Precise tuning of barnacle leg length to coastal wave action

David J. Arsenault, Kerry B. Marchinko and A. Richard Palmer[*]

Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E9 and Bamfield Marine Station, Bamfield, British Columbia, Canada V0R 1B0

Both spatial and temporal variation in environmental conditions can favour intraspecific plasticity in animal form. But how precise is such environmental modulation? Individual *Balanus glandula* Darwin, a common northeastern Pacific barnacle, produce longer feeding legs in still water than in moving water. We report here that, on the west coast of Vancouver Island, Canada, the magnitude and the precision of this phenotypic variation is impressive. First, the feeding legs of barnacles from protected bays were nearly twice as long (for the same body mass) as those from open ocean shores. Second, leg length varied surprisingly precisely with wave exposure: the average maximum velocities of breaking waves recorded *in situ* explained 95.6–99.5% of the variation in average leg length observed over a threefold range of wave exposure. The decline in leg length with increasing wave action was less than predicted due to simple scaling, perhaps due to changes in leg shape or material properties. Nonetheless, the precision of this relationship reveals a remarkably close coupling between growth environment and adult form, and suggests that between-population differences in barnacle leg length may be used for estimating differences in average wave exposure easily and accurately in studies of coastal ecology.

Keywords: morphology; phenotypic plasticity; wave exposure; hydrodynamics; marine invertebrate; Crustacea

1. INTRODUCTION

Many animal species exhibit different forms in different environments (Stearns 1989; Travis 1994; Schlichting & Pigliucci 1999). This intraspecific variation may be striking in some marine invertebrates. For example, encrusting sponges (Palumbi 1984), arborescent stony corals (Chamberlain & Graus 1975) and intertidal snails (Kitching *et al*. 1966; Vermeij 1973) produce more flow-tolerant forms under conditions of high wave exposure, colonial soft corals produce larger colonies on shores with higher wave action (Sebens 1984), intertidal snails produce thicker shells where crab predation is more intense (Kitching *et al*. 1966; Appleton & Palmer 1988; Palmer 1990) and food supply significantly affects skeletal form in herbivorous snails (Kemp & Bertness 1984), mussels (Hickman 1979) and in both the larvae (Hart & Strathmann 1994) and adults (Levitan 1991) of sea urchins. In addition, many animals exhibit conspicuous trophic polymorphisms (Travis 1994) and predator-induced morphological differences (Tollrian & Harvell 1999). Clearly, phenotypic plasticity is widespread in animals (Stearns 1989). But how precisely does animal form track local environmental conditions?

Studies of conspicuous intraspecific variation have provided many insights into the costs and benefits of particular morphologies, the mechanisms of adaptation and the adaptive significance of plastic versus constitutive responses to environmental variation (reviewed in Travis 1994; Schlichting & Pigliucci 1999; Tollrian & Harvell 1999). However, while induced differences are often predictable in magnitude and direction under controlled experimental conditions, responses to stimuli under natural conditions may differ because other factors also influence adult form. In addition, quantitative estimates of stimulus intensity (food supply, predation intensity, water flow conditions, etc.) are often difficult to obtain in the field, so robust conclusions about the precision of morphological responses to environmental stimuli under natural conditions have been elusive.

Barnacles are ideal animals for studying the precision of phenotypic plasticity. First, they are famous for being able to produce different forms under different conditions: crowding promotes elongate shells that become trumpet shaped under extreme conditions (Barnes & Powell 1950; Bertness 1989), contact with predatory snails induces a radically bent form in *Chthamalus anisopoma* where the aperture is rotated nearly perpendicular to the substratum (Lively 1986) and differences associated with water motion induce differences in the length of their feeding legs (Pentcheff 1995). Second, post-larval barnacles are sessile so local environmental effects are not blurred by animal movements. Third, barnacles are easy to manipulate in the field because they settle on a variety of substrata and may be readily transplanted for determining the causes of between-population variation (selective settlement, differential mortality or phenotypic plasticity). Fourth, some intertidal species occur over a wide range of environmental conditions, thereby setting the stage for many possible ecophenotypic responses. Finally, the extended period of larval dispersal (which is up to 4 weeks in *Balanus glandula*) (Strathmann 1987) appears to yield a low between-population genetic heterogeneity (< 4%) (Hedgecock 1986), which suggests most observable morphological variation is ecophenotypic.

