

Feeding in extreme flows: behavior compensates for mechanical constraints in barnacle cirri

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ABSTRACT: Plastic morphological changes in response to environmental cues can allow organisms to adapt to their local environment. Barnacle feeding legs (cirri) exhibit substantial plasticity in size and shape along wave exposure gradients on rocky shores, but only up to a certain limit in maximum water velocities. Above the limit, the morphology of the cirri becomes invariant. Behavioral observations of barnacles feeding at a wave-exposed shore indicate that the fast response time for feeding motions allows barnacles to avoid potentially damaging flows associated with breaking waves, while still allowing feeding between wave impacts. The ability of barnacles to avoid individual waves indicates that the apparent limit in morphological plasticity may not be a result of physiological limits in cirral form, but rather a result of the barnacles reacting to some measure of the environment besides extreme flow speeds.

KEY WORDS: Phenotypic plasticity · Suspension feeding · Waves · Water velocity · *Chthamalus fissus*

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INTRODUCTION

Suspension feeders use a wide variety of methods to capture food items from the fluid in which they live. In many cases, some form of filter, net, or sieve-like structure is employed to intercept particles as they pass by the organism, such as the baleen of whales (Sanderson & Wassersug 1993), gill rakers in fish (Lauder 1983), modified mouth parts of invertebrates (Zhang 2006), or other modified body parts such as legs (Crisp & Southward 1961, Mauchline 1989) and tube feet (LaBarbera 1978). Trapping food particles in flowing water can place unique constraints on the form and function of feeding structures in suspension feeders. The size and form of the filtering apparatus must balance particle capture efficiency against mechanical constraints such as the drag created by fluids passing through and around the filter (Cheer & Koehl 1987). While many suspension feeders (e.g. filter-feeding vertebrates, or animals that actively pump water: Lauder 1983, Sanderson & Wassersug 1993, Vogel 1994) dictate the rate of flow through their feeding apparatus, the subset of suspension feeders that extends the feeding apparatus into flowing fluids is somewhat at the mercy of the

surrounding flow conditions. Because drag increases as the square of fluid velocity, the forces accompanying extreme flow speeds may impose limitations on the usefulness of the feeding structure at certain times.

Phenotypic plasticity in response to flow conditions has been reported in several phyla (Kaandorp 1999, Okamura & Partridge 1999, Arsenault et al. 2001, Marchinko 2003, von Dassow 2005, Zhang 2006). In habitats with relatively constant flow conditions, the form of the body, colony, or feeding apparatus may be tuned to suit the habitat. However, in habitats where flow speeds vary greatly over short time scales, behavior may be a more important tactic for dealing with unpredictable changes in flow speed.

Barnacles extend their feeding legs (cirri) into flowing water to capture food particles. The size and shape of the cirri therefore affect the drag imposed on the feeding net. As flow speeds increase, barnacles may have difficulty keeping a large cirral net extended, limiting their ability to feed effectively (Marchinko 2007). Barnacle cirral morphology varies plastically among habitats along a flow-speed gradient and has traditionally been correlated with maximum flow speeds experienced at sites over several weeks

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(Arsenault et al. 2001, Marchinko & Palmer 2003, Chan & Hung 2005). Barnacles growing in slow-moving, wave-protected waters grow longer, thinner cirri than conspecifics growing at wave-exposed sites, and these cirral traits can be altered between molts in response to changing flow patterns (Marchinko 2003).

There may be limits to the extent of the plastic response to flow. Li & Denny (2004) found that the correlation between cirral morphology and maximum water velocity at a site no longer held for barnacles from sites on the open coast. As peak water velocities at a site increase beyond 4 m s^{-1} , cirri do not continue to decrease in size or change shape. If the cirral net does not continue to get smaller as maximum flow speed, and consequently drag, increases, how do barnacles exposed to extreme flows maintain intact cirral nets and feed effectively? The proposed hypothesis is that behavior substitutes for further morphological variation and allows barnacles to avoid damaging flows, yet feed when flow speeds allow it (Marchinko & Palmer 2003, Li & Denny 2004). To address this hypothesis, I observed barnacle feeding behavior in the field. I sampled *Chthamalus fissus* barnacles along a wave-exposure gradient to determine whether they exhibit the same invariant cirral traits as previously studied species at high-flow sites, and gauged feeding behavior under breaking waves along with concurrent water velocity measurements to determine whether barnacles alter their feeding behavior to accommodate short-term changes in water velocity. An analysis of the distribution of water velocities at the wave-swept site was performed to determine if barnacles might be using a measure of the environment besides maximum water velocity to dictate cirral morphology.

