



# The fluid dynamics of *Balanus glandula* barnacles: Adaptations to sheltered and exposed habitats

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## ABSTRACT

Suspension feeders use a wide range of appendages to capture particles from the surrounding fluid. Their functioning, either as a paddle or a sieve, depends on the leakiness, or amount of fluid that passes through the gaps between the appendages. *Balanus glandula* is the most common species of barnacle distributed along the Pacific coast of North America. It shows a strong phenotypic response to water flow velocity. Individuals from exposed, high flow sites have short and robust cirral filters, whereas those from sheltered, low velocity sites have long, spindly appendages. Computational fluid dynamics (CFD) simulations of these two ecophenotypes were done using a finite volume method. Leakiness was determined by simulating flow velocity fields at increasing Reynolds numbers, results that have been unattainable at higher velocities by observation. CFD also allowed us to characterize flow in hard to see regions of the feeding legs (rami). Laser-illumination experiments were performed at low to medium flow velocities in a flume tank and corroborated results from CFD. Barnacle filters from a sheltered site become completely leaky at  $Re = 2.24$  (0.16 m/s), well above the maximum habitat velocity, suggesting that this ecophenotype is not mechanically optimized for feeding. Barnacles from exposed environments become fully leaky within the range of habitat velocities  $Re = 3.50$  (0.18 m/s). Our CFD results revealed that the drag force on exposed barnacles feeding appendages are the same as the sheltered barnacles feeding appendages despite their shape difference and spacing ratio.

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## 1. Introduction

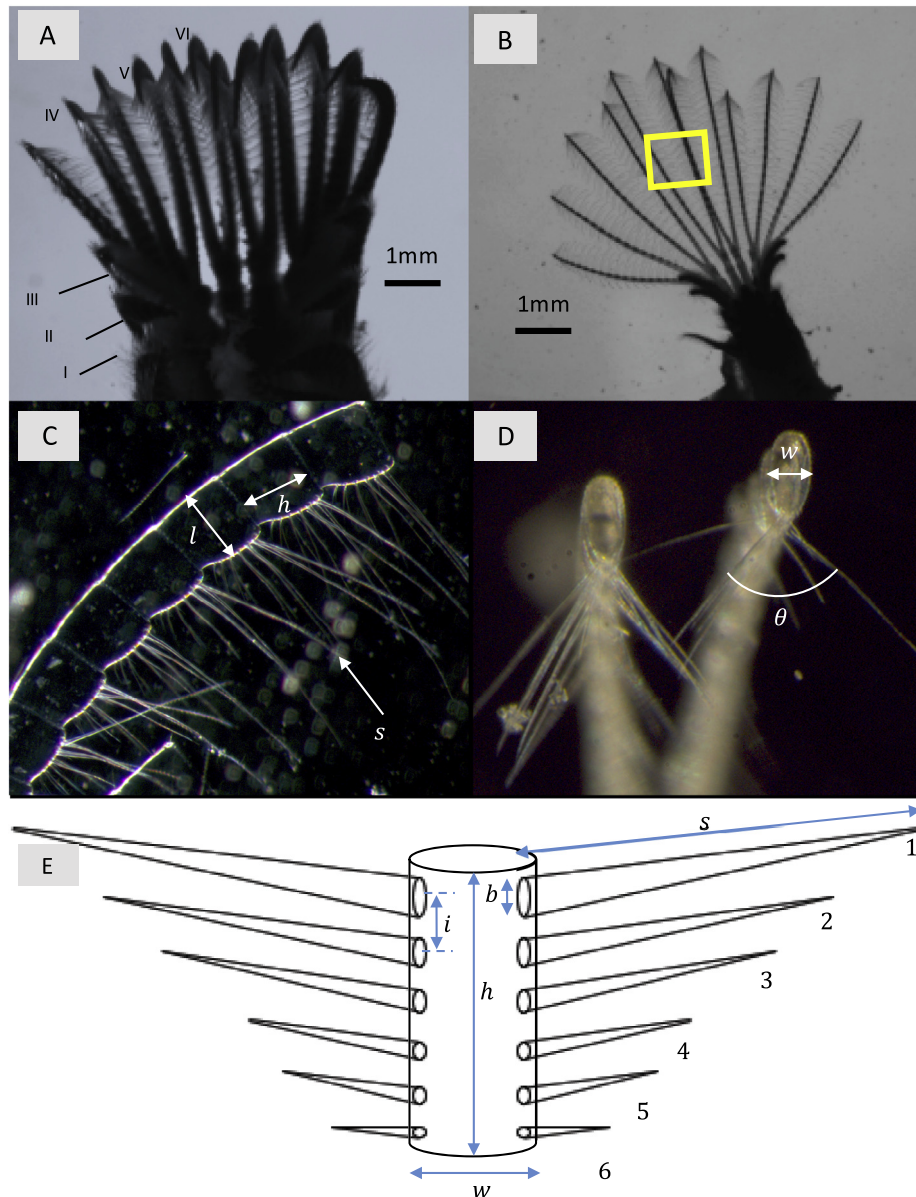
Suspension feeders use a diverse range of filamentous appendages to capture particles from the surrounding water (Mehrabian et al., in press; Riisgård and Larsen, 2010). Most appendages essentially consist of arrays of bristles or cylinders, and some behave as sieves to intercept particles from suspension passing through (e.g. bands of cilia, arthropod setae, and mucous nets), while others create feeding currents or act as paddles to direct pockets of fluid for further processing (e.g. flagella, cirri, or tentacles) (Riisgård and Larsen, 2010; Vogel, 2003). The performance of these appendages (i.e. paddle vs. sieve) depends on their interactions with the surrounding medium. Fluid can either pass readily through the gaps between filaments, creating a 'leaky' appendage that functions as a sieve, or it may flow around the perimeter of the appendage that functions as a paddle.

