



Knots and tangles weaken kelp fronds while increasing drag forces and epifauna on the kelp

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ABSTRACT

In shallow coastal areas, the fronds of long, flexible kelp can become knotted (a single frond tied around itself) and tangled (multiple fronds intertwined) as they move back and forth with ocean waves. We investigated the ecological and physical consequence of being knotted and tangled for the intertidal kelp *Egrecia menziesii* in northern California. Knots increased the hydrodynamic forces on fronds of the kelp *Egrecia menziesii* by 56% and weakened fronds by 18% when pulled in tension. There were more and larger epifauna (including many herbivores) on tangled fronds, which suffered greater damage by grazers than did untangled fronds. Tensile forces required to break herbivore-damaged fronds were 31% lower than forces to break undamaged fronds. Kelp with knotted and tangled fronds were more likely to break than kelp with unknotted, untangled fronds, and knots and tangles occurred most frequently in the autumn, thereby pruning the fronds and reducing the risk of whole kelp being ripped off the shore by large waves during winter storms.

1. Introduction

Ocean waves in shallow coastal habitats impose hydrodynamic forces on the benthic organisms in those habitats. The magnitudes of hydrodynamic forces are affected by the water motion and the morphology of the organisms experiencing the forces (Koehl, 1984; Denny, 1988). Excessive hydrodynamic forces can damage or dislodge benthic organisms from the substrata (e.g., Carrington, 1990; Carrington et al., 2009). Motile benthic organisms can modify their behavior such that they avoid times and places with unfavorable water motion (Hobday, 1995; Harley and Helmuth, 2003; Pardo and Johnson, 2006), and they can potentially recover if dislodged (Miller et al., 2007). Sessile organisms, on the other hand, are not able to actively avoid events of extreme water motion (e.g., mussels, corals) (Madin and Connolly, 2006; Denny et al., 2009). Many sessile organisms have morphologies and life cycles that reduce the hydrodynamic forces acting on their bodies during periods of water motion (e.g., macroalgae, anemones) (Koehl, 1977, 1999; Wolcott, 2007; Martone et al., 2012; de Bettignies et al., 2013).

Kelp are among the largest sessile organisms occurring on the wave-swept shorelines along the west coast of North America (Abbott and Hollenberg, 1976). Growing to large sizes allow kelp to outcompete neighboring organisms for both light and space (Dayton et al., 1999), but large organisms can experience bigger hydrodynamic forces in

waves than do smaller organisms (Denny et al., 1985, 1998; Gaylord et al., 2008). Many of the largest kelp (e.g., *Macrocystis pyrifera*, *Nereocystis luetkeana*, *Egrecia menziesii*) have flexible stipes or fronds (Abbott and Hollenberg, 1976) that allow the kelp to passively move with the water motion of each wave (“going with the flow”), which reduces the water motion relative to the kelp and thus decreases the magnitude of the hydrodynamic forces on the kelp (Koehl, 1984, 1999; Burnett and Koehl, 2017). If the wave moves water for a distance that is longer than the length of the kelp, the kelp goes with the flow until it is fully extended and comes to a stop. Jerking to a halt after being fully extended by the flow can impose an inertial force on the stipe (Denny et al., 1998; Gaylord et al., 2008). Furthermore, when the kelp is fully extended in the direction of flow, it then experiences ambient water flow relative to its surface and the consequent hydrodynamic forces (Koehl, 1984). In subtidal kelp populations, alongshore currents can reorient the kelp away from the nearby shoreline and prevent the kelp from being fully extended in the direction of waves moving toward the shore. The interaction of the alongshore currents and ocean waves can reduce the magnitude of ambient water flow relative to the kelp and the magnitude of hydrodynamic forces on the kelp (Gaylord et al., 2003). Although growing to long lengths can help reduce hydrodynamic forces on the kelp, being too long increases the risk of the kelp being damaged or dislodged during periods of more severe waves (e.g., seasonal storms) (Wolcott, 2007; Denny et al., 2009).

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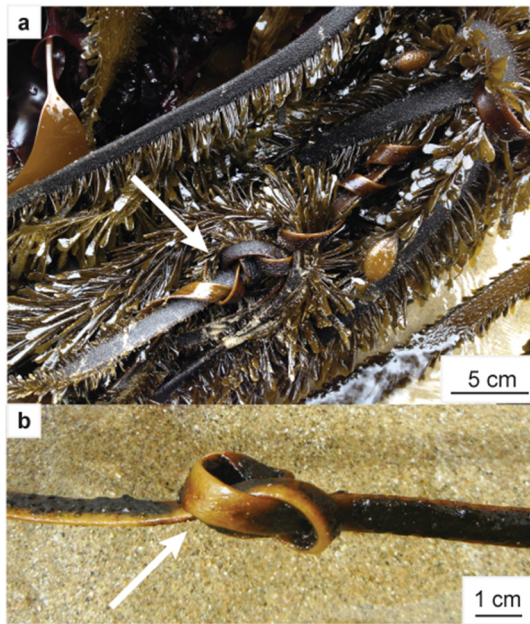


Fig. 1. Fronds of the kelp *Egregia menziesii* tied into complex configurations. (a) Tangles are formed by multiple fronds, where (b) knots are formed in a single frond. The knot and tangle are indicated by the arrow in the respective photographs.