MATERIALS AND METHODS

Cirral morphology. *Chthamalus fissus* barnacles were collected from 8 sites on the Monterey Peninsula in California, USA, in October 2006. Two protected sites in the Monterey Harbor were chosen to collect barnacles that experience no breaking waves and contend only with slow surge and tidal currents ('WharfSouth' $36^{\circ} 36.327' \text{ N}$, $121^{\circ} 53.662' \text{ W}$; 'Harbor-Beach' $36^{\circ} 36.221' \text{ N}$, $121^{\circ} 53.600' \text{ W}$, WGS84; inset, Fig. 1). Li & Denny (2004) collected *Balanus glandula* barnacles at these 2 low-flow locations. Barnacles were also collected from sites along the wave-exposed Mussel Point at Hopkins Marine Station (HMS) in Pacific Grove, approximately 1.5 km from the harbor site ($36^{\circ} 37.302' \text{ N}$, $121^{\circ} 54.258' \text{ W}$; individual sites marked in Fig. 1). Mussel Point is exposed to the full force of incoming ocean swells. Water velocities in excess of 20 m s^{-1} have been measured at the wave-exposed end

of Mussel Point (Denny et al. 2003). The 6 collection sites at HMS were chosen to encompass a broad range of wave exposure and resultant water velocities. *Chthamalus* were collected at sites along a horizontal transect 1.5 m above Mean Lower Low Water (MLLW). The relationship between offshore wave height and water velocity at each transect point has previously been described (Helmuth & Denny 2003).

In the laboratory, the barnacle prosoma was dissected from the rest of the shell. Egg masses were removed, and the prosoma was blotted dry and weighed, following the protocol of Marchinko & Palmer (2003). The sixth biramus cirrus was then dissected from both the left and right sides of the cirral net and digitally photographed under a dissecting microscope, allowing for a resolution of $0.0011 \text{ mm pixel}^{-1}$. The length of the ramus from the base to the tip and the diameter of the ramus at the suture between the first and second articles were measured using image analysis software, producing a measurement SE of approximately 0.0015 mm for ramus length and 0.001 mm for ramus diameter (Image-J, National Institutes of Health). An ordinary least squares regression was fitted to $\log(\text{leg length})$ versus $\log(\text{prosoma wet mass})$, as well as to $\log(\text{ramus diameter})$ versus $\log(\text{prosoma wet mass})$ in order to facilitate comparison of barnacle traits among sites. An analysis of covariance was carried out to compare ramus length and diameter among sites, with prosoma wet mass as the covariate.

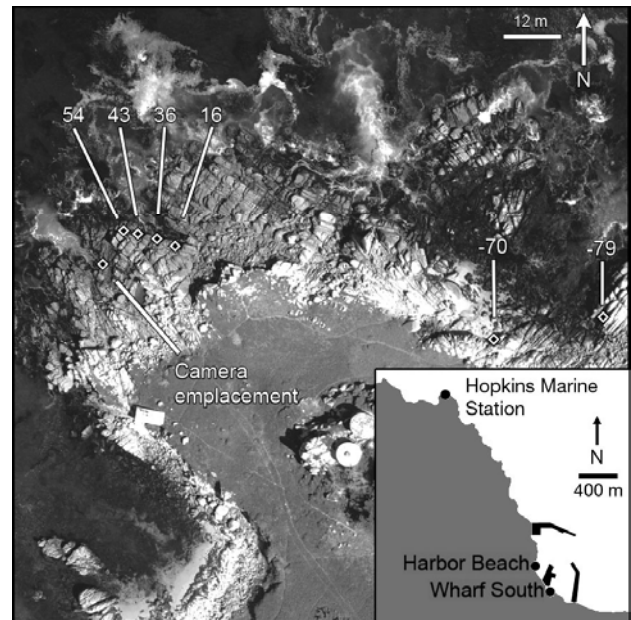


Fig. 1. *Chthamalus fissus* collection sites. Sites at Hopkins Marine Station are marked on aerial image, and collection sites in Monterey Harbor are marked on inset map. Site of camera emplacement used in behavioral studies is also noted

Average daily maximum water velocities at the collection sites were estimated for the 30 d prior to collection. Estimates were based on published relationships of average daily maximum water velocities at each site with the offshore significant wave height during the same time period (Helmuth & Denny 2003, Li & Denny 2004). The significant wave height was measured using a Seabird SBE-26 pressure gauge mounted at 10 m depth, 50 m off the point at HMS.

