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Geographic correlation between reciprocally adaptive traits of an exotic decapod predator and native gastropod prey: evidence of an arms race?

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ABSTRACT

Question: Is there evidence of an arms race between the predatory crab *Carcinus maenas* and herbivorous snail *Littorina obtusata* in the northwest Atlantic?

Data description: We compared crab claw volume (both master/crusher and minor/handler claws of males and females) and snail shell mass, standardized for a range of predator and prey body sizes, across 26 sites in the Gulf of Maine and Bay of Fundy.

Search methods: We assessed geographically based correlations between (i) crab master claw volume and snail shell mass, (ii) crab minor claw volume and shell mass, and (iii) latitude and phenotype of both crabs and snails. The size-dependency of these relationships was explored by first using population-level regressions to estimate armament sizes for crabs and snails of different body sizes (10th to 90th percentiles), and then using these phenotypic estimates to test for changes in interspecific and latitudinal trait correlations with increasing body sizes.

Conclusions: Size-standardized snail shell mass and crab master claw volume are positively correlated to one another, and the strength of these correlations increases with increasing body size of combatants. We interpret these results as evidence of a size-dependent antagonistic interaction, and possibly an arms race, between *C. maenas* and *L. obtusata* in the northwest Atlantic. These correlations do not appear strictly due to environmental confounds (e.g. temperature), because trait correlations involving snail shell mass and crab minor claw size are substantially weaker and generally insignificant, as are those involving latitude and predator or prey size-standardized trait.

Keywords: arms race, biogeography, *Carcinus, Littorina*, predator–prey.

INTRODUCTION

Co-evolution results from an intensive and reciprocating ecological antagonism between species (Rosenzweig and MacArthur, 1963; Ehrlich and Raven, 1964). In a co-evolutionary arms race, reciprocally adaptive traits of antagonistic species escalate directionally (Rosenzweig, 1973; Dawkins and Krebs, 1979; Brodie and Brodie, 1999; Benkman *et al.*, 2003). An expected outcome of a

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co-evolutionary arms race is that the expression of antagonistic phenotypes will covary over broad spatial or temporal scales.

In North America, the introduction and subsequent range expansion of the European green crab *Carcinus maenas* (L.) correlates temporally with an escalation in anti-predatory adaptations of the intertidal snail *Littorina obtusata* (L.). Over a span of approximately 60–100 years, snail shells in the northwest Atlantic underwent a dramatic morphological transition from thin to thicker, and from high to lower spire (Seeley, 1986). These patterns were initially interpreted as evidence of evolution by natural selection, because green crabs killed thin-shelled and high-spired *L. obtusata* disproportionately to thick-shelled and low-spired conspecifics (Seeley, 1986). Recent studies have questioned the mechanism underlying this phenotypic transition, with evidence that the magnitude of variation in shell thickness having occurred in about 100 years (Seeley, 1986) can be induced within a single generation by exposing snails to predatory chemical cues during development (Trussell and Smith, 2000; Trussell and Etter, 2001). These latter findings suggest that evolution is unlikely to be acting on shell thickness as a particulate trait, but rather on its developmental reaction norm (Schlitching and Pigliucci, 1998).

Recent studies suggest that *C. maenas* has reciprocated the escalation of gastropod shell defences: crabs from a region in the southern Gulf of Maine, where *L. obtusata* have relatively thick shells, are better at crushing snails than crabs from the northern Gulf, where sympatric snails have relatively thin shells (Smith, 2004; Rochette *et al.*, 2007). If *L. obtusata* and *C. maenas* have co-evolved, we would expect geographic variance in prey (*L. obtusata*) defensive traits (Trussell, 2000) to correlate with geographic variance in predator (*C. maenas*) offensive traits.

Heterochelous decapods (i.e. species with left–right claw asymmetry, like *C. maenas*) are good models for studies of adaptive variability because selection operates asymmetrically on structurally similar, although functionally different, appendages of the same individual, providing a useful control for potential effects of confounding factors. For example, the ability of a crab to crush hard-shelled prey is directly affected by the strength of its crushing claw (master claw), but not by the strength of its handling claw (minor claw) (Behrens Yamada and Boulding, 1998; Schenk and Wainwright, 2001). Therefore, if natural processes (e.g. selection or induction) are acting to increase the fitness of individuals that rely on shell-crushing to subjugate prey, the outcome should only be apparent among master, but not minor, claws.

In this study, we test the hypothesis that the ecological antagonism between green crab *C. maenas* and the herbivorous snail *L. obtusata* has caused an escalation in adaptive phenotypes of both predator and prey. Since *C. maenas* is heterochelous, we predict that master and minor claws should show different patterns of variability. More specifically, we predict that geographic variance of crab master claw strength should covary with snail shell thickness, but minor claw strength should vary randomly with respect to snail shell thickness. We also test for shifts in trait correlations that may occur during the lifetime of interacting cohorts, a likely scenario considering that both prey susceptibility to crab predation, and crab dietary preferences, are reported to vary with body size (Elner, 1978; Behrens Yamada and Boulding, 1998; Rangeley and Thomas, 1987).

MATERIALS AND METHODS

Green crabs, *Carcinus maenas,* and intertidal snails, *Littorina obtusata*, were collected from 26 sites in the Gulf of Maine and Bay of Fundy (Fig. 1, Table A1). All sites

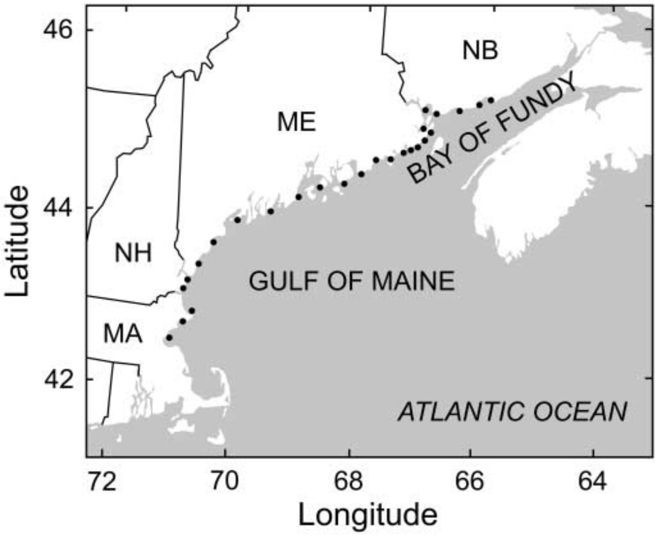

Fig. 1. Illustration of the coastline in the northwest Atlantic, including the positions of the 26 sites used in this study. Site names, coordinates, and specimen collection dates are indicated in Table A1. Longitude and latitude scales are in degrees. New Brunswick (NB), Maine (ME), New Hampshire (NH), Massachusetts (MA).