Because the feeding appendages of barnacles must be extended out of the shell in order to capture food, they must be able to function under a wide range of wave exposure conditions. In addition, *B. glandula* appears to be able to produce legs of different length in response to

Table 1. *Field study sites.*

(Sites where exposure meters were deployed and barnacles collected, in order of increasing wave action in Barkley Sound, Vancouver Island, British Columbia, Canada. The shore height values are relative to the Canadian Hydrographic Service datum.)

name	sampling location	north latitude	west longitude	shore height (m)	
				transducers	barnacles sampled
Ross Islets	south-facing side of southern-most, fully treed island in the Ross Islets	48°52′24″	125°09′37″	2.0	3.1
Self Point	south-facing side of point, east side of Helby Island	48°50′54″	125°09′42″	2.1	3.2
Wizard Islet	west-facing side of western islet, below light	48°51′30″	125°09′45″	2.0	3.4
Kelp Bay	south-facing side of point at north end of bay	48°51′49″	125°06′21″	2.3	3.4
Bordelais Island	south-facing side of southwestern point	48°49′02″	125°13′54″	4.0	5.1
Seppings Island	western-most rocks on southwest-facing side	48°50′30″	125°12′30″	2.8	3.6

different levels of water motion (Pentcheff 1995). We therefore set out to determine how precisely *B. glandula* adjusts the length of its limbs to local wave exposure conditions.

2. METHODS

(a) *Field sites*

Transducers for measuring wave exposure were deployed at and barnacles collected from six sites of varying wave exposure in Barkley Sound on the west side of Vancouver Island, British Columbia, Canada (table 1). These sites ranged from very protected conditions with minimal swell to sites exposed to the full fury of northeastern Pacific Ocean swell during the winter months.

(b) *Wave exposure measurement*

The maximum water velocity at each site was estimated using two mechanical transducers (Carrington Bell & Denny 1994) that were fastened to a rock *ca.* 2 m apart. Each transducer consisted of a hollow plastic golf ball that was attached to a spring inside a PVC pipe housing by a 27 kg test monofilament line. Drag on the ball extended the spring and a small rubber disc slid along the lubricated monofilament line inside the housing to record its maximum extension. We used springs of different compliance at the different sites in order to maximize the sensitivity of the transducers ($k = 92.1$ N m^{-1} with range = 83–110 N m^{-1}, $k = 173.9$ N m^{-1} with range = 150–194 N m^{-1} and $k = 378.1$ N m^{-1} with range = 299–453 N m^{-1}). Spring extension was calibrated by suspending known masses to the balls. Force measurements were converted to velocity using a published calibration curve (Carrington Bell & Denny 1994). Transducers were deployed concurrently at all six sites on 16 days (7, 15, 16 and 18–21 July, 30 July–4 August and 14–16 August 2000) and re-zeroed after each 24 h period, thereby yielding 16 independent estimates of the maximum velocity experienced during the preceding 24 h. The average hourly maximum offshore wave height during high tide during this time-period at the La Pérouse buoy, which is maintained by Environment Canada (buoy no. 46206) (48°50′06″ N, 129°59′54″ W), *ca.* 50 km west of our nearest site, was 1.37 ± 0.453 m (mean ± s.d. and $n = 16$).

(c) *Collection and measurement of barnacles*

We collected solitary, uncrowded barnacles from bare rock surfaces in the lower third of the *B. glandula* zone immediately upshore from the location of the transducers on 3 August 2000. Shell dimensions were recorded with Vernier calipers. The prosoma (the fleshy part of the body, excluding the shell but including the legs) was removed, blotted dry and weighed to the nearest 0.1 mg in order to obtain their body wet mass. The posterior three cirri (legs 4, 5 and 6) were dissected from the left side of the prosoma and splayed in seawater on a microscope slide. The lengths of the exopodite and endopodite of each leg were measured from the tip to the base of the ramus (i.e. protopodite segments were not included) and the average of these two lengths was standardized to a common prosoma wet mass of 0.0219 g (*ca.* 3.8 mm opercular length) by ANCOVA. Ramus lengths were measured at magnifications of ×40–50 using a camera lucida connected to a dissecting microscope and a digitizing tablet with a precision of 20 dots mm^{-1}.

