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REPORT

Community-wide character displacement in barnacles: a new perspective for past observations

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Abstract

We tested for community-wide character displacement of feeding leg length and shell morphology in two barnacle communities on the west coast of North America (southern California, USA and Vancouver Island, Canada). Neither community exhibited even displacement in shell morphology. Both barnacle communities, however, exhibited remarkably evenly displaced feeding leg length, despite large differences in geography and species composition (between the orders Pedunculata and Sessilia). Previous experiments suggest that this pattern results from competition, although the competitive mechanism remains unknown. Displacement of leg length may reflect dietary specialization, spatial competition, or both. In some cases the results from two null models differed, illustrating the importance of employing a null model that considers mean and variance, rather than character means alone. Overall, the observed pattern of character displacement provides a new perspective for re-examining the complex relationship between morphology and interspecific competition among intertidal barnacles.

Keywords

Barnacle, body size, character displacement, null model, resource competition, rocky intertidal, suspension feeding, sympatry.

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INTRODUCTION

'Community-wide character displacement' refers to even differentiation in morphological traits resulting from resource competition among similar species (Strong *et al.* 1979). Among the best known examples are terrestrial mammal communities where differences in dentition are thought to reflect differences in resource use, thus promoting competitive coexistence (Dayan *et al.* 1990; Dayan & Simberloff 1994; Ben-Moshe *et al.* 2001). Some authors, however, argue that several methodological criteria should be met before concluding the existence of character displacement (Schluter 2000a,b). First, morphological patterns should be assessed with an appropriate null model (Strong *et al.* 1979; Simberloff & Boecklen 1981; Gotelli & Graves 1996). Second, competitive interactions should be evaluated directly, as other factors, (e.g. adaptations to environmental conditions) may also generate patterns similar to character displacement (Grant 1975). To date, few studies have met these criteria (see Gotelli & Graves 1996; Schluter 2000a) and the pervasiveness of community-wide character displacement remains uncertain, particularly in marine systems.

Barnacles are a conspicuous component of marine intertidal communities throughout the world's oceans. Intertidal barnacle assemblages are repeatedly comprised of two to four species, often differing in size and competing for space (Connell 1961; Dayton 1971; Stephenson & Stephenson 1972; Delany *et al.* 2003). Inferior competitors are often competitively excluded from lower intertidal habitat via two mechanisms. First, larger, faster growing species actively overgrow and undercut smaller species, pushing them higher on the shore (Connell 1961; Newman & Stanley 1981). Second, species with dense larval settlement early in the season may competitively exclude those settling later in the year (Wethey 1983; Dungan 1985). However, physical stress, disturbance and predation may mediate such competitive interactions, allowing smaller barnacle species to co-exist with larger species (Connell 1961; Dayton 1971; Paine 1981; Dungan 1985). Although interspecific differences in size and morphology within barnacle assemblages have been documented for over a century (Darwin 1854; Connell 1961; Dayton 1971; Stephenson & Stephenson 1972; Newman & Stanley 1981; Paine 1981; Dungan 1985; Miyamoto *et al.* 1999;

Applebaum *et al.* 2002), the relationship between morphology and competitive interactions remains unclear.

Competition may generate community-wide character displacement in two ways (Schluter 2000b). First, evenly displaced phenotypes may arise evolutionarily via natural selection for divergent phenotypes that reduce competition for limited resources. Second, competition may limit community membership to species whose phenotypes were non-overlapping prior to living in sympatry via local extinction (i.e. 'ecological sorting'). However, selection and sorting are not mutually exclusive and both may contribute to character displacement (Schluter 2000a). As interspecific competition is commonly documented among barnacle species differing in body size (Connell 1961; Dayton 1971; Paine 1981; Dungan 1985; see Miyamoto *et al.* 1999 for exception), we hypothesized that community-wide character displacement of body size should occur among sympatric barnacle species. To test this hypothesis, we examined community-wide character displacement of body size and feeding leg length in two taxonomically distinct barnacle communities from widely separated sites on the west coast of North America (southern California, USA and Vancouver Island, Canada) using Poole & Rathcke's (1979) null model and a newly derived null model. Null model analyses revealed character displacement in feeding legs alone and we discuss the possible mechanisms responsible for this pattern.

