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Feeding in flow extremes: dependence of cirrus form on wave-exposure in four barnacle species

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Summary

Wave-exposure influences the form of many organisms. Curiously, the impact of flow extremes on feeding structures has received little attention. Barnacles extend feather-like legs to feed, and prior work revealed a highly precise association between leg length and water velocity in one species. To assess the generality of this flow-dependence, we quantified variation in four leg traits (ramus length, ramus diameter, seta length, and intersetal spacing) in four intertidal barnacles (*Balanus glandula, Chthamalus dalli, Semibalanus cariosus, Pollicipes polymerus*) over a wave-exposure gradient in the North-Eastern Pacific. All species exhibited a negative allometric relation between leg length and body mass. Proportionally longer feeding legs may permit smaller barnacles to avoid lower flow and particle flux associated with boundary layers. Although coefficients of allometry did not vary with wave-exposure, form differences among wave-exposures were substantial. Depending on the species, acorn barnacles of the same size from protected shores had feeding legs that were 37–80% longer and 18–25% thinner, and setae that were 36–50% longer and up to 25% more closely spaced, than those from exposed shores. Differences were less pronounced for the gooseneck barnacle, *P. polymerus*. Moreover, *in situ* water velocity explained an impressive percentage of overall leg-length variation: 92% in *B. glandula,* 67% in *C. dalli,* 91% in *S. cariosus,* and 92% in *P. polymerus*. Clearly, both size and shape of barnacle feeding legs respond to local flow conditions. This response appears widespread – across two orders of thoracican barnacles, Pedunculata and Sessilia, and two superfamilies of acorn barnacles (Balanoidea and Chthamaloidea) – and likely adaptive. Longer rami and setae would yield a larger feeding area in low flow, whereas shorter, stouter rami with shorter setae would be less vulnerable to damage in high flow. Finally, the proportionally most variable species was abundant in the widest range of habitats, suggesting that increased plasticity may permit a wider niche breadth.

Key words: allometry, Cirripedia, morphology, phenotypic variation, suspension feeding

Introduction

Flow can have a significant impact on the form, behaviour and distribution of aquatic organisms (Allan, 1995; Wildish and Kristmanson, 1997; Zhang and Malmqvist, 1997; Leonard et al., 1998). In wave-swept environments, flow variation is extreme, with water velocities ranging from 0.05 m/s to well over 10 m/s (Denny, 1988). In response to these extremes, many organisms exhibit conspicuous plasticity of body size and shape. Intertidal snails produce flow-tolerant shells and a larger foot to increase tenacity on wave-exposed shores (Kitching et al., 1966; Trussell, 1997a, b). On wave-exposed shores, barnacles produce shorter feeding legs (Pentcheff, 1995; Arsenault et al., 2001), and shorter, thicker shells that are more resistance to impact (Pentcheff, 1991); mussels have thicker shells and a lower height/width ratio (Seed, 1968; Raubenheimer and Cook, 1990; Akester and Martel, 2000); and sponges, hydrozoans, hexacorals and octocorals all exhibit a more compact body shape (Patterson, 1980; Kaandorp, 1999).
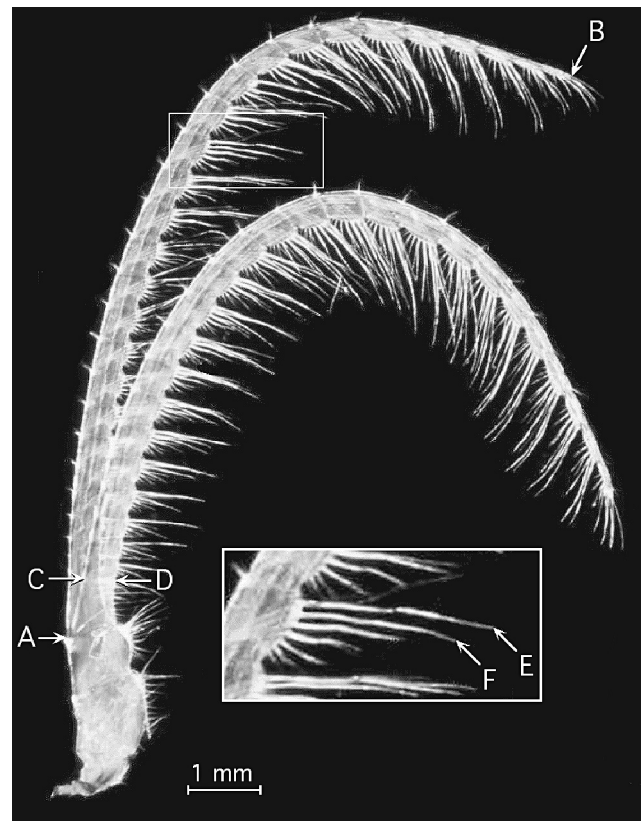
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Many intertidal invertebrates rely on ambient flow to bring them food. This creates two problems. First, a feeding structure must be strong enough to withstand extreme flow conditions, yet fine enough to capture food effectively. Second, flow may affect growth rate by influencing the rate of food supply or feeding efficiency (Okamura, 1992). On wave-exposed shores, barnacles grow more rapidly (Crisp and Bourget, 1985; Sanford et al., 1994; Sanford and Menge, 2001), whereas bryozoans (Okamura, 1992) and sponges (Palumbi, 1986) grow more slowly. In mussels, the effects of wave-exposure appear species-dependent (Seed, 1968; McQuaid and Lindsay, 2000). Higher growth rates on wave-exposed shores likely result from an increased flux of food particles, due to higher velocities and to greater turbulent mixing (Fréchette et al., 1989). However, an optimal flow for feeding and growth likely exists for many species, where feeding and growth are suppressed when flow is too fast or too slow (Eckman and Duggins, 1993; Okamura and Partridge, 1999). Curiously, although wave-exposure affects body size, shape, and growth rate in many species, surprisingly little is known about how flow affects the form of suspension feeding structures (Okamura and Partridge, 1999).

Maintaining feeding performance under different flow conditions is a challenge for suspension feeders. Both flow velocity and the size and shape of feeding structures may affect feeding performance (Cheer and Koehl, 1987). As a consequence, behavioural and morphological adaptations have arisen to maintain feeding performance under different flow conditions. For example, barnacles, anemones, phoronids, and articulate brachiopods modify either body position or position of feeding structures (Barnes and Reese, 1960; Emig and Becherini, 1970; Koehl, 1977; LaBarbera, 1977; Trager et al., 1990), whereas gorgonian sea fans and scleractinian corals alter colony form, in response to differences in the direction and velocity of water flow (Leversee, 1976; Helmuth and Sebens, 1993). By re-orienting feeding structures or the entire body, these animals likely enhance the rate of feeding while reducing hydrodynamic forces (Wildish and Kristmanson, 1997).

Feeding structure form may also vary with flow conditions. Bryozoan lophophores are smaller in diameter and have fewer tentacles under higher flow conditions (Okamura and Partridge, 1999). The primary labral fan of black flies has fewer rays and a smaller feeding area in higher velocity streams (Zhang and Malmqvist, 1997). Finally, overall leg length varies with wave-exposure in one barnacle species (Pentcheff, 1995; Arsenault et al., 2001). However, the response of other features of the feeding fan, and the extent of this response in other species, is unknown. Therefore, we examined variation in both the size and shape of feeding legs over a wave-exposure gradient in four morphologically and phylogenetically distinct species of northeastern Pacific barnacles.

Barnacles feed by extending feather-like legs (cirri) into ambient flow to capture small particles and plankton, although a few species capture larger prey (Howard and Scott, 1959; Jones, 1968). In very low flow barnacles may actively sweep-feed (Trager et al., 1990). Six pairs of biramous cirri (Fig. 1) make up the feeding net. Each ramus, or branch, of a cirrus has many segments and each segment bears four to seven pairs of evenly spaced setae. Because changes in flow regime, and the size and spacing of filtering elements, affect feeding performance of suspension feeders (Cheer and Koehl, 1987), both the size of a ramus, and the length and spacing of setae, may affect the ability of barnacles to feed under different flow conditions.

Barnacles are ideal organisms for studying how flow environment influences feeding structure form. They are sessile, and they settle and grow under wide a range of environmental conditions. As a consequence, they exhibit considerable lability of form. Crowding induces

Fig. 1. A single, biramus cirrus of *Balanus glandula* showing the four traits measured: *ramus length*- the curvilinear distance along the dorsal margin from the base to the tip, excluding the terminal seta (from A to B); *ramus diameter*- diameter of the ramus at the suture between the first and second articles, linear distance from C to D; *seta length*- length of the longest seta (E); *intersetal space*- distance between the two longest setae measured at the base of setae E and F. Modified from Fig. 1 of Arsenault et al. (2001).

longer, narrower shells in many species (Crisp and Bourget, 1985), contact with a predatory snail induces 'bent' shells in *Chthamalus anisopoma* (Lively, 1986*a, b*), and higher salinity promotes a squatter shape in *Semibalanus balanoides* (Barnes and Barnes, 1962). A long period of larval dispersal (Strathmann, 1987) and low among-population genetic heterogeneity (Hedgecock, 1986; Brown et al., 2001) suggest morphological changes with wave exposure are not likely complicated by local genetic differentiation. Finally, all barnacles must grow from a newly settled cyprid into an adult at the spot where they attach initially, so the ontogeny of form may be monitored in individual barnacles under different flow regimes (Marchinko, 2003).

We examined three aspects of wave-exposure dependence of feeding leg form: 1) variation in the relative size and shape of feeding legs (ramus length, ramus diameter, seta length, intersetal spacing), 2) body-size dependence (allometry) of leg size and shape, and 3) magnitude and similarity of variation among four co-occurring species.

Materials and methods

Study sites

Barnacles were collected from three exposure regimes along a wave-exposure gradient in Barkley Sound, Vancouver Island, British Columbia, Canada (Table 1). These sites ranged from sheltered inlets that experienced only weak tidal currents to shores fully exposed to open Pacific swell. Two replicate populations of each species were sampled under each exposure regime. A third population was sampled from the sheltered regime for a total of seven populations.

Water velocity measurements

The maximum water velocity under breaking waves for the four more exposed sites (Kelp Bay, Self Point, Bordelais Island and Sepping's Island) were from Arsenault et al. (2001). Velocities were recorded with two mechanical transducers (Carrington Bell and Denny, 1994) per site and deployed concurrently over 16 days in July and August 2000. These 16 velocities were averaged to yield a single 'average maximum velocity' for each of these sites (see Arsenault et al., 2001 for details). Maximum water velocities at the three sheltered sites were too slow to be recorded using mechanical transducers and were obtained using an Acoustic Doppler Velocimeter (SonTek/YSI Inc. 10-MHz ADV). Velocities were recorded in the lower section of the *B. glandula* zone on six days between May 9 and June 5, 2001. Five of the six sampling days fell within two days of spring tides and sampling times were between one and two hours before or after slack tide, so these measurements provided reasonable estimates of maximum tidal-current velocity. The ADV probe was placed 5 cm above the substrate and instantaneous velocity was recorded at a sampling rate of 25 Hz for five minutes in the x, y, and z dimensions. Each sampling day a single value of velocity for each

Table 1. Collection site descriptions.

Wave exposure	Site Name	Location description and species sampled	North latitude	West longitude	Water velocity m/s*
Sheltered	Grappler Narrows	East-facing shore of Grappler Inlet narrows *Balanus glandula, Semibalanus cariosus*	48°49′94″	125°07′07″	0.0052
	Grappler Mouth	West-facing shore at mouth of Grappler Inlet *B. glandula, Chthamalus dalli*	48°49′91″	125°07′65″	0.0066
	Bamfield Inlet	West-facing shore of Bamfield Inlet near mouth *B. glandula, C. dalli, S. cariosus*	48°50′06″	125°08′20″	0.0123
Intermediate	Self Point[1]	South-facing shore on southeastern point of Helby Is. *B. glandula, C. dalli, S. cariosus, Pollicipes polymerus*	48°50′90″	125°09′70″	2.66
	Kelp Bay[1]	South-facing shore on north end of Kelp Bay *B. glandula, C. dalli, S. cariosus, P. polymerus*	48°51′82″	125°06′35″	3.17
Exposed	Bordelais Island[1]	South-facing shore on southwestern point *B. glandula, C. dalli, S. cariosus, P. polymerus*	48°49′03″	125°13′90″	4.26
	Seppings Island[1]	Southwest -facing shore, gentlest slope of sites *B. glandula, C. dalli, S. cariosus, P. polymerus*	48°50′50″	125°12′50″	4.41

[1] Site descriptions from Arsenault et al 2001.
*Sustained velocity of tidal current (sheltered), or average maximum velocity of breaking waves (intermediate and fully exposed).

site was calculated as the mean of individual velocities $(u^2 + v^2 + w^2)^{1/2}$, where u, v, and w represent velocity in the x, y, and z direction (Okamura and Partridge, 1999). These single velocities were then averaged over the six sampling days to obtain the single value of water velocity for each sheltered site (Table 1).

Although the type of velocity measurement differed between the sheltered regime and the two wave-exposed regimes, both provide reasonable estimates of the maximum velocities barnacles were likely to experience during the summer months at these sites. However, even if flow was around 1 m/s at the sheltered sites, the conclusions we report here on the relationship between water velocity and cirrus form would not be altered significantly. For example, increasing flow by 1 m/s in all sheltered sites increased the slope of the relationship between ramus length and water velocity for *B. glandula* by only 23%. The difference between this slope and the original slope was non-significant (one-way ANCOVA, *P* (equality of slopes) = 0.25).

Study species

We examined four sympatric species of intertidal barnacles: three balanomorph (acorn) barnacles, *Balanus glandula* Darwin, *Chthamalus dalli* (Pilsbry), *Semibalanus cariosus* (Pallas), and one pedunculate (gooseneck) barnacle, *Pollicipes polymerus* (Sowerby). Although *Semibalanus balanoides* may occur in British Columbia and may sometimes be confused with *B. glandula*, no *S. balanoides* were encountered in this study. We focused on the posterior three cirri because these extend furthest from the shell and are used primarily for food capture. The three anterior cirri are shorter and scrape food off the posterior cirri towards the mouth (Anderson and Southward, 1987). All three acorn barnacles were found over the entire wave-exposure gradient. *Pollicipes,* however, was absent from shores lacking wave action.

Collection and measurement of barnacles

For each species, 10 solitary individuals, representing at least a four-fold range in body size (Digital Appendix 1), were collected in the lower one-third of their respective vertical zone at each site. Barnacles from Kelp Bay, Self Point, Bordelais Is. and Sepping's Is. were collected in the area immediately adjacent to the location of wave-force transducers. Transducers were located in the upper third of the *S. cariosus* zone. Barnacles were collected in August and early September 2000, within 18 days of the last wave-force measurement (Arsenault et al., 2001).