(d) *Analyses*

Least-squares linear regression analyses were conducted with STATVIEW II (version 1.03) and analyses of covariance (ANCOVA) were conducted with SUPERANOVA (version 1.11), both from Abacus Concepts (Berkeley, CA). All regression and ANCOVA analyses were conducted on log$_{10}$-transformed data. Least-square means of barnacle leg length for a standard body mass were computed assuming a common slope for all six sites.

3. RESULTS

(a) *Magnitude and form of the variation*

The lengths of the three primary pairs of feeding legs of the intertidal barnacle *B. glandula* increased with increasing barnacle size at the six sites we studied (table 2), as seen in other barnacles (Crisp & Maclean 1990). This increase was not statistically significant for some sites because the size range we chose was too narrow, but ANCOVA confirmed that this increase was highly significant for each of the three legs when all sites were analysed concurrently ($p < 0.001$) (table 3). In addition, the slope of this relationship did not differ between

Table 2. *Barnacle body sizes and least-squares linear regression equations for log(ramus length) (mm) of the sixth thoracic leg as a function of log(body wet mass) (g) of B. glandula from six sites.*

(Wet mass is the mass of the prosoma only (i.e. the body exclusive of the shell and mantle) and ramus length is the average of the exopodite and endopodite (exclusive of the protopodite) of the left leg. Similar slopes but different intercepts were observed for legs 4 and 5, but are not reported here.)

		regression statistics ($\pm$ s.e.)				mean body size ($\pm$ s.e.)	
site	n	slope	intercept	r^2	p	operculum length (mm)	prosoma wet mass (g)
Ross Islets	10	0.137 ± 0.2033	0.942 ± 0.0188	0.054	0.519	3.67 ± 0.079	0.021 ± 0.001
Self Point	10	0.202 ± 0.0972	0.920 ± 0.0138	0.350	0.072	3.75 ± 0.139	0.023 ± 0.002
Wizard Islet	10	0.178 ± 0.0911	0.856 ± 0.0147	0.323	0.087	3.53 ± 0.074	0.028 ± 0.003
Kelp Bay	10	0.288 ± 0.0872	1.032 ± 0.0136	0.577	0.011	3.87 ± 0.187	0.028 ± 0.002
Bordelais Island	10	0.330 ± 0.0443	1.063 ± 0.0086	0.874	< 0.001	4.21 ± 0.173	0.016 ± 0.002
Seppings Island	10	0.334 ± 0.1091	1.055 ± 0.0161	0.539	0.016	3.75 ± 0.176	0.022 ± 0.002

Table 3. *ANCOVA results.*

(Results from the ANCOVA tests for equality of slopes and the statistical significance of the differences in the intercepts between sites. When testing the equality of slopes, the residual degrees of freedom was 48 and the residual mean squares was 3.5–7% larger than tabled here.)

source of variation	d.f.	mean square	F	p
log(ramus length of fourth thoracic leg)				
field site	5	0.03638	22.65	< 0.001
covariate (log(prosoma wet mass))	1	0.08813	54.88	< 0.001
residual	53	0.00161	—	—
equality of slopes	5	0.00038	0.22	0.95
log(ramus length of fifth thoracic leg)				
field site	5	0.05309	34.50	< 0.001
covariate (log(prosoma wet mass))	1	0.08409	54.65	< 0.001
residual	52	0.00154	—	—
equality of slopes	5	0.00044	0.27	0.93
log(ramus length of sixth thoracic leg)				
field site	5	0.06236	40.22	< 0.001
covariate (log(prosoma wet mass))	1	0.07240	46.70	< 0.001
residual	53	0.00155	—	—
equality of slopes	5	0.00104	0.65	0.66

Table 4. *Least-squares linear regression equations for the average log(leg length) (mm) of B. glandula as a function of the average log(water velocity) (m s^{-1}) under breaking waves (data in figure 2).*

