidal sites in northern California we found that pruning was positively correlated with herbivory. We also measured growth rates and long-term survival of kelp to determine if they were correlated with kelp pruning or size. For kelp of any size, heavy pruning led to reduced growth rates in every season except autumn. Contrary to suggestions in the literature that pruning enhances kelp survival, we found that heavily pruned kelp were less likely than lightly pruned kelp to survive winter storms, and heavy pruning led to reduced long-term survival. Thus, the reduction in growth rate caused by pruning of *E. menziesii*, which renders kelp unable to recover from tissue loss, appears to be more important to long-term survival of this strong perennial kelp than is the danger of being swept away by waves.

Introduction

Macroalgae are important components of marine ecosystems because they provide food and habitat to a diversity of other organisms (Graham et al. 2007). The size of macroalgae (i.e., length, surface area, volume) can strongly influence these roles because epibiota are more likely to colonize large macroalgae than small macroalgae (Ojeda and Santelices 1984; Smith et al. 1996). The growth of a macroalga is

strongly linked to local water chemistry, water motion, and light levels (e.g., Schiel and Foster 2015), but the macroalga can also decrease in size when parts of its thallus break away or are consumed by herbivores (de Bettignies et al. 2012, 2013). Other morphological features of macroalgae can also influence the abundance of epibiota on the macroalgae (reviewed by Teagle et al. 2017). For instance, epibiotic loads on macroalgae tend to be greater if the structural complexity of the thallus is high (e.g., increased branching or tangling of blades and fronds) (Arnold et al. 2016; Burnett and Koehl 2018). Furthermore, the morphology and structural complexity of many species of macroalgae can vary between habitats (e.g., Armstrong 1987; Koehl and Alberte 1988; Holbrook et al. 1991; Koehl et al. 2008; Bekkby et al. 2014).

Ambient waves and currents exert hydrodynamic forces on macroalgae (e.g., Koehl and Wainwright 1977; Denny 1988; Carrington 1990; Gaylord et al. 2008). A macroalga can break if the hydrodynamic forces impose mechanical stresses that exceed the strength of a macroalga's tissues (e.g., Delf 1932; Koehl and Wainwright 1977; Armstrong 1987; Burnett and Koehl 2019), and an entire macroalga can be dislodged if the hydrodynamic forces exceed the strength

Responsible Editor: K. Bischof.

Reviewed by undisclosed experts.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00227-020-3663-5>) contains supplementary material, which is available to authorized users.

✉ Nicholas P. Burnett
burnetnp@gmail.com

¹ Department of Integrative Biology, University of California, Berkeley, CA 94720, USA

² Department of Neurobiology, Physiology, and Behavior, University of California, Davis, CA 95616, USA

of the holdfast's attachment to the substratum (e.g., Koehl and Wainwright 1977; Carrington 1990; de Bettignies et al. 2015). The hydrodynamic forces that macroalgae experience depend on the flow regimes in their habitats, which can be unidirectional water currents or back-and-forth wave-driven flow (e.g., Koehl 1986, 1999; Johnson and Koehl 1994). In each flow regime, the magnitude of the hydrodynamic drag is proportional to the square of the velocity of water relative to a macroalga (e.g., Koehl 1986, 1999; Denny et al. 1998). In habitats exposed to unidirectional water currents, flexible macroalgae can be bent over parallel to the direction of flow and experience the full velocity of the ambient current relative to their surfaces. In contrast, flexible macroalgae in wave-driven flow can move back-and-forth with the ambient water motion, thereby reducing the velocity of the water relative to their surfaces, and thus lowering the drag. However, if the distance that the water moves in a wave before it reverses direction is greater than twice the length of a flexible macroalga, then the water moves past the macroalga once the alga becomes fully strung out in the direction of the flow (Koehl 1986, 1999). When a macroalga in a wave reaches the end of its tether, it is jerked to a halt and is exposed to drag as water flows past it (Koehl 1986, 1999; Denny et al. 1997, 1998). While hydrodynamic forces generally increase with a macroalga's size (i.e., the projected area exposed to the moving water) (Carrington 1990; Gaylord and Denny 1997; Wolcott 2007; Gaylord et al. 2008), large macroalgae in wave-driven flow can experience reduced hydrodynamic forces if they are long enough that they are never completely strung out during a wave and thus do not experience the full velocity of the water (Koehl 1986, 1999; Denny et al. 1997, 1998). Thus, the effect of thallus size on the magnitudes of hydrodynamic forces acting on macroalgae depend on the flow regime and are not always intuitive.

Both field monitoring and laboratory studies of several species of macroalgae have reported that large individuals are more likely to be dislodged from the substratum than are small individuals (Black 1976; Santelices et al. 1980; Carrington 1990; Dudgeon and Johnson 1992; Blanchette 1997; Kawamata 2001; Wolcott 2007; de Bettignies et al. 2013, 2015). However, other studies have shown that in the back-and-forth flow in waves, flexible macroalgae that are long enough to move with the water until the flow direction reverses can experience reduced water motion relative to their surfaces, thereby avoiding large forces (Koehl 1986, 1999; Denny et al. 1997, 1998). Damage to and dislodgement of macroalgae increases during seasonal storms that produce large waves, which subject the thalli to high flow velocities and accelerations of longer duration, and thus to greater forces than during periods of small waves and slower ambient flow (Seymour et al. 1989; Dayton et al. 1992; Johnson and Koehl 1994; Graham et al. 1997; Filbee-Dexter and Scheibling 2012). Structural and mechanical features of

macroalgae other than size can also be correlated to survival (e.g., flexibility that enables macroalgae to collapse into streamlined shapes that reduce drag; strength and toughness of thallus tissues) (e.g., Koehl and Wainwright 1977; Denny et al. 1997; Stewart 2006; Boller and Carrington 2007; Demes et al. 2013). The interplay between the size and morphology of flexible macroalgae in affecting their ability to survive periods of heavy wave action is not well understood.