1.1. Knots and tangles

The back-and-forth water motion of waves can cause flexible kelp to become tangled or knotted (e.g., Meluzzi et al., 2010), which may alter the hydrodynamic forces acting on the kelp or the local stresses (force per cross-sectional area of material bearing the force) in kelp tissues, thereby affecting susceptibility to being broken. When kelp are tangled (i.e., multiple kelp structures intertwined, Fig. 1a) only a subset of the kelp end up supporting the hydrodynamic forces of the entire group, and this increase in mechanical loads can cause the load-bearing kelp to break (Koehl and Wainwright, 1977; Friedland and Denny, 1995). This is most evident when the tangled kelp, sometimes including the holdfasts, wash ashore (Koehl and Wainwright, 1977).

A knotted kelp frond (i.e., a single kelp frond tied into a knot, Fig. 1b) may also experience larger hydrodynamic forces and higher stresses (force per cross-sectional area of material bearing a load) in its tissues than unknotted fronds. Knotting changes the overall shape of the frond, which may make the frond less streamlined, resulting in increased hydrodynamic forces on the frond (e.g., Vogel, 1994). Studies of non-kelp structures showed that knots weaken the structures (reviewed by Meluzzi et al., 2010) because the curvature of material in a knot pre-stresses the material in and near the knot even before a load is added to the structure (Pieranski et al., 2001). Whether knots affect the susceptibility of kelp to breakage by pre-stressing fronds or by increasing the hydrodynamic forces they experience is not yet known.

Knots and tangles may also modify the interaction of the kelp with its epifauna by creating protected spaces where epifauna can live. In general, an increase in habitat complexity provided by a seaweed (e.g., amount of branching or number of small spaces between fronds or blades) increases the amount of epifauna a seaweed can hold (Hauser et al., 2006; Norderhaug et al., 2007; Teagle et al., 2017). Thus, it is likely that a tangled or knotted kelp can host more epifauna than untangled, unknotted individuals. Kelp exposed to hydrodynamic forces often break at wounds caused by herbivores (Black, 1976; Koehl and Wainwright, 1977; Lowell et al., 1991; Duggins et al., 2001; Krumhansl et al., 2011), thus an increase in herbivorous epifauna on knotted or tangled kelp might lead to more frond breakage than experienced by unknotted, untangled kelp.

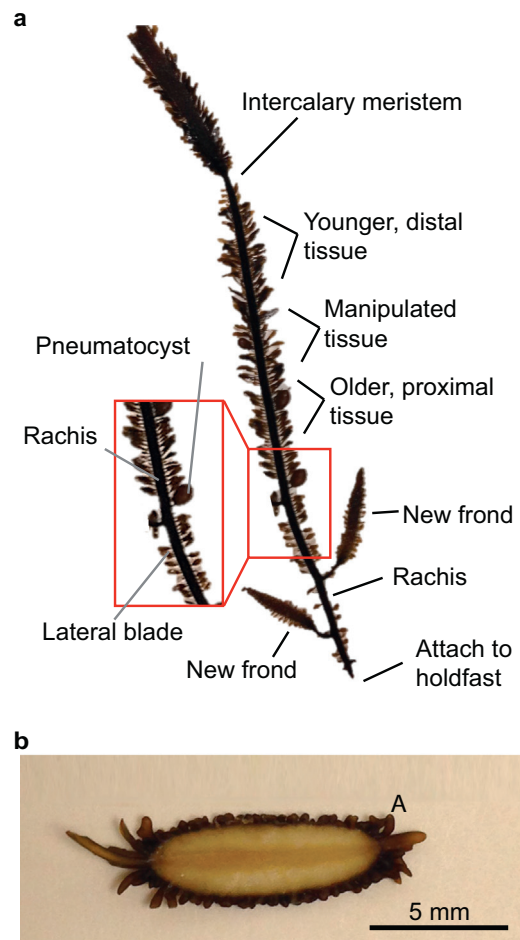


Fig. 2. (a) The anatomy and relative age of regions of a frond of *E. menziesii*. (b) The rachis of *E. menziesii* has an ellipsoidal cross-section.

1.2. The kelp *Egregia menziesii*

Egregia menziesii is one of the largest kelp on the wave-exposed rocky shores of the west coast of North America (Abbott and Hollenberg, 1976) and is an ecologically important species because it can modify the biological community in the areas under its thallus (Hughes, 2010). An *E. menziesii* has numerous strap-like fronds with ellipsoidal cross-sections (Fig. 2), which grow from a perennial holdfast and can reach lengths of > 5 m (Abbott and Hollenberg, 1976). The fronds of *E. menziesii* have been observed to become knotted and tangled (e.g., Friedland and Denny, 1995).

From spring until fall, the long fronds enable *E. menziesii* to be a dominant member of the rocky intertidal ecosystem, but long fronds in the winter increase the risk of the whole kelp being dislodged by the larger waves of winter storms (Gaylord et al., 2008). Frond breakage reduces the kelp's size and can thereby decrease the risk of the entire kelp being dislodged. Damage to the kelp by the limpet *Lottia insessa* has been shown to facilitate frond breakage and aid in the kelp's perennial survival (Black, 1976). Each frond has an intercalary meristem, such that frond breakage between the intercalary meristem and the holdfast may initially decrease the length of the frond and the overall size of the kelp, but *E. menziesii* responds to frond breakage by branching and producing new fronds from the original broken frond (Black, 1974, 1976). This growth pattern allows the kelp to survive and increase its numbers and lengths of fronds after periods of frond breakage (e.g., during winter storms), which is different from kelp that only have apical meristems and can experience mortality after frond or blade breakage (Krumhansl et al., 2015). Given the importance of frond

breakage for the survival of *E. menziesii* and the observed knotting and tangling of the kelp's fronds, we used *E. menziesii* to study how knotting and tangling affect kelp.

