

Pneumatocysts provide buoyancy with minimal effect on drag for kelp in wave-driven flow



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ABSTRACT

Many seaweeds have buoyant gas-filled bladders (pneumatocysts) that hold fronds upright in the water column and enhance their access to light for photosynthesis. However, ambient water currents bend flexible seaweeds, pushing fronds closer to the substratum where light is lower, so the hydrodynamic drag on pneumatocysts may counteract their buoyancy in flowing water. The effects of pneumatocysts on frond hydrodynamic drag were investigated in this study, as well as how the positions of pneumatocysts along fronds affect their motion and height in wave-driven water flow. The kelp *Egria menziesii* was used as a model organism because it is abundant on wave-swept rocky shores and because our field surveys revealed that this species shows great variation in pneumatocyst size, number, and location on fronds. In laboratory towing-tank studies, it was found that drag on pneumatocysts was reduced when they were bent over by flowing water. The drag due to pneumatocysts was small compared to the drag on a whole frond. At flow speeds up to 0.58 m s^{-1} , the buoyant force exerted by a pneumatocyst was greater than the drag it experienced. In wave-tank experiments using models of fronds with pneumatocysts at different positions, the pneumatocysts were most effective at lifting fronds high in the water column when they were located at the distal tips of the fronds, both in small and large waves. However, if fronds had pneumatocysts that were not at the tip, an increase in the peak velocities of waves led to an increase in the heights of the fronds in the water column. In the field, pneumatocysts did not affect the back-and-forth horizontal motion of *E. menziesii* exposed to waves, but fronds with pneumatocysts were higher in the water column than fronds with no pneumatocysts, even when the number of pneumatocysts on a frond was low. Our results indicate that pneumatocysts can exhibit great variability in size, number, and location with only a small effect on hydrodynamic forces on a kelp, that pneumatocysts at frond tips are most effective at holding kelp high in the water column, but that only a few pneumatocysts at any location along a frond can enhance the frond's height in waves.

1. Introduction

The intertidal zones of many temperate rocky shores are populated by large seaweeds whose abundance is highly correlated with increased biodiversity because they serve as a food source and habitat for many other organisms (e.g., Abbott and Hollenberg, 1976; Graham, 2004; Christie et al., 2009). Moving water from ocean currents and waves impose hydrodynamic forces on the seaweeds (e.g., Koehl, 1984; Denny, 1988; Gaylord, 1999). On the west coast of North America, waves generally have periods between 8 and 20 s (NOAA Buoy Center, www.ndbc.noaa.gov), resulting in thousands of waves each day that move onto the shore and exert forces on the seaweeds. If the magnitudes of the forces exceed the seaweed strength, the seaweeds can be dislodged from the substratum or suffer a partial breakage of the thallus (Koehl and Wainwright, 1977; Carrington, 1990; Demes et al., 2013),

resulting in the removal of the seaweed and its epibiota from the ecosystem (Krumhansl and Scheibling, 2012).

The morphological and mechanical traits of a seaweed can alter the hydrodynamic forces it experiences. A seaweed with a flexible thallus can be reconfigured by moving water into a small, streamlined shape that reduces hydrodynamic forces on the seaweed (Koehl, 1984; Carrington, 1990; Martone et al., 2012). In back-and-forth wave-driven flow, flexible seaweeds move with the water in the direction of flow, thus the water velocity relative to the seaweed is reduced and hydrodynamic forces on the seaweed are lower than they would be if the seaweed were rigid (Koehl, 1986). However, moving with the ambient water motion may not always minimize forces on the seaweed: when the seaweed becomes fully extended it can experience inertial loading (i.e., “jerk” sensu Denny et al., 1998) due to the sudden thallus deceleration, in addition to the hydrodynamic forces from water that

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continues moving past the seaweed (Koehl, 1986).

Many flexible seaweeds rely on buoyancy to remain upright in the water column and to access light for photosynthesis (e.g., Stewart et al., 2007). When hydrodynamic forces become sufficiently large, a buoyant seaweed can be pushed closer to the substratum, but return to its upright position once the water motion slows (Stewart, 2004). Unidirectional currents moving along shore can re-orient buoyant seaweeds with the current, reducing the magnitude of the hydrodynamic forces the seaweeds experience from waves moving toward the shoreline (Gaylord et al., 2003). Buoyancy has also been shown to interfere with the passive reconfiguration of a seaweed into a compact, streamlined shape when in flowing water, and thus buoyancy counteracts this mechanism of hydrodynamic force reduction (Stewart, 2006a).

The buoyancy of many species of seaweeds is provided by gas-filled bladders (pneumatocysts), which have a variety of forms across seaweed taxa (Abbott and Hollenberg, 1976). For example, *Nereocystis luetkeana* has a single, large pneumatocyst at the end of its stipe, whereas *Macrocystis pyrifera* has numerous small pneumatocysts at regular intervals along the thallus, with pneumatocysts near the holdfast being larger than more distal pneumatocysts. Most studies of the biomechanics and hydrodynamics of seaweed buoyancy have focused on small species (thallus < 0.5 m in length; pneumatocysts smaller than 2 cm in diameter) to investigate the trade-off between the flexibility of the whole thallus and pneumatocyst buoyancy (e.g., Stewart, 2004, 2006a,b; Stewart et al., 2007). However, little is known about the influence of pneumatocysts on the forces on and movement of large seaweeds (thallus longer than 1 m) in ambient flow. Furthermore, the consequences to drag of the size and deformability of a pneumatocyst have not been explored, and the effects of the positions of pneumatocysts along fronds on the behavior of seaweeds in flowing water are not understood. Understanding basic principles about how buoyant pneumatocysts affect the hydrodynamic forces on and movement of large, flexible structures, such as ecologically-important seaweeds, can not only improve predictions of how those seaweeds will be affected (e.g., growth, damage, dislodgement) by changes in flow conditions (e.g., increased frequency of storms) or by other environmental factors that can directly damage the pneumatocysts (e.g., herbivory, abrasion against the substratum).