were intertidal to shallow-subtidal boulder fields dominated by the brown macroalgae *Ascophyllum nodosum* and *Fucus* spp. Most sites were semi-sheltered from wind and waves, except for five that we considered to be moderately exposed. Linear morphometrics were recorded with digital callipers (± 0.01 mm) and mass measurements were made with an analytical balance (± 0.0001 g). Morphometric measurements of crabs were done in the field, whereas snails were measured in the laboratory. Statistical analyses were performed with JMP® v.5 statistical software.

Green crab sampling and morphometrics

Crabs were collected by hand from beneath rocks and macroalgae during low tide and, at 7 of the 26 sites, also by snorkelling because sufficient numbers were not found during one low-tide period. Sampling continued until approximately five males and five females were obtained for each 5-mm increment in carapace width, ranging from 9 to 80 mm, measured as the distance between the most distant lateral teeth of the carapace. Searches covered approximately 40–100 m of coastline and ranged in elevation from mid-intertidal to shallow subtidal. Body sizes of crabs collected subtidally were on average larger than those collected intertidally, but these were nevertheless pooled in subsequent analyses because carapace width–claw volume relationships for crabs from both tidal areas were similar in slope and intercept at any given site.

The maximum amount of force generated by marine decapod claws is a function of various morphological and physiological parameters [e.g. claw size, mechanics, muscle physiology (Warner and Jones, 1976; Elner and Campbell, 1981; Taylor *et al.*, 2000)]. We used claw size to proxy claw strength, since size is a good indicator of intra-specific variation in force generation

(Elner and Campbell, 1981; Lee, 1993; Taylor *et al.*, 2000) and, in *C. maenas,* is likely responsible for variability in feats of strength (see Sneddon *et al.*, 1997, 2000; Smith, 2004). It should be noted that although larger claws can produce more force than smaller claws, the relationship between volume and strength is unlikely to be linear.

Claw volume was estimated as the product of three linear claw dimensions [length × height × width (mm^3)]. Claw length was measured as the linear distance between the most proximal, ventral point of the manus to the ventral point of dactylus insertion. Claw height was measured from the dorsal plane of the manus (immediately anterior to the dactylus joint) to the closest ventral surface. Claw width was the greatest distance perpendicular to the longitudinal axis of the manus. Male and female crabs were analysed separately because preliminary work showed them to differ both in terms of size of their master claw (standardize for body size) and mechanical advantage of their chela lever system (standardize for claw size, data not shown).

Snail sampling and morphometrics

Littorina obtusata with a shell length greater than 4 mm were collected from ten 0.25 × 0.25-m quadrats positioned randomly at each site along 20-m, mid-tide height transect lines. Transects were parallel to the water line. Snails were sorted into 1-mm shell-length increments, and then random sub-samples were taken until all size increments were represented by 3–5 shells. Shell length was recorded with digital callipers to the nearest 0.01 mm as the longest linear dimension parallel to the plane of the aperture. Soft tissue was extracted after gently cracking the shell, and shell fragments dried at 60°C for 48 h in a convection oven before weighing to the nearest 0.0001 g. We used length-standardized shell mass as a surrogate for resistance to crushing (Lowell *et al.*, 1994).

Latitudinal variances and interspecific covariances of predator–prey phenotypes

Before testing for interspecific and latitudinal trends in phenotypes, it was first necessary to confirm that adaptive morphologies varied significantly among sites. Because both claw volume and shell mass increase with increasing body size, we standardized trait values by their respective covariates – that is, carapace width for crabs and shell length for snails. Analyses were run on log–log transformed data, as these successfully linearized the relation between body size and armament size for both species.

Analysis of covariance (ANCOVA) revealed a significant interaction between the covariate and site in all tests except for that involving male master claws (Table 1), which approached significance ($P = 0.075$). These interactions suggest that crab claw volume and snail shell mass do not scale with body size similarly at all sites, thus precluding the use of mean residuals derived from pooled population regressions as a morphometric descriptor for testing latitudinal and interspecific correlations of phenotypes. Instead, we developed population-level regression lines to predict trait sizes for a range of crab and snail body sizes; crab claw volume and snail shell mass were estimated for the 10th, 20th . . . 90th percentiles of body sizes, which were based on pooled body-size distributions of all sampled crabs (males and females separately) and snails.

Size-dependent estimates of offensive predator and defensive prey traits were used to address the study's main objectives. The arms race hypothesis was tested by the correlation between estimated crab master claw volume and estimated snail shell mass across all 26 sites.

Table 1. Summary of ANCOVA results testing for consistency between body size and trait size relationships among study sites

		Master claws			Minor claws		
Effect	d.f.	MS	*F*	*P*	MS	*F*	*P*
Male claw volume							
Carapace width	1	2523.86	56917.31	<0.0001	2287.48	28656.97	<0.0001
Site (random)	25	0.27	4.27	0.0003	0.12	0.85	0.65
Interaction	25	0.064	1.44	0.075	0.14	1.77	0.011
Error	1212	0.044			0.080		
Female claw volume							
Carapace width	1	1388.59	50835.87	<0.0001	1322.65	26534.69	<0.0001
Site (random)	25	0.28	3.20	0.0025	0.12	1.25	0.29
Interaction	25	0.086	3.16	<0.0001	0.096	1.93	0.0039
Error	1232	0.027			0.050		
Snail shell mass							
Shell length	1	931.628	7.96×10^5	<0.0001			
Site (random)	25	0.389	3.242	0.0023			
Interaction	25	0.120	10.256	<0.0001			
Error	1109	0.0117					

Note: All analyses performed on log–log transformed data. See ‘Methods’.

