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INTRASPECIFIC SHELL VARIATION IN THREE SPECIES OF ROCKY SHORE GASTROPODS FROM HONG KONG: CORRELATIONS AMONG HABITATS AND A COMPARISON WITH TEMPERATE SPECIES

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ABSTRACT

To determine if subtropical gastropods exhibited magnitudes and patterns of intraspecific morphological variation comparable to those of more thoroughly studied temperate species, I collected three species of rocky shore gastropods from a total of eleven intertidal sites along the shores of Hong Kong. Two species were predatory muricids (*Thais clavigera* and *T. leuteostoma*) and the third was a common, herbivorous trochid (*Monodonta labio*). I examined traits sensitive to pollution levels (penis size), traits related to desiccation resistance/susceptibility to dislodgment (aperture area, projected area, shell capacity) and traits related to predation intensity/resistance (number of repaired shell injuries, apertural tooth height, lip thickness, development of shell sculpture, shell weight and occupied volume).

For both *Thais clavigera* and *T. leuteostoma*, masculinized females were more common at Cape d'Aguilar than at any other site, perhaps because of its proximity to major shipping lanes. More samples along Hong Kong's southern shores would be required to substantiate this pattern. For traits where data could be compared quantitatively, both *T. clavigera* and *Monodonta labio* exhibited magnitudes of shell variation comparable to those of temperate species. The frequency of repaired shell injuries also compared favourably with published values for rocky shore species from the North Atlantic. Hence, Hong Kong gastropods did not appear to be unusual in either respect. Of some interest, the relative variability of morphological traits was significantly correlated between *T. clavigera* and *M. labio:* traits more variable in *T. clavigera* also tended to be more variable in *M. labio*. In addition, the species found over a broader range of sites (*T. clavigera*) was most variable, while the species found at the fewest sites (*T. leuteostoma*) was least variable, with *M. labio* in between.

Using regression techniques, I compared shell traits both among populations and among species. Aperture size exhibited the most striking variation among habitats: for both *Thais clavigera* and *Monodonta labio*, populations from more wave exposed shores had proportionally larger apertures. These taxonomically and ecologically distant species thus exhibited similar morphological responses over a wave exposure gradient. Somewhat surprisingly, I found little evidence of correlated responses to variation in predation intensity. In both species, the relative development of defensive attributes was not significantly correlated with shell repair frequency among sites. In addition, the only significant correlation of comparable defensive traits between species was a negative one: thicker lipped *T. clavigera* were generally found on shores with thinner lipped *M. labio*. Thus wave action and predation risk did not appear equally capable of inducing shell variation in these species. The interspecific comparisons revealed that both *T. clavigera* and *M. labio* displayed a remarkably similar weight of shell per unit body weight and per unit shell capacity. Hence, in spite of their different sizes and shapes, these two species invested in roughly equivalent amounts of shell to protect the same body mass or living space.

INTRODUCTION

Most extensive studies of intraspecific variation in the shell morphology of rocky shore gastropods have focused on species from temperate latitudes, mainly muricids (Kincaid 1957; Luckens 1970; Phillips *et al.* 1973; Kitching and Lockwood 1974; Crothers 1985; Appleton and Palmer 1988; Palmer 1990) and littorinids (Newkirk and Doyle 1975; Smith 1981; Johannesson 1986; Seeley 1986; Janson, 1987). A few have examined tropical or subtropical species (Struhsaker 1968; Palmer 1979; Hamilton 1980; Wellington and Kuris 1983; Foin 1989). Coupled with the much higher diversity and relatively lower abundances of tropical species (Vermeij 1978; 1987), one is left with the impression that temperate species are intrinsically more variable morphologically than tropical ones. To address such a question, however, similar sampling intensity and quantitative techniques have to be applied over a comparable range of habitats.

Among rocky shore gastropods exhibiting pronounced intraspecific variation, shell form correlates most commonly with the level of water movement and the intensity of predation by shell-breaking predators (Kitching *et al.* 1966; Struhsaker 1968; Crothers 1985; Johannesson 1986; Etter 1988b) although it may also correlate with growth rate and food availability (Vermeij 1980; Wellington and Kuris 1983; Kemp and Bertness, 1984; Appleton and Palmer 1988). To determine whether subtropical gastropods exhibit comparable magnitudes and directions of intraspecific morphological variation in response to a variable environment, I conducted a quantitative study of such variation in three species of rocky shore gastropods from the shores of Hong Kong: the predatory muricids *Thais clavigera* Küster and *Thais leuteostoma* Holten, and the herbivorous trochid *Monodonta labio* (L.).

MATERIALS AND METHODS

Collection sites

Snails were collected during low tides from a total of eleven sites within five different geographic regions along the shores of Hong Kong between 12 and 21 April 1989.

1. Cape d'Aguilar, exposed (CD1)—114°15'43" E, 22°13'02" N (approximate). *Thais clavigera* and *Monodonta labio* were collected from the upper 75 cm of the *Megabalanus volcano* zone in crevices and on shelves on a steep bedrock shore along the south-east edge of the cape. Because of high swell and a poor low tide, only the upper shore could be collected. *T. leuteostoma* were collected from a high pool where they appeared to have been thrown during storms as no food was available, and the shells appeared bleached compared to those from CD2. This sample of *T. leuteostoma* may not have been representative of those present intertidally.
2. Cape d'Aguilar, intermediate (CD2)—114°15'43" E, 22°13'02" N (approximate). *T. clavigera, T. leuteostoma*, and *M. labio* were collected from the upper 50 cm of the *Megabalanus volcano* zone in crevices and on shelves on a steep bedrock shore at southernmost tip of the cape.
3. Ping Chau, exposed bench (PC1)—114°26'07" E, 22°32'22" N. *T. clavigera* and *T. leuteostoma* were collected at mid shore from among *Tetraclita* on bedrock ledges and crevices at the southernmost end of the island.
4. Ping Chau, high pools (PC2)—114°26'07" E, 22°32'22" N. *T. clavigera* and *T. leuteostoma* were collected from among a dense cover of what appeared to be *Chthamalus* intermingled with articulated coralline algae on a bedrock ledge just above water line of a large tidepool into which waves continued to break even during low tide. Most snails were rapidly growing juveniles and young adults, and hence this sample may not have reflected the adult form in these pools accurately. *M. labio* were sparse here, and only a few individuals were found among a rather larger number of mid and upper shore tide pools examined. Most of those found were small.
5. Hoi Ha Wan, exposed (HH1)—114°20'20" E, 22°28'51" N. *T. clavigera* and *M. labio* were collected from the middle and upper portions of the *Saccostrea* zone from bedrock crevices, boulders, and pools at the northernmost tip of Koon Tsoi Kok, at the eastern edge of the mouth of the bay.
6. Hoi Ha Wan, intermediate (HH2)—114°20'06" E, 22°28'32" N. *T. clavigera* and *M. labio* were collected from the middle of the *Saccostrea* zone on boulders and cobbles along the south-western edge of the first major promontory along the east shore of the bay.
7. Hoi Ha Wan, protected (HH3)—114°20'01" E, 22°28'04" N. *T. clavigera* and *M. labio* were collected from the middle and upper portions of the *Saccostrea* zone among mixed boulders and bedrock along the west edge of the second major promontory along the east shore of the bay.
8. Hoi Ha Wan, very protected (HH4)—114°19'37" E, 22°27'47" N. *T. clavigera* and *M. labio* were collected from among *Saccostrea* on boulders surrounded by sand in front of the village of Hoi Ha.
9. Hoi Sing Wan, exposed (HS1)—114°14'44" E, 22°26'09" N. *T. clavigera* were collected from the middle, and *M. labio* from along the upper edge, of the *Saccostrea* zone on a bedrock headland projecting out into Tolo Harbour.

10. Hoi Sing Wan, protected (HS2)—114°14'36" E, 22°26'06" N. *T. clavigera* were collected from the middle, and *M. labio* from along the upper edge, of the *Saccostrea* zone, on the tip of small point, approximately two-thirds of the way along the north shore between HS1 and the head of the bay.
11. Tai Tan (TT)—114°20'02" E, 22°26'22" N. Only snails at the upper edge of their range were collected from the boulder substratum at this site because the low tide was very poor.

At each site, 50–100 snails of as many sizes as possible were collected by searching intensively over a contiguous area of shore. From this initial sample, a subsample (N = 25–50) was taken which included roughly equal numbers of individuals across the available size range. The goal of this sampling strategy was to ensure an accurate description of the size-dependence of morphological variation at each site. This subsample was selected purely based on size, otherwise it reflected a random sample of phenotypes available on a given shore. Snails not selected for measurement were returned to the shore. Those to be measured were taken to the lab alive.

Identification of *Thais* species

For the most part, *Thais clavigera* and *T. leuteostoma* were easy to distinguish. *T. leuteostoma* generally had larger knobs at the shoulder of the body whorl, e.g., see Figure 6C below, and their shells were both lighter and more uniformly coloured than those of *T. clavigera*. In mature animals, as the name indicates, *T. leuteostoma* also had a characteristic yellowish, cream-coloured aperture whereas *T. clavigera* usually had noticeable dark patches along the outer lip associated with the spiral ribs. Both species, however, exhibited considerable variation in these traits, e.g., see Abe 1985a, particularly among smaller rapidly growing individuals. I found that individuals ambiguous for the above traits could be distinguished most reliably by the numbers and distribution of very fine spiral striae between the most prominent two spiral rows of knobs adjacent to the suture. For *T. clavigera*, the number of striae between the tips of adjacent rows of knobs was usually seven (occasionally up to 9 or 10). *T. leuteostoma*, on the other hand, exhibited twice as many striae between knob rows. The spiral striae of *T. leuteostoma* were also much finer and were repeated axially all the way across the tips of the knobs, whereas those of *T. clavigera* were coarser and were not present in the central 20% of a knob. The reliability of these characters was confirmed among the present samples by examining mature individuals otherwise identifiable unambiguously, based on shell sculpture and colour.

Shell handling, weights, volumes, sexing

Prior to any measurements, shells were cleaned of encrusting organisms, rinsed briefly in fresh water, and allowed to dry. Identifying numbers were written on each shell with a fine-tipped waterproof pen, and coated with cyanoacrylate glue to prevent abrasion.

Two measurements had to be made while the animals were still alive: weight of the whole animal in air (to 1 mg), and the unoccupied volume of the shell (to 1 mg). Prior to measuring whole weight, snails were chased back into their shells with a soft modelling brush and then absorbent tissue was pressed firmly up against the operculum to remove as much extravisceral water as possible. After the outer surface of the shell had dried, snails were weighed on a digital balance.

Unoccupied volume of a shell was measured by weighing the amount of fresh water needed to fill the volume of the shell between the operculum of the living snail and the plane of the aperture. After recording the whole weight of a snail, the balance was tared with the snail on it so that only the added water would be weighed. Fresh water was then introduced into the aperture with a Pasteur pipette while holding the apex downward until the unoccupied volume was filled approximately half way. This prevented bubbles from being trapped around the operculum or up towards the apex if the animal could withdraw very far into the shell. The shell was then positioned on a lump of modelling clay with the plane of the aperture parallel to the surface of the weighing pan. Additional fresh water was introduced into the aperture until the water formed a flat surface (neither bowed nor sagged) flush with the outer lip and the ventral surface of the columella. After the desired flat surface was achieved, the total weight of water added to the aperture was recorded. With care, this method is repeatable to well less than 5% (Palmer 1990). Throughout the paper, 'volumes' are reported as mg of fresh water. These weights may be converted to actual volumes as follows: 1000 mg = 1 ml = 1 cc.

After the weights were completed, snails were placed in boiling water for several minutes, and the flesh extracted from the shells using a curved probe. Snails were sexed either by penis size (*Thais*) or gonad colour (*Monodonta labio*). The size of the penis (if present) was estimated by eye, and both the length and diameter, as a fraction of the right tentacle, were recorded. For *M. labio*, the gonad was either cream coloured or a deep forest green. Microscopic examination of macerated green gonad revealed eggs, so cream-coloured gonads were assumed to be from males.

Shells were dried overnight at 60 °C in a drying oven and weighed to the nearest mg. Flesh dry weights were only measured for a subsample of all three species. After removing the body from the shell as above, the flesh was dried to a constant weight at 60 °C in a drying oven (between 24 and 48 h). These subsamples yielded very accurate reduced major axis (RMA) regressions of Y = log(body dry weight) as a function of X = log(estimated body wet weight) (Fig. 1A; slopes and adjusted means ± SEM; see Statistical analyses for a discussion of model II regression techniques).

Both *Thais* species pooled: RMA slope = 1.0304 (± 0.0231), mean X = 2.9281, expected Y at mean X = 2.3480 (± 0.0068) ($F_{1,45}$= 1949, $P < 0.0001$).
For *Monodonta labio*: RMA slope = 1.0428 (± 0.0467), mean X = 2.8272, expected Y at mean X = 2.0739 (± 0.0125) ($F_{1,16}$= 483, $P < 0.0001$).

Body wet weight for these regressions was estimated by computing the difference between the total weight (shell plus live animal) and shell dry weight. Body dry weights for all remaining animals were estimated using the above regressions.

