

Feeding Behavior Reveals the Adaptive Nature of Plasticity in Barnacle Feeding Limbs

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*Barnacle feeding limbs are extremely plastic in response to spatial and temporal differences in wave exposure: individuals have long, thin feeding limbs in habitats with little wave action, and short, thick feeding limbs in wave-exposed habitats. This difference in feeding limb morphology is assumed to be adaptive. Individuals with shorter limbs may have the ability to feed in breaking waves because their limbs are better suited to withstanding drag forces than are those of individuals with longer feeding limbs. I tested this hypothesis by observing the feeding behavior of two populations of *Balanus glandula* (one from a protected shore and one from a wave-exposed shore) subjected to five different water velocities. Differences between populations in the ability to feed with the cirral net fully extended were highly significant. The wave-exposed population fed with the cirral net fully extended at all velocities tested (up to 49 cm/s), whereas full cirral extension ceased between 7.25 and 21.4 cm/s in all individuals from the protected-shore population. Clearly, barnacles possessing long, thin feeding limbs experience a strong disadvantage when feeding in faster flowing water, confirming earlier hypotheses that differences in feeding limb length between protected and wave-exposed shores are adaptive.*

Acorn barnacles are suspension feeders that extend three pairs of modified thoracic limbs (cirri) into ambient flow to capture plankton and smaller food particles (1). The feeding apparatus of many barnacle species is remarkably plastic with respect to wave exposure (2–4). In the northeastern Pacific, the common intertidal barnacle *Balanus glandula* Darwin, 1854, shows the greatest degree of plasticity in feeding leg form. Individuals from wave-protected shores

possess feeding limbs nearly twice as long and 25% thinner at the base than conspecifics living on wave-exposed shores (3), and experiments show that this species can alter the length and width of its feeding limbs to suit local flow conditions in one or two molts (2). Because of the functional importance of barnacle feeding limbs, their phenotypic plasticity is assumed to be adaptive—shorter, stouter legs may allow barnacles to feed in high-velocity flow under breaking waves. However, the consequences of possessing differently shaped feeding limbs have not been investigated, and thus the adaptive nature (5) of differences in feeding limb length remains speculative.

I examined the effect of water velocity on the feeding behavior of long-limbed *versus* short-limbed populations of *B. glandula* by observing individuals collected from two locations differing in wave exposure in Barkley Sound, British Columbia, Canada. The long-limbed population, characterized by a mean feeding limb length of 4.1 mm, came from a wave-protected shore, Bamfield Inlet, with a mean maximum tidal current velocity of 1 cm/s (see ref. 3 for further detail). The short-limbed population, characterized by a mean feeding limb length of 2.7 mm, came from a wave-exposed shore, Bordelais Island, with an average maximum velocity of breaking waves of 426 cm/s (3). Limb lengths of both populations were standardized to a mean prosomal wet mass of 0.01 g (3).

The effect of unidirectional water velocity on feeding behavior differed significantly between the long- and short-limbed populations (Table 1A and B; $P < 0.001$ Population * Water velocity interaction), and the two populations exhibited highly significant differences in the ability to feed with fully extended limbs and the number of cirral beats per minute (Table 1A and B; $P < 0.01$ Population effect; Fig. 1A and B). The short-limbed, wave-exposed population was able to feed with limbs fully extended at all velocities tested,

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Table 1

Results from two-factor repeated measures ANOVA testing the effects of population and experimental water velocity on (A) the proportion of *Balanus glandula* feeding with the cirral net fully extended, and (B) the number of cirral beats per minute

Source of variation	df	Mean-square	F	P
A. Proportion feeding with fully extended cirral net				
between subjects				
Population (long vs. short limbs)	1	46080	21.229	<0.001
Error	34	2171		
within subjects				
Water velocity	4	21982	31.636	<0.001
Population * Water velocity	4	15142	21.792	<0.001
Error	136	695		
B. Number of cirral beats per minute				
between subjects				
Population (long vs. short limbs)	1	5248.8	8.979	0.005
Error	34	584.5		
within subjects				
Water velocity	4	284.4	1.795	0.133
Population * Water velocity	4	2391.5	15.101	<0.001
Error	136	158.4		

up to 49 cm/s. In contrast, the long-limbed, protected-shore population stopped extending limbs into flows between 7.25 and 21.4 cm/s, after which the cirri remained curled while beating just above the operculum (Fig. 1A). The inability of long-limbed barnacles to fully extend during feeding at even modest velocities indicates a strong disadvantage to possessing feeding limbs too long and thin for the greater flow conditions experienced on wave-exposed shores.