1.3. Objectives of this study

We used *E. menziesii* to address the following questions: (1) How do knots affect the hydrodynamic forces on kelp fronds? (2) How do knots affect the strength of kelp fronds? (3) How do tangles affect the epifaunal load on fronds? (4) How does damage by herbivorous epifauna affect the strength of kelp fronds? (5) How common are knotted and tangled fronds during different seasons?

2. Materials and methods

2.1. Field sites

Collection for experiments and surveys of *Egrecia menziesii* were made at sites along a 26-km range of northern California coastline between May 2015 and August 2016 (Fig. S1). Two sites were located in the Point Reyes National Seashore (CA, USA): Kehoe Beach (KB; 38°9'56.08" N, 122°57'6.04" W) and McClures Beach (MC; 38°11'2.70" N, 122°58'2.33" W), and two sites were located near Bodega (CA, USA): Horseshoe Cove (HC; 38°18'47.55" N, 123°4'13.78" W) in the Bodega Head Marine Reserve (Bodega, California, USA), and Miwok Beach (MW; 38°21'53.10" N, 123°4'15.90" W) in the Sonoma Coast State Beach (Bodega, California, USA). Collections were made from adult kelp (Stage IV sporophytes sensu Henkel and Murray, 2007).

2.2. Hydrodynamic forces on knotted fronds

We tested whether overhand knots increased the drag on fronds in moving water. Overhand knots were chosen because they were the most common knot formed by single *E. menziesii* fronds in the field. Drag is the hydrodynamic force acting parallel to the direction of water movement relative to a body (Vogel, 1994). In December 2015 and January 2016, fronds that were at least 0.5 m in length were haphazardly collected from kelp at MC and MW, and transported to the University of California, Berkeley for testing. Drag measurements were made by towing intact fronds (frond length range = 0.5 to 1.2 m) with a stepping motor at a constant velocity through still water in a tank (2.5 × 0.2 × 0.2 m). The measurements on each frond occurred in < 10 min, involved only the interaction of the frond's shape with water, and did not produce any noticeable changes to the frond's structure, thus the freshwater in the tank likely did not affect the drag on the kelp. Each frond was towed at only one velocity (0.3, 0.4, 0.5, 0.6 or 1.0 m s⁻¹), which was in the range of ambient water velocities experienced by the kelp (Friedland and Denny, 1995; Gaylord et al., 2008). A spring scale (Ohaus Models 8001-MN, 8261-M, 8263-M, Ohaus, Pine Brook, NJ) recorded the maximum force with which the frond resisted the movement through the water (Bell and Denny, 1994). Three replicate measurements of drag forces were made at the tow velocity for each unknotted frond. Then each frond was tied into an overhand knot and three replicate measurements of drag were made at the same velocity. To be consistent across all of the measured fronds, the overhand knot was always positioned in the middle of each frond, which was within the range of positions where knots were observed in nature (see Results). Fronds did not break during these measurements. Each frond was photographed prior to testing, and planform area was calculated using ImageJ software (National Institutes of Health, version 1.49b).

The drag force on an object is determined, in part, by the object's shape, as indicated by the drag coefficient, C_D (Vogel, 1994). We calculated C_D for fronds in their knotted and unknotted configurations:

$$C_D = \frac{2F}{u^2\rho A}$$

where F was the measured drag force, u was the tow velocity, ρ was the density of the freshwater in the tow tank at 20 °C (1000 kg m⁻³) (Vogel, 1994), and A was the planform area of the frond in its unknotted configuration.

2.3. Breakage of knotted fronds

We tested whether knots reduced the force required to break a frond in tension. We compared the force required to break knotted sections of frond with the force required to break adjacent unknotted sections of the same frond. In December 2015, unwounded fronds that were at least 1 m in length were haphazardly collected from kelp at MC and MW, and transported to the University of California, Berkeley for testing. A model 5844 Instron (Norwood, MA, USA) materials-testing machine was used to measure the maximum tensile force required to break sections of the fronds 25 cm in length that were unknotted or tied into overhand knots (Fig. 1b). Immediately after collection, fronds were placed in a covered container with their residual sea water. Fronds were kept in air, inside the covered container, between 4 and 10 °C until testing. For each frond, no > 15 min elapsed between being removed from storage and being measured by the materials-testing machine. Preliminary experiments showed no difference in breaking force between kelp that were measured after 12 h at 4 °C and separate kelp that were measured immediately after collection (Mann-Whitney U test, $P > .05$, $n = 5$ for each time period). The fronds of *E. menziesii* have a distal intercalary meristem (Fig. 2a), hence frond tissue close to the holdfast is older and stronger than more distal tissue near the meristem (Abbott and Hollenberg, 1976; Demes et al., 2013; Krumhansl et al., 2015). To control for the effects of aging on the strength of the unknotted frond tissue, the unknotted breaking force of each frond was calculated as the mean of the breaking forces for unknotted tissues immediately distal and proximal to the frond tissue used for the knotted measurement (Fig. 2a). Samples were blotted dry with a paper towel, pieces of paper towel were glued to the ends of the fronds with cyanoacrylate glue to protect them from damage and provide friction with the Instron grips, and the paper-towel-covered ends were clamped into the grips of the Instron (Koehl and Wainwright, 1985).