While macroalgae are valuable habitats for herbivorous epifauna, they are also frequently wounded by the grazing of those herbivores (Black 1976; Burnett and Koehl 2018). Damage from herbivores (e.g., holes, cracks) can make parts of the thalli break easily when pulled on by hydrodynamic forces (Koehl and Wainwright 1977; Santelices et al. 1980; Lowell et al. 1991; Burnett and Koehl 2018, 2019). Losing tissue from a thallus can reduce its size and decrease the hydrodynamic forces acting on the whole macroalga (Wolcott 2007; Gaylord and Denny 1997; Gaylord et al. 2008), or can have no effect or can increase the forces on very long macroalgae in waves (Koehl 1986, 1999; Denny et al. 1997, 1998). Correlations between herbivory and thallus breakage have been shown for several species of macroalgae (Black 1976; Santelices et al. 1980; de Bettignies et al. 2013). However, we still do not know if there is a direct link between thallus breakage and mortality in macroalgae. Although previous studies have suggested that thallus breakage prunes macroalgae to smaller sizes thereby reducing their mortality during seasonal storms (Black 1976; Santelices et al. 1980; Harder et al. 2006; de Bettignies et al. 2012; Demes et al. 2013; Burnett and Koehl 2019), this has not been tested.

Research system

We use the intertidal kelp *Egregia menziesii* to examine the relationship between herbivory, breakage, and thallus morphology, and how those factors affect the ability of the kelp to survive seasonal periods of heavy wave action. *Egregia menziesii* is a dominant kelp on wave-swept shores along the west coast of North America, between Baja, Mexico and southern Alaska. The thallus of *E. menziesii* is made of numerous strap-like fronds, each of which can grow to several meters in length, and the edges of each frond are generally bordered by small lateral blades that are usually < 15 cm long (Abbott and Hollenberg 1976). The fronds are commonly colonized and grazed by herbivorous epifauna, including the specialized limpet *Lottia insessa* and at least seven genera of amphipods. Wounds inflicted by these epifauna can make weak spots along fronds, where they tend to break when exposed to hydrodynamic forces (termed 'pruning') (Black 1976; Chapman 2007; Burnett and Koehl 2018). Because Black (1976) found that *E. menziesii* with small thalli (few, short fronds) were more likely than *E. menziesii*

with large thalli (numerous, long fronds) to survive winter storms, he hypothesized that pruning caused by herbivory helped *E. menziesii* survive winter storms by reducing thallus size. Here we test this hypothesis.

Objectives of this study

The objectives of this study are to examine the relationship between pruning and survival of *E. menziesii*. We test (1) whether pruning is a common phenomenon that is associated with herbivory, (2) whether pruning affects the kelp's growth, and (3) whether pruning helps kelp survive the rapid water motion of winter storms.

Methods

Field site and data collection

We monitored the morphology of *Egregia menziesii* over two years at two intertidal sites in northern California that were approximately 18 km apart (Fig. S1). At each site, kelp were measured at two rocky shorelines that were within 6 km of each other. All four shorelines were wave-exposed and were a combination of rocky benches and boulder fields (Burnett and Koehl 2018, 2019). Near Bodega, CA ('Bodega sites'), we monitored *E. menziesii* at Miwok Beach (38° 21' 25" N, 123° 4' 2" W) and at Horseshoe Cove (38° 18' 59" N, 123° 4' 12" W). In the Point Reyes National Seashore ('Point Reyes sites'), we monitored *E. menziesii* at Kehoe Beach (38° 9' 56" N, 122° 57' 6" W) and at McClures Beach (38° 11' 3" N, 122° 58' 2" W).

We visited each shoreline roughly once per month from March 2015 until March 2017, as permitted by low tides and wave conditions. During each visit, we surveyed *E. menziesii* along a 20-m transect that was parallel to the shoreline and placed haphazardly within the zone occupied by *E. menziesii*. One or two transects were run per visit, depending on the timing of the tides and the abundance of kelp. We selected every third individual along the transect to measure three morphological features: size, number of fronds, and pruning. We defined size as the total length of all fronds on an individual kelp, measured to the nearest 1 cm with a measuring tape. Number of fronds was the total number of fronds on an individual kelp. Pruning was the proportion of broken fronds on a kelp (i.e., number of broken fronds divided by the total number of fronds), where a frond was classified as broken if it was missing its intercalary meristem (Fig. 1). Only fronds that were longer than 10 cm were included in these measurements. We also checked each kelp for the presence of herbivory from the limpet *Lottia insessa* and from amphipods, each of which leaves a distinctive wound on the kelp (Black 1976; Burnett and Koehl 2019)

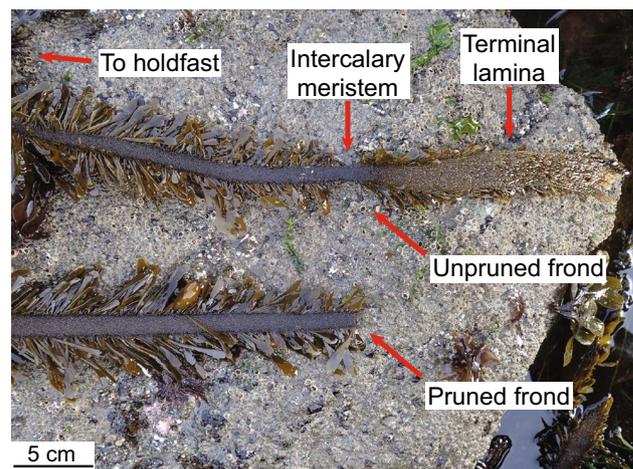


Fig. 1 (Above) A frond of *Egregia menziesii* that is unpruned (i.e., has its intercalary meristem and terminal lamina) and (below), a frond that is pruned (i.e., missing its intercalary meristem and terminal lamina)

(Fig. 2). A subset of kelp that was surveyed in each visit was also tagged with a nylon cord and numbered acrylic tile tied around the stipe. A total of 279 kelp were tagged at both sites across the whole study period. Tagged kelp were surveyed on subsequent visits when possible.