Total internal volume of a shell (shell capacity) was also only measured for a subsample of snails. To minimize problems with surface tension, 1 or 2 ml of ethyl alcohol was introduced with a Pasteur pipette into a previously dried and weighed shell while holding the apex downwards. While in this position, the apex was snapped with a fingernail to try to dislodge any possible bubbles in the tip of the apex. The shell was then inverted and the alcohol vigorously shaken out. Next, the shell was mostly filled with freshwater while holding the apex down and again snapped with a fingernail to

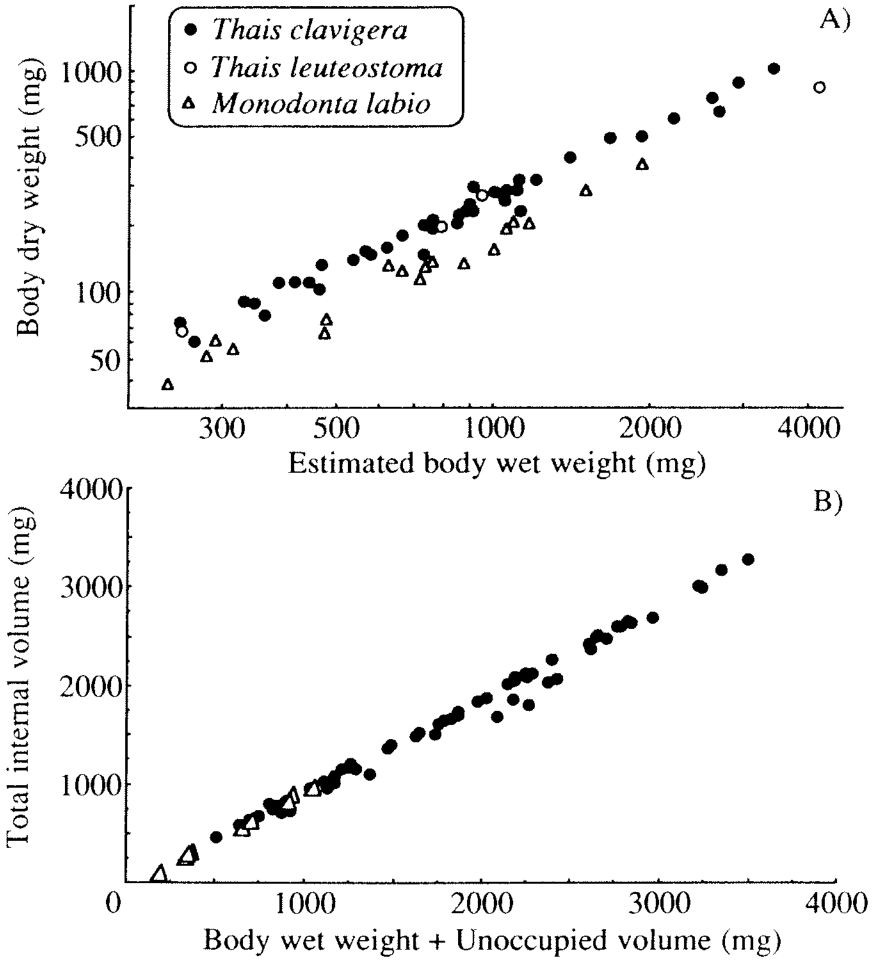

Fig. 1. Subsamples from which estimates of *A*, body dry weight, and *B*, total internal volume of the shell (= shell capacity) were determined for three species of gastropods from Hong Kong. See Materials and Methods for regression equations.

dislodge bubbles. It was then placed on a lump of clay with the apertural plane parallel to the weighing pan of a digital balance, and remainder of the internal volume filled with water as for unoccupied volume. Care was taken not to allow any air to displace water in the apex when positioning the shell on the balance. Total internal volume was calculated by subtracting the shell dry weight from the weight of the shell filled with fresh water. The subsamples also yielded very accurate RMA regressions for Y = total internal volume as a function of X = estimated body wet weight + occupied volume (Fig. 1B; slopes and adjusted means ± SEM).

For both *Thais* species: RMA slope = 0.9466 (± 0.0126), mean X = 1849, expected Y at mean X = 1695.1 (± 9.80) ($F_{1,57}$ = 5626, $P < 0.0001$).
For *Monodonta labio*: RMA slope = 0.9956 (± 0.0174), mean X = 589.2, expected Y at mean X = 562.1 (± 6.05), ($F_{1,7}$= 3271, $P < 0.0001$).

Total internal volume for all remaining snails was estimated via these regressions. Occupied volume was computed simply by subtracting the unoccupied volume, which was measured directly, from the estimate of total internal volume.

Shell morphometrics

Several morphological attributes of shells were selected for measurement because of their utility for inferring functional relationships. In the list below, 'calipers' indicates measurements recorded to the nearest 0.1 mm using Vernier calipers, or to the nearest 0.02 mm with dial calipers (lip thickness only). 'Digitized' indicates measurements obtained by superimposing, via a camera lucida, the image of a shell under a dissecting microscope over that of a calibrated graphics tablet (MacTablet, Summagraphics Corp., Fairfield, CT, USA; 500 × 500 DPI resolution).

Shell length (calipers)—from the apex to tip of the siphonal canal for *Thais*, or from the apex to the distal-most margin of the aperture parallel to the axis of coiling for *Monodonta labio* (repeatable to ± 0.2 mm).

Aperture length (digitized)—from the posterior margin of aperture at the suture to the tip of the siphonal canal for *Thais*, or from the line described by the adapical margin of the aperture adjacent to the suture, to a point perpendicular to this reference line on the abapical margin of the aperture, for *M. labio* [mean % errors ± SEM (N = 10) were 0.7 ± 0.17% and 2.4 ± 0.38% for *T. clavigera* and *M. labio*, respectively].

Aperture area (digitized)—the area described by the outermost margin of the apertural lip and the polished parietal callus when viewed perpendicular to the plane of the aperture [mean % errors ± SEM (N = 10) were 1.8 ± 0.50% and 3.5 ± 0.96% for *T. clavigera* and *M. labio*, respectively].

Apertural tooth height (digitized)—the elevation of the tip of the tooth perpendicular to the inner margin of the aperture when viewed roughly perpendicular to the plane of the aperture (*Thais* only, the tooth heights of *M. labio* were not measured because they were conspicuous in all samples). When present, the heights of the two most abaxial teeth were measured. In specimens where teeth were quite prominent, these teeth were the second and third teeth abapically from the suture; the fourth and fifth teeth were usually larger but were more difficult to orient for accurate measurement.

Lip thickness (calipers)—In *Thais*, lip thickness was measured from a point inside the lip at the location of apertural teeth, to a point outside the lip lying between the two prominent spiral rows of knobs nearest the suture. It was measured from the tip of the apertural tooth at this position if one was present. Before conducting statistical analyses, however, the height of the apertural tooth was subtracted from this measure of total lip thickness. In *M. labio*, lip thickness was measured from a point between the third and fourth apertural teeth adapically from the columella, to a point between the spiral cords on the outer surface of the shell, as perpendicular as possible to the margin of the aperture. Lip thickness was repeatable to ± 0.06 mm.

Projected area (digitized)—Projected area was measured as the total area of the shell when viewed perpendicular to the axis of coiling from the right side of the shell. Shells were attached to an adhesive vertical surface (duct tape attached to a rectangular supporting block) with the axis of coiling perpendicular to the line of sight [mean % errors ± SEM (N = 10) were 1.1 ± 0.27% and 1.1 ± 0.22% for *T. clavigera* and *M. labio*, respectively].

Knob height (digitized)—Knob height was measured as the elevation of the tip of the knob perpendicular to the outer surface of the shell when viewed roughly perpendicular to what would have been the plane of the aperture at the time the knob was being produced (*Thais* only). Two knobs were measured on each individual—the highest two of the first four, proceeding away from the apertural margin, along the row adjacent to the suture. Knobs in this row were generally more pronounced than those in the other, more anterior rows.

Statistical analyses

Statistical analyses were conducted with the microcomputer statistical packages Statview II (Ver. 1.03; descriptive regressions) and SuperANOVA (Ver. 1.01, analysis of covariance), both from Abacus Concepts (Berkeley, California, USA). Slopes from least squares linear regressions (LLR) were converted to reduced major axis slopes (the RMA is one form of model II regression) by dividing them by the correlation coefficient; the standard errors of the slopes remain the same (LaBarbera 1989). The standard errors for adjusted means are not precisely defined for model II regression, so to compare differences among means in the figures, I graphed the standard error for the expected Y at mean X as determined from the LLR analysis. To construct the figures that compare traits among populations, I computed values at a standard size using only the regressions based on individuals from each site as follows:

$$\text{log(standardized value)} = \{[\text{log(standard X)} - \text{log(sample mean of X)}] * \text{RMA slope}\} + \text{log(expected Y at mean X)}$$

These standardized values were detransformed prior to graphing.

Statistical inference of significant differences among populations was complicated for most traits because populations differed not only in their average development of particular traits, but also in their allometric relations (see Appendices I–III). Hence, although averages differences were clearly apparent among populations, the precise value of the differences depended upon the reference size used to compare populations. To avoid potentially misleading patterns that might result when estimating population means using a common slope across all populations when slopes did in fact differ, I computed regressions of functionally related pairs of traits for each population separately rather than with analysis of covariance (ANCOVA). These population-specific regressions were then used to compute expected means at three different sizes for each population. This allowed me to determine to what extent the among-population patterns reported below varied in response to the choice of standard size. Qualitative patterns of variation among populations that depended upon the choice of reference size are noted in the text. All of the population-specific regressions for the traits examined are presented in Appendices I–III.

To examine most patterns of variation among populations, the reference size used was approximately the average size across all populations for each species separately. For traits where quantitative comparisons between species were also relevant, I used a single reference size for all three species which was close to the average for them all.

When examining correlations between characters within species or between species, I computed both a standard parametric correlation coefficient and a non-parametric correlation statistic (Spearman's coefficient of rank correlation; Sokal and Rohlf 1981).

RESULTS

Variation in adult size

I estimated adult size by computing the average shell length of the largest 20% of the sample used for morphometric analyses. Because a roughly uniform distribution of snails was collected across the size range available at each site, this seemed like a reasonable measure of adult size.

Adult size varied significantly among sites for all three species, but was most pronounced for *T. clavigera* (Fig. 2). Of interest, the largest sized adults of both *T. clavigera* and *Monodonta labio* were found at the intermediate sites of Hoi Ha Wan (HH2 and HH3). Also, for *T. clavigera*, the smallest sized adults tended to be found at the most wave-exposed sites (Ping Chau and Cape d'Aguilar).

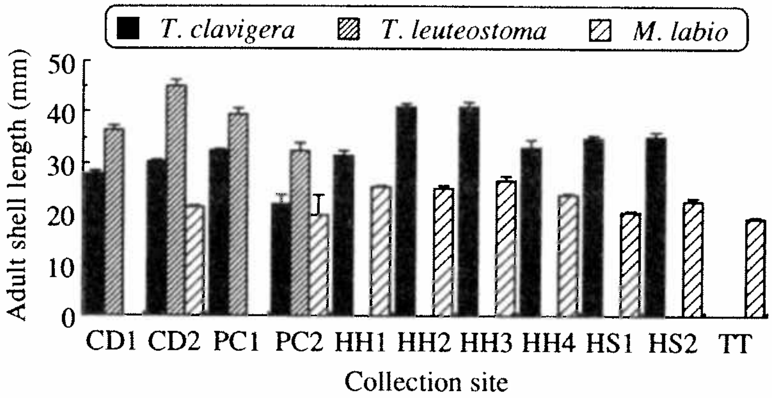

Fig. 2. Average shell length (mean ± SEM) of the largest 20% of each sample of three species of gastropods from 11 sites along the shores of Hong Kong. Sites are ordered roughly in order of decreasing wave exposure (see Materials and Methods for site abbreviations), missing bars indicate no data. Data for PC2 were not included because the sample was unavoidably biased towards smaller snails. See Appendices I–III for sample sizes.

Variation in penis size and sex ratio

Penis size varied in an unexpected manner among the four regions studied (Fig. 3). Among *Thais* from Hoi Sing Wan, Hoi Ha Wan and Ping Chau, penes were either well developed or effectively absent. This pattern was the same whether or not smaller snails were included (compare Fig. 3A with 3B and 3C with 3D). At Cape d'Aguilar the distribution of penis sizes was still bimodal, but the penis size in presumptive females was consistently larger there than at the remaining sites. Significantly, both *T. clavigera* and *T. leuteostoma* exhibited the same pattern.