Correlations were tested for trait estimates from all 81 percentile size-class combinations of predator and prey to determine if interspecific trait correlations vary with body size of combatants.

We attempted to control for possible environmental confounds that could affect either crab or snail phenotypes in two ways. First, correlations involving crab master claws were compared with those involving minor claws; since master claws are adaptive for shell crushing but minor claws are not, we expected to observe stronger interspecific correlations involving the former than the latter. Second, we compared interspecific correlations to correlations between adaptive traits and latitude, since several factors that vary along a latitudinal cline, such as water temperature and seasonal climate, could affect phenotype. If environmental factors other than the predator–prey interaction are driving geographic variation in crab or snail phenotypes, then we would expect latitude to be a better predictor of trait variance than the antagonistic phenotype of the putative antagonists.

RESULTS

Geographic variation in predator and prey armaments

Regressions between crab carapace width and claw volume showed a high degree of model fit (mean r^2 ± standard deviation: male master claws = 0.98 ± 0.015, male minor claws = 0.96 ± 0.035, female master claws = 0.98 ± 0.009, female minor claws = 0.96 ± 0.032; see Tables A2 and A3). Analysis of covariance revealed a significant carapace width × site interaction effect for female master claws and both male and female minor claws (Table 1); this interaction term similarly approached significance for master claws of male crabs.

The relationship between crab body size and the extent of inter-population variation in claw size differed between master and minor claws. Among-site variation in master claw volume estimates increased with increasing body size for both male and female crabs. For 10th percentile male crabs (carapace width = 18.02 mm), the largest-clawed population had an estimated claw volume that was 24% greater than that of same body-size conspecifics from the smallest-clawed population. A similar comparison between claw volume estimates for 90th percentile male crabs (56.20 mm carapace width) showed the largest-clawed population to have a claw volume estimate 48% larger than that of same body-size conspecifics from the smallest-clawed population. Comparisons between female crabs similarly showed variation in master claw volume estimates to range from 37% to 55% between 10th (17.82 mm) and 90th (47.49 mm) percentile crabs, respectively. In contrast, minor claw estimates show most among-site variation to occur between 10th percentile body sizes for both male (62% difference) and female (125% difference) crabs; the least amount of among-site variation occurred among 50th (23% difference) and 90th (30% difference) percentile body sizes for male and female crabs, respectively.

The proportion of left- and right-handed crabs varied among shores. On average, 83% of males (range = 67–100%) and 83% of females (70–98%) had right-handed master claws. We designated the master claw as the larger of the two claws, irrespective of handedness.

Population-level regressions between snail shell length and shell mass showed a high degree of fit for all populations (mean $r^2 \pm$ standard deviation $= 0.99 \pm 0.0085$; Table A4). Analysis of covariance revealed a highly significant shell length × population origin interaction effect (Table 1). Among-site differences in *L. obtusata* shell mass generally decreased with shell length, ranging from 106% for 5.95-mm shells (10th percentile) to 34% for 13.42-mm shells (90th percentile).

Interspecific trait correlations

Master claw volumes of male and female crabs showed strong positive correlations among sites, whereas minor claw correlations were substantially weaker (Fig. 2). Furthermore, master claw volume correlated positively and significantly with snail shell mass (Fig. 3), and the strength of these correlations generally increased with increasing size-class comparison (refer to change in correlation along diagonal in Fig. 4; see also Table 2). This pattern suggests that, on average, larger individuals are better fit to their antagonist's armament than smaller individuals. In contrast to the patterns involving the master claw, the correlations between crab minor claw volume and snail shell mass were substantially weaker, and generally statistically insignificant, except for some marginally significant correlations between the largest crabs and snails (Figs. 3, 4).

Latitudinal variation in adaptive traits

Table 2 summarizes the relationships between latitude and adaptive trait estimates. There are marginally significant correlations (negative slopes) between latitude and estimates of snail shell mass for 10th, 20th, 30th, 40th, and 50th percentile shell lengths, when $\alpha = 0.05$. Similarly, there are marginally significant correlations (negative slopes) between latitude and master claw volume estimates for female crabs of intermediate body sizes (30th, 40th,

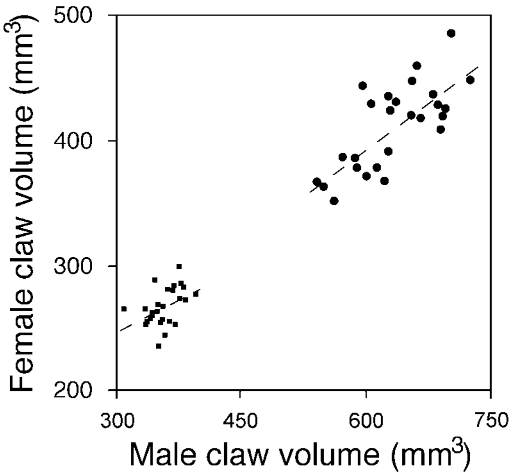

Fig. 2. Master claw volume of male and female crabs was correlated positively among sites (circles: $t_{2(0.05),\ 24,\ 24} = 5.24$, $r = 0.73$, $P < 0.0001$, $n = 26$ sites) and, to a lesser extent, so was minor claw volume (squares: $t_{2(0.05),\ 24,\ 24} = 2.44$, $r = 0.45$, $P = 0.022$, $n = 26$ sites). Results shown here are for 50th median size class of male (35.06 mm) and female (34.23 mm) crabs. Seventy-nine of 81 correlations involving master claws had $P < 0.05$ and 73/81 had $P < 0.005$. In contrast, only 18/81 correlations involving minor claws were significant when $\alpha = 0.05$ and 0/81 when $\alpha = 0.005$.