Analysis of pruning and herbivory

Morphology of *E. menziesii* can change seasonally (Black 1974; Burnett and Koehl 2019), so we compared pruning between seasons. Seasons were defined as spring (March through May), summer (June through August), autumn (September through November), and winter (December through February). For seasonal comparisons, we used data from both the untagged and tagged kelp, but we used only the first observation of each kelp (i.e., the first time a kelp was measured during the whole study period) so there were no repeated measurements on the same individual. Pruning values were not normally distributed within each season and showed different variances between seasons, so we used non-parametric statistical tests to make seasonal comparisons. We first checked whether there were differences in pruning between the locations at each site using Mann–Whitney *U* tests ($p < 0.05$ for significance) when there was a sufficient sample size ($n > 4$) from each location, with separate tests for each season and site. At each site, data were pooled between locations (see “Results”), but each site was analyzed separately. For each site and season, we then compared seasonal pruning data between years (e.g., spring 2015 vs. spring 2016) using Mann–Whitney *U* tests ($p < 0.05$ for significance). Data were then pooled between years (see “Results”) with the sites kept separate, and seasons were compared within a site using Kruskal–Wallis tests

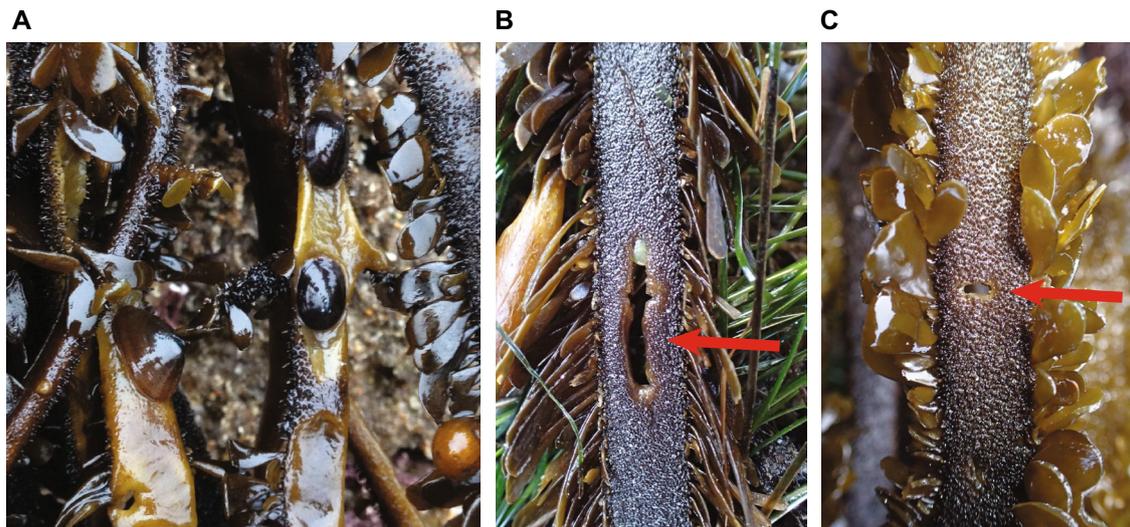


Fig. 2 Damage to the rachises of *Egregia menziesii* can be caused by two common herbivores: **a** the limpet *Lottia insessa*, which creates homescars and large wounds on the rachises, and **b, c** gammarid

amphipods, which chew holes (red arrows) through the rachises. Holes from amphipods can vary in size. The rachises in each photo are between 1 and 2 cm wide

with posthoc Dunn's tests (Ogle et al. 2018) ($p < 0.05$ for significance).

We tested whether pruning was correlated with herbivory at each site. For each site and season, we calculated the median pruning ($\text{Prune}_{\text{median}}$) and the percent of the kelp population that showed signs of herbivory from *L. insessa* and amphipods (Herbivory). Following the seasonal comparisons of pruning, we used data from both untagged and tagged kelp, but we used only the first observation of each kelp (i.e., the first time a kelp was measured during the whole study period) so there were no repeated measurements on the same individual. We used a linear regression model to test for a linear correlation between $\text{Prune}_{\text{median}}$ and Herbivory, and we also included a term for site (Site) in the model to account for all site-specific features, such as topography and local wave heights, in our analysis:

$$\text{Prune}_{\text{median}} = \alpha_1 + \alpha_2 \text{Herbivory} + \alpha_3 \text{Site}, \quad (1)$$

where α_1 , α_2 , and α_3 were the regression coefficients.

Thallus growth after pruning

We tested whether pruning was correlated with the growth rates of *E. menziesii*. We used survey data of tagged kelp to test for a linear correlation between the pruning of an individual kelp (Prune) and the subsequent growth rate of that kelp (Growth Rate) (i.e., rate of change in size, where size is the total length of all fronds on the kelp). We included the kelp's size (Size) in the model because size is already known to affect the growth rates of *E. menziesii* (Black 1974;

Burnett and Koehl 2019), and we included site (Site) in the model:

$$\text{Growth Rate} = \beta_1 + \beta_2 \text{Prune} + \beta_3 \log_{10}(\text{Size}) + \beta_4 \text{Site}, \quad (2)$$

where Growth Rate had units of cm d^{-1} and β_1 , β_2 , β_3 , and β_4 were the regression coefficients. Size was \log_{10} -transformed for normality and to be on a similar scale to Prune. We used separate models for each season (pooled between years) because the kelp's morphology and growth can change seasonally (Black 1974; Burnett and Koehl 2019). Within each season, we used only the first-occurring record of a kelp's growth rate, so there were no repeated measurements on the same individual. In each season, Prune was normally distributed. Sample sizes ranged from 52 to 107 in each season.

Overwintering

We tested whether pruning was correlated with surviving the large waves of winter storms, as has been hypothesized by others (see "Introduction"). An El Niño Southern Oscillation event occurred in the middle of our study and produced large waves at the study sites in the winter of 2015 (Barnard et al. 2017). We used a logistic regression model (Peng et al. 2002) to test whether the pruning of kelp in the autumn of 2015 ($\text{Prune}_{\text{autumn}}$) was correlated with the kelp's survival into the spring of 2016 (Overwinter), and we included the kelp's size in the autumn of 2015 ($\text{Size}_{\text{autumn}}$) and the site (Site) in the model.

$$\text{logit(Overwinter)} = \gamma_1 + \gamma_2 \text{Prune}_{\text{autumn}} + \gamma_3 \log_{10}(\text{Size}_{\text{autumn}}) + \gamma_4 \text{Site}, \quad (4)$$

where γ_1 , γ_2 , γ_3 , and γ_4 were the regression coefficients. $\text{Size}_{\text{autumn}}$ was \log_{10} -transformed to be on the same scale as $\text{Prune}_{\text{autumn}}$ and to be normally distributed. There was only one datapoint per kelp.