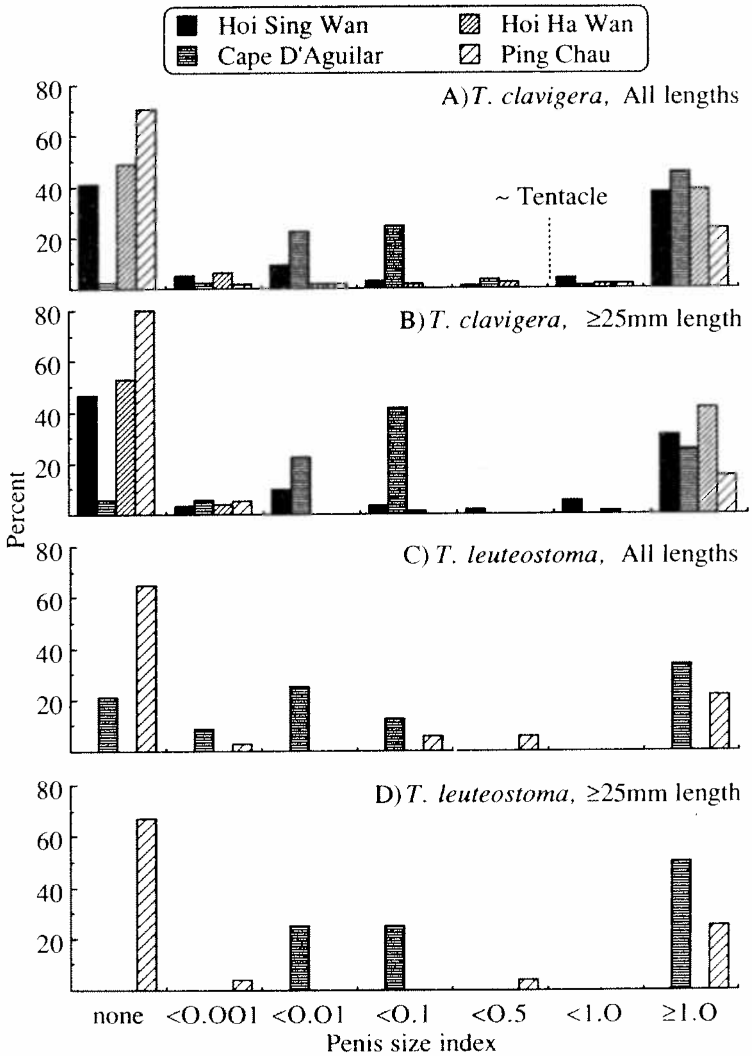

Fig. 3. Frequency distributions of relative penis size in two species of *Thais* from four regions of Hong Kong. Penis size index was computed as [$\pi \cdot (\text{diameter}/2)^2 \cdot$ length]/2, where diameter and length were expressed as proportions of the equivalent dimension of the right tentacle. Index values less than 0.5 indicate a penis whose volume was approximately equal to or less than that of the tentacle. Data were pooled for all sites within each region.

Females were, on average, more common than males in the samples for all three species (Table 1). Sex ratio varied among sites, but departures from 50:50 were only significant at Ping Chau, where females formed a larger proportion of the sample, and at Cape d'Aguilar, where males were more common.

Table 1
Numbers of males and females of three species of rocky shore gastropods collected from various sites around Hong Kong.

	Thais clavigera			*Thais leuteostoma*			*Monodonta labio*		
Site	M	F	?	M	F	?	M	F	?
CD1	21	19	0		2	20			
CD2	34	21	0	8	14	0	0	0	40
PC1	10	30	0	6	16	1			
PC2	3	8	0	6	9	0	3	3	3
HH1	16	21	3				9	19	2
HH2	12	26	2				11	11	8
HH3	27	18	0				12	16	1
HH4	5	14	1				14	9	7
HS1	14	24	0				0	0	24
HS2	20	20	0				0	0	24
TT							1	5	14
All pooled	163	200	6	20	41	22	50	63	123
Chi-square:*		25.5			0.74			4.46	
d.f.:		9			2			3	
P:		0.002			0.69			0.22	

Note: For *Thais,* individuals with a penis that was clearly larger than the right tentacle were considered males, those with no penis or a penis clearly smaller than the right tentacle were considered females. For *M. labio,* sex was determined by gonad colour (see Materials and methods). ?—sex either ambiguous or not sexed. See Materials and Methods for site abbreviations.
*Contingency table analysis on M and F categories only for sites containing ≥ 10 sexed snails.

Variation in shell repair frequency

The incidence of repaired shell injuries varied by several-fold among sites (Fig. 4). For *Thais clavigera,* the average number of injuries per shell varied significantly from 0 to 0.32 (chi-square = 17.6, d.f. = 9, $P = 0.040$). Rather remarkably, the incidence of repairs dropped consistently with decreasing wave exposure among sites in all four regions studied. Only at Ping Chau, however, did there appear to be an overall lower incidence of repair.

Although the incidence of repairs also varied among sites for *Thais leuteostoma* and *Monodonta labio,* these differences were not significant statistically (chi-square = 1.09, d.f. = 3, $P = 0.78$, and chi-square = 9.1, d.f. = 8, $P = 0.33$, respectively). Somewhat surprisingly, there was no concordance of repair frequency between either of these species and *T. clavigera.*

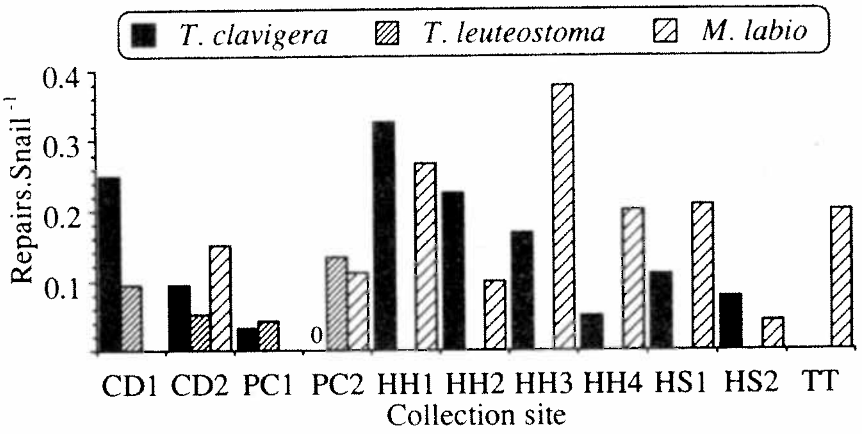

Fig. 4. Average number of repaired shell injuries (total repairs per sample/total snails per sample) for three species of gastropods from 11 sites along the shores of Hong Kong. Sites are ordered roughly in order of decreasing wave exposure (see Materials and Methods for site abbreviations), missing bars indicate no data except where indicated.

Allometric variation

All populations of *Thais clavigera* and *T. leuteostoma*, and all but two populations of *Monodonta labio*, exhibited positive allometry for lip thickness relative to aperture length (Fig. 5A). At all but one site *T. clavigera* exhibited the most pronounced allometry, and it was also the most consistently allometric of the three species (statistically significant in 8 of 10 populations). In addition, three of the seven statistically significant allometries for *T. clavigera*, and two of the three for *M. labio*, occurred at Hoi Ha Wan sites.

In contrast, all populations of *Thais leuteostoma* and *Monodonta labio*, and all but two populations of *T. clavigera*, exhibited negative allometry of aperture size relative to shell capacity (Fig. 5B). *M. labio* exhibited the most consistent allometry (6 of 9 populations significant), whereas that exhibited by *T. clavigera* was somewhat less consistent (5 of 10 populations significant). Among geographic regions, the extent of allometry in *M. labio* tended to increase with increasing wave exposure (Tai Tan → Hoi Sing Wan → Hoi Ha Wan → Ping Chau. The sample from Cape d'Aguilar, however, was not consistent with this trend. Very similar patterns were also exhibited by all three species for aperture size relative to projected area, both within and among geographic regions, although the average allometry exhibited by all three species was somewhat less pronounced (see Appendices I–III).

All three species were approximately isometric for shell dry weight relative to body dry weight, when averaged across all sites (Fig. 5C). The magnitude of allometry, however, varied rather markedly among sites. Although *Thais leuteostoma* and *Monodonta labio* did not exhibit any notable patterns, the allometry of *T. clavigera* varied in a curious way. First, with one exception, allometry increased with decreasing exposure among sites within each of the four geographic regions examined; the exception was HH1. Second, in contrast to the first pattern, the average allometry for each region increased with increasing wave exposure (0.85, 1.04, 1.09 and 1.19 for Hoi Sing Wan, Hoi Ha Wan, Ping Chau and Cape d'Aguilar, respectively).

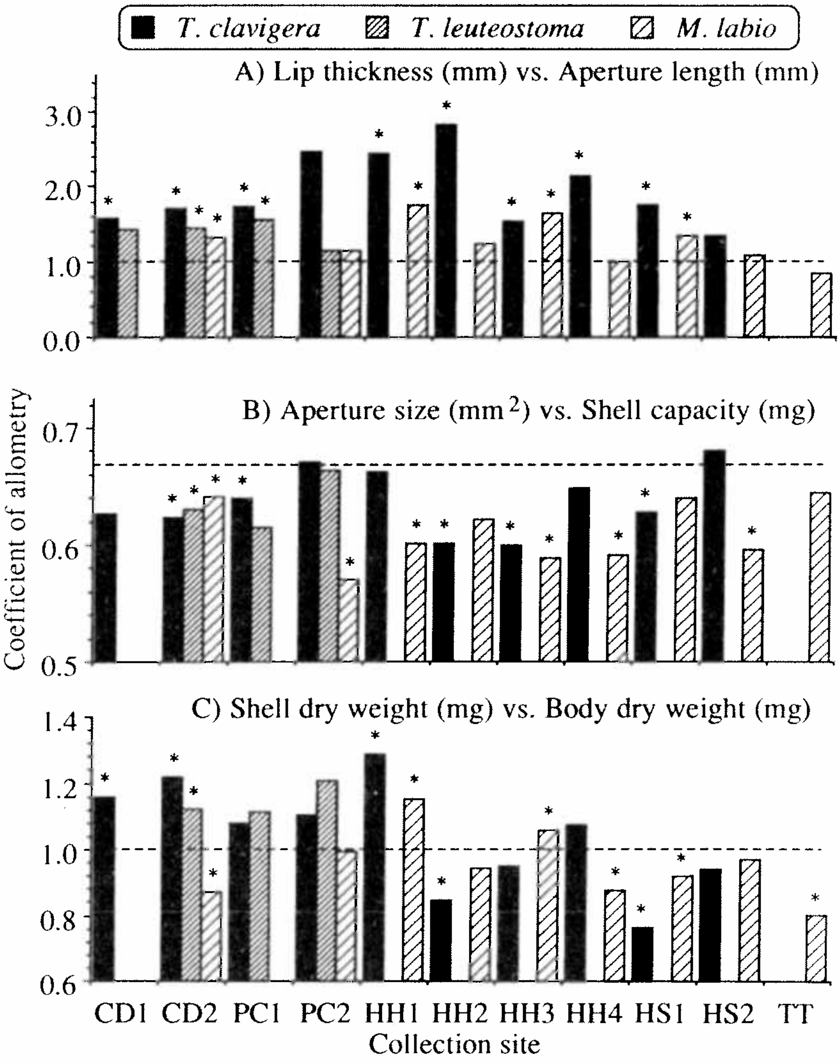

Fig. 5. Coefficients of allometry (RMA slopes) for *A*, apertural lip thickness relative to aperture length; *B*, aperture size relative to shell capacity; and *C*, shell dry weight relative to body dry weight, for three species of gastropods from 11 sites along the shores of Hong Kong. Dashed lines indicate isometry. Asterisks indicate samples exhibiting significant allometry (P <0.05); see Appendices I–III for actual slopes and results of t-tests. Sites are ordered roughly in order of decreasing wave exposure (see Materials and Methods for site abbreviations), missing bars indicate no data.

Variation in antipredatory shell features: tooth height, lip thickness, and knob height

Of the two *Thais* species, only *T. clavigera* consistently exhibited apertural teeth. Only two of 84 *T. leuteostoma* were found with apertural teeth, and in these individuals, teeth were not overly well developed (0.05 and 0.2 mm from HH2 and PC1, respectively). The greatest development of apertural teeth in *T. clavigera* was at HH1 and CD2 (Fig. 6A), but the extent of tooth development did not vary in any notable way, either within or among geographic regions. The lack of apertural teeth at PC2 was probably an artefact of having sampled predominantly juveniles and small adults at this site (see site descriptions in Materials and methods). The least well-developed teeth among the remaining samples were at HH2.

All three species exhibited roughly equivalent variation in lip thickness among sites (Fig. 6B; note that lip thickness did not include apertural tooth height). As for apertural tooth height, lip thickness in *Thais clavigera* was highest at HH1 and CD2, and lowest at HH2. Too few sites yielded *T. leuteostoma* for any patterns to emerge. In *Monodonta labio*, lip thickness tended to increase with decreasing wave exposure not only among sites within geographic regions (Hoi Ha Wan, Hoi Sing Wan), but also among geographic regions (1.14, 1.48, 1.44, 1.50 and 1.56 mm for Cape d'Aguilar, Ping Chau, Hoi Ha Wan, Hoi Sing Wan and Tai Tan, respectively).

Except for unusually well developed knobs in the tidepool sample from Ping Chau (PC2), neither species of *Thais* exhibited very pronounced variation in the development of shell sculpture over the sites examined (Fig. 6C). Nonetheless, both *T. clavigera* and *T. leuteostoma* produced strikingly larger knobs in the Ping Chau pools, suggesting a strong, commonly experienced effect of environment.