At the two highest velocities tested (33.15 and 49 cm/s) individuals from the long-limbed, protected-shore population were observed to decrease the frequency of cirral beating (Fig. 1B). This decrease in beat frequency indicated a behavioral switch from the normal beat, in which cirri are fully extended for suspension feeding, to a pumping beat, in which cirri remain curled and protected near the barnacle operculum (1). The pumping beat generates water currents within the barnacle shell for respiration and possibly for feeding on smaller food items without extending the feeding limbs (1). In the 21.4 cm/s velocity treatment, protected-shore individuals were commonly observed employing a test beat (1), which occurs when a barnacle extends just one or two cirri into flow. During the test beat, the extended cirrus immediately deflected downstream and was retracted into the shell. Test beats were irregularly performed by a few individuals in the two highest velocity treatments (33.15 and 49 cm/s), but at these velocities feeding limbs buckled quickly and were retracted. In contrast, the short-limbed, wave-exposed population increased cirral beat frequency as water velocity increased. This increase in beat frequency with increasing water movement is likely a pas-

sive consequence of higher velocities increasing particle capture rates (1). In faster flow, individuals capture a greater number of particles per unit time, requiring a greater number of beats to clear the limbs of captured food.

Although differences in feeding behavior indicate a disadvantage to feeding in high velocity with long, thin limbs, I did not observe any behavioral disadvantages to feeding with short limbs in low flow. Marchinko and Palmer (3) suggested that energy expended actively feeding—feeding with regularly beating cirri *versus* passive, prolonged extension of cirri—in low flow might be greater for shorter limbed barnacles than longer limbed ones. Shorter limbed barnacles have less surface area in which to capture food and therefore must increase the number of cirral beats per unit time to achieve the same capture rate as those barnacles with longer limbs and a greater surface area of the cirral net. This was not apparent in my data: there was no statistical difference in beat rate between populations in the lower three velocity treatments ($P > 0.15$); in contrast to expectation (3), barnacles from the short-limbed population beat, on average, nine fewer times per minute than the long-limbed population in the still-water treatment (0 cm/s; Fig. 1B). Moreover, the short-limbed population in the still-water treatment exhibited a rather low proportion of individuals feeding with cirri fully extended (Fig. 1A). Quite possibly, short-limbed, wave-exposed populations require current or other mechanical stimuli to begin feeding, as seen in some pedunculate barnacle species that live only on wave-exposed shores (6).

The lack of behavioral differences between populations may indicate that there is little disadvantage for barnacles feeding with short limbs in low-velocity currents. However, unless there is little cost to maintaining a plastic response in barnacle populations, the symmetrical ability of wave-exposed and protected-shore barnacles to lengthen limbs in slow flow and shorten limbs in fast flow (2) suggests that the disadvantage of feeding with short limbs in slow flow should be quite strong. Perhaps that disadvantage is simply due to a decrease in the efficiency of feeding with a smaller cirral net (3). For example, larval blackflies with shorter, more closely spaced feeding limbs suffer from lower particle capture rates than individuals with longer, more widely spaced feeding limbs (7). Testing the efficiency of particle capture of long- and short-limbed populations may identify the disadvantage of feeding with short, thick limbs in the quiet waters of protected shores.

Recently, Li and Denny (8) documented that the plastic response of barnacle limb length to changes in water velocity does not hold for velocities above 4 m/s. They substantiate earlier work suggesting that barnacles cease feeding at the highest velocities under breaking waves, instead feeding in the slower backwash currents after waves break (2, 6). Thus, the abundance and vertical and horizontal distributions of barnacle species along wave-exposure gradients