Frond specimens were stretched at a strain rate of $3.3 \times 10^{-3} \text{ s}^{-1}$ (i.e., 0.2 min⁻¹) (strain rate = change in length of specimen per unit time, divided by the initial length of the specimen between the grips of the Instron). Previous in situ measurements of hydrodynamic forces on *E. menziesii* (Gaylord et al., 2008) showed that forces on individual fronds of the kelp can increase at instantaneous rates on the order of 10 N s⁻¹ when a wave breaks on the kelp (i.e., wave impingement) and on the order of 1 N s⁻¹ during the wave surge after the wave breaks. Wave impingement is very brief (generally < 0.5 s) in each wave cycle, whereas wave surge lasts several seconds during the remainder of the wave cycle (Gaylord, 1999). Therefore, we measured the rate of change of force in a specimen as a function of strain rate to identify the strain rates that would produce rates of force-increase similar to those encountered by kelp during wave surge. We found no significant difference in the rate of force-increase for strain rates between $3.3 \times 10^{-3} \text{ s}^{-1}$ and $15.8 \times 10^{-3} \text{ s}^{-1}$ (linear regression, $P < .05$), which produced rates of force-increase within the range of those encountered by kelp during wave surge. Therefore, all subsequent tests were done at a strain rate of $3.3 \times 10^{-3} \text{ s}^{-1}$.

2.4. Frond configuration and epifaunal communities

We investigated whether tangled and untangled fronds of *E. menziesii* had different structural characteristics (i.e., wounds, lateral blades) and epifaunal loads. From September to December 2015, we collected tangled fronds from the intertidal zones at McClures Beach

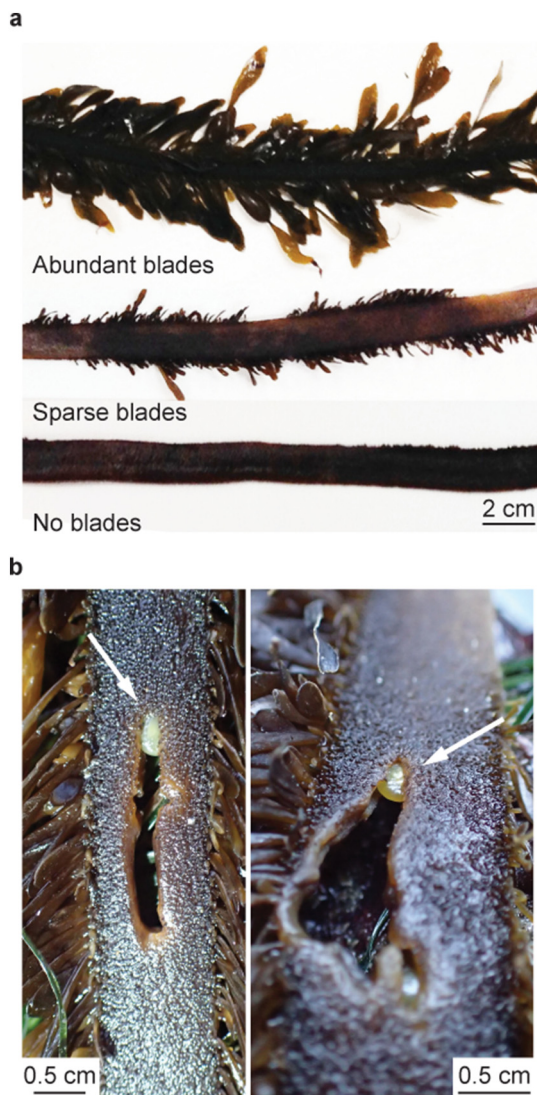


Fig. 3. (a) the lateral blades of fronds could occur in different abundances. (b) Herbivorous epifauna, such as amphipods (white arrows), can burrow into and feed on fronds of the kelp.

and Miwok Beach (cumulative length of tangled fronds ranged from 1.81 to 16.90 m). We also haphazardly collected untangled fronds that were adjacent to the collected tangled fronds (cumulative length of untangled fronds ranged from 1.81 to 8.65 m). Comparing the tangled fronds with adjacent fronds that were untangled allowed us to control for local environmental factors beyond frond configuration that could have influenced a frond's structure and epifauna (e.g. temperature, light, water motion, rock topography). Fronds and their epibiota were collected and immediately bagged and preserved with 45% isopropyl alcohol. Fronds were brought to the laboratory where they were untangled and all macrofauna were removed.

We measured morphological features and quantified epifauna on the collected fronds. The lengths of the fronds from each collection were measured to the nearest 1 cm. Small lateral blades generally border the edges of *E. menziesii* fronds (Fig. 2a) but can be removed by processes such as abrasion and herbivory. We rated the abundance of lateral blades on each frond (0 = none, 1 = lateral blades on less than half the length of the frond, or 2 = lateral blades on at least half the length of the frond; Fig. 3a). The total “bushiness” of each group of tangled or untangled fronds was calculated as the sum of these lateral blade scores, divided by the total length of the fronds in that group. We also counted the number of discrete wounds on each frond (Fig. 3b).

Many of the wounds were obviously caused by herbivory, while the cause of damage for other wounds was difficult to distinguish (e.g., herbivory vs. abrasion) so we counted the total number of wounds regardless of the cause of wounding. Epifauna in each collection were separated into taxonomic groups (gammarid amphipods, isopods *Idotea* spp., kelp crab *Pugettia producta*, barnacles, mussels *Mytilus* spp., limpets *Lottia* spp., and littorinid snails), photographed, and counted. The total dry weight of each epifaunal group on each set of fronds was determined to the nearest 0.0001 g (Mettler Toledo AG245, Mettler Toledo, Columbus, OH) after drying them to a constant weight in a drying oven at 60 °C. All metrics of frond morphology, wounds, and epifaunal loads were standardized to the length of the fronds.