Variation in aperture size and shape

All three species exhibited similar patterns of variation in relative aperture size (expressed as aperture area at a given shell capacity): aperture size increased with increasing wave exposure not only among sites within geographic regions (Fig. 7A), but also among geographic regions (Table 2). These patterns were even more pronounced for smaller-sized snails (Fig. 7B, Table 2).

Aperture shape (expressed as apertural area at a given aperture length) did not exhibit such consistent patterns (Fig. 7C). *Thais clavigera* from Cape d'Aguilar and Ping Chau had relatively wider apertures than those from other regions, and *T. leuteostoma* from Cape d'Aguilar had relatively wider apertures than those from Ping Chau. Neither of these species, however, exhibited consistent patterns of variation among sites within regions. Rather strikingly, *Monodonta labio* exhibited no significant variation in aperture shape among sites, even though it did vary in aperture size. This lack of variation was also apparent when adjusted means were computed for either smaller (reference shell length = 13.0 mm) or larger (reference shell length = 23.0 mm) *Monodonta labio* (data not shown; see Appendix III).

Variation in shell weight and occupied volume

Because weights and volumes are less arbitrary than linear dimensions of supposedly comparable features of different species, e.g., shell 'length' and aperture 'length', I was able to compare relative shell weights and occupied volumes quantitatively among

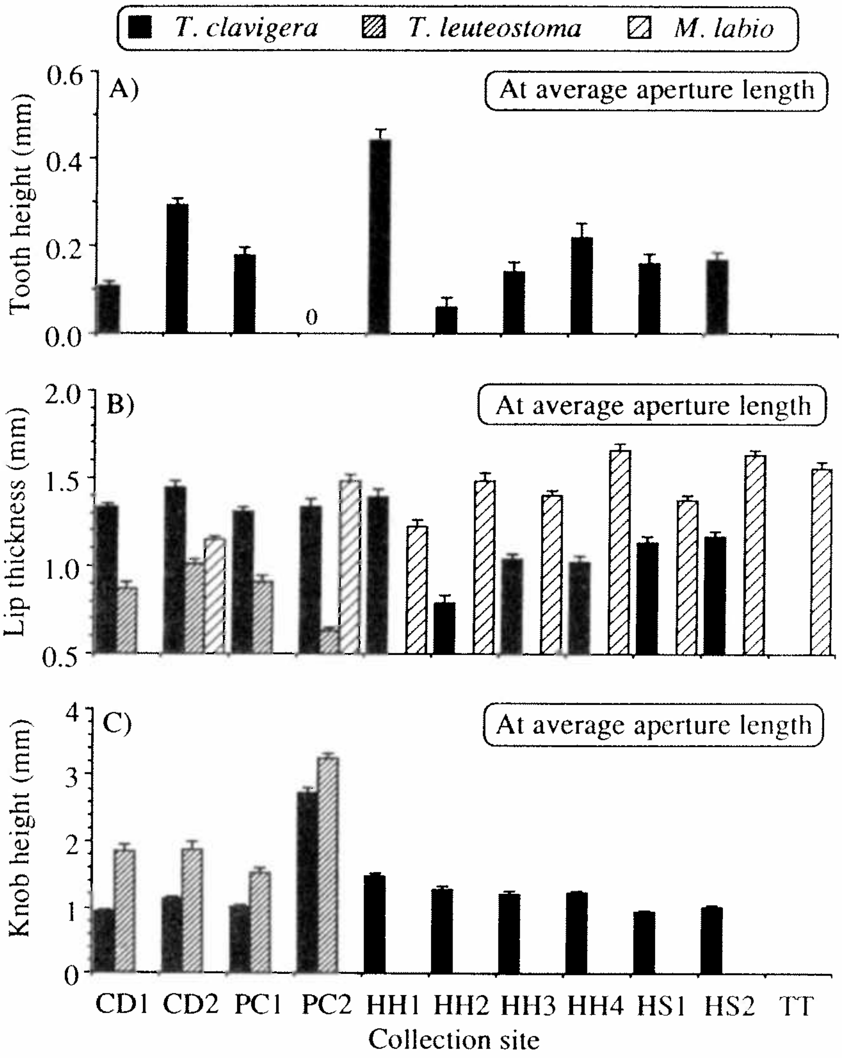

Fig. 6. *A*, average apertural tooth height; *B*, average apertural lip thickness; and *C*, average sculpture height, for three species of gastropods from 11 sites along the shores of Hong Kong. All bars are mean ± SEM for snails at a common aperture length specific to each species (approximately average aperture length: 19.3, 21.3 and 12.2 mm for *Thais clavigera, T. leuteostoma* and *Monodonta labio,* respectively). Sites are ordered roughly in order of decreasing wave exposure (see Materials and methods for site abbreviations), missing bars indicate no data unless noted by a zero. Approximate significance levels from ANCOVA for common slope = 0, equality of slopes among populations, and equality of adjusted means (assuming equal slopes) were as follows. *T. clavigera:* A = <0.001, <0.001, <0.001; B = <0.001, <0.001, <0.001; C = <0.001, <0.001, <0.001; *T. leuteostoma*: B = <0.001, 0.15, <0.001; C = <0.001, 0.30, <0.001; *M. labio*: B = <0.001, <0.001, <0.001. See Materials and Methods for a discussion of the limitations of these analyses.

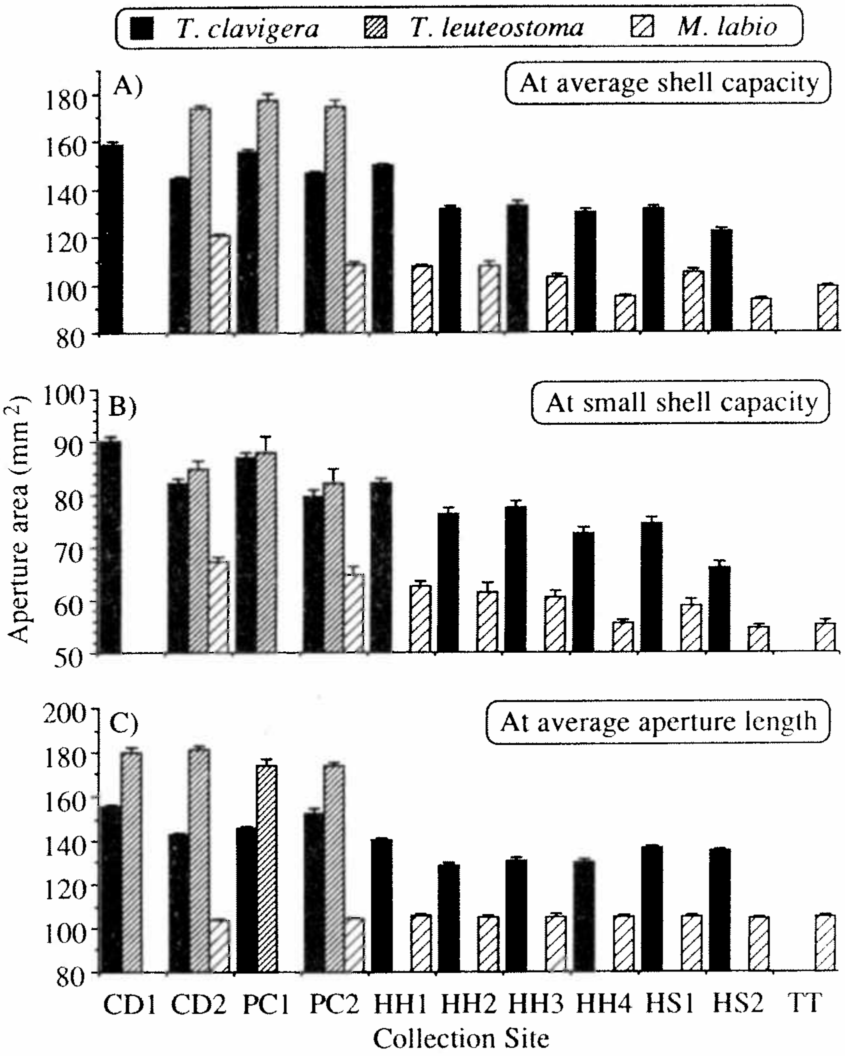

Fig. 7. Variation in apertural traits for three species of gastropods from 11 sites along the shores of Hong Kong. *A*, aperture area at average shell capacity (1215, 1726 and 897 mg for *Thais clavigera*, *T. leuteostoma* and *Monodonta labio*, respectively); *B*, aperture area at small shell capacity (491, 556 and 363 mg for *T. clavigera*, *T. leuteostoma* and *M. labio*, respectively); and *C*, aperture area at average aperture length (19.3, 21.3 and 12.2 mm for *T. clavigera*, *T. leuteostoma* and *M. labio*, respectively). All bars are mean ± SEM. Sites are ordered roughly in order of decreasing wave exposure (see Materials and methods for site abbreviations), missing bars indicate no data. Approximate significance levels from ANCOVA for common slope = 0, equality of slopes among populations, and equality of adjusted means (assuming equal slopes) were as follows. *T. clavigera*: A, B = <0.001, 0.004, <0.001; C = <0.001, 0.07, <0.001; *T. leuteostoma*: A, B = <0.001, 0.64, 0.15; C = <0.001, 0.009, <0.001; *M. labio*: A, B = <0.001, 0.02, <0.001; C = <0.001, 0.18, 0.87. See Materials and Methods for a discussion of the limitations of these analyses.

Table 2

Average aperture area (mm²) at a standardized shell capacity for two sizes of three species of rocky shore gastropods from five geographic regions around Hong Kong.

	Thais clavigera		*Thais leuteostoma*		*Monodonta labio*	
Region	Ave.*	Juv.*	Ave.	Juv.	Ave.	Juv.
Cape d'Aguilar	151.5	86.0	173.5	84.9	120.4	67.4
Ping Chau	149.3	83.4	175.6	85.1	108.7	64.8
Hoi Ha Wan	136.2	77.0			103.4	60.0
Hoi Sing Wan	126.9	70.2			99.5	56.8
Tai Tan					99.0	55.3

Note: Tabled values are averages of the adjusted means from Figure 8A and B.

*The shell capacities at which aperture sizes were compared were computed for each species using the following RMA regressions tabulated in the Appendices: I-144, II-51, and III-112 for *T. clavigera*, *T. leuteostoma* and *M. labio*, respectively. The shell lengths for which 'average' shell capacities were computed were, 27.5, 30.0 and 18.0 mm, while those for 'juvenile' shell capacities were 20.0, 20.0 and 13.0 mm for *T. clavigera*, *T. leuteostoma* and *M. labio*, respectively.

species as well as within species. For these comparisons, I chose a reference value close to the average of the log-transformed values of body dry weight for all species combined (150 mg, actual detransformed mean = 148.2 mg) and shell capacity (1000 mg, actual detransformed mean = 992.8).

In spite of their very different shapes, both *Thais clavigera* and *Monodonta labio* exhibited remarkably similar overall shell weights at a given body weight (Fig. 8A). *T. clavigera*, however, exhibited much more dramatic variation among sites than did *M. labio* (1.77 *vs* 1.18, ratio of maximum to minimum adjusted mean among sites). *T. clavigera* also exhibited a dramatic decline in relative shell weight with decreasing exposure among sites within three of the four regions examined (Ping Chau, Hoi Ha Wan, Hoi Sing Wan), although the pattern was reversed at Cape d'Aguilar. No trend in relative shell weight was apparent among regions, however. Of the three species examined, *T. leuteostoma* produced the least shell per unit body weight, but showed no significant variation among sites.

When expressed as a function of shell capacity, *Thais clavigera* had the heaviest shells of the three species examined (Fig. 8B). Significantly, the pattern of variation among sites was very similar to that exhibited at a standard dry body weight, hence this geographic variation was not primarily a product of variation in relative body size. As before, both *T. leuteostoma* and *Monodonta labio* exhibited only slight variation in shell weight when snails with a common shell capacity were compared. In contrast to Figure 8A, however, both species had comparable shell weights even though their shapes were quite different.

Thais clavigera occupied a larger fraction of the internal shell volume than either *T. leuteostoma* or *Monodonta labio*, both of which were quite similar to each other (Fig. 8C). This fraction of the internal volume actually occupied by a snail also varied significantly among sites for both *T. clavigera* and *M. labio*, although the variation was much more pronounced for *T. clavigera*. The three highest values for *T. clavigera* occurred in the two most wave-exposed regions (Cape d'Aguilar and Ping Chau), but *M. labio* exhibited no noteworthy pattern of variation. Once again, differences among sites for *T. leuteostoma* were not significant.