MATERIALS AND METHODS

Barnacle collection and measurement

Barnacles, excluding newly settled cyprids and early juveniles, were collected from two geographically distant (*c.* 1700 km) marine communities on the west coast of North America (Fig. 1a): Bamfield, Vancouver Island, British Columbia, Canada (48°50′N, 125°22′W), and County Line State Beach, Los Angeles, California, USA (34°06′N, 118°38′W). Each community was comprised of four species (Fig. 1a), occurring within five genera and across two orders, *Balanus glandula* Darwin and *Pollicipes polymerus* (Sowerby) at both locations, *Chthamalus dalli* Pilsbry and *Semibalanus cariosus* (Pallas) at Bamfield, and *Tetraclita squamosa rubescens* Darwin and *Chthamalus fissus* Darwin at County Line. Although the maximum density of each species occurs at different vertical heights along the intertidal zone (Stephenson & Stephenson 1972), species vertical distributions overlap considerably (Fig. 1b; Stephenson & Stephenson 1972).

Between 30 and 50 individuals of each species were haphazardly collected from a moderately wave-exposed shore

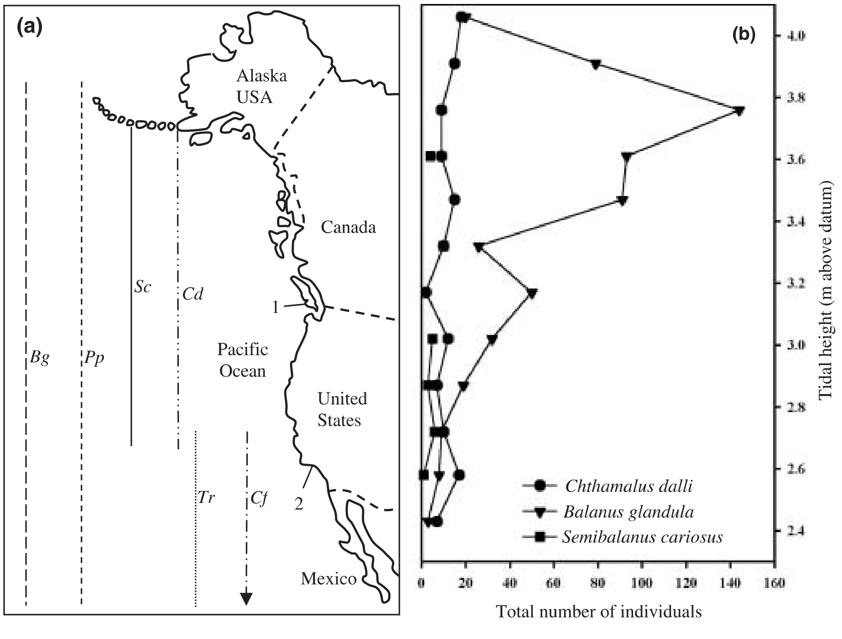

Figure 1 (a) Geographical distribution of the intertidal barnacles *Balanus glandula* (*Bg*), *Pollicipes polymerus* (*Pp*), *Semibalanus cariosus* (*Sc*), *Chthamalus dalli* (*Cd*), *Tetraclita s rubescens* (*Tr*), and *C. fissus* (*Cf*). Arrow indicates distribution extends beyond map. Numbers represent the two collection sites: (1) Bamfield, Vancouver Island, British Columbia, Canada (48°50′N, 125°22′W), and (2) County Line, California, USA (34°06′N, 118°38′W). Distributions taken from Morris *et al.* (1980). (b) Vertical distribution (tidal height) of sympatric acorn barnacles *B. glandula*, *S. cariosus* and *C. dalli* at Bamfield (collection site 1). Total number of individuals = the number of all individuals (counted at 10-cm intervals) adjacent to vertical transects through the intertidal zone, summed over three transects.