Table 2. Summary of the correlations between phenotype and latitude for male and female crab master claw volume estimates, and for snail shell mass estimates, for a range of body sizes among 26 sample sites. Correlations for same-percentile crab master claw estimates versus snail shell mass estimates are also reported for comparison

	Latitude						Predator vs. prey			
	Male crab		Female crab		Snail		Male vs. snail		Female vs. snail	
Body size percentile	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
10th	0.31	0.12	0.32	0.11	0.42	0.03*	0.15	0.49	0.21	0.30
20th	0.29	0.15	0.37	0.06	0.41	0.04*	0.26	0.20	0.34	0.09
30th	0.26	0.20	0.40	0.05*	0.41	0.04*	0.35	0.08	0.44	0.03*
40th	0.23	0.26	0.40	0.04*	0.40	0.04*	0.42	0.03*	0.52	0.007*
50th	0.19	0.34	0.38	0.05*	0.38	0.05*	0.48	0.01*	0.57	0.003**
60th	0.16	0.42	0.37	0.06	0.37	0.07	0.52	0.006*	0.59	0.001**
70th	0.14	0.50	0.35	0.08	0.34	0.09	0.55	0.004**	0.60	0.001**
80th	0.11	0.59	0.33	0.10	0.30	0.14	0.57	0.003**	0.59	0.002**
90th	0.09	0.68	0.30	0.14	0.24	0.24	0.56	0.003**	0.55	0.004**

Note: Body sizes correspond to 10th, 20th, . . . , 90th percentiles from pooled sample population distributions.
* Significant when $\alpha = 0.05$. ** Significant when $\alpha = 0.005$.

and 50th percentiles) (Fig. 5). Estimates of male master claw volumes do not correlate with latitude. Overall, correlations between crab and snail phenotype are much stronger than those between phenotype and latitude (Table 2).

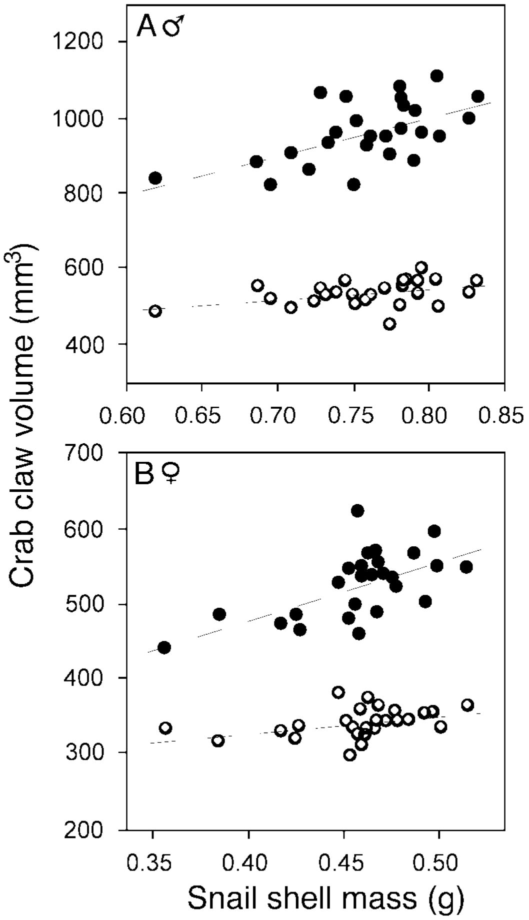

Fig. 3. Correlation between body-size standardized shell mass of snails and claw volume of male (A) and female (B) crabs (master claw: closed circles; minor claw: open circles) across 26 sites in the northwest Atlantic. Results depicted here are for body size combinations that yielded the maximum coefficients of correlation between estimates of crab master claw and snail shell mass (male master claw between 60th and 90th percentile crabs and snails: $t_{2(0.05),24,24} = 3.53$, $r = 0.58$, $P = 0.0017$; male minor claw: $t_{2(0.05),24,24} = 2.16$, $r = 0.40$, $P = 0.041$; female master claw between 60th and 70th percentile crabs and snails: $t_{2(0.05),24,24} = 3.67$, $r = 0.60$, $P = 0.0012$; female minor claw: $t_{2(0.05),24,24} = 2.17$, $r = 0.41$, $P = 0.040$). Variation in correlation coefficients for different size-class comparisons is depicted in Fig. 4.

DISCUSSION

Carcinus maenas and *Littorina obtusata* as ecological adversaries

Large-scale correlations between function-valued traits and selective gradients represent one of the most powerful first steps to understanding the ecological and evolutionary significance of phenotypic variation in the wild (Endler, 1986; Vermeij, 1987). We show that variance in reciprocally adaptive traits of *C. maenas* and *L. obtusata*, species that are