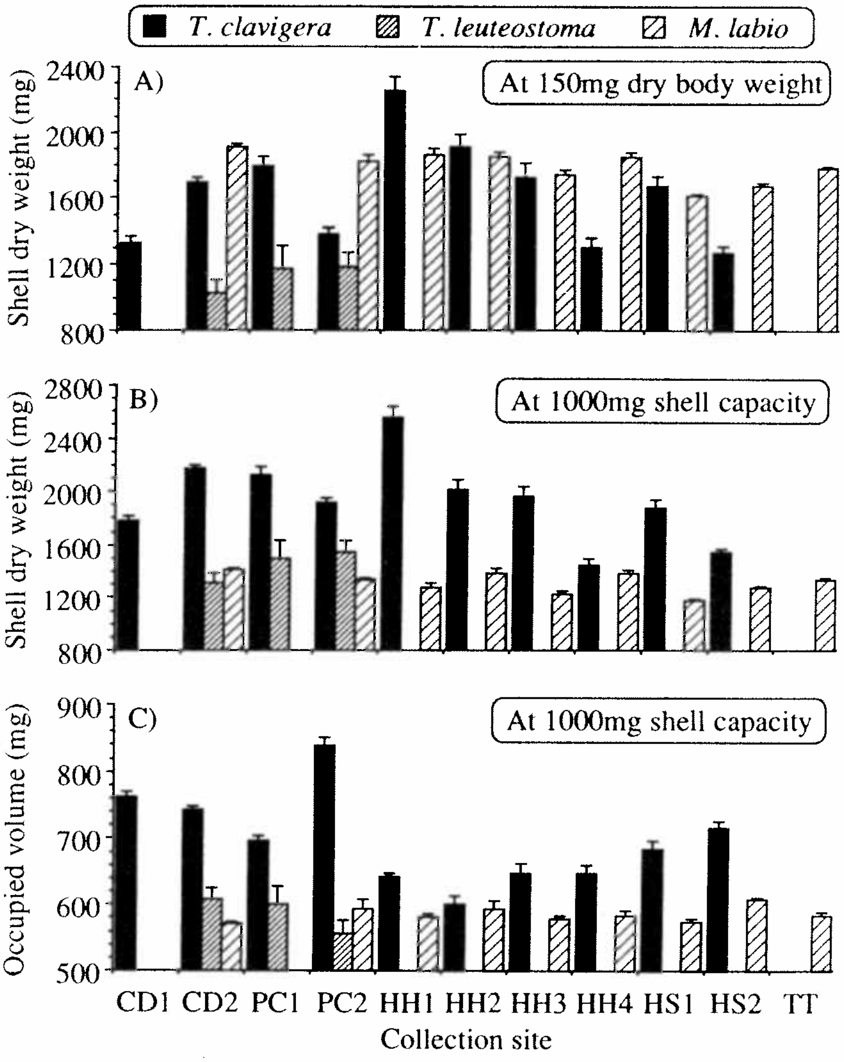

Fig. 8. Variation in relative shell weight and the volume of occupied shell for three species of gastropods from 11 sites along the shores of Hong Kong. *A*, shell dry weight at a common body dry weight (150 mg for all three species); *B*, shell dry weight at a common shell capacity (1000 mg for all three species); and *C*, occupied volume at a common shell capacity (1000 mg for all three species). All bars are mean ± SEM. Sites are ordered roughly in order of decreasing wave exposure (see Materials and methods for site abbreviations), missing bars indicate no data. Approximate significance levels from ANCOVA for common slope = 0, equality of slopes among populations, and equality of adjusted means (assuming equal slopes) were as follows. *Thais clavigera*: A = <0.001, <0.001, <0.001; B = <0.001, <0.001, <0.001; C = <0.001, <0.001, <0.001; *T. leuteostoma*: A = <0.001, 0.88, 0.15; B = <0.001, 0.86, 0.13; C = <0.001, 0.20, 0.14; *Monodonta labio:* A = <0.001, <0.001, <0.001; B = <0.001, <0.001, <0.001; C = <0.001, <0.001, <0.001. See Materials and Methods for a discussion of the limitations of these analyses.

DISCUSSION

Selection of characters and analyses

In any study of morphometric variation, the characters measured and the number of analyses conducted are in principle limited only by one's imagination and patience. In practice, the characters measured and the comparisons conducted should be selected in advance to address particular questions of functional or ontogenetic interest. In this manner, one may avoid drawing unjustified conclusions based upon small numbers of statistically significant associations after having conducted many possible analyses on arbitrary sets of characters. In this study, the characters I chose to measure, and the analyses which I chose to conduct, were selected for the following reasons.

Penis size was measured because increasing evidence suggests that 'masculinization' of female gastropods may be induced by the antifoulant tributyltin (Bryan *et al.* 1986; Gibbs *et al.* 1988).

Shell length was used primarily to provide a description of the 'size' dependence of attributes for all populations in units commonly used in other studies, e.g., see RMA regression equations in Appendices I–III. Although convenient, shell length may not always be a useful descriptor of 'size' (Palmer 1990).

Aperture length was used to scale out size differences for traits functionally or developmentally related to the aperture (apertural tooth height, lip thickness, knob height, aperture area). This avoided potentially confounding effects that might have arisen from using shell length as a general size metric, due to differences commonly observed in the proportional or allometric relations between aperture length and total shell length among populations (Crothers 1985; Palmer 1990).

Aperture area was selected because of its relation to tenacity (Branch and Marsh 1978) and to desiccation resistance (Lowell 1984). Aperture area relative to projected area should approximate the relative susceptibility to dislodgment by moving water: tenacity (proportional to foot area) relative to the maximum drag force experienced (proportional to maximum area in the direction of flow). In addition, aperture area relative to shell capacity should be an index of desiccation resistance: water loss rate (proportional to foot area) relative to water reserve (proportional to the total internal volume of the shell).

Lip thickness and *apertural tooth height* were selected for measurement because they are directly related to vulnerability to attack by shell-peeling crabs (Vermeij 1978; 1982d).

Knob height was measured because such knobs reduce vulnerability to shell-crushing fish (Palmer 1979).

Projected area was measured because it is proportional to the maximum force likely to be experienced by shells in breaking waves (Denny *et al.* 1985).

Shell dry weight was measured because of its general value as a deterrent against shell-breaking predators of all types (Vermeij 1978; Palmer 1979), and also because shell weight at a given body weight should be roughly proportional to the energetic investment in morphological defense.

Body dry weight was measured to allow the relative investment in morphological defense (weight of the shell relative to weight of body) to be compared among populations.

Shell capacity was measured as a component of desiccation resistance and as a means of comparing the relative amount of shell invested in protecting a given volume of living space of a shell.

Occupied volume was measured to compare the relative amount of living space actually occupied by the snail because this may vary in response to environmental stimuli (Palmer 1990).

Masculinization of female *Thais*

The concordant geographic variation in the extent of penis development in presumptive females of *Thais clavigera* and *T. leuteostoma* (Fig. 3) suggests very strongly a common cause. In *Nucella*, masculinization of females is widespread along shores exposed to even very low levels of the antifoulant tributyltin (TBT) (Bryan *et al.* 1986; Gibbs *et al.* 1988). These data thus suggest that Cape d'Aguilar experiences higher levels of TBT than any of the other sites in Mirs Bay or Tolo Channel. Little more can be said, however, without a more thorough survey of masculinization on other Hong Kong shores.

Shell variation: genetic or ecophenotypic?

Patterns of interpopulation morphological variation by themselves are not very informative about the mechanisms responsible for that variation. Consistent differences may arise among populations via at least four pathways: (1), the cumulative effects of selection over several generations coupled with low gene flow among populations; (2), intense selection for a subset of genotypes from a large pool of genotypes arriving in each generation; (3), selective recruitment of particular genotypes to particular habitats; or (4), ecophenotypic effects where even genetically homogenous populations may diverge from each other in response to environmental stimuli.

I think the first mechanism may be rejected for the three species examined here. If *Monodonta labio* and the two *Thais* species studied here are like their congeners, they will have planktonic larval stages (Fretter and Graham 1962; Spight 1976), whose planktonic period will be on the order of one (Fretter and Graham 1962) to two weeks or more (Webber 1977), respectively. Hence it seems unlikely that larvae released by parents from a particular site on the shore would return to that same site.

The second mechanism would also seem unlikely to account for the variation observed here. This mechanism should result in decreased character variance with increasing size, but scatter plots on log-transformed axes revealed that the variation in larger individuals was at least equivalent to, or somewhat larger than, that of smaller ones.

Although I cannot reject the third mechanism—preferential settlement is always possible yet very difficult to detect without reliable genetic markers—I feel that the fourth mechanism, ecophenotypic plasticity, is a more likely explanation for the bulk of the interpopulation variation reported above. Numerous studies have now demonstrated experimentally that gastropod shell shape (Kemp and Bertness 1984; Etter 1988a), shell weight and apertural defenses (Appleton and Palmer 1988; Palmer 1990), and life-history attributes (Crowl and Covich 1990) can all show plasticity in response to environmental stimuli.

Magnitude of shell variation: differences among Hong Kong species

The morphological variability exhibited by the three species examined appeared to depend upon the range of habitats over which they were found. *Thais clavigera* was found at all ten sites which were thoroughly sampled (Tai Tan was not included here because the tide was too poor to determine which species were present), and for all but one character (relative aperture length), it exhibited the broadest range of variation (Table 3). *Monodonta labio* was found at eight of the ten thoroughly sampled sites and was more variable than *T. leuteostoma* for two-thirds of the traits they shared in common. *T. leuteostoma* was found at the fewest number of sites (four) and for the majority of characters examined, it exhibited the least variation. Although the sample size is not large here, these data are consistent with the view that ecological generalists are more morphologically variable than ecological specialists.

Relative character variability also appeared to be correlated between the two species which occurred over the broadest range of habitats: characters which were relatively more variable in *Thais clavigera* also appeared to be relatively more variable in *Monodonta labio* (Fig. 9). For both species, apertural traits (size, shape, and allometry) were relatively less variable than those related to morphological defense (shell weight and lip thickness). Here again, too few species have been examined to draw any strong conclusions. Nonetheless, the proportionally greater variation in defensive attributes compared to those relating to desiccation resistance or tenacity is intriguing, particularly if the bulk of this variation is ecophenotypic. Perhaps selection has been stronger for plasticity in defensive characters than for characters related to physical stresses (but see below).

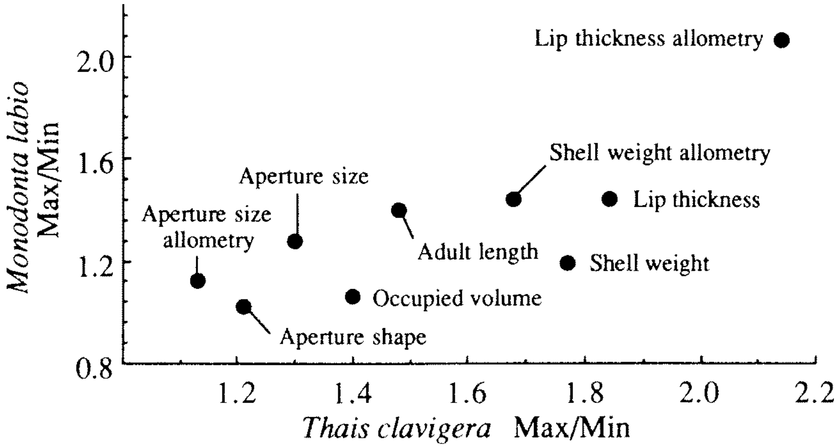

Fig. 9. Association between the relative variability of morphological traits in *Thais clavigera* and *Monodonta labio* ($r = 0.82$, $P = 0.007$, Spearman $P = 0.067$). Each point represents the ratio, for a single trait, of the maximum population mean over the minimum population mean observed among all the sites sampled (data from Table 3).

Table 3

Ranges of morphological variation in three species of rocky shore gastropods from Hong Kong.

Trait	Fig.	*Thais clavigera* Min.	Max.	Max./Min.	*Thais leuteostoma* Min.	Max.	Max./Min.	*Monodonta labio* Min.	Max.	Max./Min.
'Adult' shell length	2	27.9	41.2	1.48	32.4	45.2	1.40	19.1	26.7	1.40
Lip thickness allom.	5A	1.33	2.84	2.14	1.14	1.55	1.36	0.85	1.75	2.06
Aperture area allom.	5B	0.6	0.68	1.13	0.62	0.66	1.06	0.57	0.64	1.12
Shell weight allom.	5C	0.77	1.29	1.68	1.11	1.21	1.09	0.8	1.15	1.44
Tooth height[1]	6A	0.06	0.44	7.33						
Lip thickness[1]	6B	0.79	1.45	1.84	0.63	1.01	1.60	1.15	1.66	1.44
Sculpture height[1]	6C	0.94	2.74	2.91	1.53	3.25	2.12			
Aperture length[2]	—[2]	18.4	20.7	1.13	21.0	21.6	1.03	11.3	13.2	1.17
Aperture size (area)[3]	7A	122.1	158.8	1.30	173.5	176.8	1.02	93.7	120.4	1.28
Aperture shape (area)[1]	7C	128.6	155.3	1.21	174.0	181.4	1.04	103.9	106.1	1.02
Shell weight[4]	8A	1271	2253	1.77	1025	1184	1.16	1610	1908	1.19
Occupied volume[5]	8C	601	839	1.40	556	607	1.09	571	608	1.06

Note: Tabled values are the minimum and maximum adjusted means for each of the three species as depicted in the indicated figures (units as in figures).

[1] At a given aperture length.

[2] At a given shell length, computed from regressions I-112 to I-121 (for *T. clavigera*), II-38 to II-41 (for *T. leuteostoma*), or III-83 to III-91 (for *M. labio*), in the Appendices.

[3] At a given shell capacity.