The feeding behaviour and flow about several species of barnacles have been described, especially in *Balanus glandula* (Geierman and Emler, 2009; Marchinko, 2007; Marchinko and Palmer, 2003; Miller, 2007; Southward, 1955; Trager et al., 1990). *B. glandula* (Fig. 1) is a common Northeast Pacific species of acorn barnacle found in a wide range of wave-exposed habitats. It has been subject to questions about how morphology and fluid dynamics affect appendage functioning. Its feeding legs demonstrate a great degree of phenotypic plasticity in response to water velocity (Marchinko, 2007; Marchinko and Palmer, 2003; Southward, 1955). Its sessile nature facilitates easy observations and manipulation in the field or lab (Arsenault et al., 2001). The parameters of the feeding structures, including rami length and width, and seta length and spacing, of individuals found at low and high flow velocities is well characterized (Arsenault et al., 2001; Marchinko and Palmer, 2003).

Less well known are how the water and appendage interact in confined, small, and hard to see regions close to the appendages. Also, observations at realistic, high flow velocities have not been

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**Fig. 1.** Microscopic image of the entire feeding appendage of A: Exposed and B: Sheltered *Balanus glandula*. I, II, III, IV, V, and VI refer to the cirrus numbers. Each cirrus consists of 2 rami. The box shows the portion of cirri VI used for CFD modeling. C: Microscopic image of a ramus and segments of a feeding appendage. D: Frontal view of the two rami of cirrus VI. E: Schematic front view of a ramus segment.  $h$  is the length of the segment,  $w$  is segment width,  $b$  is the setae diameter,  $i$  is the centre-to-centre setae spacing,  $s$  is the setae length, and  $l$  is segment length, which is in the flow direction. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

reported in the literature. Several mathematical and physical models of fluid velocity profiles around rows of cylinders of finite width have demonstrated that the transition to leakiness depends largely on the Reynolds number and setae spacing ratio (Cheer and Koehl, 1987a,b; Hansen and Tiselius, 1992; Koehl, 1993; Loudon et al., 1994; Mehrabian et al., in press; Tamada and Fujikawa, 1957). The Reynolds number represents the ratio of inertial to viscous forces:

$$Re = Ub/\nu \quad (1)$$

where  $U$  is the free flow velocity,  $b$  the characteristic length, in our case the base diameter of the longest setae (see Fig. 1E) and  $\nu$  the kinematic viscosity of the surrounding fluid. For an incompressible isothermal flow, this number fully characterizes the fluid flow around a given geometry pattern, like a filament (Vogel, 2003). For most biological filaments, the Reynolds number ranges from

$10^{-5}$  to 10 (Cheer and Koehl, 1987b; Jorgensen, 1983; LaBarbera, 1984; Rubenstein and Koehl, 1977; Shimeta and Jumars, 1991). At low values, viscous forces dominate, velocity boundary layers are thick relative to the dimensions of the body, and the flow about the appendage is laminar (Happel and Brenner, 2012; Vogel and Savage, 1996). But, from dimensional analysis, when geometry varies, geometrical ratios have to be considered. For example, the setae spacing ratio,  $i/b$  (the ratio of setae center-to-center spacing,  $i$ , to setae diameter  $b$ , see Fig. 1E) increases from sheltered to exposed barnacles and is known to have an important effect on leakiness (Marchinko and Palmer, 2003). In general, for  $Re = 0.5$ , high leakiness is observed when  $i/b$  becomes larger than 5 (Cheer and Koehl, 1987b; Koehl, 1996, 2001). However, for  $Re$  of the order of  $10^{-3}$ , changes to this ratio has little influence on leakiness (i.e. morphological and behavioural diversity without performance consequences) (Koehl, 1996).

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