2.5. Weakening of fronds by herbivore damage

Many of the epifauna found on fronds, either tangled or untangled, were herbivores that wounded the frond tissue. We measured the breaking forces of fronds that had herbivore damage using the materials-testing machine described above. Undamaged fronds were collected from McClures Beach and Miwok Beach from October to December 2015. We used a metal hole punch to inflict a wound that was similar in size and shape to the wounds on the fronds that were caused by amphipods (Fig. 3b). Each inflicted wound was ellipsoidal in shape (approximately 1 cm × 4 mm), with the long axis of the wound aligned with the long axis of the frond, and was punched entirely through the frond. We chose to inflict wounds for these experiments rather than use naturally occurring damage so that we could standardize the size, shape, and age of the wound (some seaweeds are able to change the strength of their tissues following damage; Lowell et al., 1991). We measured the force required to break a section of a frond with mimicked damage and the force to break unwounded sections of the same frond (the average breaking force of unwounded tissue distal and proximal to the wounded section of the frond). Sample preparation and measurement protocols were the same as described for breakage of knotted fronds.

2.6. Prevalence of knots and tangles

The sites were visited approximately once per month when the tidal heights were between −0.4 and 0.1 m relative to MLLW. At each site, kelp were surveyed along a horizontal transect in the intertidal zone that spanned the full range of microhabitats (e.g., surge channel, rocky bench, boulder), selecting every third kelp that was encountered. Kelp were selected if they were mature sporophytes (Type IV sporophytes sensu Henkel and Murray, 2007) and had stipes that were distinguishable from those of other individuals. The lengths of all fronds on the selected kelp were measured to the nearest 1 cm, and the presence of any knotted or tangled fronds was noted. When a knotted frond was encountered, we measured the length of the frond as the distance between the distal and proximal ends of the frond in its knotted configuration. We also measured the distance of the knot from the proximal end of the frond to the nearest 1 cm. Kelp with tangled fronds were untangled to measure frond lengths to the nearest 1 cm. A subset of the surveyed kelp were also marked with nylon paracord and a 2.5 × 2.5 cm acrylic identification tag. Tagged kelp was surveyed again on subsequent months and the total frond lengths were compared with those of tagged untangled kelp over the same time period and at the same sites.

We define each season as three months: spring was March–May; summer was June–September; autumn was August–November; winter was December–February.

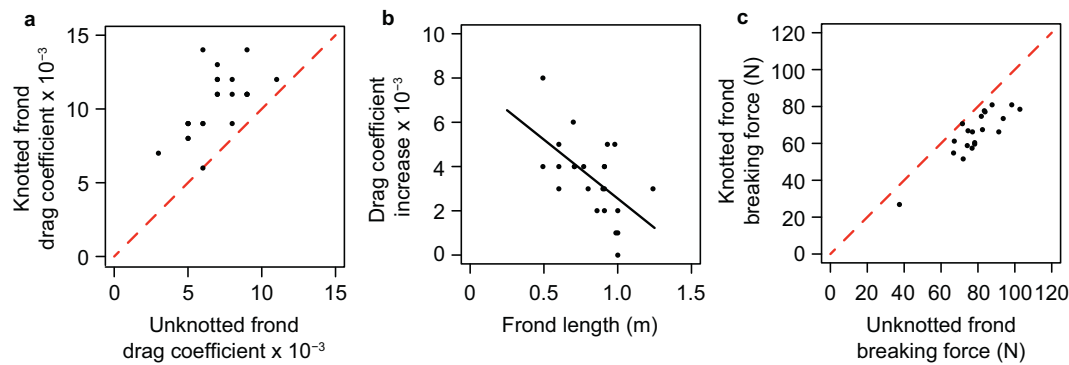


Fig. 4. Effects of being tied into a knot for kelp fronds. (a) Drag coefficients of fronds were greater when fronds were tied into a knot than when the same fronds were unknotted (paired *t*-test, $P < .0005$, $df = 19$). Slope of dashed line = 1, thus all points above the line indicate an increased drag coefficient for knotted fronds, whereas points below the line show a decrease. (b) Knots had a larger effect on the drag of short fronds than of long fronds (linear regression: $y = -5.2x + 8.0$, $P < .005$, $R^2 = 0.34$). (c) Knotted sections of frond broke with 18% lower forces than unknotted sections of the same frond (paired *t*-test, $P < .0005$, $df = 19$).

3. Results

3.1. Hydrodynamic forces on knotted fronds

Overhand knots increased the drag coefficient of the fronds of *Egregia menziesii* by 56% (paired *t*-test, $P < .0005$, $df = 19$). This effect was more pronounced for short fronds than for long fronds (Fig. 4a). Drag coefficient did not vary with towing velocity for either knotted or unknotted fronds (linear regressions, $P > .05$).

3.2. Breakage of knotted fronds

Sections of fronds tied into an overhand knot always broke at the entrance to the knot (arrow, Fig. 1b), and broke at forces that were on average 18% lower than those required to break an adjacent unknotted section from the same frond (Fig. 4c).

3.3. Epifaunal communities on fronds with vs. without knots or tangles

The most common animals found on the fronds of *E. menziesii* were amphipods, kelp crabs, isopods, littorinid snails, and limpets, all of which eat kelp tissue. Suspension-feeding mussels and barnacles were also common. Tangled fronds had more amphipods (Fig. 5a), mussels, and kelp crabs than did untangled fronds, whereas untangled fronds had more littorinid snails than did tangled fronds (paired *t*-tests, $P < .05$, $df = 15$). In contrast, there were no differences between tangled and untangled fronds in the abundances of the other types of animals tallied (paired *t*-tests, $P > .05$, $df = 15$). On both tangled and untangled fronds, amphipods, including species that can burrow and consume tissue from inside the fronds (Sotka, 2007), occurred in greater numbers (paired *t*-test, $P < .05$, $df = 31$) and higher biomass than littorinid snails (paired *t*-test, $P < .05$, $df = 31$), which only browse the surfaces of the fronds.