Feeding behavior. Barnacles used in the feeding behavior trials settled onto clear acrylic settlement plates deployed in the mid-intertidal zone at HMS. The plates were attached to the rock surface on wave-exposed areas of the shore adjacent to existing *Chthamalus fissus* beds. After the initial deployment of settlement plates in the spring of 2004, the plates were left undisturbed until the spring of 2005. By this time, a mixture of *C. fissus* and *Balanus glandula* barnacles had settled on the plates and grown to a basal shell diameter of 3 to 5 mm.

The clear acrylic settlement plates made the underside of the barnacles visible. *Chthamalus fissus* does not lay down a calcareous base plate, but instead grows a thin, partially transparent membrane. When the barnacles are still small, it is possible to see through the membrane and observe the movement of the prosoma mass of the barnacle inside the shell.

A waterproof camera housing was constructed using plastic plumbing pipe to house a Watec 502B video camera. The camera housing was mounted to the underside of a large aluminum plate with a hole bored through the middle. A settlement plate was then secured onto the top of the aluminum plate with the barnacles in view of the camera through the hole in the plate. An O-ring was placed between the settlement plate and the lens of the camera housing to provide a water-tight air space in the camera view path. This prevented water from getting between the camera and the settlement plate where it would obscure the view.

Prior to deployment in the field, the camera-and-settlement-plate apparatus was tested in an aquarium. Using a split-screen video system, the feeding behavior of the barnacles was observed from above and below simultaneously. These tests demonstrated that feeding movements viewed from above corresponded to movements of the prosoma within the barnacle test seen from below. The prosoma moved in time with the extension of the cirral net, and with the same rhythm of slow extension and fast withdrawal as described by other researchers (Crisp & Southward 1961). Small testing movements were distinguishable from full cirral extension based on the distance that the prosoma must necessarily shift back and forth in order to fully extend and withdraw the cirri. Active feeding, where

the cirri were extended and withdrawn in a regular rhythm, and passive feeding, where the cirri were extended into flow for several seconds continuously before withdrawing, were distinguishable based on the amount of time the prosoma was shifted into the extended position.

In the field, the entire apparatus was mounted in a concrete emplacement 1.5 m above MLLW, which exposed the barnacles to breaking waves. The emplacement was situated adjacent to the original deployment site of the settlement plates (Fig. 1). Rocks offshore of the site caused the largest waves to break prior to impacting the barnacles, so that the majority of wave impacts was caused by turbulent bores rushing up the shore rather than by waves directly crashing on top of the barnacles.

Wave forces acting on a small sphere adjacent to the experimental barnacles were measured using a 2-axis force transducer in a modified housing based on the basic design described by Boller & Carrington (2006). The force transducer had a 1.9 cm diameter roughened plastic sphere mounted on its post, and the transducer was bolted to the top surface of the aluminum mounting plate, 8 cm from the barnacles being filmed. The transducer was calibrated prior to deployment by hanging known weights off of the drag sphere. Power, video data, and voltage data from the force transducer were transmitted to dry land by cable.

The video and wave force data were simultaneously recorded onto video tape using a split-screen video camera arrangement. Voltages from the 2 horizontal axes of the force transducer, sampled at 100 Hz, were displayed in graphical form on the video recording, and a net force vector was calculated from the 2 signals for each wave impact. In total, 7 barnacles were deployed in the field on 6 d during October 2005 and 3 d during April 2006. Video recordings were made during high tide when the site was washed by waves.

Videotapes were analyzed with a video cassette player that allowed single frame stepping. A number of wave impacts was haphazardly selected for analysis from each 2 h video tape. For each wave that impacted the barnacles and force transducer, a score was assigned to each barnacle in view. Prior to the wave hitting, the barnacle was scored as either feeding or not feeding. During the impact of the wave (generally 10 to 15 frames, or approximately 0.3 to 0.5 s) the barnacle was scored as either withdrawing from the impact or staying out in flow.

The maximum force recorded during each wave impact was recorded off the video playback and converted to a velocity using the equation:

$$U = \sqrt{\frac{2F}{A\rho C_d}} \quad (1)$$

where U is the velocity of the water, F is the force exerted on the force transducer, A is the projected area of the drag sphere, ρ is the density of seawater, and C_d is the coefficient of drag of the drag sphere. C_d was assumed to be 0.45 based on data obtained in the laboratory (M. W. Denny unpubl.).

