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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 *Egregia menziesii* in northern California. Knots increased the hydrodynamic forces on fronds of the kelp *Egregia 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, Egregia 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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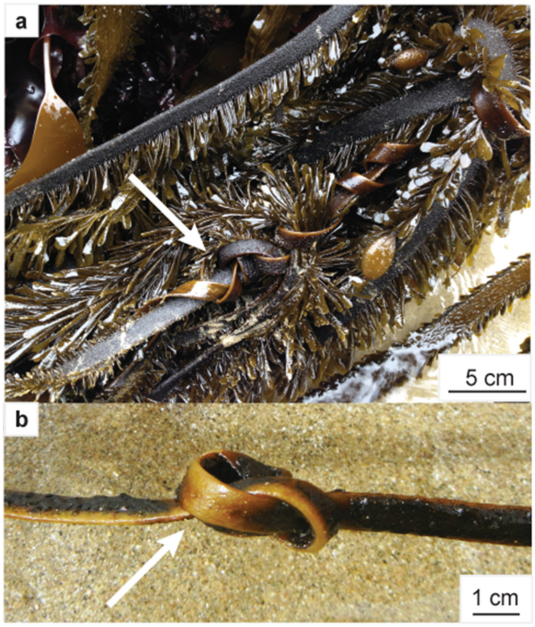

Fig. 1. Fronds of the kelp *Egregia menziesii* tied into complex configurations. (a) Tangles are formed by multiple fronds, where (b) knots are formed in a single frond. The knot and tangle are indicated by the arrow in the respective photographs.

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.

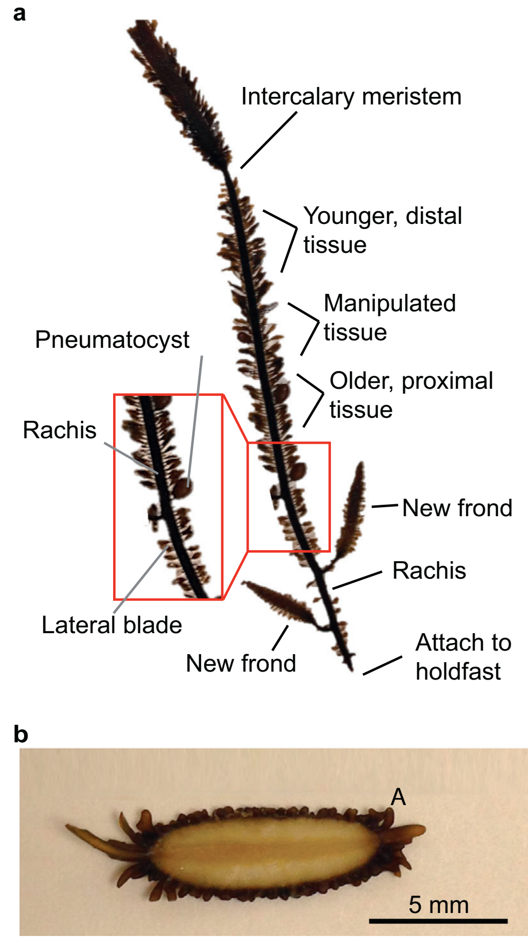

Fig. 2. (a) The anatomy and relative age of regions of a frond of *E. menziesii*. (b) The rachis of *E. menziesii* has an ellipsoidal cross-section.

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