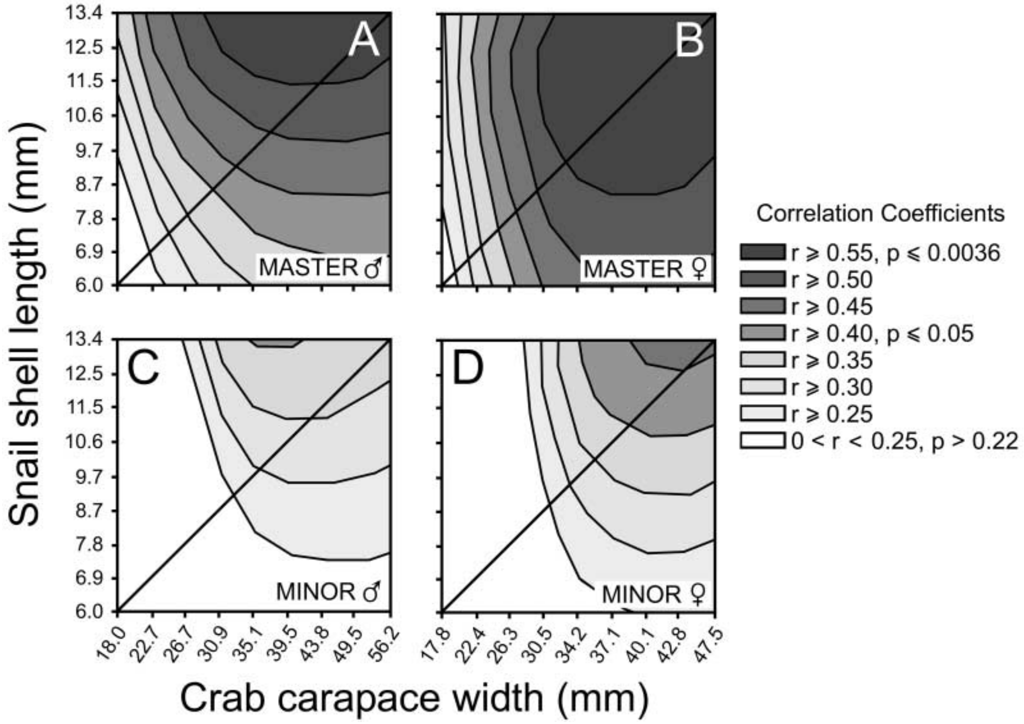

Fig. 4. Contour plots depicting variation in correlation coefficients for relationships between snail shell mass and male (A) and female (B) master claw volume, and male (C) and female (D) minor claw volume. Position of contours is based on correlation coefficients estimated for all eighty-one 10th percentile combinations of crab and snail body sizes, which were estimated from pooled body size frequency distributions. The diagonal line refers to correlations of the 1 : 1 body size percentiles of crabs and snails (e.g. 10th:10th, 20th:20th, . . . , 90th:90th). Ranges of correlation coefficients are outlined in the key.

known to interact as predator and prey (Reimchen, 1982; Seeley, 1986; Tyrrell and Harris, 2000), correlate positively along approximately 600 km of coastline. Several lines of evidence suggest that this correlation is at least partly due to the antagonistic relationship between these species, and is not simply the result of confounded responses to a common biotic or abiotic factor.

First, the amount of among-population variance in both crab claw volume and snail shell mass is biologically significant. For instance, significant differences in predatory success of *C. maenas* feeding on *L. obtusata* have been attributed to 9.4% differences in mean claw height (Smith, 2004), whereas we found up to 48% and 55% differences in master claw volumes (corresponding to ~15 and 17% differences in claw height) among shores for male and female crabs, respectively. Similarly, among-site variation in size-standardized shell mass likely accounts for the significant geographic variation in *L. obtusata* shell-breaking resistance (Lowell *et al.*, 1994; Trussell, 2000) and susceptibility to crushing predation by *C. maenas* (Seeley, 1986; Smith, 2004; Rochette *et al.*, 2007).

Second, master claw volumes of male and female crabs are strongly correlated across sites, whereas minor claw volumes are not, suggesting the former but not the latter are

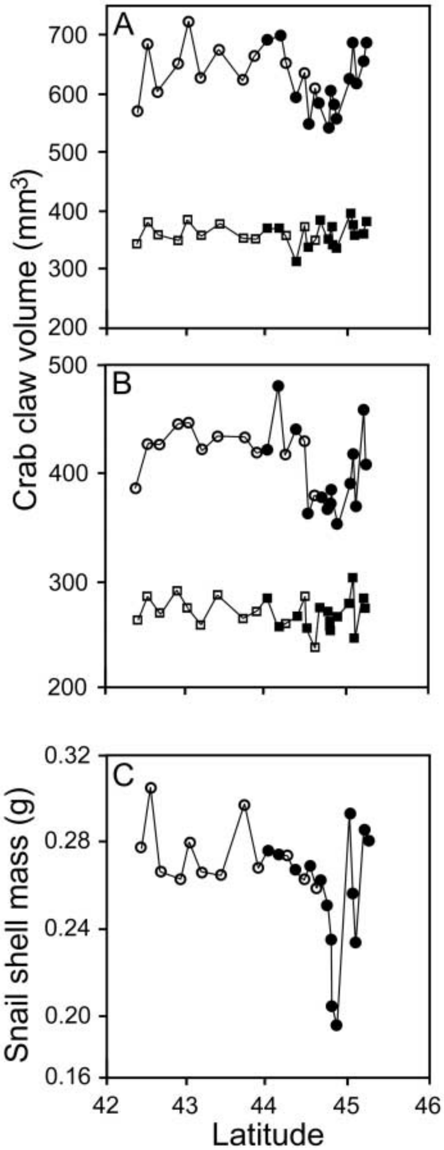

Fig. 5. Latitudinal distribution of claw volume for male (A) and female (B) crabs, and shell mass for snails (C), from 26 shores in the northwest Atlantic. Master (circles) and minor (squares) claw volumes were estimated for crabs of median carapace widths (35.06 and 34.23 mm for male and female crabs, respectively). Snail shell mass was similarly estimated for the median shell length (9.69 mm). Line equations for traits at each site are listed in Tables A2, A3, and A4. Open symbols indicate sites where predatory decapods, other than *C. maenas*, were found intertidally.

responding to a common external factor, which is likely related to maximum force production (e.g. shell crushing).

Third, and perhaps most convincingly, *C. maenas* master claw volume correlates significantly and strongly with *L. obtusata* shell mass across sites, but crab minor claw volume generally does not, except for marginally significant correlations involving the largest crabs and snails (Fig. 4). The significance of these contrasting patterns is intuitive, since master claws are used for shell crushing whereas minor claws are used for prey handling, not crushing, so the former are expected to evolve in response to prey armour but the latter are not (we address below the potential cause of significant correlations involving minor claws). Moreover, the correlation between antagonistic traits is greater in comparisons involving larger than smaller predator and prey (Fig. 4, diagonal), suggesting that older individuals are better suited to their adversarial phenotype than younger individuals. These patterns could result if either selection or induction were causing changes in mean phenotype expression within the lifetime of a cohort, or if growth trajectories have evolved to express adaptive phenotypes at times during ontogeny when antagonistic interactions are most likely to exist.

Although the dynamics of these trait correlations are suggestive of a reciprocal interaction and trait escalation, a similar pattern could also result if the phenotype of one of the two interactors was driven by variation in its antagonist's phenotype, while the phenotype of the 'antagonist' was driven by external (to the interaction) biotic or abiotic factors. We address the potential for external environmental heterogeneity to affect either crab or snail phenotype by comparing interspecific trait correlations with correlations between traits and latitude. Although this does not completely resolve the problem, results do corroborate the predator–prey co-evolution hypothesis. For instance, the correlation between reciprocally adaptive traits (i.e. master claw volume vs. shell mass) is much stronger than any correlation between phenotype and latitude for either species (Table 2).