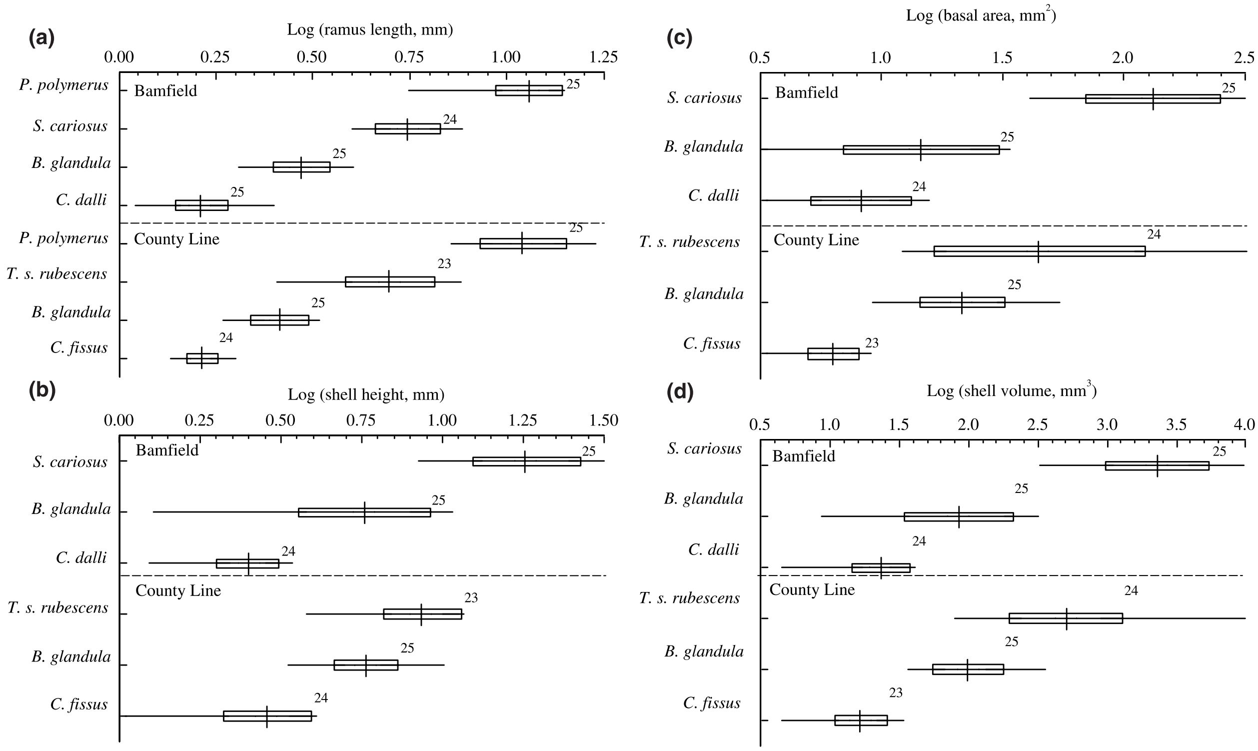

Figure 2 (a) Feeding leg length, (b) shell height, (c) basal area of shell and (d) shell volume of sympatric, intertidal barnacles from two widely separated locations (*c.* 1700 km) on the west coast of North America (Bamfield, British Columbia, Canada, and County Line, California, USA). Symbols represent log-transformed: means (vertical lines), standard deviations (bars), and ranges (horizontal lines). Numbers adjacent to symbols represent sample sizes.

at both sites, frozen, and then transported to the Bamfield Marine Sciences Centre. Twenty-five individuals of each species (see Fig. 2 for exceptions) were then randomly selected for measurement. We measured a wide size range of individuals from each species, because competition for space occurs throughout an individual's lifetime, as each species grow from a small cyprid to an adult. However, the average body size of each species fell within previously published estimates of the reproductive size range of adults (Hines 1978; Morris *et al.* 1980) and should be indicative of true adult body size. We chose four measures of barnacle morphology – feeding leg length, shell height, basal area of the shell and shell volume – for two reasons: (1) overall body size (shell dimensions) influences competition for space (i.e. larger species competitively exclude smaller species; Connell 1961; Dayton 1971) and (2) leg length is strongly influenced by selection (Marchinko 2003), highly correlated with both body size (Arsenault *et al.* 2001) and probably affects food capture rate (Crisp & MacLean 1990; Bertness *et al.* 1998; Marchinko 2003). Thus, we may expect differences in body size to reflect competition for space, whereas difference in leg length may reflect competition for space, food or a combination of both.