To measure body size, the soft tissue (prosoma) – excluding egg masses and opercular plates – was removed from the shell, blotted dry for 20 seconds on a dry

Kimwipe® EX-L (Kimberley-Clark®), and weighed to the nearest 0.1 mg (prosomal wet mass). Although solitary individuals should not exhibit the effects of crowding, shell measurements were not used to describe body size because shell form is so plastic (Crisp and Bourget, 1985; Lively, 1986*a, b*). The posterior three cirri (legs 4, 5 and 6) were dissected from the left side of the prosoma and mounted in seawater on a microscope slide. As barnacles are bilaterally symmetrical, we assumed measurements from the left side were representative of both sides. We measured four traits on each cirrus (Fig. 1): ramus length – curvilinear distance traced from base to tip on the dorsal side of the ramus, ramus diameter – distance between the dorsal and ventral side of the first (basal) segment, maximum seta length – length of the longest seta on mid-leg segments, and intersetal space – length of the space between the two longest adjacent setae on mid-leg segments. To obtain a single value of ramus length and ramus diameter for each cirrus, values from both the endo- and exopodite were averaged. To obtain a single value of seta length and intersetal space for each cirrus, we took the average value from three middle segments of the endopodite. All traits were measured at 25–50× magnification using a dissecting scope mounted with a camera lucida, and a digitizing tablet with a precision of 20 dots/mm.

Statistical analyses

Where error exists in both X and Y variables, reduced-major-axis (RMA) regression is often recommended over ordinary-least-squares (OLS) regression when describing scaling relationships, because error associated with the X-axis consistently biases the OLS slope downwards (McArdle, 1988; LaBarbera, 1989). However, we examined the slopes of four independent traits, each regressed on body mass. Because the covariate was the same for all four traits, and because Analysis of Covariance (ANCOVA) methods for model II regression are not well developed, OLS regression and ANCOVA (StatView 5.0, 1998 SAS Institute Inc., Cary, NC; SuperANOVA 1.11, Abacus Concepts, Inc., Berkeley, CA) were used to describe and test for differences in the relationships of cirral dimensions to body mass and water velocity.

Allometry

Cirral traits and body size were log10 transformed to linearize relations between variables and to meet assumptions of ANCOVA. Body size (prosomal wet mass) was used as the covariate in all allometric analyses. A one-factor ANCOVA (main effect = population) tested for differences in the dependence of cirral characters on body mass among populations from habitats of different wave-exposure. Two-factor AN-

COVA (main effects = species and population) was used to test for differences in these relationships among species. Only the sites where all four species co-occurred (Self Pt., Kelp Bay, Bordelais Is., and Sepping's Is.) were used in interspecific comparisons. Departures from isometry (expected slope of 0.333) were tested with a one-sample t-test. Where conclusions about statistical significance might have been confounded by conducting multiple tests, significance levels were also assessed by a sequential Bonferroni test (Rice, 1989).

Wave-exposure and cirrus form

To remove body-size effects, the least-squares mean of each cirral trait for a standard body mass was calculated for each site and each species using ANCOVA (slopes were assumed to be equal if slope differences were not significant). These least-squares means were then regressed on water velocity. The standard prosomal wet mass used for each species reflected the average body
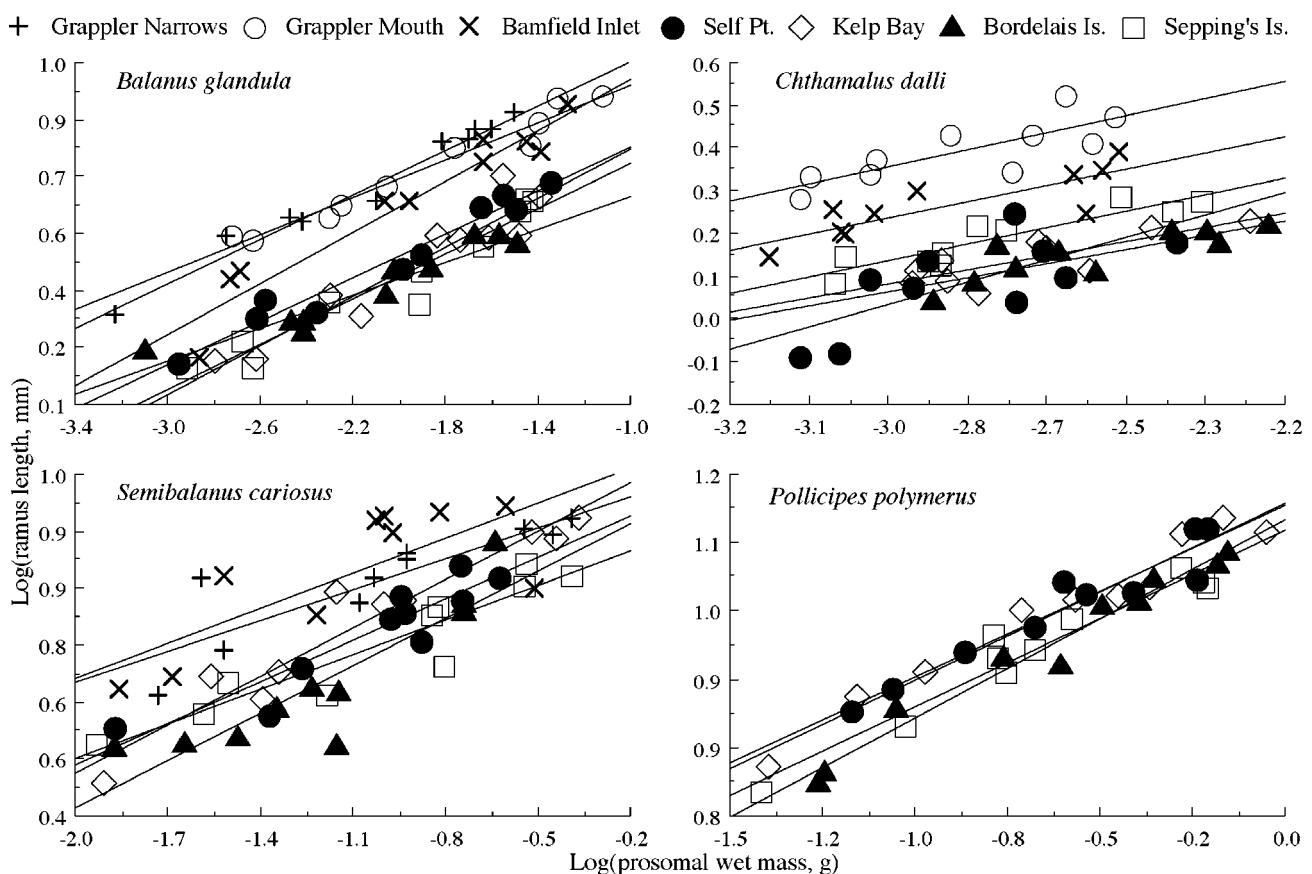
size of that species: 0.0096 g for *B. glandula*, 0.0018 g for *C. dalli*, 0.084 g for *S. cariosus*, and 0.23 g for *P. polymerus*. A one-factor ANCOVA (main effect = leg number) tested whether the relation between water velocity and cirral dimensions varied among the three cirri. Again, cirral traits were $\log_{10}$ transformed to meet assumptions of ANCOVA; however, the covariate, water velocity, was not transformed. A one-factor ANCOVA (main effect = species) was also used to test for differences in the dependence of cirral dimensions on water velocity among species.

Results

Scaling of cirral traits with body mass
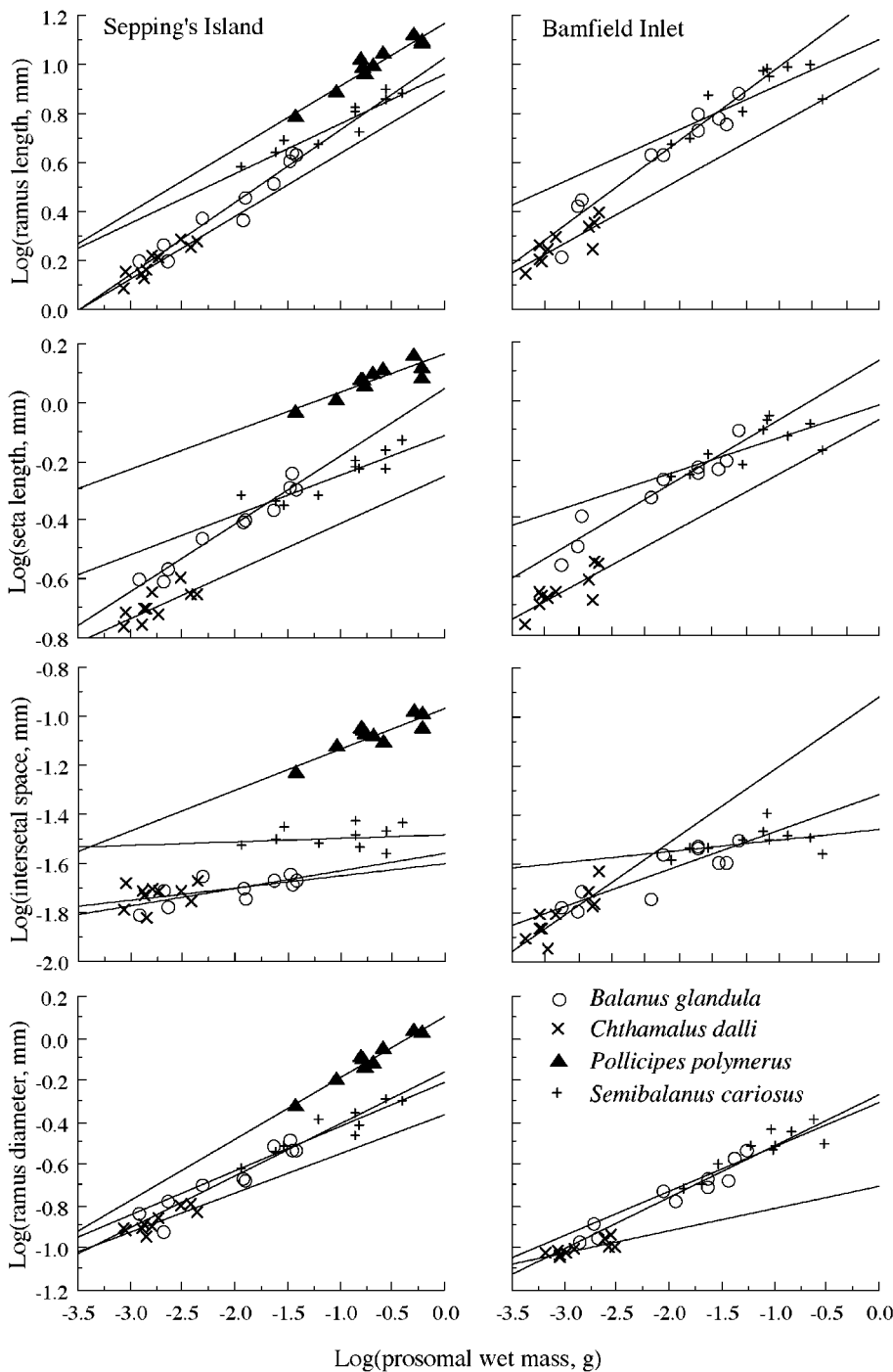
Intra-specific comparisons

All four cirral dimensions increased with increasing body mass in all four species (Figs. 2 and 3). This rela-

Fig. 2. Log-log relationships of leg 6 length versus body mass for four species of intertidal barnacle from different sites in Barkley Sound, British Columbia, Canada. Sites are listed, from left to right, in order of increasing wave exposure. Each point represents an individual barnacle (n = 10 for each species). Differences in slope among populations were non-significant when corrected for multiple tests ($P > 0.11$, Table 2). The relationships of seta length, intersetal space, and ramus diameter to prosomal wet mass exhibited similar patterns for each species and for legs 4 and 5 (see Digital Appendices 1 and 2).

tionship held true for all three feeding legs (legs 4, 5 and 6) at all sites, as observed previously for ramus length (Crisp and MacLean, 1990; Arsenault et al., 2001). This relationship was significant for each trait ($P < 0.05$) in 245 of 278 OLS regressions (Digital Appendix 1). Only setae length in one population of *C. dalli* and the intersetal space in four populations of *C. dalli* and *S. cariosus* were consistently non-signifi-

cant. However, for each species, body mass was a significant covariate ($P < 0.01$) for ramus length (Table 2), and all remaining cirral traits (Digital Appendix 3), when all populations were analyzed concurrently.

Within each species, the slopes of cirral dimensions versus body mass did not differ significantly among populations ($P > 0.05$) for ramus length (Table 2), seta length, intersetal space, or ramus diameter (Digital Ap-

Fig. 3. Cirral trait variation of leg 6 as a function of body mass for four barnacle species: *Balanus glandula*, *Chthamalus dalli*, *Semibalanus cariosus*, and *Pollicipes polymerus*. Each point represents and single individual (n = 10 for each species). Only one wave-exposed (Sepping's Is.) and one sheltered site (Bamfield Inlet) is shown for clarity. Differences in slopes among species were non-significant ($P > 0.11$) for ramus and seta length, while the slope of ramus diameter and the intersetal space to body mass differed significantly among species ($P < 0.013$, Table 4). See Digital Appendix 1 for OLS statistics for each trait in each population.

Table 2. Results from ANCOVA testing for differences in trait means and equality of slopes of the relationship between length of leg 6 and prosomal wet mass among populations of four barnacle species, *Balanus glandula*, *Chthamalus dalli*, *Semibalanus cariosus*, and *Pollicipes polymerus*. Populations of each species were from habitats differing in wave exposure (see Table 1). All data were $\log_{10}$-transformed.

Source of variation	*Balanus glandula*			*Chthamalus dalli*			*Semibalanus cariosus*			*Pollicipes polymerus*		
	df	MS	*P*	df	MS	*P*	df	MS	*P*	df	MS	*P*
Population	6	0.149	<0.001	5	0.147	<0.001	5	0.042	<0.001	3	0.006	<0.001
Log(wet mass)	1	1.584	<0.001	1	0.192	<0.001	1	0.597	<0.001	1	0.400	<0.001
Error	62	0.002		53	0.002		53	0.003		35	0.001	
Equality of slopes[1]	6	0.005	0.0362[2]	5	0.001	0.8289	5	0.004	0.3227	3	0.0004	0.5831

[1] When testing for equality of slopes, the error degrees of freedom were 56 for *B. glandula*, 48 for *C. dalli* and *S. cariosus*, and 32 for *P. polymerus*, and the error MS were 1.7–13.8% larger than tabled here.

[2] Interaction became non-significant (P = 0.11) after Sequential Bonferroni correction (3 legs = 3 tests for each species)

pendix 3) when corrected for multiple tests. So for each species, a common scaling coefficient was calculated for each trait using ANCOVA (Table 3). Cirral traits exhibited negative allometry for each species in all but one case ($P < 0.01$, Table 3). However, the extent of negative allometry differed among traits. Seta length and intersetal space tended to exhibit the strongest neg-

ative allometry whereas ramus length and diameter tended to exhibit weaker negative allometries (the principal exception to this pattern was *C. dalli*).