[4] At 150 mg dry body weight.

[5] At 1000 mg shell capacity.

Magnitude of shell variation: comparison with temperate species

As emphasized in the introduction, most of the extensive studies of morphological variation in marine gastropods have concentrated on temperate species. Unfortunately, lack of a common methodology rather limits the ability to compare quantitatively the extent of intraspecific morphological variation. To conduct a preliminary examination, I computed comparable measures of shell variability for three notoriously variable species of north-temperate *Nucella* upon which I have worked. Rather surprisingly, *Thais clavigera* in the vicinity of Hong Kong exhibited a range of variation nearly equivalent to these species (Table 4). However, the rather impressive magnitude of variation exhibited by *T. clavigera* may not be representative of tropical *Thais*. It is more a subtropical than a tropical species because it appears to be near the southern end of its range in Hong Kong (Abe 1985b).

Allometric variation

The patterns of allometric variation (Fig. 5A–C) were somewhat difficult to interpret. The consistent positive allometry of lip thickness exhibited by all three species (Fig. 5A) occurs commonly in marine gastropods (Vermeij 1980; Palmer 1990). Such allometry could arise if the maximal rate of body growth was limited by the rate of shell deposition (Palmer 1981). If this were the case, however, sites exhibiting the most pronounced allometry should also exhibit the highest occupied volume, because the bodies of rapidly growing snails should have expanded to fill as much of the habitable volume as possible. Yet for both *Thais clavigera* and *Monodonta labio*, sites with the highest lip allometry were associated with relatively low occupied volumes (e.g., in HH1 and HH2). Perhaps the occupied volumes at the time of collection were not representative of differences in growth rates among populations. In addition, none of the three species consistently exhibited any allometry of shell weight relative to body weight (Fig. 5C), further suggesting that the rate of shell production does not limit the rate of body growth in these snails.

Perhaps the most interesting allometry was exhibited by aperture size. On the whole, all three species exhibited proportionally smaller apertures with increasing size (negative allometry, Fig. 5B). This was true even for populations from wave exposed shores where average aperture size was larger (Fig. 7A, B), suggesting that the size-dependence of aperture area was less relevant to tenacity than to some other factors, e.g., desiccation or predation resistance.

Concordant variation of characters within species

Assuming that most of the observed variation reported here arose ecophenotypically (as argued above), concordant variation of characters among populations within a species may reflect: (a), developmentally independent responses of different characters to the same environmental stimuli; (b), developmentally independent responses of different characters to separate but otherwise correlated environmental stimuli; (c), correlated change due to developmental interdependence, either via some form of tradeoff or via linked developmental pathways; or (d), geometric non-independence. I have avoided making any comparisons which might fall in this last category, and have tried to con-

Table 4

Ranges of morphological variation in three temperate species of rocky shore gastropods.

	Nucella lamellosa[1]			*Nucella emarginata*[2]			*Nucella lapillus*[3]		
Trait	Min.	Max.	Max./Min.	Min.	Max.	Max./Min.	Min.	Max.	Max./Min.
Lip thickness (mm)[4]							1.81	3.56	1.97
Aperture length (mm)[4]				13.6	15.7	1.15	16.8	20.3	1.21*
Aperture shape (area, mm^2)[5]				91.4	104.4	1.14			
Shell weight (mg)[6]	2477	5402	2.18	782	1463	1.87	2811	4578	1.63

Note: Tabled values are minimum and maximum adjusted means at roughly average size for each of the three species.

[1] Computed from data partially presented in Appleton and Palmer 1988.

[2] Palmer, unpublished data from 10 sites over a wave exposure gradient in Barkley Sound, BC.

[3] Computed from regressions in Palmer 1990.

[4] At 20 mm (*N. emarginata*), or 25 mm (*N. lapillus*) shell length.

[5] At 14.5 mm aperture length.

[6] At approximately 150 mg dry body weight.

*This value compares quite closely with the range in a much larger data set presented by Crothers (1985; figure 29, excluding the Severn estuary).

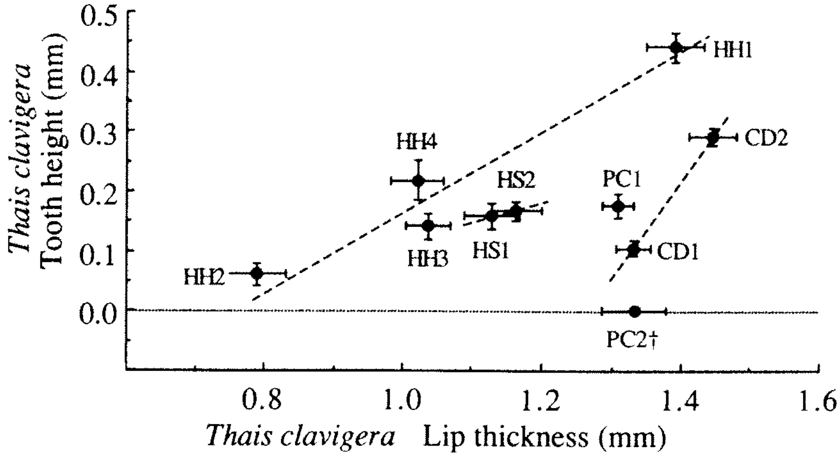

Fig. 10. Correlation between relative apertural tooth height and relative lip thickness in *Thais clavigera* from 10 sites along the shores of Hong Kong (see Materials and methods for site abbreviations; $r = 0.63$, $P = 0.07$, Spearman $P = 0.11$). Each point represents the mean ± SEM along each axis for a single collection site (data from Fig. 6A, B). Note that lip thickness does not include the height of apertural teeth. The sample from PC2 (identified by †) was excluded from the analysis because it was biased towards younger, more rapidly growing snails where teeth were less likely to develop. Note that within each region (Hoi Sing Wan, Hoi Ha Wan and Cape d'Aguilar), tooth height was also positively correlated with lip thickness (*dashed lines*).

centrate on characters of particular functional significance (lip thickness, apertural tooth height, aperture area) or characters that showed substantial variation among populations (shell weight, occupied volume; see Table 3).

In *Thais clavigera*, populations with thicker lips tended to have larger apertural teeth, although the association was not quite significant statistically (Fig. 10). Note that the same pattern was evident among sites within the three regions having reliable tooth-height measurements. Thus, the positive association between tooth height and lip thickness does seem valid. Because these characters are geometrically independent (see Materials and methods), and because both are intimately associated with reducing vulnerability to predation by shell breaking crabs (Vermeij 1978), this correlation seems most likely to be a product of mechanisms (a) or (c).

For both *Thais clavigera* and *Monodonta labio*, lip thickness was also positively correlated with occupied volume (a measure of relative body size; Fig. 11A). Although these correlations could have arisen if thicker lips cramped the internal volume of the shell forcing the body to occupy a larger fraction of this space (mechanisms (c) or (d)), the expected negative correlation between relative shell weight and occupied volume did not materialize ($r = 0.14$, $P = 0.71$, N = 10 for *T. clavigera* and $r = 0.11$, $P = 0.78$, N = 9 for *M. labio*; both estimated at a common shell capacity of 1000 mg). Hence, neither mechanism (c) nor (d) seems likely to account for these correlations. In addition, these correlations are the reverse of what would be expected based on studies of predator induction: experimentally induced thicker lips are associated with a *decreased* occupied volume in both *Nucella lamellosa* and *N. lapillus* (Appleton and Palmer 1988;

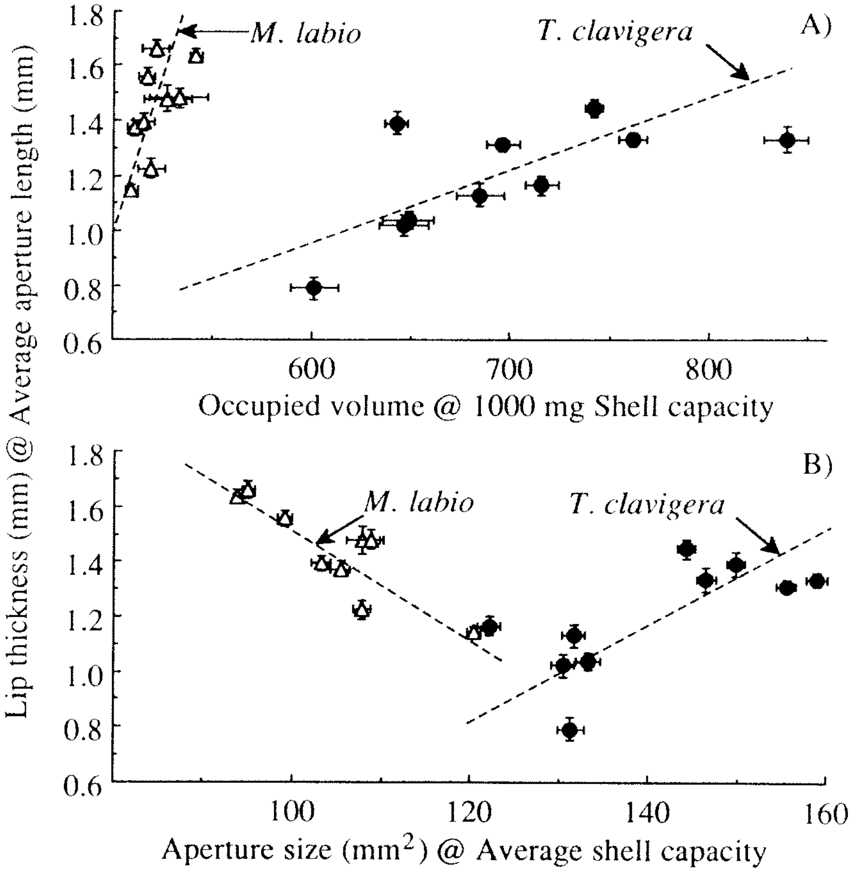

Fig. 11. *A*, correlation between relative lip thickness and relative occupied volume in *Thais clavigera* and *Monodonta labio* from 10 and 9 sites respectively along the shores of Hong Kong. Each point represents the mean ± SEM along each axis for a single collection site (data from Figs. 6B and 8C). For *T. clavigera*, $r = 0.71$, $P = 0.031$, Spearman $P = 0.090$; for *M. labio*, $r = 0.62$, $P = 0.078$, Spearman $P = 0.053$); *B*, correlation between relative lip thickness and relative aperture size in the same samples of *T. clavigera* and *M. labio*. The data are from Figs. 6B and 7A. For *T. clavigera*, $r = 0.69$, $P = 0.028$, Spearman $P = 0.053$; for *M. labio*, $r = 0.87$, $P = 0.002$, Spearman $P = 0.044$. Note that lip thickness does not include the height of apertural teeth. Dashed lines were fitted by eye.

Palmer 1990). Thus a correlated response to common environmental stimuli associated with predation by crabs (mechanism (a)) also does not seem likely. Taken together, these patterns suggest that lip thickness and occupied volume reflect independent responses to separate but correlated features of the environment (mechanism (b), e.g., growth rate or food availability, and predation intensity).

Curiously, the association between lip thickness and aperture size differed between *Thais clavigera* and *Monodonta labio* (Fig. 11B): larger apertured populations of *T. clavigera* tended to have thicker lips whereas lip thickness decreased with increasing aperture size in *M. labio*. For both species, larger apertures were associated with increased wave exposure (Fig. 7A, Table 2; see also Fig. 12 below), thus for some reason *T. clavigera* produced thicker lips and *M. labio* thinner lips on more wave exposed shores. Mechanisms (a), (c) and (d) all seem unlikely causes because they would generate parallel patterns in both species. Thus these contrasting correlations most likely reflect some other differences in the biology of these two species. Since *T. clavigera* is a predator of oysters and small bivalves (Taylor 1980) while *M. labio* is presumably a microherbivore like other trochids, and since these species have very different shell microstructures, most notably extensive development of nacre in *M. labio* (personal observation), many explanations for these contrasting patterns are possible.

Concordant morphological variation of sympatric species across environments

As with correlations among characters within species, many possible correlations could have been examined between species. However, I chose to analyze only four characters shared by *Thais clavigera* and *Monodonta labio* for interspecific correlations. Two of these exhibited consistent associations across habitats within species (aperture size and lip thickness), and two exhibited a particularly high range of variation (shell weight and occupied volume; Table 3). These seemed the most interesting to examine because either the presence or absence of correlations would be informative. Unfortunately, the third species, *T. leuteostoma,* was not found at enough sites to include in these analyses.

Table 5

Summary of the strength and direction of association of shell traits with two major aspects of the environment in two species of rocky shore gastropods from Hong Kong.

		Wave exposure[1]			Crab predation intensity[2]		
Trait	Fig.	*T. clav.*	*T. leut.*	*M. labio*	*T. clav.*	*T. leut.*	*M. labio*
'Adult' shell length	2	–	?	?	?	?	?
Tooth height[3]	7A	?	x	x	?	x	x
Lip thickness[3]	7B	?	?	—	+/?	–	?
Sculpture height[3]	7C	–/?	–	x	?	–	x
Aperture size (area)[4]	8A	+++	0	+++	?	0	?
Aperture shape (area)[3]	8C	?	+	0	?	?	0
Shell weight[5]	9A	+	0	?	+/?	0	?
Occupied volume[6]	9C	?	0	?	–/?	0	?