Shell dimensions were measured with digital callipers, and basal area (mm^2) was calculated assuming an elliptical shape:

$$\text{Basal area} = \pi \times R_\text{l} \times R_\text{t}$$

where R_l is longitudinal radius (radius between carinal and rostral plates) and R_t is transverse radius (radius between lateral plates) of the barnacle shell at its base. Shell volume (mm^3) was calculated using the formula for a symmetrical truncated cone following Pentcheff (1991):

$$\text{Shell volume} = \pi/3 \times h \times [(R_\text{b})^2 + (R_\text{o})^2 + (R_\text{b} \times R_\text{o})]$$

where h is shell height, R_b is basal radius, and R_o is opercular radius. Basal and opercular radii were calculated as (length + width)/4. Due to considerable differences in shell form between the stalked barnacle *P. polymerus* and acorn barnacles, direct comparisons of shell morphology was not possible; thus, *P. polymerus* was only used in the analysis of feeding leg length. Measurements of feeding leg length were made on the sixth cirrus from the left side of each barnacle (following Arsenault *et al.* 2001). The leg was slide-mounted in seawater, and photographed with a Nikon CoolPix 995 digital camera (Nikon Inc., Melville, NY, USA) mounted on a dissecting microscope. Feeding leg length was measured as the distance traced from base to tip on the dorsal side of each ramus, and then averaged from both rami on single cirrus. All leg measurements were made on digital JPEG files using the public domain NIH Image program (v. 1.62; US National Institutes of Health, http://rsb.info.nih.gov/nih-image/).

To determine if phenotypic clines (in traits exhibiting character displacement) occur between communities, we employed a two-way ANOVA testing for intraspecific differences between sites on the two species that occurred in both locales, *P. polymerus* and *B. glandula*, using species and site as factors.

Null model

Two null model analyses were used to test for evidence of character displacement. We employed the model of Poole & Rathcke (1979), with modifications by Williams (1995) to test for even differentiation of average values of each morphological variable. This test, however, is potentially problematic as it considers only differences in the average morphology of each species. Given that a community exhibiting evenly displaced traits may nevertheless show pronounced and irregular differences in variances, we developed a new null model to evaluate both the mean and variance of feeding leg length and shell volume of each species.

Our new model is based on a metric, *d/w*, commonly used to characterize niche overlap in theoretical studies (see Taper & Case 1985). It is defined as the difference between the average phenotype of two species divided by the sum of their standard deviations. To characterize overlap in leg length and shell volume distributions, *d/w* was calculated for all adjacent species pairs in the sequence of species ranked from the lowest to highest average value. The variance of these values was calculated to obtain a single metric characterizing community-level displacement in morphology. To determine whether the observed variance in *d/w* is lower than would be expected by chance, the observed variance was compared with expected variance values generated in Monte Carlo simulations.

Simulations chose random numbers representing average character values for each species from within the range of observed character means. Standard deviations were then assigned to randomly chosen values according to the observed species sequence, such that the standard deviation of the second smallest species (*B. glandula*) was always assigned to the second smallest randomly chosen value. *d/w* was calculated for all adjacent species pairs, and variance in these values was calculated to generate expected displacement values. This procedure was iterated 10 000 times in Mathematica 4.0 (Wolfram Research 1999), and the fraction of iterations generating overlap values less than observed was taken as the type I error rate (*P*-value) in tests of non-random overlap in character distributions.