We used the feather boa kelp, *Egregia menziesii*, to study the hydrodynamic consequences of having pneumatocysts of different sizes, numbers, and locations along the thallus of a long seaweed. *E. menziesii*, which is one of the largest species of kelp abundant in the rocky intertidal zone along the west coast of North America from Baja California to southeast Alaska, has numerous strap-like fronds that grow to lengths of 3 m or more from a perennial holdfast (Abbott and Hollenberg, 1976) (Fig. 1A). The rachis of each frond (about 1 to 2 cm wide) bears ellipsoidal pneumatocysts (up to 5 cm long) and narrow lateral blades (up to 5 cm long) along both edges (Henkel and Murray, 2007) (Fig. 1B).

The objective of the present study was to determine how the number, size, flexibility, and location of pneumatocysts on long kelp fronds affect the motion of and hydrodynamic forces on the fronds in wave-driven water flow. The specific questions investigated were: (1) How abundant are pneumatocysts on the fronds of *Egregia menziesii*, and do their abundances change with season? Where do pneumatocysts occur on the fronds and how large are those pneumatocysts? How variable are the locations, numbers, and sizes of pneumatocysts between individuals? (2) What is the magnitude of the hydrodynamic force on a single pneumatocyst, and how do the size and the reconfiguration of a pneumatocyst in moving water affect the force on the pneumatocyst? (3) How much do pneumatocysts increase the drag on a frond? (4) How does the location of pneumatocysts on a frond affect the depth of the frond in the water column under different wave conditions? (5) How do pneumatocysts in natural arrangements on kelp in the field affect the horizontal movement and depth of fronds in ambient waves?

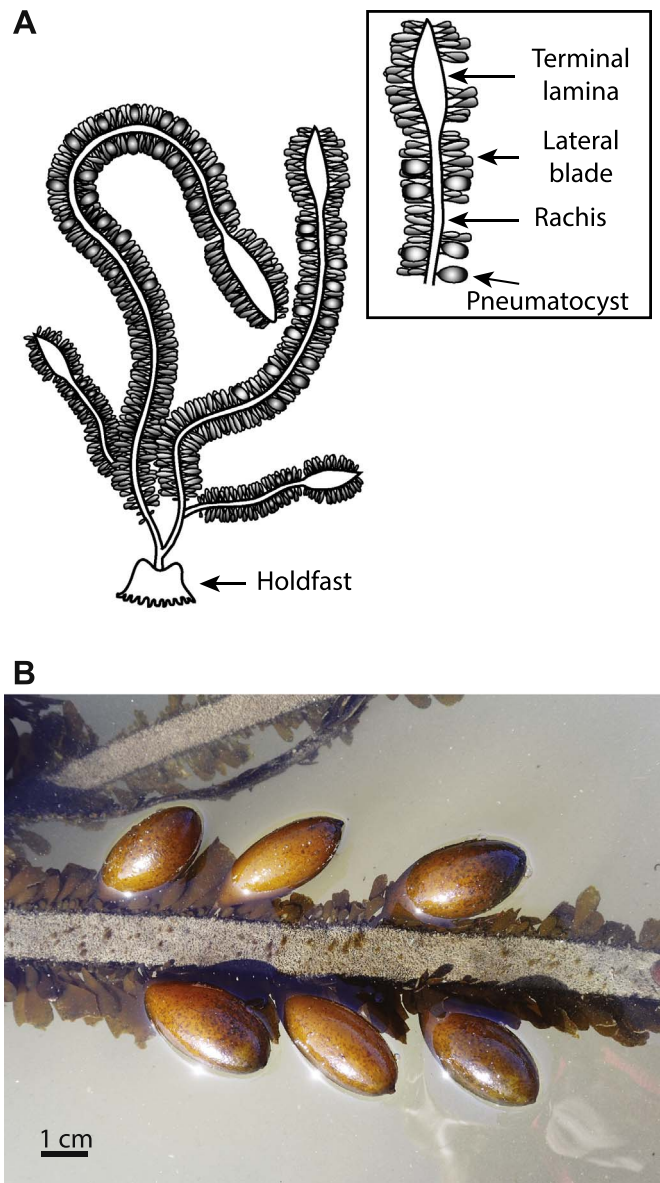


Fig. 1. (A) Anatomy of an *Egregia menziesii* sporophyte. Individual fronds on the kelp are strap-like and can grow to > 3 m in length. (B) Each frond's rachis bears lateral blades and ellipsoidal pneumatocysts along both edges.

2. Methods

2.1. Pneumatocyst surveys

2.1.1. Field sites

Pneumatocysts on *Egregia menziesii* were surveyed at four rocky intertidal sites in northern California. Two moderately wave-exposed sites were located near Bodega, CA, USA: Horseshoe Cove (HC) (38°18'59" N, 123°4'12" W) and Miwok Beach (MW) (38°21'25" N, 123°4'2" W). Two wave-exposed 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). Waves were attenuated as they moved across the wide, gently-sloping surf zones at HC and MW, whereas the steep rocky faces at KB and MC were hit by bigger, unattenuated waves (Denny, 1995; Johnson et al., 2015a,b). Furthermore, the fauna colonizing *E. menziesii* at HC and MW are dominated by herbivorous invertebrates, and the fauna colonizing *E. menziesii* at KB and MC are dominated by sessile suspension feeders (Burnett, 2017). These communities are

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