(Water velocity is the average maximum daily water velocity recorded over 16 days and leg length is the least-squares mean ramus length from ANCOVA at a common prosoma wet mass of 0.0219 g (*ca.* 3.8 mm operculum length).)

		regression statistics ($\pm$ s.e.)			
trait	n	slope	intercept	r^2	p
leg 4	6	-0.324 ± 0.0349	0.623 ± 0.0081	0.956	< 0.001
leg 5	6	-0.414 ± 0.0187	0.748 ± 0.0043	0.992	< 0.001
leg 6	6	-0.433 ± 0.0161	0.775 ± 0.0037	0.994	< 0.001

sites ($p > 0.6$ for all three legs) (table 3), so we could therefore compute a leg length for a standard-sized barnacle at each site. Legs from the quiet water site were from 55 to 77% longer than those from the most wave-exposed site (tables 2 and 4) for a common prosoma wet mass of 0.0219 g (*ca.* 3.8 mm opercular length). More dramatically, at a very protected site in Grappler Inlet, which is only exposed to weak tidal currents and no ocean swell, the barnacles' feeding legs were 63, 71 and 90% larger than those from the most wave-exposed site (legs 4, 5 and 6, respectively). Legs of similar sized barnacles differed not only in length, but also in stoutness and the length and spacing of setae (figure 1).

(b) *Precision of the variation*

The lengths of the barnacles' feeding legs exhibited surprisingly precise relationships with the maximum water velocities under breaking waves recorded on the adjacent
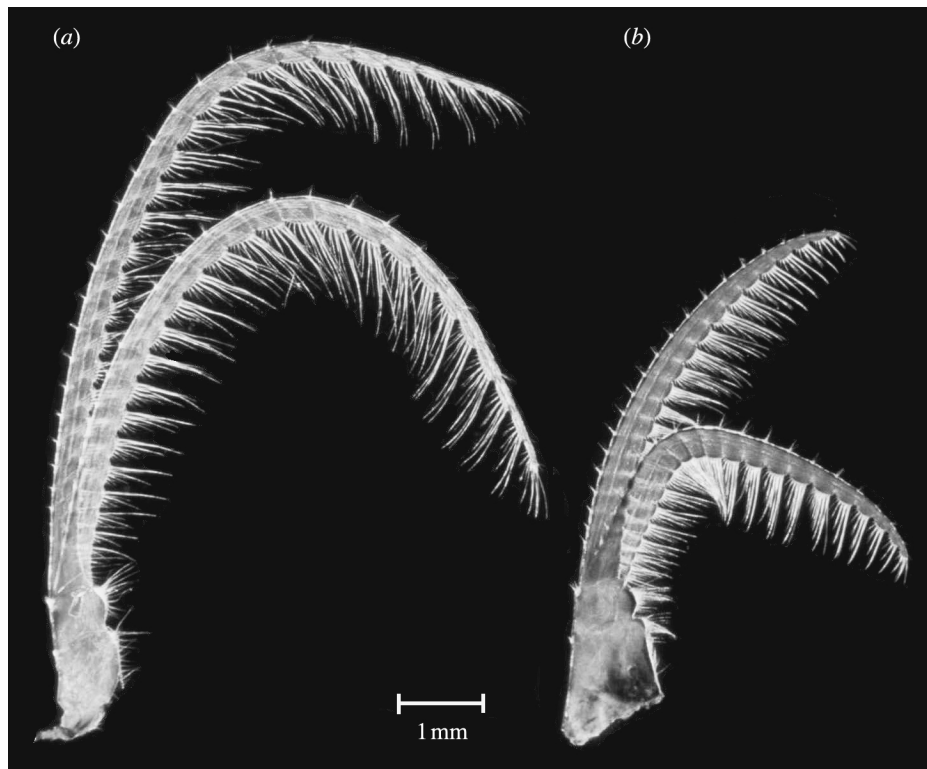
Figure 1. Feeding legs of similar sized barnacles (*B. glandula*) from two sites: (*a*) a protected harbour (Bamfield Inlet) (prosomal wet mass $= 0.059$ g and operculum length $= 6.7$ mm) and (*b*) an exposed outer coast (Seppings Island) (prosomal wet mass $= 0.069$ g and operculum length $= 6.9$ mm), both in Barkley Sound, Vancouver Island, British Columbia, Canada. The sixth (posterior-most) thoracic leg from the left side is shown for each barnacle.
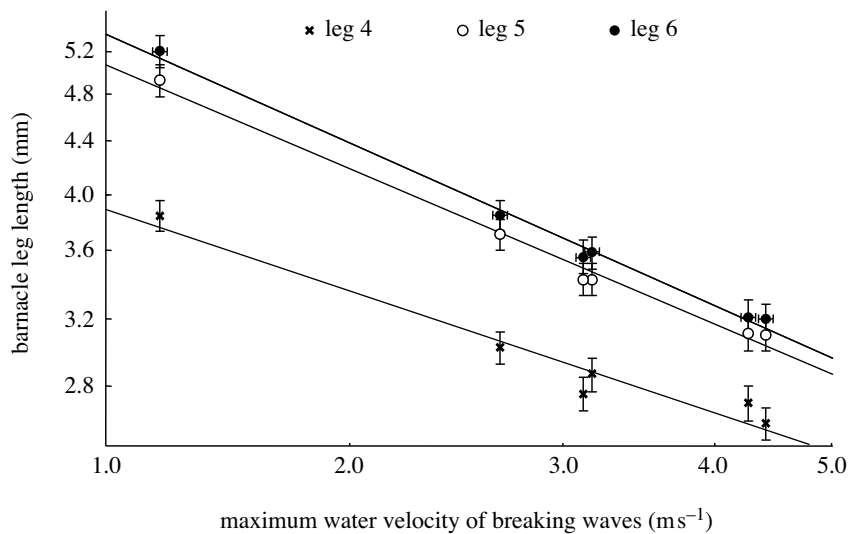