Ashton *et al.* (1988) demonstrated that equating the randomization interval to the observed range of phenotypic values increases expected values of overlap and underestimates the type I error rate. To remove this 'edge effect', the smallest and largest species were held constant during all iterations (following Simberloff & Boecklen 1981). Therefore, both the observed and 'null' range of phenotypic values never differed. Finally, to avoid the confounding effects of multiple tests (shell measurements were used to calculate shell height, basal area and shell volume), we employed a sequential Bonferonni correction (Rice 1989) to all analyses involving shell traits.

RESULTS

Null model analyses revealed community-wide character displacement of feeding leg length (Fig. 2a; Table 1). The Poole & Rathcke (1979) model revealed that average feeding leg length was evenly displaced at Bamfield ($P < 0.001$), but not at County Line ($0.05 < P < 0.10$; Table 1). Similarly, only one in 10 000 iterations of the *d/w* model of feeding leg length was more evenly displaced than observed leg length at Bamfield ($P = 0.0001$), and 64 of 10 000 iterations were more evenly displaced than observed at County Line ($P = 0.0064$; Table 1). Two-way ANOVA showed that *B. glandula* had significantly shorter feeding legs than *P. polymerus* ($F_{1,25} = 1243.99$, $P < 0.001$) and that both species had shorter legs at County Line ($F_{1,25} = 4.24$, $P = 0.042$). The between factors interaction was non-significant ($F_{1,25} = 1.141$, $P = 0.288$).

Patterns in shell morphology were somewhat different (Fig. 2b–d). The Poole & Rathcke (1979) model revealed that

Table 1 Results (*P*-values) from the Poole & Rathcke (1979) and *d/w* null models

	Bamfield		County Line	
	Poole and Rathcke	*d/w*	Poole and Rathcke	*d/w*
Leg length (mm)	<0.001	0.0001	$0.05 < P < 0.100$	0.0064
Shell height (mm)	>0.100	0.2965	$0.05 < P < 0.100$	0.0919
Basal area (mm^2)	>0.100	0.5325	>0.100	0.621
Shell volume (mm^3)	>0.100	0.3194	$0.025 < P < 0.05$*	0.2164

*Non-significant after sequential Bonferroni correction.

shell height, basal area and shell volume were not evenly displaced at Bamfield or County Line ($P > 0.05$ after sequential Bonferroni correction; Table 1). Similarly, the d/w null model provided no evidence of even displacement of shell height ($P = 0.30$ and 0.09), basal area ($P = 0.53$ and 0.62) and shell volume ($P = 0.32$ and 0.22, Bamfield and County Line respectively; Table 1).

DISCUSSION

Results revealed a striking pattern of community-wide character displacement in feeding leg length in two distinct barnacle communities separated by nearly 1700 km. This is particularly unique because very few examples of character displacement exist at the taxonomic level of order (Schluter 2000a). Within each community, character displacement occurs among four genera, one in the order Pedunculata and three in Sessilia. Furthermore, the replacement of *S. cariosus* and *C. dalli* by *T. s. rubescens* and *C. fissus* between communities is consistent with the least common mode of character displacement, a phenomenon known as species-for-species matching (Schluter 2000b), which refers to groups of ecologically similar species showing similar patterns of habitat use or morphology in different locales (Schluter 1990). Moreover, because community-wide patterns of character displacement were upheld despite the unidirectional change in leg length in species common to both locations (i.e. a geographical cline in phenotype), it appears that similar processes are responsible for the parallel pattern of character displacement at both locations. Although experimental work suggests that the causal process is competition (Connell 1961; Dayton 1971; Dungan 1985), the competitive mechanism is unclear.