Longevity of kelp

We tested whether pruning was correlated with the longevity of kelp. We defined the Longevity of an individual as the number of days between the date in the autumn of 2015 when the kelp was tagged and the date of the last visit during which that kelp was still present. We tested for a linear correlation between the pruning of kelp in autumn of 2015 ($\text{Prune}_{\text{autumn}}$) and its subsequent Longevity. We also included the kelp's size in autumn of 2015 ($\text{Size}_{\text{autumn}}$) and the site (Site) in the model:

$$\text{Longevity} = \delta_1 + \delta_2 \text{Prune}_{\text{autumn}} + \delta_3 \log_{10}(\text{Size}_{\text{autumn}}) + \delta_4 \text{Site} \quad (5)$$

where δ_1 , δ_2 , δ_3 , and δ_4 were the regression coefficients. $\text{Size}_{\text{autumn}}$ was \log_{10} -transformed to be on the same scale as $\text{Prune}_{\text{autumn}}$ and to be normally distributed. Kelp that were present at the final surveys of each site were removed from the analysis (i.e., we could not determine their lifespan without observing their mortality). There was only one datapoint per kelp.

All analyses were done in R Statistical Software (R Core Team 2019).

Results

Seasonal patterns of pruning

Pruning (proportion of broken fronds on a kelp) of *Egregia menziesii* was similar between locations at each study site (Mann–Whitney U tests, $p > 0.05$, $n > 4$ individuals for each location and season), with only four exceptions out of 12 comparisons done (see Supplementary Materials). Even in those four cases, there were large overlaps in the distributions of pruning values between locations at a site. Therefore, to test for differences in pruning between years for each season at each of the sites, we pooled pruning data between locations but analyzed each site separately.

There were no differences in pruning between years for each season at each of the sites (Mann–Whitney U tests, $p > 0.05$, $n > 9$ individuals in each season), with two exceptions: springs at Bodega ($p = 0.007$, $n = 37$ and 43 for the first and second years, respectively) and summers at Point Reyes

($p = 0.006$, $n = 51$ and 24 for the first and second years, respectively) (Fig. S2). However, the pruning data for these two seasons each showed a large overlap in the numerical distributions between years, so there were likely no biologically significant differences between the two years. Therefore, to test for differences between seasons at each site, we pooled pruning data from both years (e.g., spring 2015 pooled with spring 2016) but analyzed each site separately.

We compared pruning between seasons at each site using Kruskal–Wallis tests ($p < 0.05$ for significance). Pairwise comparisons were made with posthoc Dunn's tests and Bonferroni p -value adjustments for multiple comparisons (Ogle et al. 2018). Pruning varied with season, and the seasonal pattern of pruning differed between sites. At Bodega, pruning was similar in all four seasons (Kruskal–Wallis test, $df = 3$, $p = 0.071$), and seasonal medians ranged from 0.33 (summer) to 0.47 (spring) (Fig. 3a). At Point Reyes, pruning increased significantly from spring (median = 0.00) to winter (median = 0.44) (Kruskal–Wallis test with posthoc Dunn's tests, $p < 0.05$) (Fig. 3b).

Herbivory and pruning

Median pruning ($\text{Prune}_{\text{median}}$) in each season was well-predicted by a linear regression model (Eq. 1) with factors of Herbivory (percent of kelp population with signs of herbivory) and Site ($p = 0.002$, $r^2 = 0.56$). Within that model, Herbivory was positively correlated with median pruning ($t = 3.83$, $p = 0.002$) while Site was not correlated with median pruning ($t = -0.39$, $p = 0.703$) (Fig. 3c).

Thallus growth after pruning

The correlation between pruning (Prune) and growth rate (Growth Rate) depended on season (Eq. 2; Fig. 4). In spring, growth rates decreased with pruning ($t = -3.36$, $p = 0.001$) but were unaffected by size (Size) ($t = 1.75$, $p = 0.084$) and site (Site) ($t = -1.15$, $p = 0.254$). However, when considered alone, growth rates in spring increased with size (linear regression, $p < 0.005$; Fig. S3). In summer, growth rates decreased with pruning ($t = -2.35$, $p = 0.022$), increased with size ($t = 3.38$, $p = 0.001$), and were unaffected by the site ($t = 0.19$, $p = 0.849$). In autumn, growth rates were unaffected by pruning ($t = -0.99$, $p = 0.326$) and site ($t = 0.96$, $p = 0.344$), but decreased with size ($t = -2.24$, $p = 0.030$). In winter, growth rates decreased with pruning ($t = -3.61$, $p = 0.001$), increased with size ($t = 2.38$, $p = 0.019$), and were unaffected by site ($t = -0.96$, $p = 0.338$). Thus, pruning decreased growth rate in all seasons but autumn, during which pruning had no effect.