Bonferroni-Dunn tests for multiple comparisons revealed that, for a standard wet mass, sheltered populations had consistently and significantly longer rami ($P < 0.002$), longer setae ($P < 0.003$), and narrower

Table 3. Common slopes of the dimensions of leg 6 with prosomal wet mass for each species. Slopes for each species were obtained from ANCOVA on log-transformed data (Tables 2 and 4). Regressions for each population are in Digital Appendix 1. OLS Slopes were tested against an isometric slope of 0.333 using a one-sample Student's *t*-test (t_{allom}).

Species	Slope (SE)	Intercept (SE)	r	df	t_{allom}	
log (ramus length) vs. log (prosomal wet mass) (Figs. 1 and 2)						
Balanus glandula	0.287 (0.011)	1.123 (0.022)	0.975	69	4.152	***
Chthamalus dalli	0.261 (0.028)	0.919 (0.077)	0.935	59	2.550	NS
Semibalanus cariosus	0.230 (0.016)	1.036 (0.019)	0.916	59	6.385	***
Pollicipes polymerus	0.266 (0.010)	1.192 (0.008)	0.976	39	6.618	***
log (seta length) vs. log (prosomal wet mass) (Fig. 2)						
B. glandula	0.204 (0.009)	0.062 (0.018)	0.969	69	14.232	***
C. dalli	0.193 (0.027)	–0.152 (0.074)	0.875	59	5.143	***
S. cariosus	0.145 (0.012)	–0.070 (0.014)	0.912	59	15.538	***
P. polymerus	0.159 (0.013)	0.186 (0.010)	0.918	39	13.220	***
log (intersetal space) vs. log (prosomal wet mass) (Fig. 2)						
B. glandula	0.146 (0.014)	–1.377 (0.028)	0.842	69	13.263	***
C. dalli	0.181 (0.042)	–1.289 (0.116)	0.637	59	3.589	***
S. cariosus	0.071 (0.018)	–1.456 (0.021)	0.797	59	14.436	***
P. polymerus	0.183 (0.014)	–0.964 (0.010)	0.918	39	10.583	***
log (ramus diameter) vs. log (prosomal wet mass) (Fig. 2)						
B. glandula	0.231 (0.009)	–0.237 (0.019)	0.961	69	11.253	***
C. dalli	0.174 (0.024)	–0.454 (0.067)	0.869	59	6.570	***
S. cariosus	0.233 (0.014)	–0.216 (0.014)	0.926	59	7.084	***
P. polymerus	0.297 (0.012)	0.084 (0.009)	0.972	39	2.963	**

$**P < 0.01$, $***P < 0.001$, NS = non-significant.

Table 4. Results from 2-factor ANCOVA testing for equality of slopes of the relationship of the cirral dimensions of leg 6 to prosomal wet mass among the barnacle species: *Balanus glandula, Chthamalus dalli, Semibalanus cariosus*, and *Pollicipes polymerus* (see Fig. 3). Analyses were performed on log-transformed data and included only the four most wave-exposed sites, Self Point, Kelp Bay, Bordelais Island and Sepping's Island.

Source of variation[1]	df	Ramus length MS	Ramus length P	Seta length MS	Seta length P	Intersetal space MS	Intersetal space P	Ramus diameter MS	Ramus diameter P
Species (spp)	3	0.0476	<0.001 ***	0.1015	<0.001 ***	0.3616	<0.001 ***	0.1120	<0.001 ***
Population (pop)	3	0.0030	0.182	0.0002	0.948	0.0023	0.536	0.0007	0.702
Log(wet mass. g) (wm)	1	1.1298	<0.001 ***	0.5147	<0.001 ***	0.2724	<0.001 ***	0.9549	<0.001 ***
spp × pop	9	0.0024	0.211	0.0012	0.662	0.0084	0.008 **	0.0014	0.465
spp × wm	3	0.0012	0.583	0.0034	0.106	0.0119	0.013 *	0.0069	0.004 **
pop × wm	3	0.0009	0.687	0.0006	0.796	0.0080	0.064	0.0014	0.430
spp × pop × wm	9	0.0027	0.171	0.0018	0.380	0.0033	0.428	0.0016	0.385
Error	128	0.0018		0.0016		0.0032		0.0015	

$*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

[1] Main effects are not considered meaningful in these analyses. Differences among species reflect differences in body size and differences among populations are tested within species (Table 2, Digital Appendix 3).

ramus diameters ($P < 0.003$) than populations from intermediate and wave exposed habitats (Table 2; Fig. 2; Digital Appendix 3). Ramus diameter of *P. polymerus* did not vary significantly among populations, however, because only intermediate and exposed sites were sampled for this species.

Inter-specific comparisons

All four species showed similar allometries in ramus length and seta length (Fig. 3, Table 3; P > 0.11, Table 4). The allometry of both intersetal space and ramus diameter, however, differed significantly among species (P < 0.013, Table 4). The large, low-shore *S. cariosus* exhibited the strongest negative allometry in intersetal spacing whereas the diminutive, mid- and high-shore *C. dalli* exhibited the strongest negative allometry in ramus diameter. Nonetheless, regardless of species or site, all cirral traits exhibited a consistent negative allometry with body mass (Table 3; Digital Appendix 1).

Dependence cirrus form on wave-exposure

Curiously, cirral trait allometries did not differ significantly among populations (Table 2; Digital Appendix 3). Therefore, predicted cirral dimensions could be calculated for a standard sized barnacle of each species (see methods) to determine how they varied as a function of wave-exposure. Percentage differences were computed as the total difference between the site of lowest water velocity (0.0066 m/s) and the site of highest velocity (4.41 m/s, Table 1); according to the regression equation for each species (Digital Appendix 2a and b).
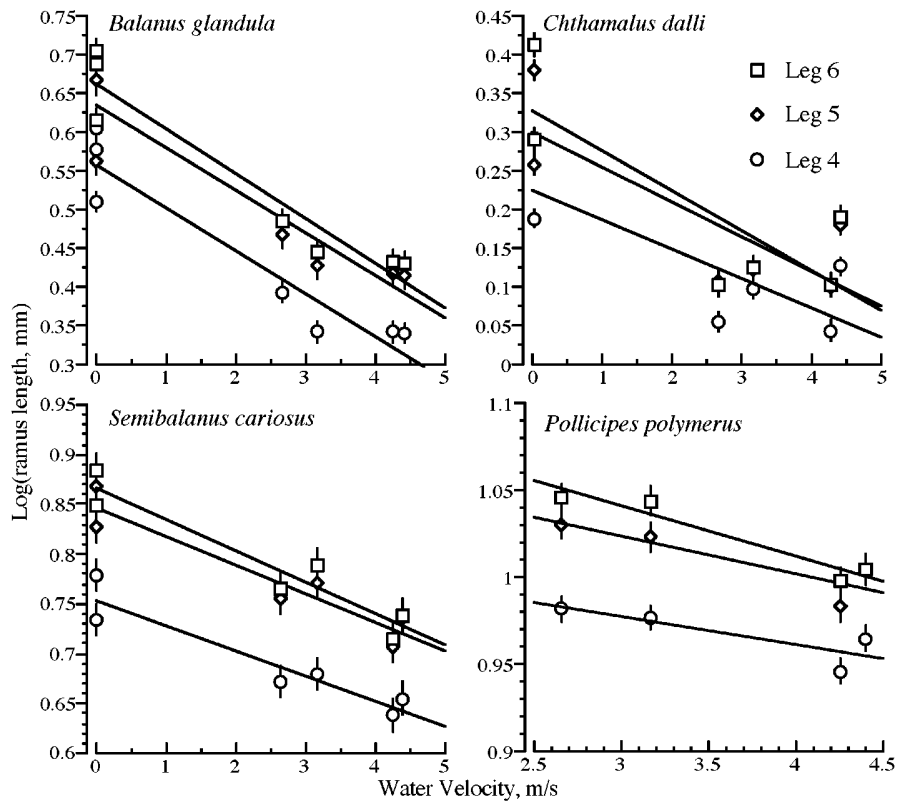
Ramus length

In each species, populations experiencing lower water velocities exhibited longer rami than populations from higher velocity habitats (Figs. 4 and 5a), as reported previously for *B. glandula* (Pentcheff, 1995; Arsenault et al., 2001). Ramus lengths of legs 4, 5 and 6 of B. glandula were 75–80% longer in the sheltered habitat compared to the most wave-exposed habitat (Fig. 4). Significant, though less dramatic, differences in ramus length were observed between these extreme sites in both *C. dalli* (47–68% longer) and *S. cariosus* (29–37% longer) (Fig. 4), and between habitats of intermediate (2.66 m/s) and high wave-exposure (4.41 m/s) in the gooseneck barnacle *P. polymerus* (7–12% longer). OLS regressions revealed a highly significant dependence of ramus length on water velocity (P < 0.005) that was also quite precise (r^2 varied from 0.89–0.92) for legs 4, 5 and 6 of *B. glandula* and *S. cariosus* (Digital Appendix 2a). For *C. dalli* and *P. polymerus* this relationship was only significant statistically for leg 6; however, the slopes did not differ significantly among legs 4, 5 and 6 for any species (Table 5).
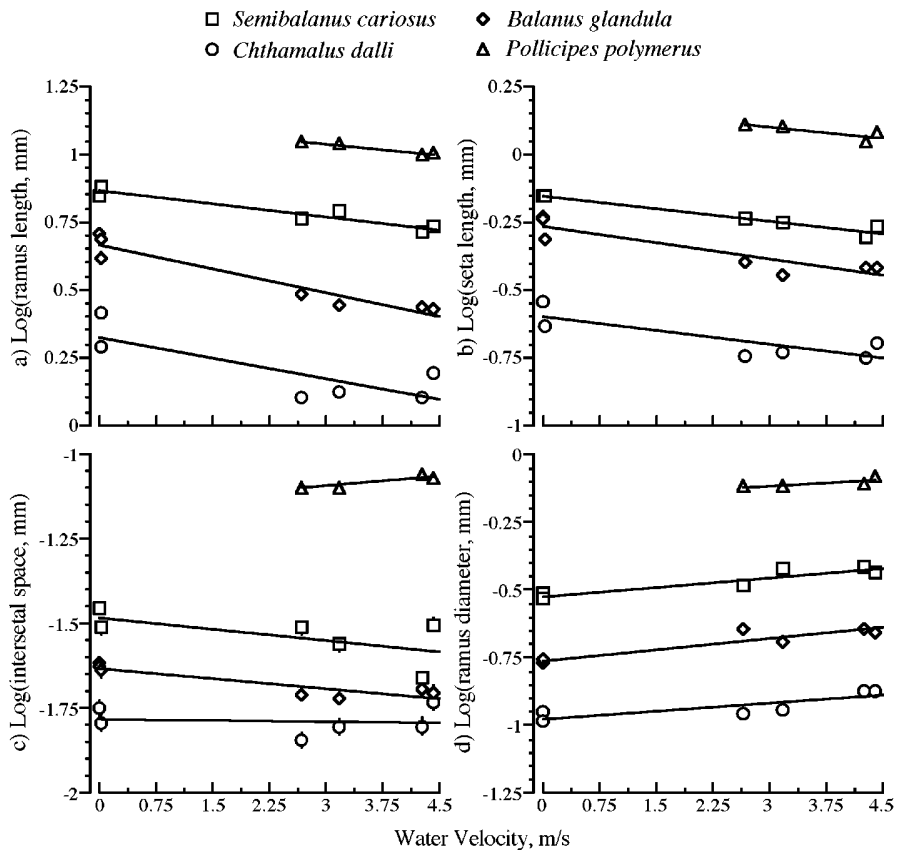
Seta length

Barnacles from quiet-water habitats tended to posses longer setae than those from wave-exposed shores (Fig. 5b). Between the two most extreme sites (Grappler Inlet, Sepping's Is.), setae of leg 6 were 50% longer in *B. glandula*, 41% longer for *C. dalli*, and 36% longer for *S. cariosus*. *Pollicipes polymerus* from intermediate wave-exposure had setae 11% longer than those from highly wave-exposed shores. The increase in seta length with decreasing water velocity was sig-

Fig. 4. Average length of the posterior three feeding legs (legs 4, 5, 6) for a standard-sized barnacle as a function of water velocity (Table 1). Each point represents the least-squares mean leg length (±SE) of 10 individuals from one of seven sites in Barkley Sound, British Columbia, Canada. Standard log10 (prosomal wet mass, g) for *B. glandula* was −2.017 (SE, 0.064), *C. dalli* −2.741 (0.031), *S. cariosus* −1.074 (0.057), *P. polymerus* −0.635 (0.060). The slopes of these relationships did not differ significantly among legs 4, 5 and 6 in any species ($P > 0.5$, Table 5). See Digital Appendix 2a for OLS statistics for these relationships.

Fig. 5. Least-squares mean trait dimension of leg 6 for a standard sized barnacle (see Fig. 4 legend) as a function of water velocity (Table 1). Each point represents the least-squares mean (±SE) for 10 individuals. Where error bars are absent they are less than the symbol size. The slope of these relationships did not differ significantly among species ($P > 0.33$, Table 6). See Digital Appendix 2b for OLS statistics for these relationships.

Table 5. Results from ANCOVA testing for equality of slopes and differences in intercept between legs 4, 5 and 6 for the relationship of leg length at a standard body mass to water velocity in *Balanus glandula, Chthamalus dalli, Semibalanus cariosus*, and *Pollicipes polymerus* (see Fig. 4 for sample means)

Source of variation	Balanus glandula			Chthamalus dalli			Semibalanus cariosus			Pollicipes polymerus		
	df	MS	*P*	df	MS	*P*	df	MS	*P*	df	MS	*P*
Leg number	2	0.019	<0.001	2	0.008	0.202	2	0.017	<0.001	2	0.003	<0.001
Water velocity	1	0.231	<0.001	1	0.118	<0.001	1	0.048	<0.001	1	0.003	<0.001
Error	17	0.002		14	0.005		14	0.0004		8	0.0001	
Equality of slopes[1]	2	0.00007	0.962	2	0.001	0.846	2	0.0002	0.671	2	0.00007	0.501

[1] When testing for equality of slopes, the error degrees of freedom were 15 for *B. glandula*, 12 for *C. dalli*, 12 for *S. cariosus*, and 6 for *P. polymerus*. The error mean squares were 1.3–13.4% larger than tabled here.

Table 6. Results from ANCOVA testing for equality of slopes and differences in intercept among barnacle species for the log-linear relationship of the dimensions of leg 6 to water velocity.