For each barnacle, a total of 600 individual waves was analyzed. Barnacles did not actively feed throughout each recording session, so the total number of waves that could be scored and used in the analysis (waves that hit a barnacle while it was feeding) was less than 600. The scored wave impacts were binned into velocity ranges with a minimum of 30 observations per bin, except for the highest water velocity bin where sample sizes ranged from 7 to 53, and the barnacles' feeding behavior was summarized as the fraction of waves in each velocity range for which they continued feeding uninterrupted.

Barnacle feeding behavior was also scored during intervals between wave impacts, while barnacles were still submerged. A series of 600 haphazardly selected time points from the various recording sessions was selected for each barnacle. This protocol was designed to measure the feeding activity of barnacles during the more benign flow conditions that make up the majority of submerged time.

Water flow conditions. In addition to scoring barnacle behavior, a random sample of water velocities was taken from each recording session used in this study in order to characterize the general water flow regime at this wave-exposed site. Water velocity was measured at 4000 haphazardly selected time points throughout the recorded sessions to produce a cumulative probability distribution. Due to limitations in the sensitivity of the force transducer, all velocities $<1.3 \text{ m s}^{-1}$ had to be binned. Using Matlab software, a curve was fit to the cumulative probability distribution using a function from Gaines & Denny (1993):

$$\text{Cumulative probability} = e^{-\left[\frac{\alpha - \beta U}{\alpha - \beta \epsilon}\right]^{\frac{1}{\beta}}} \quad (2)$$

With U as the velocity, the resulting values for the parameters α , β , and ϵ allowed for the extrapolation of the cumulative probability distribution back to 0 m s^{-1} using the known cumulative probability distribution $> 1.3 \text{ m s}^{-1}$. Taking the derivative of this curve yields the probability density function of water velocities during the recording sessions.

RESULTS

Cirral morphology. Analysis of covariance tests of log (ramus length) on log (prosoma mass) and log (ramus diameter) on log (prosoma mass) revealed heterogeneous slopes among the sample sites (for ramus length: site \times log [prosoma weight] interaction, $F_{7,139} = 2.92$, $p = 0.007$; for ramus diameter: site \times log [prosoma weight] interaction, $F_{7,139} = 2.96$, $p = 0.006$). The regression slopes are given in Table 1. At small and medium body sizes (0.1 to 1.2 mg prosoma mass), protected-site barnacles had longer rami than exposed-site barnacles, while they began to overlap in ramus length at the largest body sizes sampled here (1.2 to 2.0 mg prosoma mass). However, barnacles from wave-exposed sites also grew thicker rami at those larger body sizes, which should lead to a stiffer overall structure that is better able to withstand higher water velocities without bending (bending stiffness scales as diameter to the fourth power).

An average body mass of 0.8 mg was used to compute representative ramus lengths and diameters for barnacles from the sample sites, which were then plotted against the average daily maximum water velocity at the sites (Fig. 2).

Feeding behavior. As the wave size and peak water velocities increased, *Chthamalus fissus* withdrew more often during wave impacts (Fig. 3). There was substantial spread in the sensitivity of the barnacles to wave impacts. Five of the barnacles stayed open during $>80\%$ of the lowest measured velocity waves that

Table 1. *Chthamalus fissus*. Ordinary least squares estimates of slope and intercept for log (ramus length, mm) and log (ramus diameter, mm) versus log (prosoma wet mass, g). Sites are listed in order of increasing average daily maximum water velocity. HMS: Hopkins Marine Station. The trait value (mean \pm 95% CI) for a normalized body mass of 0.8 mg is given in the last column

Site	Slope	Intercept	r^2	p	Trait value (mm)
Length					
WharfSouth	0.1490	0.6662	0.703	0.040	1.59 \pm 0.258
HarborBeach	0.1651	0.7148	0.625	0.002	1.60 \pm 0.249
HMS -79	0.1995	0.7186	0.675	<0.001	1.26 \pm 0.073
HMS -70	0.2050	0.7841	0.764	0.005	1.41 \pm 0.179
HMS 54	0.1844	0.6812	0.779	0.013	1.29 \pm 0.185
HMS 36	0.2649	0.9361	0.884	<0.001	1.30 \pm 0.227
HMS 43	0.1687	0.6635	0.726	<0.001	1.38 \pm 0.186
HMS 16	0.2609	0.909	0.829	0.002	1.26 \pm 0.115
Diameter					
WharfSouth	0.1452	-0.6122	0.792	0.012	0.079 \pm 0.014
HarborBeach	0.1212	-0.7230	0.454	0.019	0.087 \pm 0.013
HMS -79	0.2648	-0.1544	0.483	<0.001	0.107 \pm 0.007
HMS -70	0.1881	-0.3693	0.734	0.008	0.112 \pm 0.014
HMS 54	0.2280	-0.2749	0.835	0.004	0.104 \pm 0.013
HMS 36	0.2147	-0.3436	0.787	0.004	0.098 \pm 0.019
HMS 43	0.2038	-0.3432	0.755	<0.001	0.106 \pm 0.015
HMS 16	0.2443	-0.2330	0.792	0.004	0.102 \pm 0.009