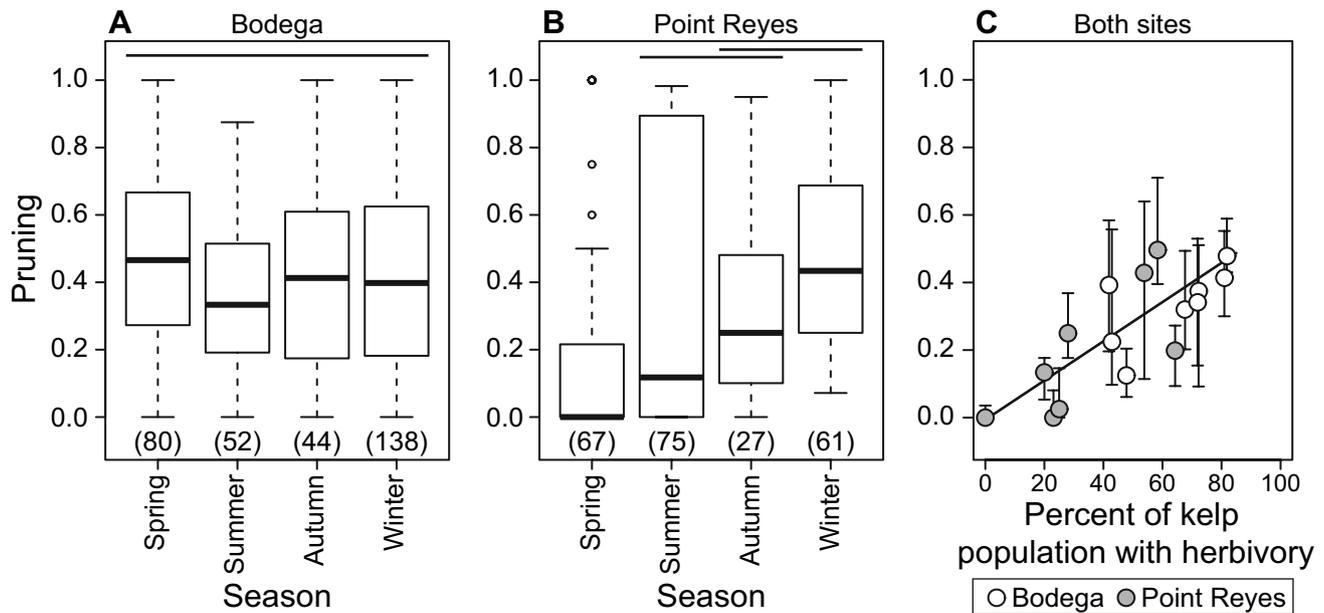


Fig. 3 Seasonality of pruning at **a** Bodega and **b** Point Reyes pooled between years, and **c** median pruning in each season plotted as a function of the percent of the kelp population with herbivory. In **a** and **b**, bars show the median, boxes show the interquartile range, error bars show the most extreme data point that is no more than 1.5 times

the interquartile range from the median, and numbers in parentheses below the plot show the sample size. In **c**, error bars show the interquartile range, and the regression line shows the correlation between median pruning and herbivory from Eq. 1 (see text)

Overwintering

Several instances of large waves occurred in the winter of 2015 (Fig. 5a), corresponding to the onset of the 2015–2016 El Niño Southern Oscillation event (Barnard et al. 2017). *Egrecia menziesii* were less likely to survive from autumn to spring (Overwinter) if they were heavily pruned in autumn ($\text{Prune}_{\text{autumn}}$) ($t = -2.58$, $p = 0.010$; Eq. 4; Fig. 5b). Overwintering was not affected by size in autumn ($\text{Size}_{\text{autumn}}$) ($t = 1.78$, $p = 0.075$; Fig. 5c) and did not differ between the sites (Site) ($t = 0.74$, $p = 0.462$).

Longevity

We were able to monitor individually tagged *E. menziesii* for more than 400 days after the autumn of 2015. The longevity of a kelp (Longevity) was the number of days between the date in the autumn of 2015 when the kelp was tagged and the date of the last visit during which that kelp was still present. Longevity was negatively correlated with the pruning of the kelp in the autumn of 2015 ($\text{Prune}_{\text{autumn}}$) ($t = -3.562$, $p = 0.001$; Eq. 5) but not correlated with the kelp's size in the autumn of 2015 ($\text{Size}_{\text{autumn}}$) ($t = 0.56$, $p = 0.580$) or the site (Site) ($t = 0.56$, $p = 0.581$). A linear regression model with pruning, size, and site predicted 16% of the variation in longevity ($p = 0.009$; Eq. 5), whereas a linear regression model with pruning alone predicted 19% of the variation

in longevity ($p = 0.001$) (Fig. 6). Thus, the longevity of kelp that were heavily pruned was lower than that of lightly pruned kelp.

Discussion

Seasonal patterns of pruning and herbivory

During each season, the degree of pruning of *Egrecia menziesii* at each study site correlated with the prevalence of herbivory (Fig. 3c), suggesting that damage from herbivores plays a role in pruning. This finding is not surprising because wounds from herbivores are known to weaken kelp (Koehl and Wainwright 1977; Biedka et al. 1987; Denny et al. 1989; Lowell et al. 1991; de Bettignies et al. 2012; Burnett and Koehl 2018). The two most common herbivores on *E. menziesii* are the limpet *Lottia insessa* (Black 1976) and various species of amphipods from at least seven genera (Chapman 2007; Burnett and Koehl 2018). These herbivores each typically consume rachis tissue: *L. insessa* rasps home scars into the rachis surface; amphipods eat holes through the rachis (Black 1976; Conlan and Chess 1992; Burnett and Koehl 2018, 2019). The reduced cross-sectional area of rachis tissue at the location of a wound must support the hydrodynamic forces acting on the section of a frond distal to the wound. As a result, mechanical stress (force per