Source of variation	Ramus length			Seta length			Ramus diameter		
	df	MS	*P*	MS	*P*	MS	*P*	MS	*P*
Species	3	0.677	<0.001	0.525	<0.001	0.536	<0.001		
Water velocity	1	0.147	<0.001	0.080	<0.001	0.037	<0.001		
Error	18	0.002		0.001		0.0005			
Equality of slopes[1]	3	0.003	0.33	0.0004	0.83	0.0003	0.68		

[1] When testing for equality of slopes, the error degrees of freedom were 15 and the error mean squares were 4.3–13.3% larger than tabled here.

nificant for *B. glandula* (*P* = 0.005), *S. cariosus* (*P* = 0.001) and *C. dalli* (*P* = 0.048), but not for *P. polymerus* (*P* = 0.14; Digital Appendix 2b).

Intersetal space

The intersetal space only increased significantly with decreasing water velocity in *B. glandula* (*P* = 0.006; Digital Appendix 2b). On leg 6, it was 21% greater at the most protected compared to the most exposed site (Fig. 5c). *S. cariosus* exhibited a similar difference between these two sites (25%), whereas the intersetal space of *C. dalli* increased by only 2%, however neither increase was significant (*P* = 0.19). In contrast, the intersetal space declined by 8% from the most exposed to intermediately exposed site in *P. polymerus*, but this decline was not statistically significant (*P* > 0.08; Digital Appendix 2b).

Ramus diameter

Ramus diameter declined with decreasing water velocity in all four species, and this decline was significant for the three acorn barnacles (*B. glandula, C. dalli*, and *S. cariosus*; *P* < 0.03), but not for *P. polymerus* (*P* = 0.20; Digital Appendix 2b). For leg 6, ramus diameter was 25% smaller for *B. glandula* from the most protected site compared to the most wave-exposed site

(Fig. 5d). This difference was similar, though less pronounced, for *C. dalli* (18%), *S. cariosus* (21%) and *P. polymerus* (6%).

Inter-specific variation in cirrus form with wave-exposure

All four species exhibited strikingly similar changes in cirrus form (except the intersetal space; Fig. 5c; Digital Appendix 2b): as water velocity increased among sites, ramus length and seta length decreased, whereas ramus diameter increased (Fig. 5). In addition, the slopes of these relationships did not differ significantly among species (*P* > 0.33, Table 6).

Discussion

Taxonomic breadth of wave-dependent variation

Wave-exposure dependent variation in feeding leg form appears to be taxonomically widespread in barnacles. All four species we examined exhibited similar, significant variation, including representatives from two free-living orders of thoracican barnacles – Pedunculata (gooseneck barnacles) and Sessilia (acorn barnacles) – and from two of the three superfamilies of intertidal

acorn barnacles (Balanoidea and Chthamaloidea; Newman and Ross, 1976; Newman, 1987). Similar variation has now also been observed in one member of the superfamily Coronuloidea (*Tetraclita rubescens*), and in one additional balanoid barnacle (*Semibalanus balanoides*; K. B. Marchinko et al., unpublished), suggesting dramatic intraspecific variation in feeding leg form like that reported here may be universal in intertidal barnacles.

Somewhat surprisingly, this conspicuous intraspecific variation occurs even in species with quite different feeding modes. Gooseneck barnacles like *Pollicipes* feed primarily on microinvertebrates dislodged by the breaking waves themselves, so they are completely at the mercy of wave action for food (Barnes and Reese, 1960). In contrast, acorn barnacles like *Balanus*, *Semibalanus* and *Chthamalus* feed largely on plankton suspended in the water, so, although wave action may increase the rate of food supply, acorn barnacles do not depend on wave action for food (Trager et al., 1990). The similar morphological responses of barnacles with different feeding modes therefore suggests that intraspecific variation in feeding legs depends more on hydrodynamics than on the idiosyncrasies of feeding behaviour.

Allometry of cirral dimensions

In all four species examined, larger barnacles exhibited proportionally shorter cirri using either OLS or RMA techniques (Table 7). This same pattern was also apparent for two of three additional species for which data were available (Table 7). Hydrodynamic theory suggests such negative allometry is adaptive. As barnacles grow larger their feeding cirri extend farther away from the substratum and therefore, as in other animals (Thomason et al., 1998), they are more likely to experience free-stream velocities. Consequently, smaller barnacles may benefit from proportionally longer cirri because they can feed further out of the boundary layer where particle flux is greater, and because they may experience less competition from nearby barnacles (Lohse, 2002). However, size-dependent differences in metabolic and feeding rates (Sebens, 1982; Denny, 1988) might also influence this pattern even in the absence of boundary-layer effects.

Curiously, the degree of negative allometry in feeding leg length did not appear to differ among populations from different wave-exposure regimes. Because boundary layers are thinner at higher velocities (Vogel, 1988), the benefits of proportionally longer cirri to smaller barnacles should be least under high-velocity conditions. Yet coefficients of allometry did not differ among exposure conditions for any of the four cirral traits examined (Digital Appendix 1). Therefore, contrary to expectation, barnacles appear to respond to differences in wave exposure not with changes in the allometry of limb growth, but rather with changes in limb size and shape specific to a particular wave-exposure regime (i.e., the intercepts of the size-dependence relationships change but the slopes do not).

Cirrus form and wave action

Feeding legs were shorter and stouter on wave-exposed shores and up to 80% longer and 25% thinner in sheltered bays. The high precision of these relationships in all four barnacle species (r^2 varied from 0.65 to 0.94 depending on trait and species; Digital Appendix 2b) suggests that strict trade-offs govern the form of feeding structures to ensure maximal feeding effectiveness under different hydrodynamic conditions.

Although striking, our quantitative results must be interpreted with caution, because of qualitative differences in the type of maximal flows experienced by barnacles and because of the way barnacles respond behaviourally to flow. At the intermediate and most exposed sites, maximal water velocities – as measured by our shore sensors – were likely experienced during wave impact, and these would be followed by lower velocities during the backwash in an oscillatory manner. At the most sheltered sites maximal water velocities arose from sustained tidal currents (see Methods). Therefore, in oscillating flow maximum drag arises due to moving water, whereas in weak tidal currents the drag on feeding legs due to ambient flow may be negligible. These flow regimes are also associated with different feeding behaviours. In oscillating flow, leg-extension is precisely timed to the frequency of oscillation (Trager et al., 1990), but legs may or may not be fully extended at the maximum velocity. In contrast, in slow, sustained currents barnacles may actively sweep-feed to increase the volume of water cleared per unit

Table 7. Slopes of leg 6 length versus wet mass for all barnacle species for which data are available (both variables log10 transformed before analysis).

Species	OLS Slope	r	RMA Slope
Balanus glandula	0.287	0.975	0.294
Chthamalus dalli	0.261	0.935	0.279
Semibalanus cariosus	0.230	0.916	0.251
Pollicipes polymerus	0.266	0.976	0.273
Semibalanus balanoides[1]	0.233	0.953	0.244
Eliminius modestus[1]	0.249	0.930	0.268
Tetraclita squamosa rubescens[2]	0.319	0.888	0.363

[1] data from Crisp and MacLean (1990).
[2] K.B. Marchinko, D.J. Arsenault, and A.R. Palmer, unpublished data

time. As a consequence, the differences in leg form observed over the wide range of velocities we examined likely reflect a complex response to mechanical forces induced by drag at high and intermediate exposure, and to ingestion rates that depend on leg form in slow currents. Although we cannot dissect the role of each of these factors in shaping this response, the sizeable differences in form we observed are likely adaptive.

Feeding in slow moving currents

Barnacles from sheltered bays experience weaker currents and thicker boundary layers that may limit the rate of food supply (Fréchette et al., 1989). Those with longer rami and setae would clear a greater volume of water per sweep and presumably have higher capture rates (Crisp and MacLean, 1990). In barnacles, as in larval black flies (Zhang and Malmqvist, 1997), a wider spacing of sieve elements in slow-moving water may permit higher capture rates because fluid transmission rates are higher (Cheer and Koehl, 1987). However, the Reynolds number for flow through *B. glandula* cirri from Bamfield Inlet was approximately 0.5 (based on a seta diameter of 35 µm, which was roughly equal to the distance between adjacent setae, and a water velocity of 0.01 m/s), suggesting that the intersetal space may be too large for spacing differences to affect fluid transmission (Cheer and Koehl, 1987). Furthermore, active sweep-feeding would also significantly increase the feeding rate of barnacles at low water velocity (Crisp and Southward, 1961; Trager et al., 1990).

Feeding in breaking waves

On wave-exposed shores barnacles possess shorter, stouter cirri, which should reduce drag (Denny, 1988) and hence the risk of damage. In addition, shorter, stouter cirri should allow barnacles to hold their cirri erect at higher velocities and feed more effectively. Flume experiments bear this out. *Balanus glandula* from a wave-exposed site maintained full cirral extension at velocities up to 1 m/s, whereas sheltered-shore individuals fully retracted their cirri around 20 cm/s (Marchinko, unpublished data). This compares favorably to observations on *Balanus hameri* from areas of high current, where cirri were held erect at velocities up to 1 m/s (Crisp and Southward, 1961).

The stouter rami of barnacles from wave-exposed shores may also be less likely to buckle when extended in high-velocity flow for two reasons. First, the cuticle of barnacle legs resembles a tube, and larger diameter tubes have material further from the neutral axis (Denny, 1988). Second, stouter rami also have a thicker cuticle (Marchinko, unpublished). Both of these factors would reduce the extent to which rami deflect downstream due to drag. Studies of how cuticle thickness

and second moment of area vary with increasing water velocity are currently underway.

Relation of feeding to growth and fitness

Feeding rate has a large impact on growth rate and fitness (Lewis and Chia, 1981; Okamura, 1992; Wildish and Kristmanson, 1997), so variation in traits that effect feeding rate should experience strong selection. The differences in limb form between exposed and protected-shore barnacles likely reflect a trade-off between feeding effectiveness and structural integrity. On the one hand, longer legs and filtering setae would allow a barnacle to sieve a larger volume of water per sweep, or to clear a larger volume of water during passive feeding. However, the longer the limb and setae, the greater the drag at a given velocity (Denny, 1988). If a limb is too long to be held erect at a given velocity, the volume of water cleared will decrease. Similarly, a stouter ramus with thicker cuticle could be held erect at higher velocities, but it would also be more costly to maintain because more cuticle would have to be replaced each molt (Wu and Levings, 1978).

If differences in limb form allow equivalent rates of feeding under different wave-exposure regimes, then growth rates should be similar in sheltered- and exposed-shore barnacles. However, many studies have reported higher rates of growth or reproduction on more wave-exposed shores (Lewis and Chia, 1981; Crisp and Bourget, 1985; Bertness et al., 1991; Sanford et al., 1994; Sanford and Menge, 2001). Each of these studies suggests the higher flux of food in wave-exposed sites promotes higher growth rate. If the feeding limbs of the barnacles in these studies vary with wave exposure as they do in the species reported here, then the costs of producing shorter, stouter cirri with thicker cuticle appear to be more than offset by the increased flux of food. In addition, barnacles feeding under low flow conditions must resort to active sweep-feeding (Trager et al., 1990), which is energetically more costly (Jørgensen, 1966). Higher water temperatures in sheltered bays would also yield higher metabolic rates, and thus greater rates of energy loss to maintenance metabolism. All of these factors may contribute to lower rates of growth in slower moving water.

Confounding effects of growth and form in studies of suspension feeders

Care should be taken when measuring growth rates of suspension feeders to ensure morphological changes do not confound the environmental variables being studied. For example, Eckman and Duggins (1993) collected juvenile barnacles from a single site and measured growth rate under different flow regimes over 54 days: *B. glan-*

dula, S. cariosus and *P. polymerus* all grew at similar rates over a 2–15 cm/s range of velocities. However, these consistent growth rates might have reflected changes in cirrus morphology. *B. glandula* can alter feeding-leg form to suit ambient flow conditions after a single molt (within 18–25 days; Marchinko, 2003). Therefore, the barnacles in Eckman and Duggins' (1993) study may have achieved similar rates of growth by altering cirrus form to suit ambient velocities.

Interspecific differences in relative variability

Although the difference in leg form for a given difference in water velocity was similar for all four species studies (Fig. 5, Table 6), some species exhibited proportionally more variation than others. The larger, lowest-shore species, *S. cariosus*, exhibited the lowest proportional difference in leg length between extreme sites (29–37%) whereas the smaller, higher shore species, *B. glandula* and *C. dalli*, exhibited much greater variation (75–80% an d 47–68%, respectively).

Three explanations might account for these differences among species. First, shore height may influence the maximal velocities experienced because, as water depth increases, the maximum water velocities at the substratum due to passing waves decreases (Denny, 1988). Therefore, wave-exposed populations of *S. cariosus* would not only have a greater opportunity to feed at lower velocities, but they would also have more opportunity to feed when waves were not breaking directly over them.

Second, body size may influence the extent of cirral variation. Adult body size of the three balanomorph barnacles differed (*S. cariosus > B. glandula > C. dalli*; see methods), and the lowest proportional differences in leg length between extreme sites occurred in the largest species. However, the larger bodied *B. glandula* exhibited proportionally greater variation than the smaller bodied *C. dalli*, suggesting that differences in variability among species are not simply due to body size differences. Nonetheless, surface rugosity may allow small individuals to hide deeper in the boundary layer, so *C. dalli* may experience lower velocities on the same shore than *B. glandula*, and therefore be less variable. This sensitivity to surface rugosity may also explain why the cirri of *C. dalli* varied less predictably with water velocity at intermediate and exposed sites (Figs. 4 and 5).

Third, relative variability may relate to the range of conditions typically experienced by each species. Our data suggest that species inhabiting a wider range of wave-exposure conditions exhibit proportionally greater variability of feeding cirri. *Balanus glandula* occurs at high density throughout the wave-exposure gradient we studied and exhibited the greatest proportional variation in leg length. In contrast, *C. dalli* and *S. cariosus* are less

common in protected bays, and exhibited intermediate variability in leg length. Finally, the leg lengths of *P. polymerus*, which can only survive on high-energy shores, were least variable. If different degrees of variability in leg form reflect different degrees of phenotypic plasticity – as seems likely based on experiments with *B. glandula* (Marchinko, 2003) – then the capacity to alter the form of feeding appendages to suit local fluid-dynamic conditions may be directly tied to the range of exposure conditions under which a species may feed and grow effectively. In other words, more phenotypically plastic species may be able to survive and grow under a wider range of hydrodynamic conditions.

Variability of different cirral traits

Within species, some traits exhibited greater variation over the wave-exposure gradient than others. However the rank order of proportional variability of the three significant traits was consistent for all four species: ramus length > seta length > ramus diameter. This rank order also parallels the rank order of trait size: the larger the trait, the more variable it was. Presumably, these differences in variability reflect the impact each trait has on feeding efficiency, or risk of damage, at different water velocities.