[1] Qualitative ranking of regions by wave exposure: Cape d'Aguilar > Ping Chau > Hoi Ha Wan > Hoi Sing Wan > Tai Tam. Within each region, seaward sites were considered relatively more exposed.

[2] Predation intensity assumed to be proportional to incidence of repaired shell injuries (Fig. 4).

[3] At a given aperture length.

[4] At a given shell capacity.

[5] At 150 mg dry body weight.

[6] At 1000 mg shell capacity.

+++ = strong and consistent positive association; + = weak or less consistent positive association; 0 = no significant differences among sites; – = weak or less consistent negative association; — = strong and consistent negative association; ? = association ambiguous; x = not applicable. Covariates used to compare traits given in figures listed.

Although lip thickness exhibited the greatest range of variation of characters shared by all three species (Table 3, excluding allometric variation), and also exhibited a consistent negative association with wave exposure at least in *Monodonta labio* (Table 5), it exhibited only a weak negative correlation between *Thais clavigera* and *M. labio* (r = 0.59, P = 0.13, N = 8, Spearman P = 0.14; data not shown). As suggested in the preceding section, this negative correlation may be a product of differences between these two species in the biology of feeding and growth or of shell production. Additional information is needed before any conclusions can be drawn. Neither of the other two shared characters which showed substantial variation were significantly correlated between *T. clavigera* and *M. labio* (shell weight at a common body dry weight: r = 0.30, P = 0.48, N = 8, Spearman P = 0.17; occupied volume at a common shell capacity: r = 0.26, P = 0.54, N = 8, Spearman P = 1.0).

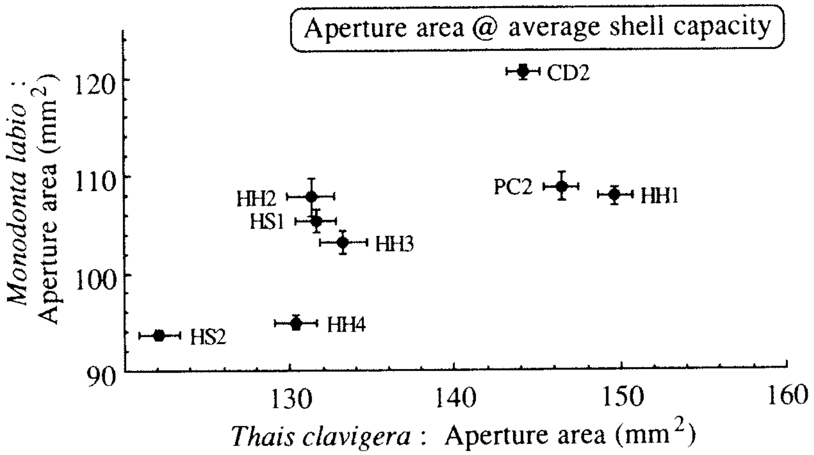

Fig. 12. Concordant variation in relative aperture size between *Thais clavigera* and *Monodonta labio* among the eight sites sampled in Hong Kong (r = 0.72, P = 0.042, Spearman P = 0.096). Each point represents the mean ± SEM along each axis for a single collection site (data from Fig. 7A).

Relative aperture size, the trait which was most consistently associated across environments within species (Table 5), was also significantly correlated between species (Fig. 12): shores harboring large apertured *Thais clavigera* also harbored large apertured *Monodonta labio*. The occurrence of larger apertured populations on more wave exposed shores is a common pattern in rocky-shore gastropods (Vermeij 1973; Crothers 1985; Seeley 1986). The fact that these two species should exhibit concordant variation in aperture size, despite their distinctive taxonomy and ecology, suggests that water movement is an environmental force with an influence on shell form that transcends taxonomic and ecological considerations.

Phenotypic correlations with incidence of shell repair

Although the incidence of repaired shell injuries varied substantially among populations, from a low of none, to a high of 0.38 repairs per individual (Fig. 4), the overall average incidence of repair was quite comparable among species (mean ± SEM: 0.13 ± 0.033, 0.08 ± 0.021, and 0.18 ± 0.033 for *Thais clavigera*, *T. leuteostoma* and *Monodonta labio*, respectively). These frequencies compared favourably to those observed in *Nucella lapillus* (Vermeij 1982a) and *Littorina littorea* (Vermeij 1982b) from the North Atlantic. Hence, relative to other species from rocky shores, snails from Hong Kong appear to have a similar probability of experiencing and surviving a crab attack.

In spite of the roughly tenfold variation among sites, differences in predation intensity accounted for very little of the observed interpopulation shell variation. To obtain an overall index of crab predation intensity, I pooled the repair frequencies across species on the assumption that, within any particular habitat, each of these species was equally likely to be attacked, and proportionally likely to survive the attack. None of the traits considered likely *a priori* to respond to crab predation intensity exhibited significant associations with repair frequency for either *Thais clavigera* or *Monodonta labio*: apertural tooth height ($r = 0.34$, $P = 0.37$, N = 9, Spearman $P = 0.99$; *T. clavigera* only, PC2 excluded), lip thickness ($r = 0.10$, $P = 0.77$, N = 10, Spearman $P = 0.81$, and $r = -0.36$, $P = 0.34$, N = 9, Spearman $P = 0.30$ for *T. clavigera* and *M. labio*, respectively), shell weight ($r = 0.55$, $P = 0.10$, N= 10, Spearman $P = 0.22$, and $r = 0.16$, $P = 0.68$, N = 9, Spearman $P = 0.67$ for *T. clavigera* and *M. labio*, respectively), and occupied volume ($r = -0.48$, $P = 0.16$, N = 10, Spearman $P = 0.14$, and $r = -0.46$, $P = 0.26$, N = 9, Spearman $P = 0.67$ for *T. clavigera* and *M. labio*, respectively). Either, (a), larger sample sizes are required to describe the variation of repair frequency among sites more accurately; (b), repair frequency is a poor indicator of predation intensity in certain situations (Vermeij 1982c); or (c), the bulk of shell variation observed in *T. clavigera* and *M. labio* is not in response to different levels of predation. In view of the rather substantial variation observed in these species, this topic would seem worthy of further study.

CONCLUSIONS

To my surprise, in spite of considerable variation in many morphological traits, the only particularly striking association between shell form and environment revealed by this study was between aperture area and wave exposure (Figs. 7A, B and 12; Table 2). As discussed above, this pattern is common in other species of gastropods and its existence in two taxonomically and ecologically distant species suggests that wave action is a significant agent of selection on Hong Kong shores.

I find it puzzling, however, that traits related to predation resistance exhibited so little correlation between species or among environments. The incidence of repaired shell injury is sufficiently high to suggest that shell-breaking predators are an important source of gastropod mortality on Hong Kong shores (Fig. 4). In addition, studies of shell variation in temperate rocky shore gastropods have revealed that shell form may change quite rapidly in response to increased predation risk (Vermeij 1982a; Seeley 1986), a large fraction of which may be ecophenotypic (Appleton and Palmer 1988; Palmer 1990).

Part of the explanation may lie in the assumptions I have made. First, I have assumed, based on the evidence for extensive plasticity in temperate species (Vermeij 1980; Kemp and Bertness 1984; Appleton and Palmer 1988; Palmer 1990), that most of the variation observed among sites would be ecophenotypic. Perhaps this is valid for *Thais clavigera*, as muricids are commonly quite variable, but not for *Monodonta labio*. More information is needed about the length of planktonic development in these species. The lack of concordance between them does not mean that neither is responding to predation risk, only that one of them is not.

Second, I have assumed that both *T. clavigera* (a predatory muricid) and *M. labio* (an herbivorous trochid) would show similar responses to predation risk. The negative correlation between these species in lip thickness (Fig. 11A), a well-defined antipredatory trait (Vermeij 1987), immediately suggests this assumption is invalid. Perhaps the system for cueing to predation risk that has evolved in muricids is only weakly developed or absent in trochids. Laboratory experiments examining the relative responsiveness of these two species to risk stimuli would be most informative.

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APPENDICES

These appendices include the descriptive regressions used to generate standardized values for *Thais clavigera* (Appendix I), *T. leuteostoma* (Appendix II) and *Monodonta labio* (Appendix III) in the figures and tables in the text. For each regression, sites are ordered roughly in order of increasing wave exposure. For each species, regressions are ordered alphabetically by X and then Y variables. For each character pair examined in each species, a separate regression was computed for each site, i.e., slopes differed too often among sites to justify using pooled slopes from ANCOVA. See Materials and methods for details of measurement and Discussion for a justification of the variables analyzed.

Abbreviations: Regr. #—number of the regression as referred to in the text; Site—see Materials and methods for site abbreviations (All = regression computed on data for all sites pooled); N—sample size; Min., Max.—minimum and maximum *untransformed* values for the X variate; Mean—mean of the X variates actually used to compute the regression (may or may not be log-transformed); Least Sq. Linear Regr.—results from a least squares linear regression [Slope (standard error of slope), *r*—correlation coefficient]; Expected Y @ Mean X—Y value predicted from the least-squares linear regression at the mean value for X (standard error of expected Y); RMA slope—reduced major axis slope for a model II regression (= least-squares linear regression slope/r, see Statistical analyses section in Materials and methods); Ts Allom.—Student's *t* value for the difference between the observed RMA slopes and those expected for isometry (see Statistical analyses section in Materials and Methods).

APPENDIX I

Thais clavigera.

Regr. #	Site	N	X-Axis Min.	X-Axis Max.	X-Axis Mean	Least Sq. Linear Regr. Slope (SEM)	*r*	Expected Y @ Mean X (SEM)	RMA Slope	Ts Allom.
X = log (Aperture length, mm), Y = log (Aperture area, mm^2)										
I-01	HS1	38	14.1	24.5	1.296	2.062 (0.0544)	0.988	2.159 (0.0035)	2.087	1.60
I-02	HS2	40	13.3	25.3	1.281	2.064 (0.0409)	0.993	2.123 (0.0030)	2.079	1.92
I-03	HH1	40	10.2	23.2	1.234	2.009 (0.0370)	0.994	2.046 (0.0033)	2.021	0.57
I-04	HH2	37	16.5	28.5	1.327	2.167 (0.0551)	0.989	2.201 (0.0040)	2.191	3.47
I-05	HH3	44	11.6	29.7	1.333	2.013 (0.0341)	0.994	2.216 (0.0033)	2.025	0.74
I-06	HH4	19	12.3	26.2	1.240	2.029 (0.0518)	0.995	2.023 (0.0050)	2.039	0.76
I-07	PC1	40	10.1	24.6	1.256	2.153 (0.0388)	0.994	2.100 (0.0035)	2.166	4.28
I-08	PC2	11	11.9	17.0	1.151	2.233 (0.2343)	0.954	1.870 (0.0110)	2.341	1.45
I-09	CD1	40	14.6	22.4	1.260	2.033 (0.0630)	0.982	2.139 (0.0030)	2.070	1.12
I-10	CD2	55	8.8	22.5	1.201	2.055 (0.0298)	0.995	1.981 (0.0030)	2.065	2.19
X = log (Aperture length, mm), Y = log (Aperture width, mm)										
I-11	HS1	38	14.1	24.5	1.296	1.053 (0.0438)	0.970	1.000 (0.0025)	1.086	1.95
I-12	HS2	40	13.3	25.3	1.281	1.029 (0.0271)	0.987	0.988 (0.0020)	1.043	1.57
I-13	HH1	40	10.2	23.2	1.234	1.039 (0.0296)	0.985	0.947 (0.0028)	1.055	1.85
I-14	HH2	38	16.5	28.5	1.325	1.233 (0.0400)	0.981	1.008 (0.0030)	1.257	6.42
I-15	HH3	44	11.6	29.7	1.333	1.136 (0.0302)	0.985	1.019 (0.0028)	1.153	5.08
I-16	HH4	19	12.3	26.2	1.240	1.064 (0.0389)	0.989	0.923 (0.0038)	1.076	1.95
I-17	PC1	40	10.1	24.6	1.256	1.179 (0.0373)	0.981	0.976 (0.0035)	1.202	5.41
I-18	PC2	11	11.9	17.0	1.151	1.247 (0.1680)	0.927	0.837 (0.0078)	1.345	2.05
I-19	CD1	40	14.6	22.4	1.260	1.064 (0.0609)	0.943	1.009 (0.0028)	1.128	2.11
I-20	CD2	55	8.8	22.5	1.201	1.100 (0.0327)	0.977	0.919 (0.0030)	1.126	3.85
X = log (Aperture length, mm), Y = log (Knob height, mm)										
I-21	HS1	38	14.1	24.5	1.296	0.136 (0.1595)	0.140	−0.013 (0.0100)	0.971	−0.18
I-22	HS2	40	13.3	25.3	1.281	0.829 (0.1533)	0.659	−0.005 (0.0118)	1.258	1.68
I-23	HH1	40	10.2	23.2	1.234	0.732 (0.1261)	0.686	0.119 (0.0113)	1.067	0.53
I-24	HH2	40	16.5	28.5	1.323	−0.021 (0.1690)	0.020	0.149 (0.0118)	1.050	−0.30
I-25	HH3	45	11.6	29.7	1.328	0.290 (0.1230)	0.339	0.121 (0.0123)	0.855	−1.18
I-26	HH4	20	12.3	26.2	1.238	0.483 (0.1720)	0.552	0.049 (0.0158)	0.875	−0.73
I-27	PC1	40	10.1	24.6	1.256	0.717 (0.1362)	0.650	−0.028 (0.0123)	1.103	0.76
I-28	PC2	11	11.9	17.0	1.151	2.218 (0.5126)	0.822	0.076 (0.0238)	2.698	3.31
I-29	CD1	40	14.6	22.4	1.260	0.599 (0.3017)	0.306	−0.078 (0.0135)	1.958	3.17
I-30	CD2	55	8.8	22.5	1.201	0.494 (0.1313)	0.459	−0.038 (0.0125)	1.076	0.58

Appendix I (cont.)