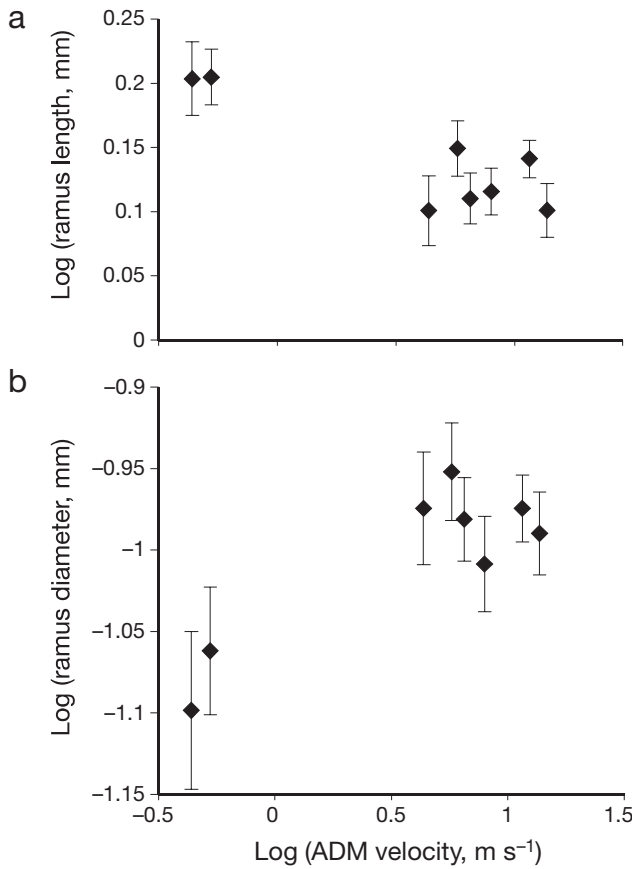


Fig. 2. *Chthamalus fissus*. Ramus length and diameter at 2 wave-protected sites and 6 wave exposed sites on the Monterey Peninsula. (a) Log (ramus length, mm) vs log (average daily maximum [ADM] water velocity, $m s^{-1}$). (b) Log (ramus diameter, mm) vs log (ADM water velocity, $m s^{-1}$). Ramus length and diameter at each site are standardized to a common prosoma wet mass of 0.8 mg based on the regression coefficients given in Table 1. Error bars: 95% CI

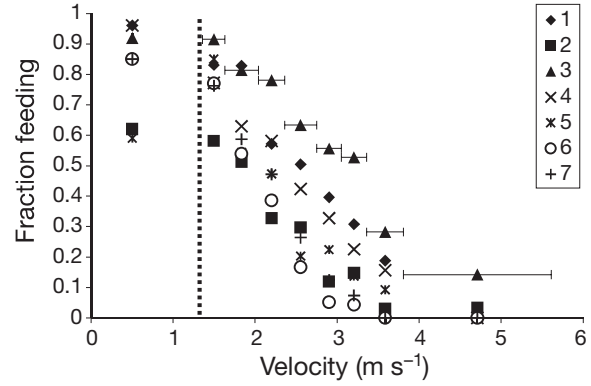


Fig. 3. *Chthamalus fissus*. Feeding behavior of 7 barnacles under a variety of wave conditions in the field. Data points to the left of dotted line: fraction of time spent feeding for water flow conditions $< 1.3 m s^{-1}$ ($n = 600$ time points for each barnacle). Data points to the right of dotted line: fraction of wave impacts during which barnacles continued feeding, binned by velocity. Horizontal error bars for barnacle 3: width of velocity bins. Sample size for each barnacle within each velocity bin ranged from 23 to 200, except for the 2 highest velocities for barnacles 6 and 7, where sample sizes ranged from 7 to 12

impacted the site ($< 1.3 m s^{-1}$). As water speeds increased above 2 to 3 $m s^{-1}$, every barnacle withdrew for a greater fraction of the sampled waves, and they avoided nearly every high speed impact at water speeds above 4 to 5 $m s^{-1}$.