Correlations involving minor crab claws

The significant correlations between crab minor claw volume and snail shell masses for comparisons involving large animals are somewhat perplexing, particularly since minor claws are not thought to be adaptive for shell-crushing predation. However, we do not believe that these patterns indicate that minor claws function as an additional crushing appendage, since their occlusive surfaces typically have fine, needle-like teeth, in marked contrast to the blunt molars of the master crushing claws (e.g. Brown *et al.*, 1979; Behrens Yamada and Boulding, 1998). The minor claw of larger crabs may show some relation to prey defence if the developmental allometries of master and minor claws are linked, either genetically or through developmental constraints, and variation in the master claw is being driven by distributions of prey armour. Whereas such a correlation between minor claw and shell strength may not directly affect crushing performance when the master claw is intact, it could infer fitness to crabs that retain an adequate replacement weapon in the event that their master claw is autotomized (Pynn, 1998).

Geographic confounds and other challenges for the arms-race hypothesis

An inherent limitation when elucidating proximate causation from biogeographic patterns derives from the many factors that can affect the expression of adaptive morphologies across broad spatial scales. At least three scenarios can explain the occurrence of the *Carcinus–Littorina* trait correlation reported here: (i) reciprocal selection or reciprocal induction, both of which may lead to co-evolution (Agrawal, 2001; Relyea, 2002; Kopp and Tollrian, 2003; Kishida *et al.*, 2006); (ii) trait variation in one species is driven by factors external to the predator–prey interaction (e.g. abiotic environment), while trait variation in the second species is caused by trait variability in the first (not co-evolution because the species–species effect on phenotype is not reciprocal) (Vermeij, 1987, 2004); (iii) phenotypes of both species covary simply because they live sympatrically, and both respond to environmental heterogeneity in a similar way – that is, the variable environment, not the predator–prey interaction, is driving geographic covariance of phenotypes. Previous studies on marine decapods and gastropods suggest that all three of the scenarios stated above could explain the *Carcinus–Littorina* geographic trait correlation, since both crabs and snails (a) have adaptive morphologies that are plastic (Appleton and Palmer, 1988; Palmer, 1990; Smith and Palmer, 1994; Trussell and Smith, 2000; Dalziel and Boulding, 2005), and (b) show significant genetic structuring over spatial scales comparable to that covered in this study (Rólan-Alvarez *et al.*, 2004; Roman and Palumbi, 2004). Although the proximate causes of phenotypic variation cannot be directly tested by our correlative data, we will briefly discuss the putative effects of (i) latitudinal temperature gradients and (ii) other crab and snail enemies, on crab and snail phenotypes to embolden our hypothesis that this *Carcinus–Littorina* trait correlation is in part a function of the species–species interaction.

In general, gastropod shell armour is less massive at higher than lower latitudes, perhaps because water temperature (which decreases with increasing latitude) affects growth rates and subsequent allometries, or because calcium carbonate, which is a major structural component of gastropod shells, is less bio-available and more soluble at colder temperatures (Graus, 1974; Vermeij, 1977, 1987; Reid, 1996). Consistent with these findings, both shell mass estimates of small *L. obtusata* and claw volume estimates of medium-sized female crabs showed marginally significant decreases with latitude (Table 2). To our knowledge, the effects of temperature on crab claw allometry have not been substantiated, although the possibility that the energetics of the ambient environment can affect claw size should not be dismissed. If the expression of adaptive morphologies of both species is primarily a function of water temperature, or any other environmental factor that affects phenotype and varies geographically, we would expect to find trait covariances among sympatric populations, whether the species interact with one another or not. We cannot dismiss the potential role of temperature (or other environmental confounds) in contributing to these patterns; however, and as stated earlier, the interspecific trait correlations were substantially stronger than the correlations between trait estimates and latitude, suggesting that the inter-species effect on phenotype is greater than the effect of temperature or other possible latitudinal confounds.

If the adaptive morphologies of *C. maenas* and *L. obtusata* are driven by antagonistic biotic interactions, we should also consider the role of other species in contributing to phenotypic change. For example, sites in the northern Gulf of Maine and Bay of Fundy have conspicuously low decapod diversity in intertidal habitats, being inhabited almost exclusively by *C. maenas*. In contrast, the diversity and abundance of other intertidal decapods, notably *Hemigrapsus sanguineus* and juvenile *Homarus americanus*, increases southward, to the point where several sites in the lower Gulf had lower densities of *C. maenas* than of these other molluscivores (T.C. Edgell, personal observation). The heavily armoured snails in the southern Gulf, relative to weakly armoured conspecifics in the northern Gulf, may have evolved in response to the collective of shell-crushing enemies, *C. maenas* being just one of them. A similar effect may also explain large-clawed *C. maenas* in the southern Gulf, since claw size and strength in these animals is also important during agonistic interactions such as defending food or mates, or escaping from predators.

Although the presence of other decapods may have an effect on *C. maenas* and *L. obtusata* phenotypes, this hypothesis does not help to explain why crabs and snails in the Bay of Fundy, which more or less do not interact with other intertidal decapods, are as heavily armoured as conspecific in the southern Gulf of Maine (see Fig. 5).

However daunting a task, more detailed information pertaining to geographic variability in the *Carcinus–Littorina* interaction – in particular, rates of snail mortality *in situ* and the importance of *L. obtusata* as prey to *C. maenas* relative to other available prey species – would contribute significantly to our understanding of this predator–prey antagonism. Moreover, a better understanding of geographic variation in factors that are known to affect phenotype (e.g. resource availability, wave energy, temperature) would greatly enhance our ability to parse predator–prey effects from the effects of other environmental variables that vary across this geographic expanse. An appropriate starting point for future research would be to explain why crabs and snails existing due south of 45° (see Fig. 5) possess claws and shells, respectively, which are distinctly, and inexplicably, less enhanced than those of conspecifics both north and south of that region.