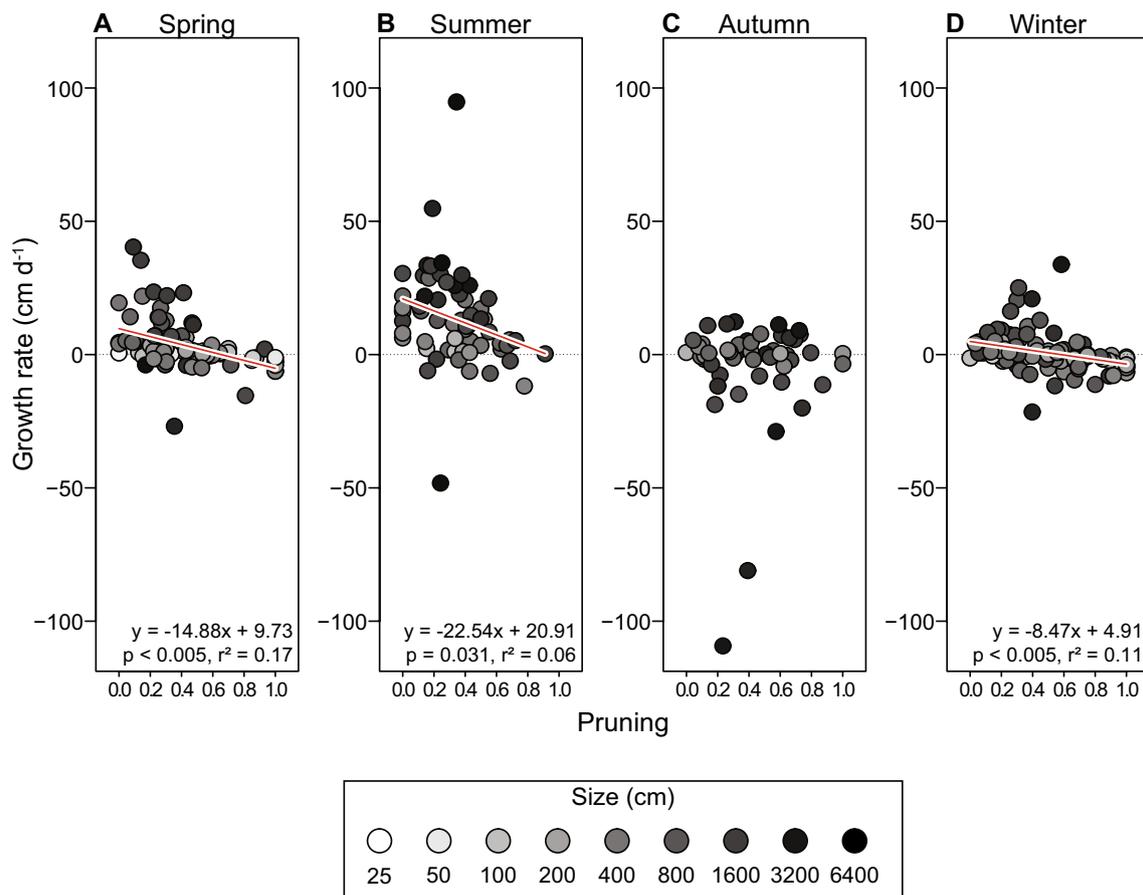


Fig. 4 Growth rates of kelp (i.e., the combined change in length of all fronds on a kelp) from both sites in (a) spring ($n=84$), (b) summer ($n=63$), (c) autumn ($n=52$), and (d) winter ($n=107$) plotted as a function of their initial pruning and color-coded by their initial size. For seasons where there was a statistically significant linear correla-

tion between growth rates and pruning (linear regression, $p < 0.05$), the regression lines and details of regression models are displayed in the panels. Within each season, each point is a separate individual. Negative growth rates show a decrease in thallus size over time

cross-sectional area of tissue) is concentrated in the tissue around a wound. If this local stress at the wound exceeds the tissue's breaking stress, the rachis breaks and the frond is pruned to a shorter length (Koehl and Wainwright 1977; Biedka et al. 1987; Denny et al. 1989; de Bettignies et al. 2012). Some macroalgae are known to heal wounded tissues by increasing tissue breaking stress (Lowell et al. 1991), or by increasing the cross-sectional area of the region of the kelp that has been wounded (Burnett and Koehl 2019). However, this healing process can be slow. For example, rachises of *E. menziesii* still have reduced strength four weeks after wounding (Burnett and Koehl 2019), during which time the kelp is exposed to hundreds of thousands of waves that could break the tissue.

Kelp at Point Reyes showed seasonal differences in pruning that correlated with large, seasonal fluctuations in herbivory (ranging from 0 to 65% of the population showing signs of herbivory), whereas kelp at Bodega showed no seasonal differences in pruning and high levels of herbivory

during all seasons (ranging from 41 to 82% of the population showing signs of herbivory) (Fig. 3). Differences in the range of herbivory between sites could be due to differences in wave exposure. In a separate study, we compared hourly significant wave heights (average wave height of the 33% of waves that were the largest during a given time period) between sites (Burnett and Koehl 2019). By pairing hourly observations between the sites we found that in each hour of the 2-year study period, the waves at Point Reyes tended to be larger than the waves at Bodega (paired *t*-test: Point Reyes waves were on average 22 cm taller than waves at Bodega, S.D. = 20 cm, $t = 147.81$, $df = 17,543$, $p < 0.005$). Site-specific, nearshore wave heights are calculated based on wave heights measured at a single offshore buoy (Buoy 46013; www.ndbc.noaa.gov; Fig. 5) and the nearshore bathymetry of each site, which can modify the structure of nearshore waves (Scripps Institution of Oceanography, <https://cdip.ucsd.edu>). However, these calculations of nearshore wave heights are not necessarily representative of onshore water