Not only did tangled fronds bear more epifauna than did untangled fronds, but those animals were bigger on the tangled kelp: amphipods (paired *t*-test, $P < .05$, $df = 14$, Fig. 5b) and isopods (paired *t*-test, $P < .05$, $df = 6$) each had a greater average body mass on tangled fronds than on untangled fronds.

3.4. Weakening of fronds by herbivore damage

Grazers can damage fronds by removing the lateral blades and by making wounds in the supportive rachis (Fig. 3). Tangled fronds had fewer lateral blades (paired *t*-test, $P < .05$, $df = 10$) and more wounds per rachis length than did adjacent untangled fronds (Fig. 5c).

To test whether the rachis wounds we found on tangled fronds made the fronds weaker, we compared the strength of fronds with wounds

like those made by amphipods to that of unwounded fronds. Wounded sections of frond rachises broke at forces that were on average 31% lower than the forces required to break adjacent unwounded sections of rachis from the same fronds (Fig. 5d).

3.5. Prevalence of knots and tangles

Surveys of *E. menziesii* in four intertidal habitats (Fig. S1) along the northern California coast revealed that knots and tangles were more abundant in the autumn than in the spring (Kruskal-Wallis test with post-hoc Dunn test; Ogle, 2017; $p < .05$) (Fig. 6a), and that they formed on kelp whose mean frond lengths were at least 49 cm ($n = 43$ kelp; Fig. S2). Knots frequently formed on the longest frond of a kelp (76% of knots, $n = 17$ kelp), and those fronds ranged in length from 1.24 to 3.59 m. However, the maximum frond length of a kelp was not a good predictor of whether or not the kelp had knotted fronds (logistic regression, $P = .081$, $X^2 = 3.042$, $df = 1$; Peng et al., 2002). The relative position of knots on fronds ranged from 29 to 95% (median = 85%, $n = 17$), where 0% is the end of the frond toward the holdfast and 100% is the end of the frond at the terminal lamina (Fig. 2a). Tangles formed on kelp whose maximum frond lengths ranged from 1.17 to 5.50 m, but maximum frond length was not a good predictor of whether kelp had tangled fronds (logistic regression, $P = .21$, $X^2 = 1.576$, $df = 1$).

Kelp whose fronds were knotted or tangled experienced more frond breakage per time than did neighboring kelp without knots or tangles (Fig. 6b,c). To control for local variation in the physical environment (e.g., wave action, light, temperature), kelp whose fronds were knotted were compared to randomly selected kelp, whose fronds were unknotted, at the same sites and over the same time period. We used the average daily change in kelp size from our survey data, beginning when knots and tangles were first observed (sampling intervals ranged from 14 days to 88 days), to calculate the percent change in size that kelp experienced over a 30-day month. Over that month when kelp had knotted fronds, the kelp tended to become smaller (median loss of total frond length = 14.0%, range = 64.2% decrease to 25.6% increase in size), while over the same time interval, kelp without knotted fronds did not (median increase in total frond length = 0.9%; range = 30.5% decrease to 95.4% increase in size) (Wilcoxon signed-rank test, $P < .05$, $n = 14$ pairs of kelp) (Fig. 6b). Similarly, kelp with tangled fronds lost more frond tissue than kelp without tangled fronds over a 30-day month beginning when tangles were first observed (Wilcoxon signed-rank test, $P < .05$, $n = 31$ pairs of kelp). The median loss of total frond length from kelp with tangled fronds was 9.5% (range = 151.4% decrease to 61.7% increase in size), while kelp without tangled fronds maintained their size during the same time interval (median = 0.3% increase in size, range = 56.2% decrease to