CONCLUSION

Co-evolutionary arms races occur when antagonistic traits escalate directionally in response to reciprocated phenotypic improvements by two or more interacting species. We demonstrated a key feature that is central to the idea of arms racing, a large-scale correlation between reciprocally adaptive traits of antagonistic species. Despite obvious limitations, mostly pertaining to proximate causation of trait variability, this correlative data set depicts real patterns of adaptive phenotypic variation among a large number of sympatric predator–prey populations, spanning a broad geographic range, a phenomenon that is documented infrequently in studies of co-evolving organisms. Now that these trait correlations have been established, future research should focus on (i) identifying factors that contribute to intraspecific variation and how they may vary along a latitudinal cline (e.g. temperature, resource availability, competition and predation), and (ii) discriminating between genetic and environmental sources of phenotypic variation, to determine the extent to which these ecological antagonists are having a reciprocating effect on the expression of each other's adaptive morphologies.

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APPENDIX

Table A1. Coordinates and names of 26 study sites in the Gulf of Maine and Bay of Fundy, northwest Atlantic

Site	Latitude	Longitude	*L. obtusata* collection date	*C. maenas* collection date
Anthony's Cove, NB	45°13.733′N	66°00.470′W	16 September	16 September
Lorneville, NB	45°11.499′N	66°08.897′W	15 August	15 August
Maces Bay, NB	45°06.178′N	66°28.594′W	9 July	9 July
St. Andrews, NB	45°04.137′N	67°02.356′W	6 July	6 July
Back Bay, NB	45°02.377′N	66°53.423′W	20 September	20 September
Johnson Bay, ME	44°51.137′N	67°00.289′W	15 July	9 June
West Quoddy Head, ME[b]	44°48.829′N	66°57.061′W	14 July	7 June
Carrying Place Cove, ME	44°48.567′N	66°58.661′W	14 July	11 June
Bailey's Mistake, ME[a]	44°46.466′N	67°03.327′W	15 July	10 June
Cutler, ME	44°39.270′N	67°12.430′W	15 July	12 June
Roque Bluffs, ME[c]	44°36.489′N	67°28.601′W	16 July	14 June
Jonesport, ME	44°31.665′N	67°38.492′W	16 July	15 June
Wyman, ME[c]	44°29.171′N	67°51.135′W	5 July	5 July
Ocean Wood, ME	44°22.602′N	68°01.501′W	16 July	16 June
Seawall, ME[c]	44°14.233′N	68°18.079′W	17 July	17 June
Burnt Cove, ME	44°10.246′N	68°42.524′W	17 July	19 June
South Thomaston, ME	44°01.500′N	69°07.204′W	3 July	20 June
Salt Pond, ME[c]	43°52.790′N	69°29.036′W	3 July	22 June
Land's End, ME[c]	43°43.079′N	70°00.157′W	3 July	23 June
Fortune's Rocks, ME[b,c]	43°25.409′N	70°22.673′W	2 July	25 June
Ogunquit, ME[a,b,c]	43°12.290′N	70°35.426′W	2 July	26 June
Odiorne Point, NH[a,b,c]	43°02.396′N	70°42.898′W	1 July	27 June
Hampton Beach, NH[a,b,c]	42°55.073′N	70°48.059′W	2 July	2 July
Folly Cove, MA[a,c]	42°41.102′N	70°38.502′W	1 July	28 June
Lobster Cove, MA[a,c]	42°33.846′N	70°46.207′W	1 July	29 June
Nahant, MA[a,c]	42°25.687′N	70°55.721′W	30 June	30 June

Note: Sites were varied from semi-sheltered to moderately exposed from wind and waves, and ranged in elevation from intertidal to shallow subtidal. Habitats consisted of boulder fields dominated by the brown algae *Ascophyllum nodosum* and *Fucus* spp. All collections were made in 2003.

[a] Sites where crabs were collected from both intertidal and shallow subtidal.

[b] Sites that were moderately exposed to wind and waves.

[c] Sites where decapod predators, in addition to *C. maenas*, were found intertidally.

Table A2. Summary of line equations used to estimate master and minor claw volume for male crabs

	Master claws			Minor claws			
Site	m	b	r^2	m	b	r^2	n
Anthony's Cove, NB	3.70	−6.63	0.99	3.34	−5.95	0.99	42
Lorneville, NB	3.58	−6.25	0.99	3.41	−6.24	0.99	48
Maces Bay, NB	3.78	−7.02	0.97	3.55	−6.75	0.97	57
St. Andrews, NB	3.65	−6.45	0.99	3.56	−6.74	0.98	64
Back Bay, NB	3.71	−6.76	0.99	3.61	−6.87	0.99	65
Johnson Bay, ME	3.47	−6.02	0.99	3.17	−5.46	0.95	50
West Quoddy Head, ME[b]	3.52	−6.15	0.93	3.39	−6.15	0.87	32
Carrying Place Cove, ME	3.56	−6.27	0.99	3.24	−5.70	0.96	37
Bailey's Mistake, ME[a]	3.61	−6.55	0.96	3.42	−6.31	0.92	61
Cutler, ME	3.56	−6.29	0.99	3.49	−6.47	0.99	35
Roque Bluffs, ME[c]	3.59	−6.36	0.98	3.42	−6.31	0.97	46
Jonesport, ME	3.49	−6.11	0.96	3.51	−6.67	0.94	52
Wyman, ME[c]	3.46	−5.86	0.99	3.36	−6.04	0.99	59
Ocean Wood, ME	3.63	−6.53	0.98	3.27	−5.90	0.88	52
Seawall, ME[c]	3.57	−6.22	0.99	3.39	−6.19	0.96	53
Burnt Cove, ME	3.62	−6.33	0.99	3.47	−6.45	0.99	59
South Thomaston, ME	3.69	−6.59	0.99	3.44	−6.33	0.96	52
Salt Pond, ME[c]	3.67	−6.56	0.98	3.67	−7.20	0.96	47
Land's End, ME[c]	3.58	−6.30	0.96	3.11	−5.21	0.89	46
Fortune's Rocks, ME[b,c]	3.62	−6.36	0.99	3.52	−6.59	0.98	52
Ogunquit, ME[a,b,c]	3.50	−6.01	0.99	3.46	−6.44	0.96	42
Odiorne Point, NH[a,b,c]	3.61	−6.26	0.99	3.51	−6.54	0.98	39
Hampton Beach, NH[a,b,c]	3.39	−5.58	0.99	3.15	−5.36	0.98	35
Folly Cove, MA[a,c]	3.70	−6.76	0.98	3.53	−6.69	0.97	50
Lobster Cove, MA[a,c]	3.69	−6.60	0.98	3.48	−6.44	0.98	49
Nahant, MA[a,c]	3.51	−6.14	0.98	3.46	−6.47	0.99	40
Total							**1264**

Note: Equations show relationship between the dependent variable, claw volume (mm^3), and its covariate, carapace width (mm), for 26 sites in the Gulf of Maine and Bay of Fundy: (log) claw volume = m[(log) carapace width] + b.