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ZOOLOGY

Feeding in flow extremes:
dependence of cirrus form on wave-exposure in four barnacle species

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Summary

Wave-exposure influences the form of many organisms. Curiously, the impact of flow extremes on feeding structures has received little attention. Barnacles extend feather-like legs to feed, and prior work revealed a highly precise association between leg length and water velocity in one species. To assess the generality of this flow-dependence, we quantified variation in four leg traits (ramus length, ramus diameter, seta length, and intersetal spacing) in four intertidal barnacles (*Balanus glandula, Chthamalus dalli, Semibalanus cariosus, Pollicipes polymerus*) over a wave-exposure gradient in the North-Eastern Pacific. All species exhibited a negative allometric relation between leg length and body mass. Proportionally longer feeding legs may permit smaller barnacles to avoid lower flow and particle flux associated with boundary layers. Although coefficients of allometry did not vary with wave-exposure, form differences among wave-exposures were substantial. Depending on the species, acorn barnacles of the same size from protected shores had feeding legs that were 37–80% longer and 18–25% thinner, and setae that were 36–50% longer and up to 25% more closely spaced, than those from exposed shores. Differences were less pronounced for the gooseneck barnacle, *P. polymerus*. Moreover, *in situ* water velocity explained an impressive percentage of overall leg-length variation: 92% in *B. glandula,* 67% in *C. dalli,* 91% in *S. cariosus,* and 92% in *P. polymerus*. Clearly, both size and shape of barnacle feeding legs respond to local flow conditions. This response appears widespread – across two orders of thoracican barnacles, Pedunculata and Sessilia, and two superfamilies of acorn barnacles (Balanoidea and Chthamaloidea) – and likely adaptive. Longer rami and setae would yield a larger feeding area in low flow, whereas shorter, stouter rami with shorter setae would be less vulnerable to damage in high flow. Finally, the proportionally most variable species was abundant in the widest range of habitats, suggesting that increased plasticity may permit a wider niche breadth.

Key words: allometry, Cirripedia, morphology, phenotypic variation, suspension feeding

Introduction

Flow can have a significant impact on the form, behaviour and distribution of aquatic organisms (Allan, 1995; Wildish and Kristmanson, 1997; Zhang and Malmqvist, 1997; Leonard et al., 1998). In wave-swept environments, flow variation is extreme, with water velocities ranging from 0.05 m/s to well over 10 m/s (Denny, 1988). In response to these extremes, many organisms exhibit conspicuous plasticity of body size and shape. Intertidal snails produce flow-tolerant shells and a larger foot to increase tenacity on wave-exposed shores (Kitching et al., 1966; Trussell, 1997a, b). On wave-exposed shores, barnacles produce shorter feeding legs (Pentcheff, 1995; Arsenault et al., 2001), and shorter, thicker shells that are more resistance to impact (Pentcheff, 1991); mussels have thicker shells and a lower height/width ratio (Seed, 1968; Raubenheimer and Cook, 1990; Akester and Martel, 2000); and sponges, hydrozoans, hexacorals and octocorals all exhibit a more compact body shape (Patterson, 1980; Kaandorp, 1999).
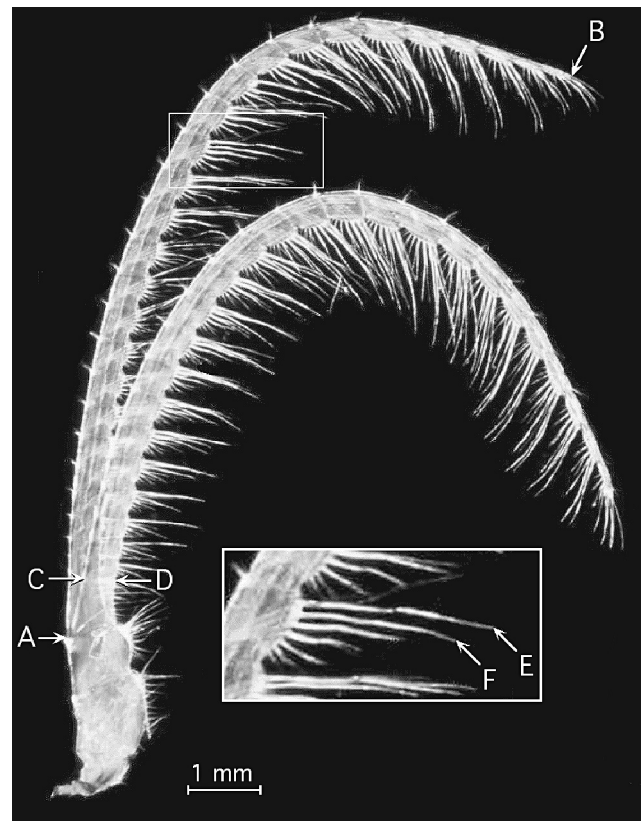
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Many intertidal invertebrates rely on ambient flow to bring them food. This creates two problems. First, a feeding structure must be strong enough to withstand extreme flow conditions, yet fine enough to capture food effectively. Second, flow may affect growth rate by influencing the rate of food supply or feeding efficiency (Okamura, 1992). On wave-exposed shores, barnacles grow more rapidly (Crisp and Bourget, 1985; Sanford et al., 1994; Sanford and Menge, 2001), whereas bryozoans (Okamura, 1992) and sponges (Palumbi, 1986) grow more slowly. In mussels, the effects of wave-exposure appear species-dependent (Seed, 1968; McQuaid and Lindsay, 2000). Higher growth rates on wave-exposed shores likely result from an increased flux of food particles, due to higher velocities and to greater turbulent mixing (Fréchette et al., 1989). However, an optimal flow for feeding and growth likely exists for many species, where feeding and growth are suppressed when flow is too fast or too slow (Eckman and Duggins, 1993; Okamura and Partridge, 1999). Curiously, although wave-exposure affects body size, shape, and growth rate in many species, surprisingly little is known about how flow affects the form of suspension feeding structures (Okamura and Partridge, 1999).

Maintaining feeding performance under different flow conditions is a challenge for suspension feeders. Both flow velocity and the size and shape of feeding structures may affect feeding performance (Cheer and Koehl, 1987). As a consequence, behavioural and morphological adaptations have arisen to maintain feeding performance under different flow conditions. For example, barnacles, anemones, phoronids, and articulate brachiopods modify either body position or position of feeding structures (Barnes and Reese, 1960; Emig and Becherini, 1970; Koehl, 1977; LaBarbera, 1977; Trager et al., 1990), whereas gorgonian sea fans and scleractinian corals alter colony form, in response to differences in the direction and velocity of water flow (Leversee, 1976; Helmuth and Sebens, 1993). By re-orienting feeding structures or the entire body, these animals likely enhance the rate of feeding while reducing hydrodynamic forces (Wildish and Kristmanson, 1997).

Feeding structure form may also vary with flow conditions. Bryozoan lophophores are smaller in diameter and have fewer tentacles under higher flow conditions (Okamura and Partridge, 1999). The primary labral fan of black flies has fewer rays and a smaller feeding area in higher velocity streams (Zhang and Malmqvist, 1997). Finally, overall leg length varies with wave-exposure in one barnacle species (Pentcheff, 1995; Arsenault et al., 2001). However, the response of other features of the feeding fan, and the extent of this response in other species, is unknown. Therefore, we examined variation in both the size and shape of feeding legs over a wave-exposure gradient in four morphologically and phylogenetically distinct species of northeastern Pacific barnacles.

Barnacles feed by extending feather-like legs (cirri) into ambient flow to capture small particles and plankton, although a few species capture larger prey (Howard and Scott, 1959; Jones, 1968). In very low flow barnacles may actively sweep-feed (Trager et al., 1990). Six pairs of biramous cirri (Fig. 1) make up the feeding net. Each ramus, or branch, of a cirrus has many segments and each segment bears four to seven pairs of evenly spaced setae. Because changes in flow regime, and the size and spacing of filtering elements, affect feeding performance of suspension feeders (Cheer and Koehl, 1987), both the size of a ramus, and the length and spacing of setae, may affect the ability of barnacles to feed under different flow conditions.

Barnacles are ideal organisms for studying how flow environment influences feeding structure form. They are sessile, and they settle and grow under wide a range of environmental conditions. As a consequence, they exhibit considerable lability of form. Crowding induces

Fig. 1. A single, biramus cirrus of *Balanus glandula* showing the four traits measured: *ramus length-* the curvilinear distance along the dorsal margin from the base to the tip, excluding the terminal seta (from A to B); *ramus diameter-* diameter of the ramus at the suture between the first and second articles, linear distance from C to D; *seta length-* length of the longest seta (E); *intersetal space-* distance between the two longest setae measured at the base of setae E and F. Modified from Fig. 1 of Arsenault et al. (2001).

longer, narrower shells in many species (Crisp and Bourget, 1985), contact with a predatory snail induces 'bent' shells in *Chthamalus anisopoma* (Lively, 1986*a, b*), and higher salinity promotes a squatter shape in *Semibalanus balanoides* (Barnes and Barnes, 1962). A long period of larval dispersal (Strathmann, 1987) and low among-population genetic heterogeneity (Hedgecock, 1986; Brown et al., 2001) suggest morphological changes with wave exposure are not likely complicated by local genetic differentiation. Finally, all barnacles must grow from a newly settled cyprid into an adult at the spot where they attach initially, so the ontogeny of form may be monitored in individual barnacles under different flow regimes (Marchinko, 2003).

We examined three aspects of wave-exposure dependence of feeding leg form: 1) variation in the relative size and shape of feeding legs (ramus length, ramus diameter, seta length, intersetal spacing), 2) body-size dependence (allometry) of leg size and shape, and 3) magnitude and similarity of variation among four co-occurring species.

Materials and methods

Study sites

Barnacles were collected from three exposure regimes along a wave-exposure gradient in Barkley Sound, Vancouver Island, British Columbia, Canada (Table 1). These sites ranged from sheltered inlets that experienced only weak tidal currents to shores fully exposed to open Pacific swell. Two replicate populations of each species were sampled under each exposure regime. A third population was sampled from the sheltered regime for a total of seven populations.

Water velocity measurements

The maximum water velocity under breaking waves for the four more exposed sites (Kelp Bay, Self Point, Bordelais Island and Sepping's Island) were from Arsenault et al. (2001). Velocities were recorded with two mechanical transducers (Carrington Bell and Denny, 1994) per site and deployed concurrently over 16 days in July and August 2000. These 16 velocities were averaged to yield a single 'average maximum velocity' for each of these sites (see Arsenault et al., 2001 for details). Maximum water velocities at the three sheltered sites were too slow to be recorded using mechanical transducers and were obtained using an Acoustic Doppler Velocimeter (SonTek/YSI Inc. 10-MHz ADV). Velocities were recorded in the lower section of the *B. glandula* zone on six days between May 9 and June 5, 2001. Five of the six sampling days fell within two days of spring tides and sampling times were between one and two hours before or after slack tide, so these measurements provided reasonable estimates of maximum tidal-current velocity. The ADV probe was placed 5 cm above the substrate and instantaneous velocity was recorded at a sampling rate of 25 Hz for five minutes in the x, y, and z dimensions. Each sampling day a single value of velocity for each

Table 1. Collection site descriptions.

Wave exposure	Site		North latitude	West longitude	Water velocity m/s*
	Name	Location description and species sampled			
Sheltered	Grappler Narrows	East-facing shore of Grappler Inlet narrows *Balanus glandula, Semibalanus cariosus*	48°49′94″	125°07′07″	0.0052
	Grappler Mouth	West-facing shore at mouth of Grappler Inlet *B. glandula, Chthamalus dalli*	48°49′91″	125°07′65″	0.0066
	Bamfield Inlet	West-facing shore of Bamfield Inlet near mouth *B. glandula, C. dalli, S. cariosus*	48°50′06″	125°08′20″	0.0123
Intermediate	Self Point[1]	South-facing shore on southeastern point of Helby Is. *B. glandula, C. dalli, S. cariosus, Pollicipes polymerus*	48°50′90″	125°09′70″	2.66
	Kelp Bay[1]	South-facing shore on north end of Kelp Bay *B. glandula, C. dalli, S. cariosus, P. polymerus*	48°51′82″	125°06′35″	3.17
Exposed	Bordelais Island[1]	South-facing shore on southwestern point *B. glandula, C. dalli, S. cariosus, P. polymerus*	48°49′03″	125°13′90″	4.26
	Seppings Island[1]	Southwest -facing shore, gentlest slope of sites *B. glandula, C. dalli, S. cariosus, P. polymerus*	48°50′50″	125°12′50″	4.41

[1] Site descriptions from Arsenault et al 2001.
*Sustained velocity of tidal current (sheltered), or average maximum velocity of breaking waves (intermediate and fully exposed).

site was calculated as the mean of individual velocities $(u^2 + v^2 + w^2)^{1/2}$, where u, v, and w represent velocity in the x, y, and z direction (Okamura and Partridge, 1999). These single velocities were then averaged over the six sampling days to obtain the single value of water velocity for each sheltered site (Table 1).

Although the type of velocity measurement differed between the sheltered regime and the two wave-exposed regimes, both provide reasonable estimates of the maximum velocities barnacles were likely to experience during the summer months at these sites. However, even if flow was around 1 m/s at the sheltered sites, the conclusions we report here on the relationship between water velocity and cirrus form would not be altered significantly. For example, increasing flow by 1 m/s in all sheltered sites increased the slope of the relationship between ramus length and water velocity for *B. glandula* by only 23%. The difference between this slope and the original slope was non-significant (one-way ANCOVA, *P* (equality of slopes) = 0.25).

Study species

We examined four sympatric species of intertidal barnacles: three balanomorph (acorn) barnacles, *Balanus glandula* Darwin, *Chthamalus dalli* (Pilsbry), *Semibalanus cariosus* (Pallas), and one pedunculate (gooseneck) barnacle, *Pollicipes polymerus* (Sowerby). Although *Semibalanus balanoides* may occur in British Columbia and may sometimes be confused with *B. glandula*, no *S. balanoides* were encountered in this study. We focused on the posterior three cirri because these extend furthest from the shell and are used primarily for food capture. The three anterior cirri are shorter and scrape food off the posterior cirri towards the mouth (Anderson and Southward, 1987). All three acorn barnacles were found over the entire wave-exposure gradient. *Pollicipes,* however, was absent from shores lacking wave action.

Collection and measurement of barnacles

For each species, 10 solitary individuals, representing at least a four-fold range in body size (Digital Appendix 1), were collected in the lower one-third of their respective vertical zone at each site. Barnacles from Kelp Bay, Self Point, Bordelais Is. and Sepping's Is. were collected in the area immediately adjacent to the location of wave-force transducers. Transducers were located in the upper third of the *S. cariosus* zone. Barnacles were collected in August and early September 2000, within 18 days of the last wave-force measurement (Arsenault et al., 2001).