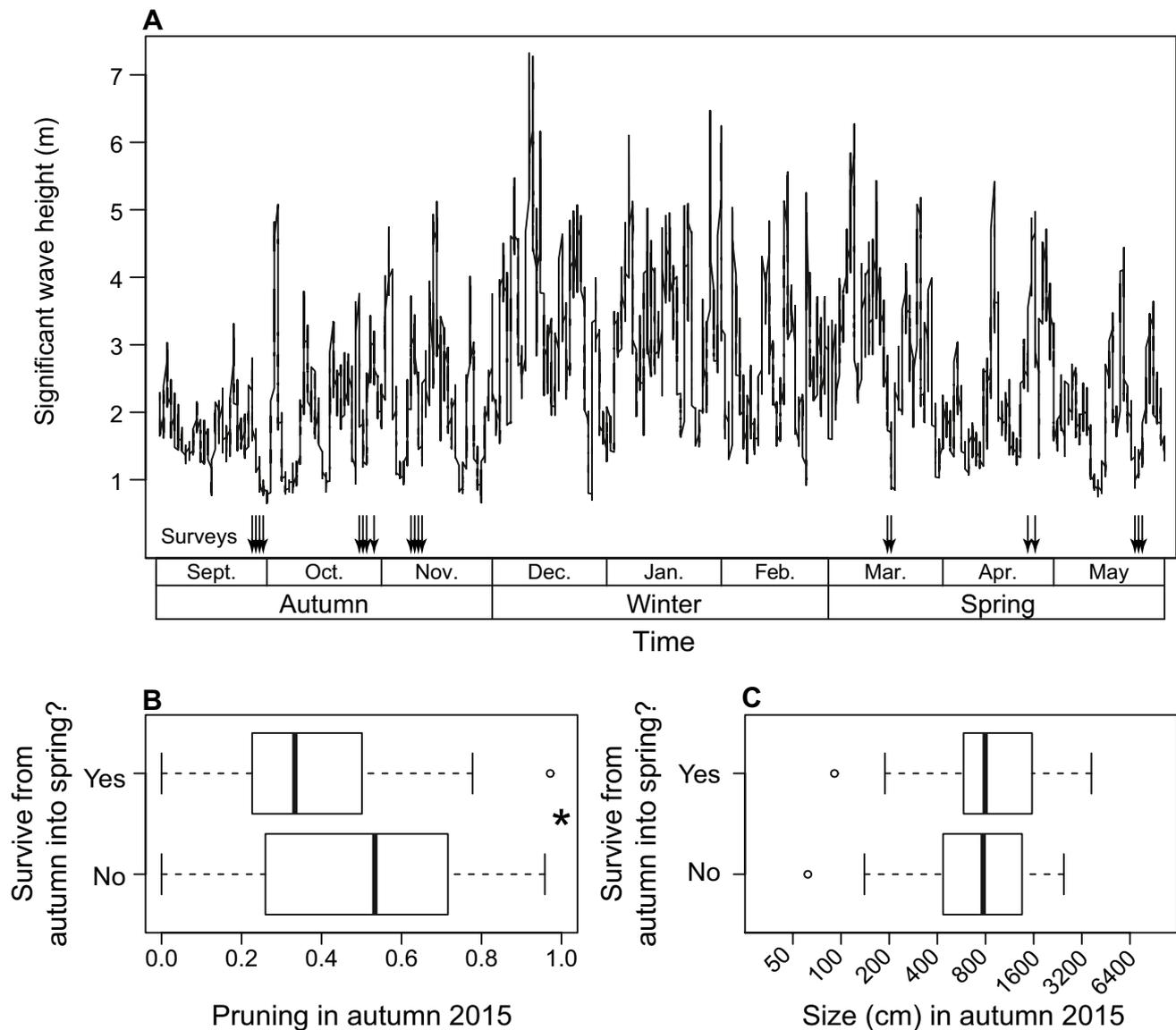


Fig. 5 **a** Hourly significant wave height data from autumn 2015 to spring 2016 measured at a buoy near the sites (Buoy 46013; www.ndbc.noaa.gov; the buoy was located between 20 and 33 km from the sites), and the overwintering survival of kelp plotted as a function of their **(b)** pruning and **(c)** size. In **a**, arrows show when sites were sur-

veyed to measure morphology in autumn and survival into spring. In **b** and **c**, asterisks show morphological features that were significantly different between kelp that successfully overwintered and kelp that did not survive (logistic regression, $p < 0.05$ for significance; Eq. 4)

velocities experienced by the kelp and their herbivores; the orientation of the shoreline, the local bathymetry of the sites, the arrangement of boulders along the shore, and the presence of neighboring kelp could each influence the size and structure of waves and the resulting water velocities as the waves moved on to the shoreline (Helmuth and Denny 2003; Gaylord et al. 2007; O'Donnell and Denny 2008). Because water motion from waves can dislodge herbivores from kelp (Duggins et al. 2001), we hypothesize that the difference in wave action between the sites might have permitted high levels of year-round herbivory at Bodega, where nearshore

waves were relatively small, but not at Point Reyes, where nearshore waves were larger. Regardless of differences in water motion and herbivory between the sites, the rachis tissues of fronds of *E. menziesii* at Point Reyes and Bodega had similar mechanical properties so a herbivore wound would have had a comparable weakening effect at both sites (Burnett and Koehl 2019).

The seasonal variation in herbivory at the wave-swept Point Reyes site was likely influenced by seasonal changes in kelp morphology and water motion, and by the herbivores' life histories. Herbivores are more likely

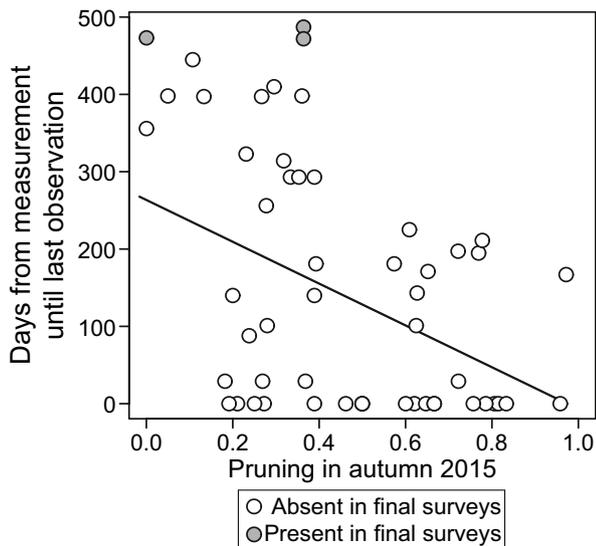


Fig. 6 Number of days kelp were monitored after they were surveyed in autumn 2015 plotted as a function of their pruning in autumn 2015. The regression line shows the linear correlation between longevity and pruning ($p=0.001$, $r^2=0.19$). Kelp that were present in the final survey (filled symbols) were not included in the regression model

to be found on old kelp and on large thalli than on young or small ones, and it has been suggested that these patterns exist because old thalli have had more time to accumulate herbivores and large thalli provide more tissue for herbivores to graze (de Bettignies et al. 2012; Teagle et al. 2017). Therefore, as *E. menziesii* increase in size during the summer and autumn (seasons with long day lengths), they are colonized and wounded by herbivores, whose populations on macroalgae have been documented to boom during these seasons (Gunnill 1983; Winkler et al. 2017). Waves hitting the coast of California are the largest in winter (Fig. 5a), and by this time, many of the kelp in the population are wounded and heavily pruned (Fig. 3). Other studies have shown that, as large waves continue through the winter, herbivores are dislodged and wounded fronds of macroalgae are pruned (e.g., Duggins et al. 2001; de Bettignies et al. 2013), which agrees with the decreased herbivory that we observed for *E. menziesii* at Point Reyes. In the spring and summer, kelp begin to grow new fronds that are free of herbivores (Black 1974), and levels of pruning in the population decrease (Fig. 3). In contrast, the high levels of year-round herbivory at Bodega (i.e., > 41% of kelp showed signs of herbivory in each season) despite winter waves pruning wounded *E. menziesii*, suggest that winter waves do not dislodge the herbivores on kelp at Bodega.