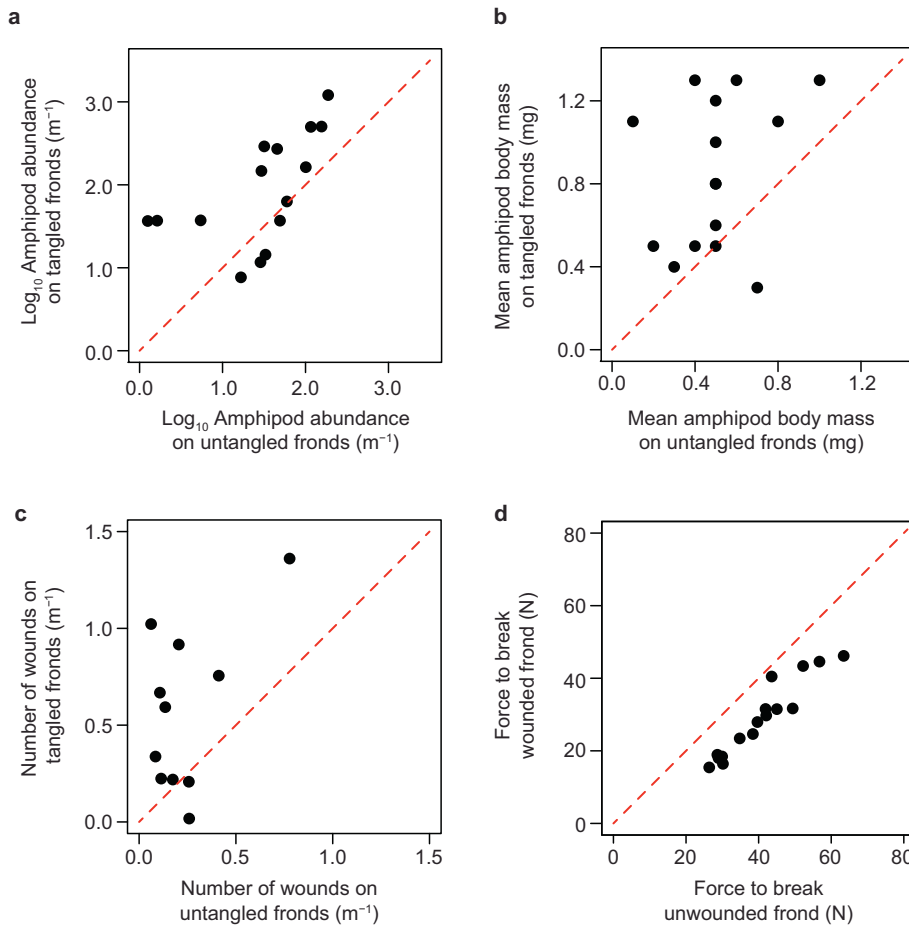


Fig. 5. Effects of being tangled for kelp fronds. (a) Tangled fronds had more amphipods per frond length (individuals m^{-1}) than did neighboring, untangled fronds (paired t -test, $P < .05$, $df = 15$). Maximum abundance of amphipods on tangled fronds was 1207 individuals m^{-1} , and 188 individuals m^{-1} on untangled fronds. Dashed lines show a slope = 1. (b) Tangled fronds had bigger amphipods (mean dried weight per amphipod) than did untangled fronds (paired t -test, $P < .05$, $df = 14$). (c) Tangled fronds had more wounds than did untangled fronds (paired t -test, $P < .05$, $df = 10$). (d) Wounds mimicking damage from amphipods made fronds break at a 31.4% lower force than unwounded frond tissue from the same frond (paired t -test, $P < .05$, $df = 15$).

101.9% increase in size) (Fig. 6c).

In our field surveys, we also scored whether the tagged kelp showed signs of herbivory (i.e., wounds characteristic of herbivores, presence of herbivores) from two of the most common herbivores at the sites, gammarid amphipods and the limpet *Lottia insessa* (Burnett, 2017). Using these data, we tested if the change in a kelp's size was correlated to herbivory (e.g., frond breakage at herbivore wounds) and not just the tangling or knotting of fronds. Of the kelp with knotted fronds, 9 kelp showed signs of herbivory while knotted, and 1 kelp did not. Of the kelp without knotted fronds, 5 kelp showed signs of herbivory, and 5 kelp did not. Among all the kelp, both knotted and unknotted, individuals that showed signs of herbivory decreased in size (median change = 12.8% decrease in size) while individuals without signs of herbivory increased in size (median change = 22.9% increase in size;

Mann-Whitney U test, $P < .05$). Similarly, of the kelp with tangled fronds, 15 kelp showed signs of herbivory, and 3 kelp did not. Of the kelp with untangled fronds, 13 kelp showed signs of herbivory, and 5 kelp did not. Among all the kelp, both tangled and untangled, there was no difference in the size change between kelp with herbivory and kelp without herbivory (Mann-Whitney U test, $P > .05$). These results suggest that the decrease in kelp size observed for kelp with knotted fronds may be due to herbivory rather than the knot, while the decrease in kelp size observed for kelp with tangled fronds is not due to herbivory alone.

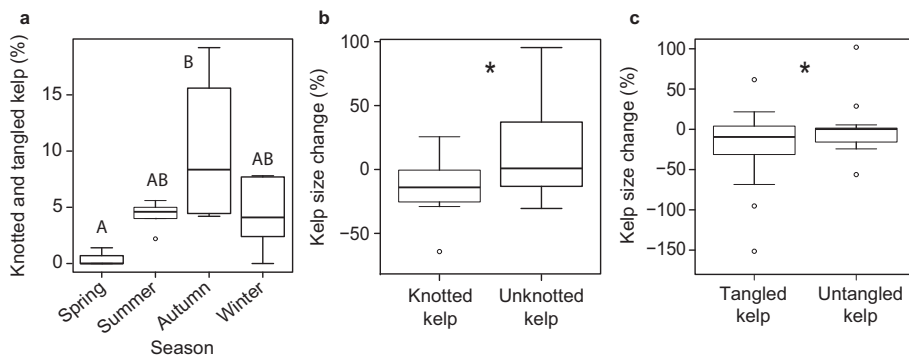


Fig. 6. Seasonality of knotting and tangling, and the consequences for kelp. (a) Kelp with knotted or tangled fronds were more common in autumn (median = 8.4%, $n = 4$) than in spring (median = 0.0%, $n = 4$). Each sample is the mean of two sites per month. Letters show significantly different groups (Kruskal-Wallis test with post hoc Dunn tests, $p < .05$). (b) Change in kelp size calculated for a 30-day period for kelp with knotted fronds versus kelp without knotted fronds and (c) kelp with tangled fronds versus kelp without tangled fronds. Asterisks show that knotting and tangling were associated with larger decreases in kelp size as compared to unknotted, untangled kelp (Wilcoxon signed-rank tests, $p < .05$). Boxes indicate the first quartiles around the median, error bars show the most extreme data point that is no > 1.5 times the interquartile range from the box, and circles indicate values

quartiles around the median, error bars show the most extreme data point that is no > 1.5 times the interquartile range from the box.