To measure body size, the soft tissue (prosoma) – excluding egg masses and opercular plates – was removed from the shell, blotted dry for 20 seconds on a dry

Kimwipe® EX-L (Kimberley-Clark®), and weighed to the nearest 0.1 mg (prosomal wet mass). Although solitary individuals should not exhibit the effects of crowding, shell measurements were not used to describe body size because shell form is so plastic (Crisp and Bourget, 1985; Lively, 1986a, b). The posterior three cirri (legs 4, 5 and 6) were dissected from the left side of the prosoma and mounted in seawater on a microscope slide. As barnacles are bilaterally symmetrical, we assumed measurements from the left side were representative of both sides. We measured four traits on each cirrus (Fig. 1): ramus length – curvilinear distance traced from base to tip on the dorsal side of the ramus, ramus diameter – distance between the dorsal and ventral side of the first (basal) segment, maximum seta length – length of the longest seta on mid-leg segments, and intersetal space – length of the space between the two longest adjacent setae on mid-leg segments. To obtain a single value of ramus length and ramus diameter for each cirrus, values from both the endo- and exopodite were averaged. To obtain a single value of seta length and intersetal space for each cirrus, we took the average value from three middle segments of the endopodite. All traits were measured at 25–50× magnification using a dissecting scope mounted with a camera lucida, and a digitizing tablet with a precision of 20 dots/mm.

Statistical analyses

Where error exists in both X and Y variables, reduced-major-axis (RMA) regression is often recommended over ordinary-least-squares (OLS) regression when describing scaling relationships, because error associated with the X-axis consistently biases the OLS slope downwards (McArdle, 1988; LaBarbera, 1989). However, we examined the slopes of four independent traits, each regressed on body mass. Because the covariate was the same for all four traits, and because Analysis of Covariance (ANCOVA) methods for model II regression are not well developed, OLS regression and ANCOVA (StatView 5.0, 1998 SAS Institute Inc., Cary, NC; SuperANOVA 1.11, Abacus Concepts, Inc., Berkeley, CA) were used to describe and test for differences in the relationships of cirral dimensions to body mass and water velocity.

Allometry

Cirral traits and body size were log10 transformed to linearize relations between variables and to meet assumptions of ANCOVA. Body size (prosomal wet mass) was used as the covariate in all allometric analyses. A one-factor ANCOVA (main effect = population) tested for differences in the dependence of cirral characters on body mass among populations from habitats of different wave-exposure. Two-factor AN-

COVA (main effects = species and population) was used to test for differences in these relationships among species. Only the sites where all four species co-occurred (Self Pt., Kelp Bay, Bordelais Is., and Sepping's Is.) were used in interspecific comparisons. Departures from isometry (expected slope of 0.333) were tested with a one-sample t-test. Where conclusions about statistical significance might have been confounded by conducting multiple tests, significance levels were also assessed by a sequential Bonferroni test (Rice, 1989).

Wave-exposure and cirrus form

To remove body-size effects, the least-squares mean of each cirral trait for a standard body mass was calculated for each site and each species using ANCOVA (slopes were assumed to be equal if slope differences were not significant). These least-squares means were then regressed on water velocity. The standard prosomal wet mass used for each species reflected the average body
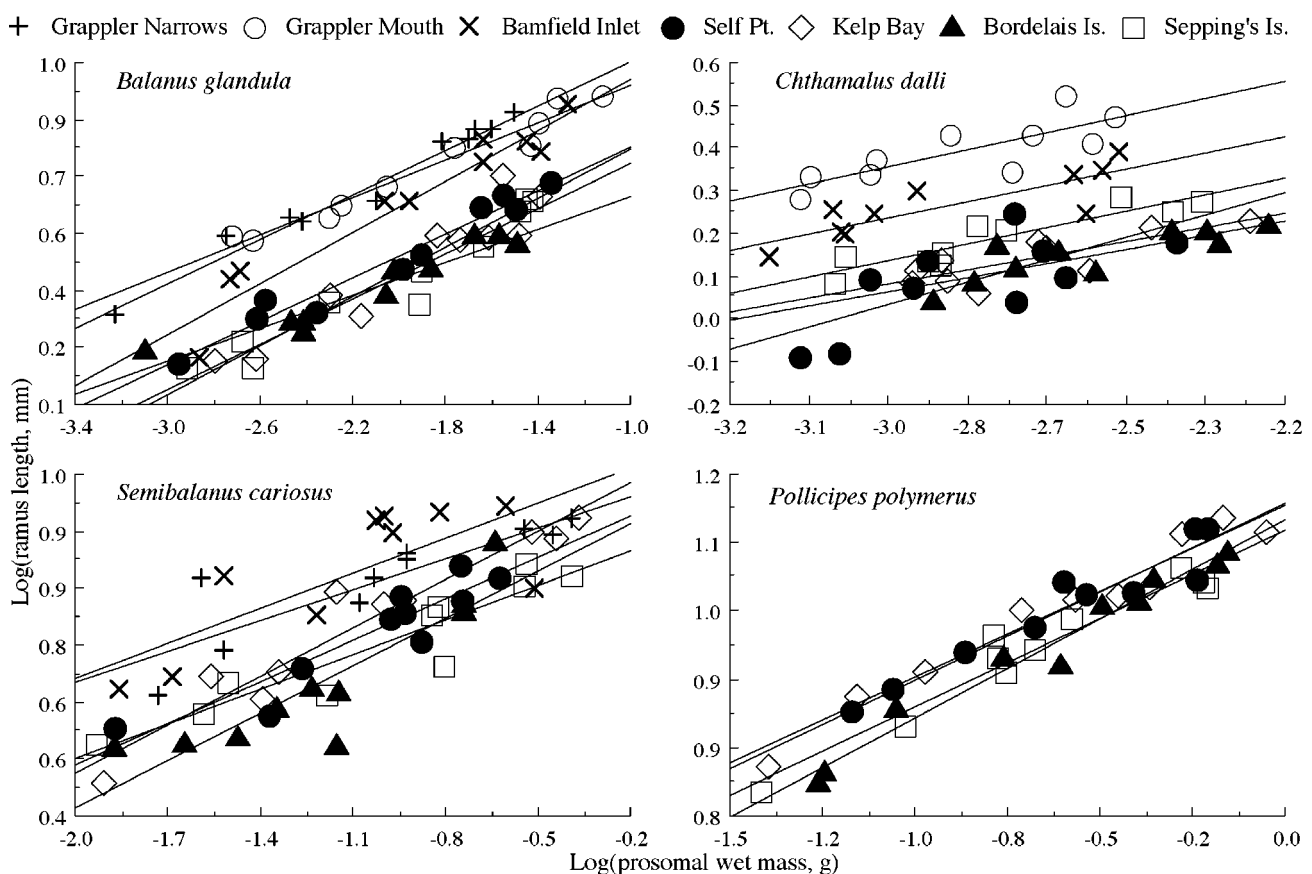
size of that species: 0.0096 g for *B. glandula*, 0.0018 g for *C. dalli*, 0.084 g for *S. cariosus*, and 0.23 g for *P. polymerus*. A one-factor ANCOVA (main effect = leg number) tested whether the relation between water velocity and cirral dimensions varied among the three cirri. Again, cirral traits were $\log_{10}$ transformed to meet assumptions of ANCOVA; however, the covariate, water velocity, was not transformed. A one-factor ANCOVA (main effect = species) was also used to test for differences in the dependence of cirral dimensions on water velocity among species.

Results

Scaling of cirral traits with body mass
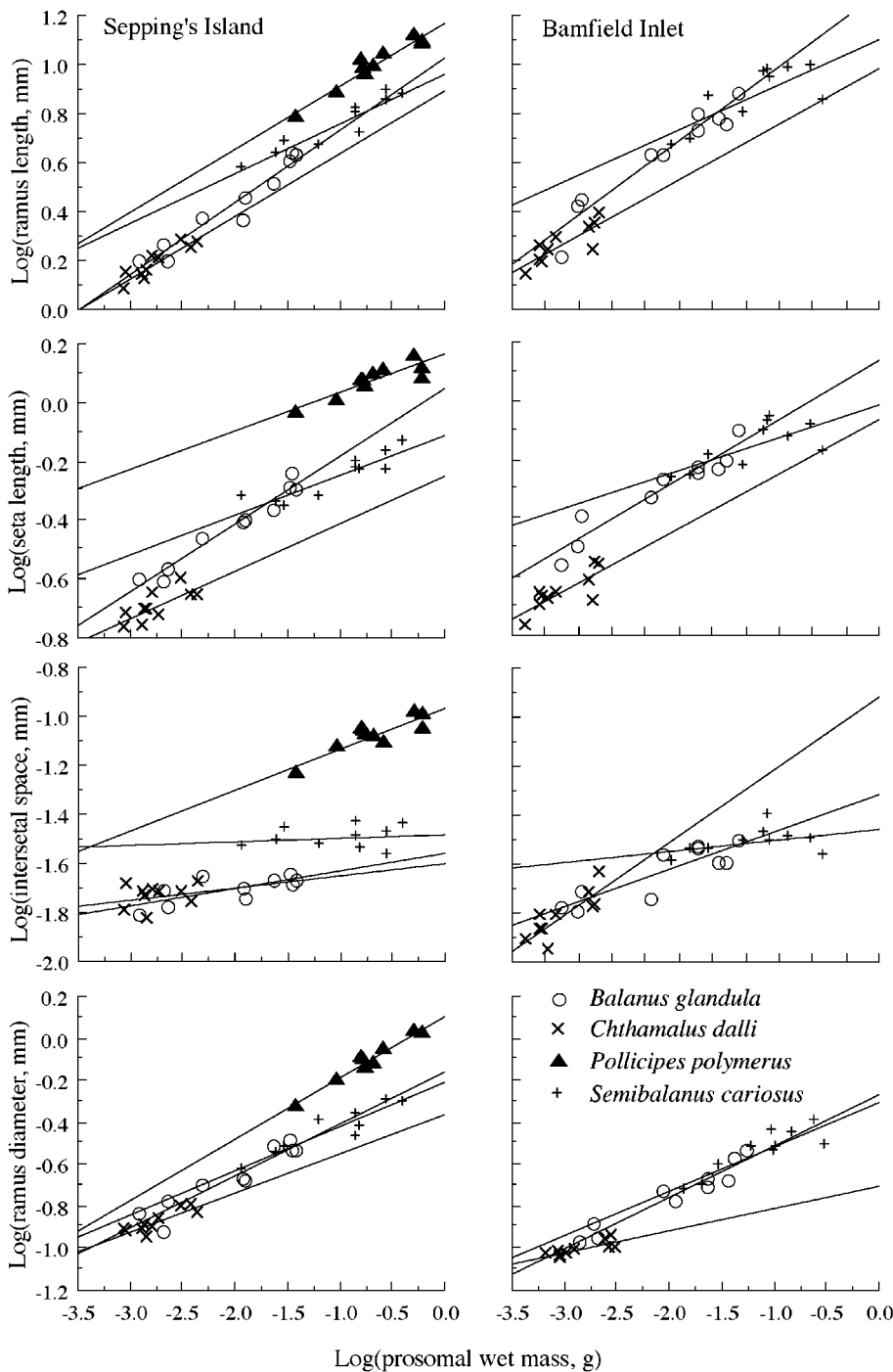
Intra-specific comparisons

All four cirral dimensions increased with increasing body mass in all four species (Figs. 2 and 3). This rela-

Fig. 2. Log-log relationships of leg 6 length versus body mass for four species of intertidal barnacle from different sites in Barkley Sound, British Columbia, Canada. Sites are listed, from left to right, in order of increasing wave exposure. Each point represents an individual barnacle (n = 10 for each species). Differences in slope among populations were non-significant when corrected for multiple tests ($P > 0.11$, Table 2). The relationships of seta length, intersetal space, and ramus diameter to prosomal wet mass exhibited similar patterns for each species and for legs 4 and 5 (see Digital Appendices 1 and 2).

tionship held true for all three feeding legs (legs 4, 5 and 6) at all sites, as observed previously for ramus length (Crisp and MacLean, 1990; Arsenault et al., 2001). This relationship was significant for each trait ($P < 0.05$) in 245 of 278 OLS regressions (Digital Appendix 1). Only setae length in one population of *C. dalli* and the intersetal space in four populations of *C. dalli* and *S. cariosus* were consistently non-signifi-

cant. However, for each species, body mass was a significant covariate ($P < 0.01$) for ramus length (Table 2), and all remaining cirral traits (Digital Appendix 3), when all populations were analyzed concurrently.

Within each species, the slopes of cirral dimensions versus body mass did not differ significantly among populations ($P > 0.05$) for ramus length (Table 2), seta length, intersetal space, or ramus diameter (Digital Ap-

Fig. 3. Cirral trait variation of leg 6 as a function of body mass for four barnacle species: *Balanus glandula*, *Chthamalus dalli*, *Semibalanus cariosus*, and *Pollicipes polymerus*. Each point represents and single individual (n = 10 for each species). Only one wave-exposed (Sepping's Is.) and one sheltered site (Bamfield Inlet) is shown for clarity. Differences in slopes among species were non-significant ($P > 0.11$) for ramus and seta length, while the slope of ramus diameter and the intersetal space to body mass differed significantly among species ($P < 0.013$, Table 4). See Digital Appendix 1 for OLS statistics for each trait in each population.

Table 2. Results from ANCOVA testing for differences in trait means and equality of slopes of the relationship between length of leg 6 and prosomal wet mass among populations of four barnacle species, *Balanus glandula*, *Chthamalus dalli*, *Semibalanus cariosus*, and *Pollicipes polymerus*. Populations of each species were from habitats differing in wave exposure (see Table 1). All data were $\log_{10}$-transformed.

Source of variation	*Balanus glandula*			*Chthamalus dalli*			*Semibalanus cariosus*			*Pollicipes polymerus*		
	df	MS	P	df	MS	P	df	MS	P	df	MS	P
Population	6	0.149	<0.001	5	0.147	<0.001	5	0.042	<0.001	3	0.006	<0.001
Log(wet mass)	1	1.584	<0.001	1	0.192	<0.001	1	0.597	<0.001	1	0.400	<0.001
Error	62	0.002		53	0.002		53	0.003		35	0.001	
Equality of slopes[1]	6	0.005	0.0362[2]	5	0.001	0.8289	5	0.004	0.3227	3	0.0004	0.5831

[1] When testing for equality of slopes, the error degrees of freedom were 56 for *B. glandula*, 48 for *C. dalli* and *S. cariosus*, and 32 for *P. polymerus*, and the error MS were 1.7–13.8% larger than tabled here.

[2] Interaction became non-significant (P = 0.11) after Sequential Bonferroni correction (3 legs = 3 tests for each species)

pendix 3) when corrected for multiple tests. So for each species, a common scaling coefficient was calculated for each trait using ANCOVA (Table 3). Cirral traits exhibited negative allometry for each species in all but one case (*P* < 0.01, Table 3). However, the extent of negative allometry differed among traits. Seta length and intersetal space tended to exhibit the strongest neg-

ative allometry whereas ramus length and diameter tended to exhibit weaker negative allometries (the principal exception to this pattern was *C. dalli*).