Effect of pruning on growth

The growth rate of a kelp is the sum of the growth rates of individual fronds. Once a frond of *E. menziesii* is pruned and loses its meristem, it can no longer grow in length (Black 1976). Therefore, it is not surprising that pruning was negatively correlated with growth rates of thalli of *E. menziesii*. While herbivory likely initiates the pruning that leads to reduced growth rates of *E. menziesii* thalli (e.g., Black 1976; Burnett and Koehl 2018), herbivores are also known to affect the physiology and growth rates of kelp without causing tissue breakage. For instance, grazing by invertebrates on *Macrocystis pyrifera* and *Lessonia spicata* can reduce the concentration of photosynthetic pigments in kelp tissues, thereby causing reduced growth rates (Poore et al. 2014). Surveys of kelp in situ have also shown negative correlations between herbivore infestation and kelp growth rates (O'Brien and Scheibling 2016; Pfister and Betcher 2018), similar to the trends observed in our study. Growth rates of *E. menziesii* were positively correlated with kelp size during the spring, summer, and winter, but negatively correlated with kelp size during the autumn (Fig. S3). The size-dependent growth rates of *E. menziesii* in spring and summer are not surprising because these are the seasons where individual unpruned fronds have the most rapid growth (Black 1976; Burnett and Koehl 2019). We hypothesize that the seasonal variation in size-dependent growth rates occurred because kelp were lightly pruned during spring and summer, and they grew by lengthening their unpruned fronds, while kelp were heavily pruned during winter and grew by generating new fronds. Kelp had many long fronds at the start of autumn (i.e., the result of high growth rates in summer), and pruning caused rapid and large decreases in the kelp's size that were not counteracted by growth (e.g., Black 1974).

Survival and longevity

It has been suggested that pruning enables perennial kelp to survive winter storms by reducing their size, thereby lowering the magnitude of hydrodynamic forces acting on the thalli and decreasing their risk of dislodgement from the substratum (e.g., Black 1976; de Bettignies et al. 2012; Burnett and Koehl 2019). Our data showed the opposite: heavily pruned *E. menziesii* were less likely than lightly pruned kelp to survive winter storms, and kelp size was not correlated with overwintering survivorship (Fig. 5). Several factors may explain this pattern. Longer fronds of flexible kelp moving with the water in back-and-forth wavy flow do not experience higher forces than shorter fronds if they are able to move with the flow during the whole wave cycle (Koehl 1984, 1986, 1999; Denny et al. 1997, 1998) and to reconfigure into drag-reducing shapes (e.g., Koehl 1986; Koehl and Alberte 1988; Martone et al. 2012), so pruning of the

very long fronds of *E. menziesii* might not reduce hydrodynamic forces. In addition, pruned fronds grow slowly, if at all (Fig. 4), so kelp that are heavily pruned to small sizes might not be able to compensate for the tissue loss caused by pruning, or to compete with neighboring kelp for light (e.g., Black 1974; Holbrook et al. 1991; Watanabe et al. 1992). As a result of intense pruning and reduced growth, heavily pruned kelp may be grazed by herbivores to the point of mortality (e.g., Leighton 1971; Tegner et al. 1995). In contrast, lightly pruned kelp with numerous intact fronds should have a better potential than heavily pruned kelp to grow throughout the winter (Black 1974; Burnett and Koehl 2019). The role of thallus age in affecting survivorship during winter storms is not known for perennial *E. menziesii*. Because fronds of *E. menziesii* are produced and pruned often, determining the age of a thallus from its morphology is not feasible, so the age structure of our tagged population was not known. While new fronds are produced and pruned over the lifetime of an individual, the stipe that supports them might accrue damage from abrasion and herbivory, as has been noted in other macroalgae (e.g., Santelices et al. 1980). Among the kelp that were surveyed in autumn 2015, the heavily pruned kelp that showed low overwintering survival might have been older than the lightly pruned kelp that had high overwintering survival. Overall, our data indicate that large *E. menziesii* are not at increased risk of dislodgement and mortality on wave-swept shores during winter storms. However, thallus size may still be an important predictor of dislodgement and mortality for other macroalgae in different water-flow environments (e.g., de Bettignies et al. 2015).

We were able to track individual kelp for more than 400 days after tagging them in autumn, so our study showed that *E. menziesii* is truly a perennial kelp that can survive multiple winters. Not only was low pruning a strong predictor of overwintering survivorship by *E. menziesii* (i.e., whether kelp survived from autumn to spring), but it was also a strong predictor of longevity (i.e., the number of days kelp survived after being tagged in the autumn). Heavily pruned kelp suffered mortality sooner than lightly pruned kelp (Fig. 6) probably due to the inability of heavily pruned thalli to grow faster after the tissue was removed by grazing and the subsequent frond breakage induced by such wounding, as described above. In contrast, thallus size was not a good predictor of longevity, most likely because the number of unpruned fronds on a thallus is not necessarily linked to the kelp's size.

In summary, our study reveals that the survival of *E. menziesii*, an abundant intertidal kelp on wave-swept rocky shores, is the result of the interaction between herbivory that weakens the kelp, hydrodynamic forces that break (prune) the fronds and remove meristems, and the kelp's ability to grow rapidly enough to recover from that breakage. In

contrast to the idea that the reduction of thallus size by pruning increases survivorship of kelp during winter storms, we found that heavy pruning reduces the survival of *E. menziesii* during winter storms and decreases longevity.

Acknowledgements We thank E. Armstrong, A. Belk, T. Burnett, D. Chan, S. Chang, J. Judge, E. King, L. Louis, W. Kumler, R. Romero, C. Runzel, E. Sathe, D. Springthorpe, R. Tanner and D. Weiler for help with field surveys.

Funding This work was funded by a Point Reyes National Seashore Marine Science Fund grant and the National Science Foundation [DGE-1106400 to N.P.B.; DGE-0903711 to R. Full, M.A.R.K., R. Dudley and R. Fearing].

Data availability The datasets collected and analyzed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare they have no conflicts of interest.

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