When the barnacles were not being impacted by waves but were still submerged in slow moving water ($< 1.3 m s^{-1}$), they spent at least half the time feeding, and in some cases $> 90\%$ of the time (Fig. 3). A representative record of 2 min of feeding behavior from barnacle 6 is depicted in Fig. 4. Waves washed over the site with a typical period of 8 to 12 s, and barnacle

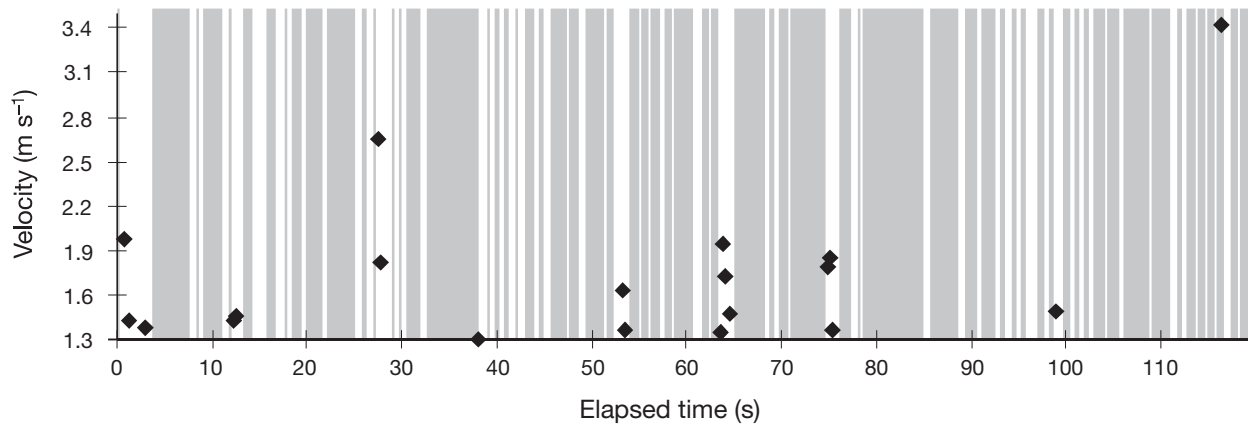


Fig. 4. *Chthamalus fissus*. Feeding behavior of a representative barnacle and associated flow speeds during a 2 min interval, sampled every 10 frames (0.333 s). Shaded vertical bars: periods when the feeding cirri were extended into flow. Points on the graph: water velocity at each sample time. Velocity measurements $< 1.3 m s^{-1}$ were excluded due to limits in the sensitivity of the force transducer

feeding paused during periods of high flow, but usually resumed quickly after the velocity decreased. There was no correlation between the water velocity of a wave impact and the time the barnacle spent retracted after the peak velocity had passed. The time periods between high water velocities consisted of many cirral extensions (gray shaded areas in Fig. 4), mainly in the active feeding pattern but with some longer duration passive feeding extensions as well.

Water flow conditions. Fig. 5a shows the cumulative probability distribution of water velocities during recording sessions at the wave-exposed HMS point. The probability is $>87\%$ that a randomly sampled water velocity is $<1.3 \text{ m s}^{-1}$; the probability increases to 99% for a velocity $<2.3 \text{ m s}^{-1}$. The extrapolated prob-

ability density function of water velocities during the recording sessions (Fig. 5b) has a mean water velocity of 0.98 m s^{-1} , and a mode of 0.52 m s^{-1} .