Figure 2. Average length of three feeding legs of *B. glandula* from six sites of differing wave exposure in Barkley Sound, Vancouver Island, British Columbia, Canada (both axes are log scale). Legs 4, 5 and 6 refer to the fourth, fifth and posterior-most (sixth) pair of thoracic legs of balanomorph barnacles. Leg lengths ($n = 10$ per site) were standardized to a common prosoma wet mass of 0.0219 g (*ca.* 3.8 mm opercular length) by ANCOVA. Daily maximum water velocities adjacent to the rock surface were obtained concurrently at high tide for all six sites on 16 days in July and August 2000 and averaged. All points are means $\pm$ s.e.s (error bars for velocity are only shown for leg 6 for clarity). The sites are (left to right) Ross Islets, Self Point, Wizard Islet, Kelp Bay, Bordelais Island and Seppings Island. See table 4 for regression statistics.

rock surface (figure 2). Between 95.6 and 99.4% of the variation in the average leg length among the six sites was explained statistically by variation in the water velocity (table 4). This effect was most pronounced for the posterior-most two legs (legs 5 and 6), but was highly significant for all three: the barnacles' leg length varied in

proportion to velocity at a power of -0.32 to -0.43 depending on the leg (table 4). Similar declines in leg length with increasing wave exposure have been observed in other northeastern Pacific acorn barnacles (*Chthamalus dalli* and, to a lesser extent, in *Semibalanus cariosus*) and in the goose-neck barnacle *Pollicipes polymerus* (K. B.

Marchinko, unpublished observations). J. Truscott (personal communication) has also confirmed that exposed-shore *Semibalanus balanoides* have shorter feeding legs than protected-shore individuals from the coast of Wales.

4. DISCUSSION

(a) *Adaptive significance and predicted pattern*

The highly precise dependence of barnacle leg form on local environmental conditions suggests some rather strict trade-offs between the costs and benefits of different forms (Travis 1994). Presumably, leg length directly affects feeding performance. Longer legs would be able to sieve a larger volume of water per sweep than shorter ones (Crisp & Maclean 1990) and, therefore, be beneficial under quiet water conditions. However, longer legs would be less able to remain erect in a higher velocity flow because the higher drag would cause them to bend downstream or buckle. Because the outcome of competitive interactions between barnacles and the ultimate fecundity of barnacles depends on their growth rate, natural selection should favour those individuals whose leg form is the most effective for feeding under local conditions of water motion.