Bonferroni-Dunn tests for multiple comparisons revealed that, for a standard wet mass, sheltered populations had consistently and significantly longer rami (*P* < 0.002), longer setae (*P* < 0.003), and narrower

Table 3. Common slopes of the dimensions of leg 6 with prosomal wet mass for each species. Slopes for each species were obtained from ANCOVA on log-transformed data (Tables 2 and 4). Regressions for each population are in Digital Appendix 1. OLS Slopes were tested against an isometric slope of 0.333 using a one-sample Student's *t*-test (t_{allom}).

Species	Slope (SE)	Intercept (SE)	r	df	t_{allom}	
log (ramus length) vs. log (prosomal wet mass) (Figs. 1 and 2)						
Balanus glandula	0.287 (0.011)	1.123 (0.022)	0.975	69	4.152	***
Chthamalus dalli	0.261 (0.028)	0.919 (0.077)	0.935	59	2.550	NS
Semibalanus cariosus	0.230 (0.016)	1.036 (0.019)	0.916	59	6.385	***
Pollicipes polymerus	0.266 (0.010)	1.192 (0.008)	0.976	39	6.618	***
log (seta length) vs. log (prosomal wet mass) (Fig. 2)						
B. glandula	0.204 (0.009)	0.062 (0.018)	0.969	69	14.232	***
C. dalli	0.193 (0.027)	–0.152 (0.074)	0.875	59	5.143	***
S. cariosus	0.145 (0.012)	–0.070 (0.014)	0.912	59	15.538	***
P. polymerus	0.159 (0.013)	0.186 (0.010)	0.918	39	13.220	***
log (intersetal space) vs. log (prosomal wet mass) (Fig. 2)						
B. glandula	0.146 (0.014)	–1.377 (0.028)	0.842	69	13.263	***
C. dalli	0.181 (0.042)	–1.289 (0.116)	0.637	59	3.589	***
S. cariosus	0.071 (0.018)	–1.456 (0.021)	0.797	59	14.436	***
P. polymerus	0.183 (0.014)	–0.964 (0.010)	0.918	39	10.583	***
log (ramus diameter) vs. log (prosomal wet mass) (Fig. 2)						
B. glandula	0.231 (0.009)	–0.237 (0.019)	0.961	69	11.253	***
C. dalli	0.174 (0.024)	–0.454 (0.067)	0.869	59	6.570	***
S. cariosus	0.233 (0.014)	–0.216 (0.014)	0.926	59	7.084	***
P. polymerus	0.297 (0.012)	0.084 (0.009)	0.972	39	2.963	**

**P < 0.01, ***P < 0.001, NS = non-significant.

Table 4. Results from 2-factor ANCOVA testing for equality of slopes of the relationship of the cirral dimensions of leg 6 to prosomal wet mass among the barnacle species: *Balanus glandula, Chthamalus dalli, Semibalanus cariosus*, and *Pollicipes polymerus* (see Fig. 3). Analyses were performed on log-transformed data and included only the four most wave-exposed sites, Self Point, Kelp Bay, Bordelais Island and Sepping's Island.

Source of variation[1]	Ramus length			Seta length		Intersetal space		Ramus diameter	
	df	MS	P	MS	P	MS	P	MS	P
Species (spp)	3	0.0476	<0.001 ***	0.1015	<0.001 ***	0.3616	<0.001 ***	0.1120	<0.001 ***
Population (pop)	3	0.0030	0.182	0.0002	0.948	0.0023	0.536	0.0007	0.702
Log(wet mass. g) (wm)	1	1.1298	<0.001 ***	0.5147	<0.001 ***	0.2724	<0.001 ***	0.9549	<0.001 ***
spp × pop	9	0.0024	0.211	0.0012	0.662	0.0084	0.008 **	0.0014	0.465
spp × wm	3	0.0012	0.583	0.0034	0.106	0.0119	0.013 *	0.0069	0.004 **
pop × wm	3	0.0009	0.687	0.0006	0.796	0.0080	0.064	0.0014	0.430
spp × pop × wm	9	0.0027	0.171	0.0018	0.380	0.0033	0.428	0.0016	0.385
Error	128	0.0018	0.0016	0.0032	0.0015				

$*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

[1] Main effects are not considered meaningful in these analyses. Differences among species reflect differences in body size and differences among populations are tested within species (Table 2, Digital Appendix 3).

ramus diameters ($P < 0.003$) than populations from intermediate and wave exposed habitats (Table 2; Fig. 2; Digital Appendix 3). Ramus diameter of *P. polymerus* did not vary significantly among populations, however, because only intermediate and exposed sites were sampled for this species.

Inter-specific comparisons

All four species showed similar allometries in ramus length and seta length (Fig. 3, Table 3; P > 0.11, Table 4). The allometry of both intersetal space and ramus diameter, however, differed significantly among species (P < 0.013, Table 4). The large, low-shore *S. cariosus* exhibited the strongest negative allometry in intersetal spacing whereas the diminutive, mid- and high-shore *C. dalli* exhibited the strongest negative allometry in ramus diameter. Nonetheless, regardless of species or site, all cirral traits exhibited a consistent negative allometry with body mass (Table 3; Digital Appendix 1).

Dependence cirrus form on wave-exposure

Curiously, cirral trait allometries did not differ significantly among populations (Table 2; Digital Appendix 3). Therefore, predicted cirral dimensions could be calculated for a standard sized barnacle of each species (see methods) to determine how they varied as a function of wave-exposure. Percentage differences were computed as the total difference between the site of lowest water velocity (0.0066 m/s) and the site of highest velocity (4.41 m/s, Table 1); according to the regression equation for each species (Digital Appendix 2a and b).
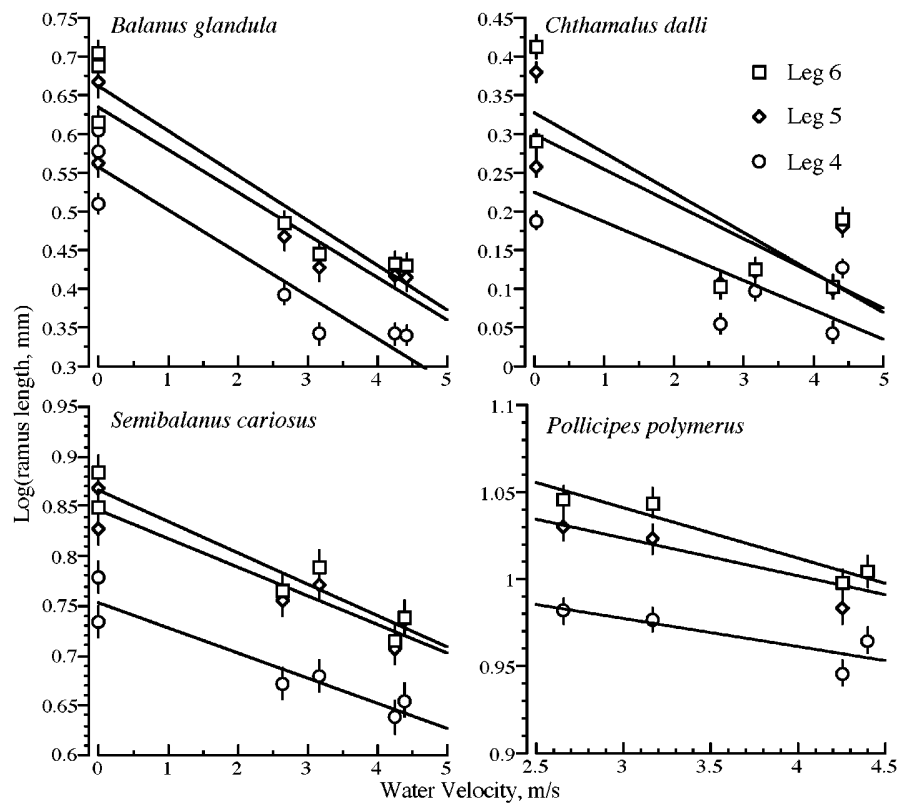
Ramus length

In each species, populations experiencing lower water velocities exhibited longer rami than populations from higher velocity habitats (Figs. 4 and 5a), as reported previously for *B. glandula* (Pentcheff, 1995; Arsenault et al., 2001). Ramus lengths of legs 4, 5 and 6 of B. glandula were 75–80% longer in the sheltered habitat compared to the most wave-exposed habitat (Fig. 4). Significant, though less dramatic, differences in ramus length were observed between these extreme sites in both *C. dalli* (47–68% longer) and *S. cariosus* (29–37% longer) (Fig. 4), and between habitats of intermediate (2.66 m/s) and high wave-exposure (4.41 m/s) in the gooseneck barnacle *P. polymerus* (7–12% longer). OLS regressions revealed a highly significant dependence of ramus length on water velocity (P < 0.005) that was also quite precise (r^2 varied from 0.89–0.92) for legs 4, 5 and 6 of *B. glandula* and *S. cariosus* (Digital Appendix 2a). For *C. dall*i and *P. polymerus* this relationship was only significant statistically for leg 6; however, the slopes did not differ significantly among legs 4, 5 and 6 for any species (Table 5).
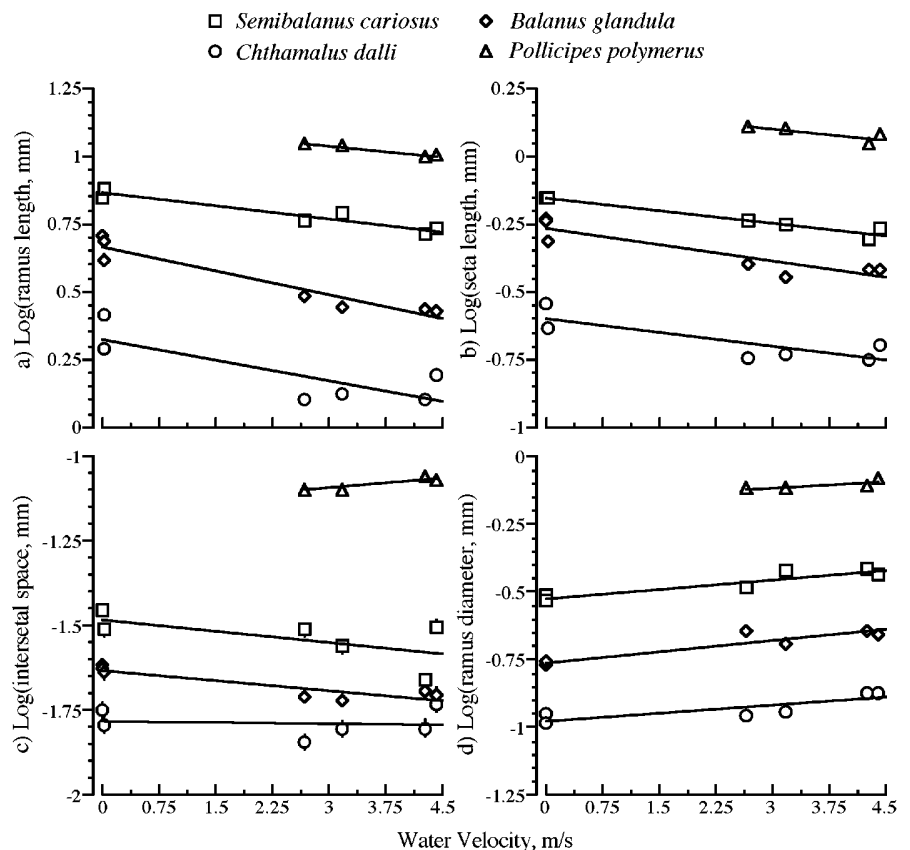
Seta length

Barnacles from quiet-water habitats tended to posses longer setae than those from wave-exposed shores (Fig. 5b). Between the two most extreme sites (Grappler Inlet, Sepping's Is.), setae of leg 6 were 50% longer in *B. glandula*, 41% longer for *C. dalli*, and 36% longer for *S. cariosus*. *Pollicipes polymeru*s from intermediate wave-exposure had setae 11% longer than those from highly wave-exposed shores. The increase in seta length with decreasing water velocity was sig-

Fig. 4. Average length of the posterior three feeding legs (legs 4, 5, 6) for a standard-sized barnacle as a function of water velocity (Table 1). Each point represents the least-squares mean leg length (±SE) of 10 individuals from one of seven sites in Barkley Sound, British Columbia, Canada. Standard log10 (prosomal wet mass, g) for *B. glandula* was –2.017 (SE, 0.064), *C. dalli* –2.741 (0.031), *S. cariosus* –1.074 (0.057), *P. polymerus* –0.635 (0.060). The slopes of these relationships did not differ significantly among legs 4, 5 and 6 in any species (*P* > 0.5, Table 5). See Digital Appendix 2a for OLS statistics for these relationships.

Fig. 5. Least-squares mean trait dimension of leg 6 for a standard sized barnacle (see Fig. 4 legend) as a function of water velocity (Table 1). Each point represents the least-squares mean (±SE) for 10 individuals. Where error bars are absent they are less than the symbol size. The slope of these relationships did not differ significantly among species (*P* > 0.33, Table 6). See Digital Appendix 2b for OLS statistics for these relationships.

Table 5. Results from ANCOVA testing for equality of slopes and differences in intercept between legs 4, 5 and 6 for the relationship of leg length at a standard body mass to water velocity in *Balanus glandula, Chthamalus dalli, Semibalanus cariosus*, and *Pollicipes polymerus* (see Fig. 4 for sample means)

Source of variation	Balanus glandula			Chthamalus dalli			Semibalanus cariosus			Pollicipes polymerus		
	df	MS	P	df	MS	P	df	MS	P	df	MS	P
Leg number	2	0.019	<0.001	2	0.008	0.202	2	0.017	<0.001	2	0.003	<0.001
Water velocity	1	0.231	<0.001	1	0.118	<0.001	1	0.048	<0.001	1	0.003	<0.001
Error	17	0.002		14	0.005		14	0.0004		8	0.0001	
Equality of slopes[1]	2	0.00007	0.962	2	0.001	0.846	2	0.0002	0.671	2	0.00007	0.501

[1] When testing for equality of slopes, the error degrees of freedom were 15 for *B. glandula*, 12 for *C. dalli*, 12 for *S. cariosus*, and 6 for *P. polymerus*. The error mean squares were 1.3–13.4% larger than tabled here.

Table 6. Results from ANCOVA testing for equality of slopes and differences in intercept among barnacle species for the log-linear relationship of the dimensions of leg 6 to water velocity.

Source of variation	Ramus length			Seta length			Ramus diameter		
	df	MS	P	MS	P	MS		P	
Species	3	0.677	<0.001	0.525	<0.001	0.536		<0.001	
Water velocity	1	0.147	<0.001	0.080	<0.001	0.037		<0.001	
Error	18	0.002		0.001		0.0005			
Equality of slopes[1]	3	0.003	0.33	0.0004	0.83	0.0003		0.68	

[1] When testing for equality of slopes, the error degrees of freedom were 15 and the error mean squares were 4.3–13.3% larger than tabled here.

nificant for *B. glandula* (*P* = 0.005), *S. cariosus* (*P* = 0.001) and *C. dalli* (*P* = 0.048), but not for *P. polymerus* (*P* = 0.14; Digital Appendix 2b).