The even displacement of feeding leg length may be explained by direct competition for food, analogous to differences in mammalian dentition that reflect differences in prey size selection (see Ben-Moshe *et al.* 2001). As food availability is limited within benthic boundary layers (Fréchette *et al.* 1989), food resource competition may have led to specialization by different species on different size fractions of available food. Indeed, size-dependent differences in diet do exist (Jianping *et al.* 1996) with larger individuals often capturing a higher proportion of larger particles (Barnes 1959; Lewis 1981). Larger barnacles, with longer legs, present a greater feeding area for food capture and also feed higher in the water column where faster currents deliver food at a quicker rate. Smaller barnacles may make use of food transporting eddies that are induced by the beating of feeding legs during active feeding (Trager *et al.* 1990; Bertness *et al.* 1998). Such species-specific feeding responses to flow properties may be a mechanism by which niche partitioning can arise in intertidal systems (Ackerman & Nishizaki 2004).

The even displacement of feeding leg length may also reflect differences in body size and competition for space. The high correlation between feeding leg length and prosomal mass, the mass of the barnacle's soft tissue (or body) within the shell (Arsenault *et al.* 2001), indicates that over-dispersion of leg length could be a consequence of over-dispersion of body size. Body size is commonly associated with competition for space, as larger species competitively exclude smaller species from the lower intertidal zone (Connell 1961). However, none of our shell measures rendered substantial evidence for character displacement (Fig. 2b–d; Table 1). Shell form is, however, extremely phenotypically plastic in response to many environmental conditions, including crowding, wave-exposure and predation (Crisp & Bourget 1985; Lively 1986a,b; Pentcheff 1991). Thus, any shell measure may be a poor estimate of body size, possibly explaining why shell characters were not as evenly displaced as feeding leg length (Fig. 2). Additionally, dense larval settlement in early summer can result in competitive exclusion of inferior competitors from the lower intertidal (Wethey 1983; Dungan 1985). Therefore, size-based competitive exclusion resulting in character displacement of body size may be weak in comparison to the influence of timing and density of larval settlement.

Competition for food, or space, or a combination of both, are plausible explanations for the pattern of character displacement observed in barnacles. However, the relationship between body size, feeding leg length and food capture must be examined directly before any competition hypothesis receives unequivocal support. Equally unclear is whether the pattern results from natural selection or ecological sorting (see Gotelli & Graves 1996; Schluter 2000a,b). Evidence of decreased body size in intertidal chthamaloids since the cretaceous suggests that body size has indeed changed over time (see Newman & Ross 1976; Paine 1981). However, both ecological sorting and selection remain plausible, and determining the role of these mechanisms in generating character displacement awaits future research.

Differences in results between the Poole & Rathcke (1979) and d/w null models highlight the importance of considering both the mean and variance of each species morphology. At County Line, the d/w null model showed strong support for character displacement in leg length, whereas Poole & Rathcke's (1979) model did not. Conflicting results between null models may be explained by irregular differences in average values at County Line, which were offset by differences in variances. Specifically, species pairs that had greater differences between means also had greater variances, resulting in even displacement in overall distributions of leg length. Thus, the d/w null model, which evaluates entire morphological distributions (i.e. mean and variance), may provide a more accurate test of community-wide character displacement than tests using means alone.

Our study revealed strong evidence of community-wide character displacement in feeding leg length, and perhaps body size, between two orders in one of the most highly competitive groups of marine organisms. Remarkably, this pattern has remained undocumented in a group where differences in size have been reported repeatedly since Darwin's monograph on the Cirripedia (Darwin 1854; Connell 1961; Dayton 1971; Miyamoto *et al.* 1999). The *d/w* null model showed that evidence for character displacement exists despite irregular variation in average morphological values. Notably, the inclusion of variance as a measure in the *d/w* null model appears to add an important dimension to models testing for character displacement. The real contribution of this work, however, is to stimulate future research into competition and character displacement in barnacles. First, barnacle communities may provide a unique opportunity to evaluate species-for-species matching, as these small, sessile organisms are well suited to experimental manipulation. Second, because barnacle communities throughout the world are frequently comprised of two to four species differing in body size (Stephenson & Stephenson 1972), we can assess if character displacement is common in barnacles, and possibly identify which ecological conditions lead to character displacement. Finally, intertidal barnacles may be ideal for developing and testing models of character displacement that incorporate the effects of depleted shared resources, disturbance and predation on the competitive interactions of multiple species.

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