Because barnacle legs probably experience free stream velocities in the turbulence of breaking waves (Denny 1988), the expected decline in leg length with increasing wave exposure can be predicted from simple hydrodynamics, assuming geometric similarity of the legs. Fluid dynamics theory predicts that, as water velocity increases under conditions of high Reynolds number R_e ($> 10^3$), structure length perpendicular to flow should vary in proportion to velocity to a power of -1 for drag to remain the same. This prediction obtains because the force experienced due to pressure drag is $F_d = 0.5\rho u^2 S_f C_d$, where ρ is seawater density, u is water velocity, S_f is the frontal or projected area in the direction of flow and C_d is the coefficient of drag (Denny 1988). Because ρ is constant and C_d lacks units, $F_d \propto u^2 S_f \propto u^2 l^2$ or $F_d^{0.5} \propto ul$, where l is structure length and structure shape is assumed to remain constant. For drag to remain constant, an increase in u must be matched by a proportional decrease in l. In our study, the observed decline in barnacle leg length (proportional to velocity to a power of -0.3 to -0.4, table 4) was considerably less extreme than the exponent of -1 predicted due to simple scaling.

Three factors might account for why exposed-shore barnacles have proportionally longer legs than predicted from fluid dynamics theory. First, exposed-shore barnacles may alter their timing of leg extension in oscillating flow (Barnes & Reese 1958; Trager *et al.* 1992) in a way that minimizes drag. Second, the sieving setae that extend perpendicularly from the rami are shorter on more wave-exposed shores (figure 1), which would affect the relation between total leg length and drag (i.e. the assumption of geometric similarity is violated). Finally, preliminary results revealed a thicker cuticle in the legs of exposed-shore *B. glandula* (K. B. Marchinko, unpublished observations), so the legs of barnacles from wave-exposed shores are probably more resistant to buckling than those of quiet water barnacles. However, the scaling of leg cuticle thickness to the velocity of breaking waves remains to be determined.

(b) *Precision of plasticity and implications*

The precision with which barnacle leg length varied in response to wave exposure (figure 2) seems remarkable: between 95 and 99% of the variation in their average leg length appears to be explained by wave action. Because individual *B. glandula* can alter the form of their feeding legs in response to water motion (Pentcheff 1995), this may be the most precise example of ecophenotypic fine-tuning of animal form to local environmental conditions yet reported. Leg length in *B. glandula* exhibits noticeable change within one or two moults following transfer to different flow conditions (D. Pentcheff, personal communication), but the precise time-course of the change and the plasticity of adult compared to juvenile barnacles is unknown and currently under study (K. B. Marchinko, unpublished observations).

The decline in barnacle leg length as the velocity of breaking waves increases (figure 2) has three significant implications. First, the striking linearity of this relationship (on log axes) implies that drag forces—even in the complex, oscillating flow of breaking waves (Denny 1994)—and material and structural changes in the feeding legs all vary as simple power functions of wave exposure. Second, since the variation in leg length is largely ecophenotypic (Pentcheff 1995), the close fit of the data to a simple power function implies that the cueing mechanisms and the architectural responses of the barnacles are surprisingly precise.

Third, the precision of this relationship suggests that barnacle leg length may provide a simple and reliable index of relative wave exposure in studies of coastal ecology. Direct measurements of wave exposure are cumbersome or time-consuming to obtain over a wide range of field sites (Denny & Gaines 1990). Indirect correlates have been proposed as indices of wave exposure (Ballantine 1961; Denny 1994), but biological indicators are limited to the geographic area of the original study and abrasion/dissolution indicators cannot be translated into actual wave forces or velocities. *Balanus glandula*, on the other hand, ranges from the Aleutian Islands of Alaska to southern California (Cornwall 1969), and therefore potentially provides a wave exposure meter for most shores of the northeastern Pacific. The circumboreal *S. balanoides* appears to exhibit a similar variation in leg length with wave exposure (J. Truscott, personal communication) and, therefore, it could provide the same tool for North Atlantic and Arctic shores.

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