Intersetal space

The intersetal space only increased significantly with decreasing water velocity in *B. glandula* (*P* = 0.006; Digital Appendix 2b). On leg 6, it was 21% greater at the most protected compared to the most exposed site (Fig. 5c). *S. cariosus* exhibited a similar difference between these two sites (25%), whereas the intersetal space of *C. dalli* increased by only 2%, however neither increase was significant (*P* = 0.19). In contrast, the intersetal space declined by 8% from the most exposed to intermediately exposed site in *P. polymerus*, but this decline was not statistically significant (*P* > 0.08; Digital Appendix 2b).

Ramus diameter

Ramus diameter declined with decreasing water velocity in all four species, and this decline was significant for the three acorn barnacles (*B. glandula, C. dalli*, and *S. cariosus*; *P* < 0.03), but not for *P. polymerus* (*P* = 0.20; Digital Appendix 2b). For leg 6, ramus diameter was 25% smaller for *B. glandula* from the most protected site compared to the most wave-exposed site

(Fig. 5d). This difference was similar, though less pronounced, for *C. dalli* (18%), *S. cariosus* (21%) and *P. polymerus* (6%).

Inter-specific variation in cirrus form with wave-exposure

All four species exhibited strikingly similar changes in cirrus form (except the intersetal space; Fig. 5c; Digital Appendix 2b): as water velocity increased among sites, ramus length and seta length decreased, whereas ramus diameter increased (Fig. 5). In addition, the slopes of these relationships did not differ significantly among species (*P* > 0.33, Table 6).

Discussion

Taxonomic breadth of wave-dependent variation

Wave-exposure dependent variation in feeding leg form appears to be taxonomically widespread in barnacles. All four species we examined exhibited similar, significant variation, including representatives from two free-living orders of thoracican barnacles – Pedunculata (gooseneck barnacles) and Sessilia (acorn barnacles) – and from two of the three superfamilies of intertidal

acorn barnacles (Balanoidea and Chthamaloidea; Newman and Ross, 1976; Newman, 1987). Similar variation has now also been observed in one member of the superfamily Coronuloidea (*Tetraclita rubescens*), and in one additional balanoid barnacle (*Semibalanus balanoides*; K. B. Marchinko et al., unpublished), suggesting dramatic intraspecific variation in feeding leg form like that reported here may be universal in intertidal barnacles.

Somewhat surprisingly, this conspicuous intraspecific variation occurs even in species with quite different feeding modes. Gooseneck barnacles like *Pollicipes* feed primarily on microinvertebrates dislodged by the breaking waves themselves, so they are completely at the mercy of wave action for food (Barnes and Reese, 1960). In contrast, acorn barnacles like *Balanus*, *Semibalanus* and *Chthamalus* feed largely on plankton suspended in the water, so, although wave action may increase the rate of food supply, acorn barnacles do not depend on wave action for food (Trager et al., 1990). The similar morphological responses of barnacles with different feeding modes therefore suggests that intraspecific variation in feeding legs depends more on hydrodynamics than on the idiosyncrasies of feeding behaviour.

Allometry of cirral dimensions

In all four species examined, larger barnacles exhibited proportionally shorter cirri using either OLS or RMA techniques (Table 7). This same pattern was also apparent for two of three additional species for which data were available (Table 7). Hydrodynamic theory suggests such negative allometry is adaptive. As barnacles grow larger their feeding cirri extend farther away from the substratum and therefore, as in other animals (Thomason et al., 1998), they are more likely to experience free-stream velocities. Consequently, smaller barnacles may benefit from proportionally longer cirri because they can feed further out of the boundary layer where particle flux is greater, and because they may experience less competition from nearby barnacles (Lohse, 2002). However, size-dependent differences in metabolic and feeding rates (Sebens, 1982; Denny, 1988) might also influence this pattern even in the absence of boundary-layer effects.

Curiously, the degree of negative allometry in feeding leg length did not appear to differ among populations from different wave-exposure regimes. Because boundary layers are thinner at higher velocities (Vogel, 1988), the benefits of proportionally longer cirri to smaller barnacles should be least under high-velocity conditions. Yet coefficients of allometry did not differ among exposure conditions for any of the four cirral traits examined (Digital Appendix 1). Therefore, contrary to expectation, barnacles appear to respond to differences in wave exposure not with changes in the allometry of limb growth, but rather with changes in limb size and shape specific to a particular wave-exposure regime (i.e., the intercepts of the size-dependence relationships change but the slopes do not).

Cirrus form and wave action

Feeding legs were shorter and stouter on wave-exposed shores and up to 80% longer and 25% thinner in sheltered bays. The high precision of these relationships in all four barnacle species (r^2 varied from 0.65 to 0.94 depending on trait and species; Digital Appendix 2b) suggests that strict trade-offs govern the form of feeding structures to ensure maximal feeding effectiveness under different hydrodynamic conditions.

Although striking, our quantitative results must be interpreted with caution, because of qualitative differences in the type of maximal flows experienced by barnacles and because of the way barnacles respond behaviourally to flow. At the intermediate and most exposed sites, maximal water velocities – as measured by our shore sensors – were likely experienced during wave impact, and these would be followed by lower velocities during the backwash in an oscillatory manner. At the most sheltered sites maximal water velocities arose from sustained tidal currents (see Methods). Therefore, in oscillating flow maximum drag arises due to moving water, whereas in weak tidal currents the drag on feeding legs due to ambient flow may be negligible. These flow regimes are also associated with different feeding behaviours. In oscillating flow, leg-extension is precisely timed to the frequency of oscillation (Trager et al., 1990), but legs may or may not be fully extended at the maximum velocity. In contrast, in slow, sustained currents barnacles may actively sweep-feed to increase the volume of water cleared per unit

Table 7. Slopes of leg 6 length versus wet mass for all barnacle species for which data are available (both variables log10 transformed before analysis).

Species	OLS Slope	r	RMA Slope
Balanus glandula	0.287	0.975	0.294
Chthamalus dalli	0.261	0.935	0.279
Semibalanus cariosus	0.230	0.916	0.251
Pollicipes polymerus	0.266	0.976	0.273
Semibalanus balanoides[1]	0.233	0.953	0.244
Eliminius modestus[1]	0.249	0.930	0.268
Tetraclita squamosa rubescens[2]	0.319	0.888	0.363

[1] data from Crisp and MacLean (1990).
[2] K.B. Marchinko, D.J. Arsenault, and A.R. Palmer, unpublished data

time. As a consequence, the differences in leg form observed over the wide range of velocities we examined likely reflect a complex response to mechanical forces induced by drag at high and intermediate exposure, and to ingestion rates that depend on leg form in slow currents. Although we cannot dissect the role of each of these factors in shaping this response, the sizeable differences in form we observed are likely adaptive.

Feeding in slow moving currents

Barnacles from sheltered bays experience weaker currents and thicker boundary layers that may limit the rate of food supply (Fréchette et al., 1989). Those with longer rami and setae would clear a greater volume of water per sweep and presumably have higher capture rates (Crisp and MacLean, 1990). In barnacles, as in larval black flies (Zhang and Malmqvist, 1997), a wider spacing of sieve elements in slow-moving water may permit higher capture rates because fluid transmission rates are higher (Cheer and Koehl, 1987). However, the Reynolds number for flow through *B. glandula* cirri from Bamfield Inlet was approximately 0.5 (based on a seta diameter of 35 µm, which was roughly equal to the distance between adjacent setae, and a water velocity of 0.01 m/s), suggesting that the intersetal space may be too large for spacing differences to affect fluid transmission (Cheer and Koehl, 1987). Furthermore, active sweep-feeding would also significantly increase the feeding rate of barnacles at low water velocity (Crisp and Southward, 1961; Trager et al., 1990).

Feeding in breaking waves

On wave-exposed shores barnacles possess shorter, stouter cirri, which should reduce drag (Denny, 1988) and hence the risk of damage. In addition, shorter, stouter cirri should allow barnacles to hold their cirri erect at higher velocities and feed more effectively. Flume experiments bear this out. *Balanus glandula* from a wave-exposed site maintained full cirral extension at velocities up to 1 m/s, whereas sheltered-shore individuals fully retracted their cirri around 20 cm/s (Marchinko, unpublished data). This compares favorably to observations on *Balanus hameri* from areas of high current, where cirri were held erect at velocities up to 1 m/s (Crisp and Southward, 1961).

The stouter rami of barnacles from wave-exposed shores may also be less likely to buckle when extended in high-velocity flow for two reasons. First, the cuticle of barnacle legs resembles a tube, and larger diameter tubes have material further from the neutral axis (Denny, 1988). Second, stouter rami also have a thicker cuticle (Marchinko, unpublished). Both of these factors would reduce the extent to which rami deflect downstream due to drag. Studies of how cuticle thickness

and second moment of area vary with increasing water velocity are currently underway.

Relation of feeding to growth and fitness

Feeding rate has a large impact on growth rate and fitness (Lewis and Chia, 1981; Okamura, 1992; Wildish and Kristmanson, 1997), so variation in traits that effect feeding rate should experience strong selection. The differences in limb form between exposed and protected-shore barnacles likely reflect a trade-off between feeding effectiveness and structural integrity. On the one hand, longer legs and filtering setae would allow a barnacle to sieve a larger volume of water per sweep, or to clear a larger volume of water during passive feeding. However, the longer the limb and setae, the greater the drag at a given velocity (Denny, 1988). If a limb is too long to be held erect at a given velocity, the volume of water cleared will decrease. Similarly, a stouter ramus with thicker cuticle could be held erect at higher velocities, but it would also be more costly to maintain because more cuticle would have to be replaced each molt (Wu and Levings, 1978).

If differences in limb form allow equivalent rates of feeding under different wave-exposure regimes, then growth rates should be similar in sheltered- and exposed-shore barnacles. However, many studies have reported higher rates of growth or reproduction on more wave-exposed shores (Lewis and Chia, 1981; Crisp and Bourget, 1985; Bertness et al., 1991; Sanford et al., 1994; Sanford and Menge, 2001). Each of these studies suggests the higher flux of food in wave-exposed sites promotes higher growth rate. If the feeding limbs of the barnacles in these studies vary with wave exposure as they do in the species reported here, then the costs of producing shorter, stouter cirri with thicker cuticle appear to be more than offset by the increased flux of food. In addition, barnacles feeding under low flow conditions must resort to active sweep-feeding (Trager et al., 1990), which is energetically more costly (Jørgensen, 1966). Higher water temperatures in sheltered bays would also yield higher metabolic rates, and thus greater rates of energy loss to maintenance metabolism. All of these factors may contribute to lower rates of growth in slower moving water.

Confounding effects of growth and form in studies of suspension feeders

Care should be taken when measuring growth rates of suspension feeders to ensure morphological changes do not confound the environmental variables being studied. For example, Eckman and Duggins (1993) collected juvenile barnacles from a single site and measured growth rate under different flow regimes over 54 days: *B. glan-*

dula, S. cariosus and *P. polymerus* all grew at similar rates over a 2–15 cm/s range of velocities. However, these consistent growth rates might have reflected changes in cirrus morphology. *B. glandula* can alter feeding-leg form to suit ambient flow conditions after a single molt (within 18–25 days; Marchinko, 2003). Therefore, the barnacles in Eckman and Duggins' (1993) study may have achieved similar rates of growth by altering cirrus form to suit ambient velocities.

Interspecific differences in relative variability

Although the difference in leg form for a given difference in water velocity was similar for all four species studies (Fig. 5, Table 6), some species exhibited proportionally more variation than others. The larger, lowest-shore species, *S. cariosus*, exhibited the lowest proportional difference in leg length between extreme sites (29–37%) whereas the smaller, higher shore species, *B. glandula* and *C. dalli*, exhibited much greater variation (75–80% an d 47–68%, respectively).

Three explanations might account for these differences among species. First, shore height may influence the maximal velocities experienced because, as water depth increases, the maximum water velocities at the substratum due to passing waves decreases (Denny, 1988). Therefore, wave-exposed populations of *S. cariosus* would not only have a greater opportunity to feed at lower velocities, but they would also have more opportunity to feed when waves were not breaking directly over them.

Second, body size may influence the extent of cirral variation. Adult body size of the three balanomorph barnacles differed (*S. cariosus* > *B. glandula* > *C. dalli*; see methods), and the lowest proportional differences in leg length between extreme sites occurred in the largest species. However, the larger bodied *B. glandula* exhibited proportionally greater variation than the smaller bodied *C. dalli*, suggesting that differences in variability among species are not simply due to body size differences. Nonetheless, surface rugosity may allow small individuals to hide deeper in the boundary layer, so *C. dalli* may experience lower velocities on the same shore than *B. glandula*, and therefore be less variable. This sensitivity to surface rugosity may also explain why the cirri of *C. dalli* varied less predictably with water velocity at intermediate and exposed sites (Figs. 4 and 5).

Third, relative variability may relate to the range of conditions typically experienced by each species. Our data suggest that species inhabiting a wider range of wave-exposure conditions exhibit proportionally greater variability of feeding cirri. *Balanus glandula* occurs at high density throughout the wave-exposure gradient we studied and exhibited the greatest proportional variation in leg length. In contrast, *C. dalli* and *S. cariosus* are less

common in protected bays, and exhibited intermediate variability in leg length. Finally, the leg lengths of *P. polymerus*, which can only survive on high-energy shores, were least variable. If different degrees of variability in leg form reflect different degrees of phenotypic plasticity – as seems likely based on experiments with *B. glandula* (Marchinko, 2003) – then the capacity to alter the form of feeding appendages to suit local fluid-dynamic conditions may be directly tied to the range of exposure conditions under which a species may feed and grow effectively. In other words, more phenotypically plastic species may be able to survive and grow under a wider range of hydrodynamic conditions.

Variability of different cirral traits

Within species, some traits exhibited greater variation over the wave-exposure gradient than others. However the rank order of proportional variability of the three significant traits was consistent for all four species: ramus length > seta length > ramus diameter. This rank order also parallels the rank order of trait size: the larger the trait, the more variable it was. Presumably, these differences in variability reflect the impact each trait has on feeding efficiency, or risk of damage, at different water velocities.

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The feeding fan of an intertidal acorn barnacle, Balanus glandula, extended to capture suspended food particles. The article by Marchinko and Palmer reports striking intraspecific variation in feeding leg form of four phylogenetically distant barnacle species: individuals from more wave-exposed shores have dramatically shorter and stouter legs. Such ecophenotypic variation likely reduces the risk of damage, while maintaining feeding performance, over a wide range of hydrodynamic conditions. Photo by Dave Denning.