DISCUSSION

Feeding versus morphology

As in previous work on *Balanus glandula* from the same field sites (Li & Denny 2004), I found little variation in the morphology of the feeding cirri of *Chthamalus* among the wave-exposed sites at HMS. This apparent limit to the extent of plastic change in cirral morphology at sites characterized by higher maximum water velocities is potentially compensated for by the ability of barnacles to alter feeding behavior as needed in response to the flow conditions. The field observations of *C. fissus* feeding behavior in a variety of flow conditions demonstrates that barnacles have the ability to withdraw and avoid individual breaking waves that generate high flow speeds. Barnacles at this wave-exposed site also continued feeding at flow speeds substantially faster than those used in previous laboratory tests of feeding behavior. Traditional laboratory flume experiments on feeding behavior have been limited to flow speeds below 50 cm s^{-1} (Trager et al. 1990, 1992, Pullen & LaBarbera 1991, Sanford et al. 1994). Marchinko (2007) attempted to determine the upper limit of water flows that would cause barnacles to stop feeding, and given the constraints of the experimental equipment, this only occurred in protected-shore individuals. When flow speeds produced drag on the cirral net that exceeded the mechanical stiffness of the cirri, buckling occurred, making feeding impossible. Barnacles taken from high-flow field sites had cirri with larger diameter rami and could continue feeding at the 50 cm s^{-1} maximum velocity of Marchinko's flume. Observations made here in the field indicate that barnacles raised in this high-flow environment may occasionally leave their cirri extended in flows up to $3.5\text{--}4 \text{ m s}^{-1}$, although feeding drops off quickly in flows above 2 m s^{-1} (Fig. 3). Based on the patterns of change in cirral morphology with wave exposure among barnacle species, I propose that a similar behavioral mechanism of high-flow avoidance may be operating in *B. glandula* and other barnacle species spanning a range of flow habitats.

Feeding behavior observations

Laboratory studies of barnacle feeding behavior have often focused on the method of feeding exhibited by barnacles in response to changing flow conditions.

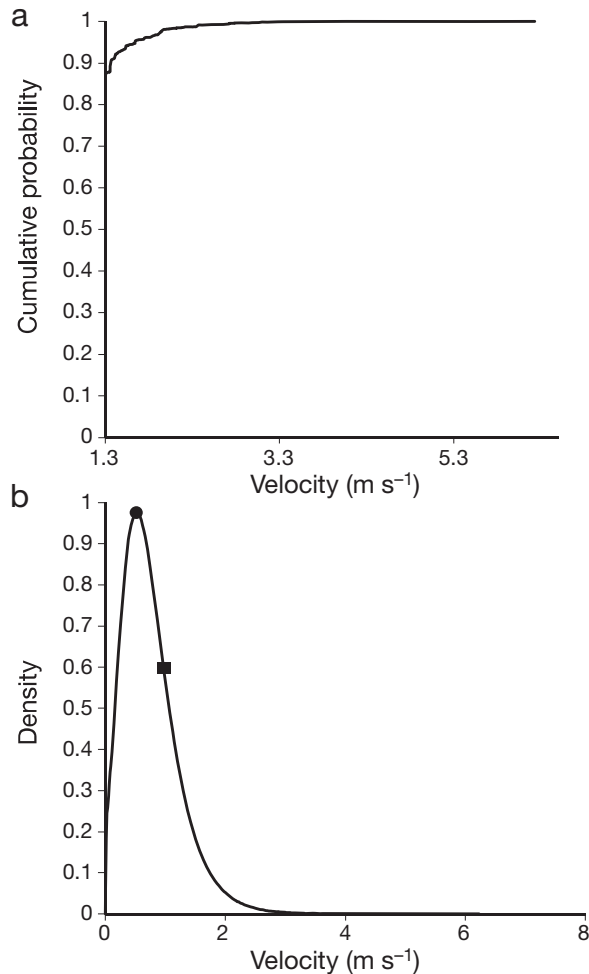


Fig. 5. (a) Cumulative probability density function of water velocities during barnacle feeding observations. All velocities below 1.3 m s^{-1} were binned due to limits in the sensitivity and noise of the force transducer at low velocities; $N = 4000$. (b) Probability density function of water velocities during feeding behavior trials, based on a curve fit to the cumulative probability density function. Mode (filled circle) and mean (filled square) are denoted on the curve

Crisp & Southward (1961) made the first detailed descriptions of the feeding behavior of several barnacle species in still water and slow flows. Among the various movement patterns exhibited by their barnacles were testing beats, pumping beats, active feeding, and passive feeding. Barnacles studied in flumes tend to switch from active beating of the cirri to passive extension as water speeds increase (Trager et al. 1990, Pullen & LaBarbera 1991), with passive feeding predominating at higher flow speeds in some species (Sanford et al. 1994). The methods used in this study limited the different types of movements that could be clearly discerned, but it was possible to distinguish the full extension of active and passive feeding from the pumping and testing movements, based on the degree to which the prosoma shifted within the test. Based on initial observations made in the laboratory, pumping and testing movements in *C. fissus* were coupled with small movements in the prosoma, while the full extension of the cirri for feeding required the prosoma to shift from one end of the test to the other. In the field, *C. fissus* used the active feeding mode for the vast majority of the time and at all flow speeds measured in this experiment. Individual barnacles occasionally switched to passive extension of the cirral net into flow for short periods of time (~3 to 5 s), but the switch happened only during long backwash periods as water receded off the shore, and was not consistent across individuals. The constantly shifting nature of the turbulent flows at this site likely precludes the use of passive feeding much of the time.