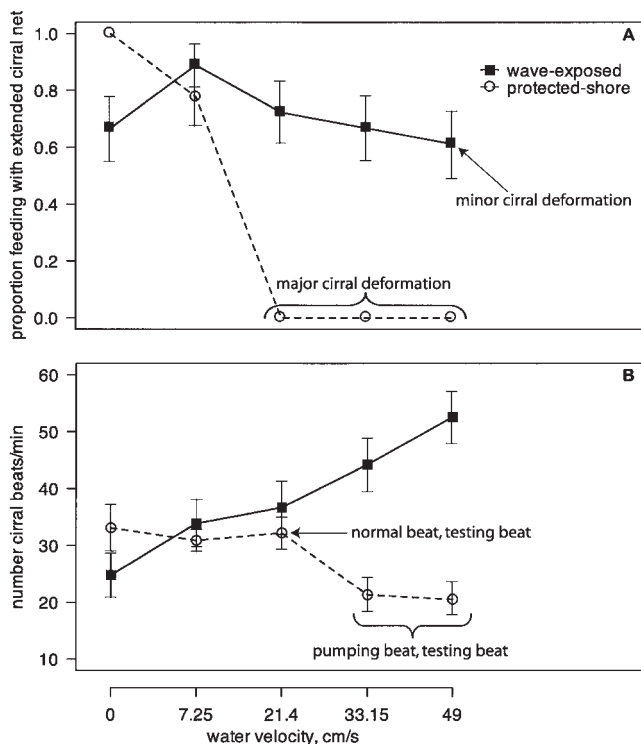


Figure 1. The effect of water velocity on feeding behavior of the intertidal barnacle *Balanus glandula* from two populations differing in wave exposure and feeding limb morphology: one short-limbed, wave-exposed population and one long-limbed, protected-shore population. (A) The proportion of individuals fully extending the cirral net into flow. Major cirral deformation indicates that all attempts at extending the cirral net resulted in full deflection of the cirrus downstream; minor cirral deformation indicates light bending of the cirrus in three individuals. (B) The number of cirral beats counted per minute. Barnacles performed a normal beat unless otherwise indicated in the figure. See text for definitions of beating behavior. Points and bars represent mean \pm 1 SE of 18 individuals tested from each population.

Barnacles were collected on mussel shells during two low tide cycles on 18 and 19 June 2001 from Bamfield Inlet and Bordelais Island in Barkley Sound, BC, Canada. Barnacles from both populations came from the same shore locations as those used by Marchinko and Palmer (3) and were of similar mean body size (mean opercular diameter $4.1 \text{ mm} \pm 0.99 \text{ SD}$ and $3.9 \text{ mm} \pm 0.86 \text{ SD}$ for Bamfield Inlet and Bordelais Isl., respectively). After collection, 18 solitary, uncrowded barnacles from each population were left out of water for the following high and low tides, during which they were labeled individually and then hot-glued (upon their mussel shell) to a single rock used in each trial throughout the experiment. Feeding trials were conducted at night under artificial lighting, during the time of the next high tide. Barkley Sound experiences a mixed semidiurnal tidal sequence; therefore the feeding trials began about 18 h after individuals were collected.

Feeding-behavior trials were performed on three barnacles from one population at a time, alternating between populations for each trial. The rock, with barnacles, was immersed in a recirculating flume for 10 min with no current before the experiment began. Velocity trials were conducted in the same order, starting with velocities of 0, 7.25, 21.4, 33.15, and 49 cm/s. Barnacles were acclimatized to each velocity treatment for 5 min before the extension and deformation of the cirral net was observed for 1 min, followed by counting the cirral beats in 30 s for each individual. The reported velocity of each treatment was measured prior to the experiment by using a Nixon Streamflo analog meter with a series 403 low-speed

propeller probe 15 mm in diameter (Novonic Instruments, Gloucester, England). To ensure accurate measurement of the velocities experienced by the feeding barnacles, the flow meter was inserted just above the rock used to support the barnacles. All trials were conducted at $12 \pm 0.5 \text{ }^\circ\text{C}$ in seawater from Bamfield Inlet.

Two-factor, repeated-measures analysis of variance (ANOVA) was conducted in the R statistical environment (13) to test for differences in feeding behavior between populations and among velocity treatments. The repeated-measures ANOVA was necessary because each individual was subjected to all velocity treatments. The binomially distributed proportional data were arcsine-transformed prior to analysis.

may be influenced not only by the range of morphological plasticity of feeding limbs (3), but also by behavioral decisions concerning the mode, direction, and timing of feeding (4, 9–11). The velocities I used were modest compared to those measured in the field by Li and Denny (8). Although the short-limbed, wave-exposed population was able to feed with full cirral extension at velocities up to 49 cm/s, the data indicate a gradual decrease in the proportion of individuals feeding with full extension at velocities higher than 7.25 cm/s (Fig. 1A). Moreover, a few individuals from the short-limbed population exhibited deformation of limbs when feeding at 49 cm/s, which is nearly an order of magnitude less than the maximum velocities measured at their collection site (3). Testing the ability of barnacles to extend feeding limbs into velocities approximating those measured in the field would allow us to compare the upper velocity limit of feeding to the upper velocity limit of their distribution. Perhaps then we may begin to dissect the roles of behavior and morphological plasticity in determining physical limits to the distribution and abundance of barnacle species inhabiting shores along wave-exposure gradients.