4. Discussion

4.1. Hydrodynamic forces on and breakage of knotted fronds

Knotted fronds of *E. menziesii* experienced higher hydrodynamic drag (Fig. 4a,b) and were weaker than unknotted fronds (Fig. 4c), suggesting that the water motion of ocean waves can break knotted fronds more easily than unknotted fronds. However, the cross-sectional shape of *E. menziesii* fronds (Fig. 2b) may have limited the weakening caused by knots. The weakening of knotted structures is thought to result from the curvature of the material within the knot and the mechanical stress (force per cross-sectional area of material) that the curvature puts on the material. When a structure is bent, the material on the inside of the curve experiences compression and the material on the outside of the curve experiences tension. If the tensile stress placed on the material on the outside edge of the curve exceeds the strength of the material, then the structure can break. The maximum stress (σ , the force per area) on a material that is bending under an applied force can be quantified by

$$\sigma = \frac{E y_{max}}{R}$$

where E is the Young's modulus (stiffness) of the material, y_{max} is the maximum distance within the material's cross-section from the neutral axis (where neither compression nor tension occur while bending), and R is the structure's radius of curvature when bent (Wainwright et al., 1976). Because the stress from bending in a knot pre-stresses the material at the knot, the tensile load on the structure due to drag can raise the local stress at the knot above the material's breaking strength. Therefore, a lower tensile load can break a knotted structure than in an unknotted one.

Structures with circular cross-sections can be weakened by up to 50% when tied into a knot (Pieranski et al., 2001; Meluzzi et al., 2010), whereas *E. menziesii*, with its ellipsoidal cross-sectional (Fig. 2b), was only weakened by 18% (median) up to a maximum of 28% (Fig. 4c). An ellipsoidal cross-section has a smaller y_{max} than does a circular cross-section of the same total area, and because y_{max} is proportional to the maximum stress (eq. 2), the ellipsoidal cross-section experiences smaller stresses than the circular cross-section for any given degree of bending (Gere and Timoshenko, 1997). Therefore, when bent inside a knot, the maximum stress in the frond is much less than if the frond had a circular cross-section.

Considering both the increased hydrodynamic drag and weakening caused by knots, knotted fronds might be expected to break more easily than unknotted fronds when exposed to moving water in the field. However, the fronds of *E. menziesii* have a high breaking strength (up to 100 N; Fig. 4c), while the forces the individual fronds experience in waves in nature are < 20 N (Gaylord et al., 2008). Thus, an 18% increase in local stress due to a knot subjected to a crashing wave (e.g., 20 N) would still be well below the stress required to break a frond. However, the decrease in kelp size that we observed for kelp with knotted fronds was correlated with herbivory on the kelp in addition to the presence of the knot. This suggests that wounds from herbivores are more likely to lead to frond breakage than are the increased stresses from knots. Similarly, because herbivores are more abundant on tangled than untangled kelp, herbivore wounds are more likely to lead to frond breakage than are the increased stresses from knots.

4.2. Frond configuration, epifaunal communities, and herbivory

Tangling was associated with an increase in the numbers and body sizes of herbivores living on the kelp. Herbivore grazing caused structural damage to the fronds, most notably by decreasing the number of lateral blades and by directly wounding the frond's rachis (Fig. 3b). Losing lateral blades, which are responsible for much of the kelp's photosynthesis (Henkel and Murray, 2007), can impact the growth of

the kelp, whereas the wounds to the rachis can cause the frond to break (Fig. 5d), also resulting in a loss of photosynthetic tissue. Thus, while the back-and-forth motion of waves can passively tie kelp fronds into knots and tangles that enhance the kelp's role as a source of habitat and food, it can ultimately lead to the breakage of kelp fronds and loss of that valuable kelp habitat from the intertidal ecosystem (e.g., Black, 1976).

4.3. Prevalence of knots and tangles

Our field surveys showed that knots and tangles, which formed on kelp with long fronds, were more likely to occur in the autumn. Knotted fronds experienced increased drag and reduced strength due to pre-stressing at the knots, while tangled fronds showed reduced strength due to enhanced herbivory. Together these suggest that knotted and tangled fronds are more likely to break when subjected to the hydrodynamic forces of waves than are unknotted and untangled fronds. Consistent with this prediction, we found that kelp whose fronds were tangled or knotted decreased in size while untangled, unknotted kelp did not (i.e., they either increased in size or showed no net change in size; Fig. 6b,c).

The seasonal occurrence of knotted and tangled fronds on *E. menziesii* further suggests that these complex frond configurations are important in the perennial life cycle of the kelp. Although knotted and tangled fronds were observed in every season of the year, they were most common in autumn, which is also when the kelp have the longest fronds and largest total size (Black, 1974; Burnett, 2017). By becoming knotted and tangled in the autumn, the kelp can decrease in size just before the arrival of the large ocean waves that are typical of winter storms. A decrease in the total number and length of fronds on a kelp should decrease the magnitude of hydrodynamic forces that its holdfast experiences, and therefore reduces the risk that the entire kelp will be dislodged from the substratum (Wolcott, 2007). Surviving the large waves of winter is an important process for perennial seaweeds, especially those that grow to large sizes. In spite of the large reductions in size of *E. menziesii* during winter, these kelp have high growth rates and quickly attain large sizes in the spring and summer (Black, 1974; Burnett, 2017), providing habitat and food to much of the surrounding biological community (Hughes, 2010). Studies of kelp demography have yet to be done to determine if knotting and tangling enhance overwintering survival, since the long-term hydrodynamic advantage of knotting and tangling relies on the fronds breaking and kelp size decreasing before the onset of winter storms. However, for the kelp populations observed in this study, knotting and tangling were associated with a significant decrease in kelp size and can therefore be added to the list of other ways in which large seaweeds undergo decreases in body size before winter, such as herbivory-induced breakage (Black, 1976; de Bettignies et al., 2012), inherently weak fronds (Demes et al., 2013), and the timing of reproductive tissue formation (Wolcott, 2007).

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Author's contributions

N.P.B. conducted field surveys and experiments, and analyzed the data with assistance from M.A.R.K., who supervised the project. Both authors contributed to the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2018.08.003>.

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