Field feeding observations also demonstrated that the fast response time of barnacles to changes in flow speed allows them to feed for much of the time that they are submerged (Figs. 3 & 4). The high peak flows of breaking waves are extremely transient, often lasting <1 s. The turbulent bore that continues up the shore and eventually washes back down moves much more slowly than the peak flows under the initial breaking wave. Barnacles in this study reacted quickly to the decelerating flows and began feeding again shortly (~0.5 to 2 s, Fig. 4) after withdrawing to avoid the initial breaking wave. These behavioral observations match the predicted behavioral pattern postulated by previous researchers for barnacles living on wave-exposed shores (Marchinko & Palmer 2003, Li & Denny 2004). Barnacles growing in high-flow sites typically have faster growth rates than barnacles at protected sites (Sanford et al. 1994, Sanford & Menge 2001). If the feeding time lost to hiding from fast flows is a small fraction of the total time spent submerged, the proposed higher food delivery rates on exposed shores and headlands could lead to a higher food capture rate and growth rate for barnacles at those exposed sites (Sanford & Menge 2001).

Characterizing the environment

Barnacles have the ability to withdraw into a robust shell that protects them from damage and dislodgement by high flow speeds (Denny et al. 1985). For this reason, large waves impinging on a shoreline may be of little concern to barnacles when considering the plastic morphology of their feeding structures. Instead, barnacles may be tuning their cirral morphology to some other measure of their flow environment besides maximum water velocity. This point may be illustrated using the measured distribution of water velocities during the feeding observations in this study (Fig. 5). The maximum water velocity measured during the time period of this experiment was 6.2 m s^{-1} , while the extrapolated probability density function in Fig. 5b indicates that the mean velocity was only 0.98 m s^{-1} , and the most common water velocity was predicted to be 0.52 m s^{-1} . The maximum water velocity measured was nearly 12 times faster than the most common water velocity at this site. The barnacles used in this experiment continued feeding at speeds well beyond 0.52 m s^{-1} . If we assume that the relationship between the maximum water velocity and modal water velocity is relatively consistent across wave-exposed sites, we would need to move to a site where the maximum water velocity is 30 m s^{-1} to increase the mode of the water velocities to 2.5 m s^{-1} , the speed at which most barnacles in this study stopped feeding. Even at this hypothetical field site, we would assume that maximum water velocities must eventually drop below 30 m s^{-1} as the swell subsides, returning flow speeds to a range that permits barnacles to feed.

If barnacles on wave-exposed shores can avoid flows beyond a certain velocity by withdrawing into the shell, it may be that in these exposed conditions they tune cirral morphology to another measure of the flow environment, such as mean or modal flow speeds. Therefore, the apparent lack of morphological change in barnacle cirri in response to increasing wave exposure among the HMS sites may be due not to a limit in the capacity for plastic change, but rather to a relatively invariant environmental cue. The gradient in maximum water velocities at the HMS sites sampled here for morphological measurements (4 to 13 m s^{-1}) might be accompanied by a relatively minor change in mean or modal flow speed. In wave-protected habitats, where there is a strong correlation between cirral morphology and maximum water velocity, flow speeds may rarely exceed the limit that would induce buckling of the cirral net and require hiding inside the shell. These protected-shore barnacles can sample the entire distribution of velocities, including the maximum water velocities, and grow cirri to accommodate the full range of flow conditions. The dimensions of the cirral

net should determine the flow speeds that the barnacle can withstand before buckling of the cirri occurs. The mechanical properties of the cirri produced during a molting cycle that set this limit are likely a result of a number of considerations, including maximizing particle capture area, maximizing potential feeding time, minimizing energy expenditures for growing the cirral net, and avoiding drag-induced buckling of the cirral net given the range of potential flow velocities at the site. While barnacles living at high-flow sites might be capable of growing shorter, stiffer cirri to avoid buckling at high water velocities, the need to maintain a cirral net with a large particle capture area likely makes this option less desirable. As a result of these considerations, and based on the feeding observations described here, plastic phenotypic change may be giving way to behavioral accommodation of the high-flow conditions at wave-exposed sites in order to maximize potential feeding time and particle capture rates.

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