Lastly, the degree to which water velocity is a major factor in determining the size of barnacle feeding fans and feeding behavior is unclear. Faster flowing water results in more food passing by the feeding fan per unit time, and thus it is difficult to separate the effects of food availability from the effects of velocity. Velocity and food availability play important but different roles in determining the form of feeding elements in suspension-feeding black flies (12). Food availability appears to have a greater effect on the number of feeding rays, whereas velocity appears more important in determining the area of the feeding fan (12). The effect of water velocity on the feeding performance of different-sized feeding fans in barnacles is clear. Barnacles with longer limbs are unable to feed by fully extending feeding limbs at moderate to high velocities. If lower opportunity to feed results in lower rates of growth and reproduction, then I would expect water velocity to be a major determinant of feeding limb size and shape, at least in the high velocities associated with wave-exposed shores.

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Literature Cited

1. **Crisp, D. J., and A. J. Southward. 1961.** Different types of cirral activity of barnacles. *Philos. Trans. R. Soc. Lond. B* **243**: 271–307.
2. **Marchinko, K. B. 2003.** Dramatic phenotypic plasticity in barnacle legs (*Balanus glandula* Darwin): magnitude, age-dependence, and speed of response. *Evolution* **57**: 1281–1290.
3. **Marchinko, K. B., and A. R. Palmer. 2003.** Feeding in flow extremes: dependence of cirrus form on wave-exposure in four barnacle species. *Zoology* **106**: 127–141.
4. **Chan, B. K. K., and O. S. Hung. 2005.** Cirral length of the acorn barnacle *Tetraclita japonica* (Cirripedia: Balanomorpha) in Hong Kong: effect of wave exposure and tidal height. *J. Crustac. Biol.* **25**: 329–332.
5. **Travis, J. 1994.** Evaluating the adaptive role of morphological plasticity. Pp. 99–122 in *Ecological Morphology*, P. C. Wainwright and S. M. Reilly, eds. University of Chicago Press, Chicago.
6. **Barnes, H., and E. S. Reese. 1959.** Feeding in the pedunculated cirriped *Pollicipes polymerus* J. B. Sowerby. *Proc. Zool. Soc. Lond.* **132**: 569–585.
7. **Zhang, Y., and B. Malmqvist. 1997.** Phenotypic plasticity in a suspension-feeding insect, *Simulium lundstromi* (Diptera: Simuliidae), in response to current velocity. *Oikos* **78**: 503–510.
8. **Li, N. K., and M. W. Denny. 2004.** Limits to phenotypic plasticity: flow effects on barnacle feeding appendages. *Biol. Bull.* **206**: 121–124.
9. **Barnes, H., and E. S. Reese. 1960.** The behaviour of the stalked intertidal barnacle *Pollicipes polymerus* J. B. Sowerby, with special reference to its ecology and distribution. *J. Anim. Ecol.* **29**: 169–185.
10. **Trager, G. C., D. Coughlin, A. Genin, Y. Achituv, and A. Gango-padyay. 1992.** Foraging to the rhythm of ocean waves: porcelain crabs and barnacles synchronize feeding motions with flow oscillations. *J. Exp. Mar. Biol. Ecol.* **164**: 73–86.
11. **Trager, G. C., J.-S. Hwang, and J. R. Strickler. 1990.** Barnacle suspension-feeding in variable flow. *Mar. Biol.* **105**: 117–127.
12. **Zhang, Y. 2006.** Balancing food availability and hydrodynamic constraint: phenotypic plasticity and growth in *Simulium noelleri* blackfly larvae. *Oecologia* **147**: 39–46.
13. **R Development Core Team. 2005.** R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. [Online]. Available: <http://www.R-project.org>.