[a] Sites where crabs were collected from both intertidal and shallow subtidal.

[b] Sites that were moderately exposed to wind and waves.

[c] Sites where decapod predators, in addition to *C. maenas*, were found intertidally.

Table A3. Summary of line equations used to estimate master and minor claw volume for female crabs

	Master claws			Minor claws			
Site	*m*	*b*	r^2	*m*	*b*	r^2	*n*
Anthony's Cove, NB	3.11	−4.98	0.98	3.00	−4.99	0.99	34
Lorneville, NB	3.29	−5.50	0.98	3.03	−5.07	0.97	41
Maces Bay, NB	3.55	−6.64	0.96	3.49	−6.83	0.95	72
St. Andrews, NB	2.97	−4.46	0.97	3.08	−5.18	0.95	36
Back Bay, NB	3.16	−5.20	0.98	3.08	−5.26	0.97	73
Johnson Bay, ME	2.92	−4.46	0.96	2.90	−4.67	0.95	45
West Quoddy Head, ME[b]	3.05	−4.83	0.98	2.84	−4.50	0.85	43
Carrying Place Cove, ME	3.15	−5.22	0.98	3.11	−5.44	0.97	42
Bailey's Mistake, ME[a]	3.05	−4.88	0.97	2.85	−4.48	0.93	42
Cutler, ME	3.19	−5.34	0.98	3.02	−5.06	0.98	35
Roque Bluffs, ME[c]	3.04	−4.81	0.99	2.91	−4.82	0.97	40
Jonesport, ME	3.00	−4.71	0.97	2.85	−4.54	0.89	52
Wyman, ME[c]	3.11	−4.93	0.99	3.08	−5.24	0.99	57
Ocean Wood, ME	3.26	−5.43	0.98	3.07	−5.27	0.94	49
Seawall, ME[c]	3.28	−5.56	0.97	3.23	−5.86	0.95	49
Burnt Cove, ME	3.29	−5.45	0.98	3.19	−5.73	0.94	42
South Thomaston, ME	3.06	−4.77	0.97	3.03	−5.07	0.99	60
Salt Pond, ME[c]	3.23	−5.38	0.96	3.18	−5.64	0.96	58
Land's End, ME[c]	3.11	−4.92	0.98	3.08	−5.31	0.96	51
Fortune's Rocks, ME[b,c]	3.06	−4.74	0.98	3.17	−5.55	0.95	69
Ogunquit, ME[a,b,c]	3.06	−4.77	0.97	3.01	−5.09	0.97	47
Odiorne Point, NH[a,b,c]	3.00	−4.50	0.98	2.94	−4.78	0.99	40
Hampton Beach, NH[a,b,c]	3.07	−4.75	0.99	3.17	−5.54	0.98	44
Folly Cove, MA[a,c]	3.16	−5.11	0.99	3.13	−5.47	0.98	55
Lobster Cove, MA[a,c]	3.18	−5.18	0.97	3.16	−5.52	0.98	63
Nahant, MA[a,c]	3.30	−5.71	0.97	3.07	−5.28	0.97	45
Total							**1284**

Note: Equations show the relationship between the dependent variable, claw volume (mm^3), and its covariate, carapace width (mm): (log) claw volume = *m*[(log) carapace width] + *b*.

[a] Sites where crabs were collected from both intertidal and shallow subtidal.

[b] Sites that were moderately exposed to wind and waves.

[c] Sites where decapod predators, in addition to *C. maenas*, were found intertidally.

Table A4. Summary of the relationship between shell mass (g) and its covariate, shell length (mm), for *L. obtusata* from all 26 study sites

	(Log) shell mass parameters			
Site	*m*	*b*	r^2	*n*
Anthony's Cove, NB	3.16	−8.45	0.99	41
Lorneville, NB	3.27	−8.68	0.99	21
Maces Bay, NB	3.55	−9.52	0.99	42
St. Andrews, NB	3.28	−8.81	0.99	46
Back Bay, NB	3.07	−8.20	0.99	55
Johnson Bay, ME	3.56	−9.72	0.95	26
West Quoddy Head, ME[b]	3.73	−10.06	0.99	41
Carrying Place Cove, ME	3.40	−9.17	0.99	52
Bailey's Mistake, ME	3.15	−8.54	0.98	41
Cutler, ME	3.40	−9.06	0.99	47
Roque Bluffs, ME[c]	3.31	−8.87	0.98	61
Jonesport, ME	3.16	−8.49	0.99	76
Wyman, ME[c]	3.32	−8.88	0.99	37
Ocean Wood, ME	3.26	−8.72	0.99	44
Seawall, ME[c]	3.11	−8.36	0.98	49
Burnt Cove, ME	3.01	−8.13	0.99	43
South Thomaston, ME	3.21	−8.58	0.98	38
Salt Pond, ME[c]	3.33	−8.88	0.98	44
Land's End, ME[c]	3.06	−8.16	0.99	50
Fortune's Rocks, ME[b,c]	3.33	−8.89	0.99	46
Ogunquit, ME[b,c]	3.23	−8.66	0.99	44
Odiorne Point, NH[b,c]	3.26	−8.68	0.99	46
Hampton Beach, NH[b,c]	3.36	−8.97	0.99	34
Folly Cove, MA[c]	3.12	−8.41	0.99	44
Lobster Cove, MA[c]	3.08	−8.18	0.99	43
Nahant, MA[c]	2.96	−8.01	0.99	49
Total				**1160**

Note: Data were log–log transformed and fit with a linear regression [(log) shell mass = m(log) shell length + b]; $P < 0.0001$ for all regressions.

[b] Sites that were moderately exposed to wind and waves.

[c] Sites where decapod predators, in addition to *C. maenas*, were found intertidally.