Regr.			X-Axis			Least Sq. Linear Regr.		Expected Y @	RMA	Ts
#	Site	N	Min.	Max.	Mean	Slope (SEM)	r	Mean X (SEM)	Slope	Allom.
X = log (Aperture length, mm), Y = log (Lip thickness excluding teeth, mm)										
I-31	HS1	38	14.1	24.5	1.296	0.983 (0.2405)	0.563	0.072 (0.0148)	1.746	3.08
I-32	HS2	40	13.3	25.3	1.281	0.802 (0.1721)	0.603	0.061 (0.0133)	1.330	2.01
I-33	HH1	40	10.2	23.2	1.234	2.112 (0.1968)	0.867	0.018 (0.0175)	2.436	8.17
I-34	HH2	40	16.5	28.5	1.323	2.379 (0.2513)	0.838	0.005 (0.0175)	2.839	7.72
I-35	HH3	45	11.6	29.7	1.328	1.333 (0.1151)	0.870	0.082 (0.0113)	1.532	5.28
I-36	HH4	20	12.3	26.2	1.238	1.909 (0.2293)	0.891	–0.092 (0.0210)	2.143	5.43
I-37	PC1	40	10.1	24.6	1.256	1.620 (0.0969)	0.938	0.067 (0.0088)	1.727	7.95
I-38	PC2	11	11.9	17.0	1.151	1.320 (0.6936)	0.536	–0.206 (0.0318)	2.463	2.11
I-39	CD1	40	14.6	22.4	1.260	0.997 (0.1976)	0.634	0.085 (0.0088)	1.573	3.18
I-40	CD2	55	8.8	22.5	1.201	1.294 (0.1521)	0.760	0.017 (0.0143)	1.703	5.72
X = Aperture length (mm), Y = Tooth height (mm)										
I-41	HS1	38	14.1	24.5	20.0	–0.002 (0.0079)	0.035	0.198 (0.0220)	0.057	
I-42	HS2	40	13.3	25.3	19.4	–0.003 (0.0049)	0.107	0.170 (0.0165)	0.028	
I-43	HH1	40	10.2	23.2	17.5	0.047 (0.0074)	0.716	0.323 (0.0250)	0.066	
I-44	HH2	40	16.5	28.5	21.3	0.022 (0.0056)	0.534	0.144 (0.0193)	0.041	
I-45	HH3	45	11.6	29.7	21.8	0.013 (0.0049)	0.370	0.229 (0.0215)	0.035	
I-46	HH4	20	12.3	26.2	17.7	0.037 (0.0084)	0.715	0.134 (0.0328)	0.052	
I-47	PC1	40	10.1	24.6	18.4	0.022 (0.0060)	0.523	0.138 (0.0203)	0.042	
I-48	PC2	11	11.9	17.0	14.2	0.000 (0.0000)	1.000	0.000 (0.0000)	0.000	
I-49	CD1	40	14.6	22.4	18.3	0.001 (0.0074)	0.017	0.048 (0.0138)	0.059	
I-50	CD2	55	8.8	22.5	16.2	0.024 (0.0046)	0.588	0.168 (0.0150)	0.041	
X = log (Body dry wt., mg), Y = log (Shell dry wt., mg)										
I-51	HS1	38	70	596	2.396	0.695 (0.0533)	0.908	3.392 (0.0113)	0.765	–4.40
I-52	HS2	40	85	596	2.400	0.920 (0.0330)	0.976	3.315 (0.0075)	0.943	–1.74
I-53	HH1	40	25	396	2.113	1.192 (0.0784)	0.927	3.272 (0.0208)	1.286	3.65
I-54	HH2	37	77	910	2.439	0.810 (0.0396)	0.958	3.502 (0.0115)	0.846	–3.90
I-55	HH3	45	35	942	2.464	0.924 (0.0342)	0.972	3.509 (0.0120)	0.951	–1.44
I-56	HH4	20	46	587	2.158	1.042 (0.0634)	0.968	3.094 (0.0200)	1.076	1.21
I-57	PC1	40	21	430	2.186	1.042 (0.0458)	0.965	3.264 (0.0140)	1.080	1.74
I-58	PC2	11	55	183	1.962	1.019 (0.1432)	0.922	2.904 (0.0223)	1.105	0.73
I-59	CD1	40	91	367	2.272	1.067 (0.0725)	0.922	3.236 (0.0103)	1.157	2.17
I-60	CD2	55	18	319	2.081	1.179 (0.0406)	0.970	3.112 (0.0115)	1.215	5.31
X = log (Projected area, mm^2), Y = log (Aperture area, mm^2)										
I-61	HS1	38	133	443	2.404	1.004 (0.0409)	0.971	2.159 (0.0050)	1.034	0.83

I-62	HS2	40	119	434	2.383	1.090 (0.0287)	0.987	2.123 (0.0040)	1.104	3.64
I-63	HH1	40	60	380	2.275	0.933 (0.0223)	0.989	2.046 (0.0043)	0.943	–2.54
I-64	HH2	37	169	574	2.487	0.932 (0.0251)	0.988	2.201 (0.0040)	0.943	–2.26
I-65	HH3	44	77	622	2.482	0.906 (0.0210)	0.989	2.216 (0.0043)	0.916	–4.00
I-66	HH4	19	82	433	2.257	0.942 (0.0349)	0.989	2.023 (0.0070)	0.952	–1.36
I-67	PC1	40	54	364	2.279	0.956 (0.0262)	0.986	2.100 (0.0053)	0.970	–1.16
I-68	PC2	11	82	194	2.072	1.028 (0.0750)	0.977	1.870 (0.0078)	1.052	0.70
I-69	CD1	40	116	311	2.275	0.886 (0.0491)	0.946	2.139 (0.0050)	0.937	–1.29
I-70	CD2	55	41	301	2.185	0.906 (0.0250)	0.980	1.981 (0.0050)	0.924	–3.02
X = log (Shell capacity, mg), Y = log (Aperture area, mm^2)										
I-71	HS1	38	411	3100	3.147	0.619 (0.0182)	0.985	2.159 (0.0038)	0.628	–2.10
I-72	HS2	40	429	3237	3.138	0.673 (0.0163)	0.989	2.123 (0.0040)	0.680	0.85
I-73	HH1	40	134	2207	2.890	0.657 (0.0146)	0.991	2.046 (0.0040)	0.663	–0.25
I-74	HH2	37	597	4464	3.222	0.595 (0.0155)	0.988	2.201 (0.0040)	0.602	–4.16
I-75	HH3	44	193	4874	3.236	0.595 (0.0122)	0.991	2.216 (0.0037)	0.600	–5.43
I-76	HH4	20	278	3213	2.943	0.644 (0.0178)	0.994	2.024 (0.0053)	0.648	–1.06
I-77	PC1	40	108	2171	2.941	0.636 (0.0124)	0.993	2.100 (0.0038)	0.640	–2.11
I-78	PC2	11	255	939	2.644	0.662 (0.0363)	0.987	1.870 (0.0060)	0.671	0.11
I-79	CD1	40	447	2009	2.986	0.611 (0.0232)	0.974	2.139 (0.0035)	0.627	–1.70
I-80	CD2	55	65	1752	2.799	0.614 (0.0143)	0.986	1.981 (0.0045)	0.623	–3.07
X = log (Shell capacity, mg), Y = log (Occupied volume, mg)										
I-81	HS1	38	411	3100	3.147	1.066 (0.0320)	0.984	2.903 (0.0065)	1.083	2.60
I-82	HS2	40	429	3237	3.138	0.997 (0.0202)	0.992	2.909 (0.0048)	1.005	0.25
I-83	HH1	40	134	2207	2.890	1.098 (0.0242)	0.991	2.592 (0.0065)	1.108	4.46
I-84	HH2	40	597	4464	3.207	1.182 (0.0246)	0.992	2.925 (0.0063)	1.192	7.79
I-85	HH3	45	193	4874	3.217	1.136 (0.0185)	0.994	2.963 (0.0060)	1.143	7.72
I-86	HH4	20	278	3213	2.943	1.189 (0.0432)	0.988	2.640 (0.0125)	1.203	4.71
I-87	PC1	40	108	2171	2.941	1.240 (0.0257)	0.992	2.663 (0.0080)	1.250	9.73
I-88	PC2	11	255	939	2.644	1.042 (0.1070)	0.956	2.444 (0.0173)	1.090	0.84
I-89	CD1	40	447	2009	2.986	1.013 (0.0357)	0.977	2.780 (0.0053)	1.037	1.03
I-90	CD2	55	65	1752	2.799	1.093 (0.0179)	0.993	2.556 (0.0055)	1.101	5.63
X = log (Shell capacity, mg), Y = log (Shell dry wt., mg)										
I-91	HS1	38	411	3100	3.147	0.743 (0.0454)	0.939	3.392 (0.0093)	0.791	–4.60
I-92	HS2	40	429	3237	3.138	0.898 (0.0263)	0.984	3.315 (0.0063)	0.913	–3.32
I-93	HH1	40	134	2207	2.890	1.183 (0.0643)	0.948	3.271 (0.0175)	1.248	3.86
I-94	HH2	40	597	4464	3.207	0.925 (0.0427)	0.962	3.502 (0.0110)	0.962	–0.90
I-95	HH3	45	193	4874	3.217	0.975 (0.0308)	0.979	3.510 (0.0103)	0.996	–0.13
I-96	HH4	20	278	3213	2.943	1.147 (0.0599)	0.976	3.094 (0.0170)	1.175	2.92
I-97	PC1	40	108	2171	2.941	1.056 (0.0402)	0.974	3.265 (0.0123)	1.084	2.09
I-98	PC2	11	255	939	2.644	0.967 (0.1474)	0.909	2.904 (0.0238)	1.064	0.43
I-99	CD1	40	447	2009	2.986	1.060 (0.0674)	0.931	3.236 (0.0097)	1.139	2.06
I-100	CD2	55	65	1752	2.799	1.086 (0.0348)	0.974	3.112 (0.0110)	1.115	3.30

Appendix I (cont.)

Regr. #	Site	N	X-Axis Min.	X-Axis Max.	X-Axis Mean	Least Sq. Linear Regr. Slope (SEM)	Least Sq. Linear Regr. r	Expected Y @ Mean X (SEM)	RMA Slope	Ts Allom.
X = log (Shell length, mm), Y = log (Aperture area, mm^2)										
I-101	HS1	38	20.8	38.5	1.459	1.897 (0.0864)	0.965	2.159 (0.0058)	1.966	−0.40
I-102	HS2	40	20.0	38.2	1.452	2.158 (0.0666)	0.982	2.123 (0.0050)	2.198	2.97
I-103	HH1	40	13.0	34.7	1.382	1.743 (0.0582)	0.979	2.046 (0.0060)	1.780	−3.77
I-104	HH2	37	24.1	44.0	1.510	1.866 (0.0652)	0.979	2.201 (0.0055)	1.906	−1.44
I-105	HH3	44	15.8	45.5	1.500	1.800 (0.0477)	0.985	2.215 (0.0050)	1.827	−3.62
I-106	HH4	19	16.5	36.3	1.384	1.922 (0.0635)	0.991	2.024 (0.0063)	1.939	−0.95
I-107	PC1	40	12.8	34.3	1.384	1.837 (0.0653)	0.977	2.100 (0.0068)	1.880	−1.83
I-108	PC2	11	15.6	23.9	1.274	2.057 (0.2176)	0.953	1.870 (0.0110)	2.158	0.73
I-109	CD1	40	18.6	30.8	1.373	1.659 (0.1017)	0.936	2.139 (0.0055)	1.772	−2.24
I-110	CD2	55	10.8	31.6	1.342	1.706 (0.0591)	0.970	1.981 (0.0065)	1.759	−4.08
X = log (Shell length, mm), Y = log (Aperture length, mm)										
I-111	ALL	369	10.8	45.5	1.415	0.828 (0.0101)	0.974	1.265 (0.0013)	0.850	−14.84
I-112	HS1	38	20.8	38.5	1.459	0.914 (0.0380)	0.970	1.296 (0.0025)	0.942	−1.52
I-113	HS2	40	20.0	38.2	1.452	1.043 (0.0273)	0.987	1.281 (0.0020)	1.057	2.08
I-114	HH1	40	13.0	34.7	1.382	0.866 (0.0255)	0.984	1.234 (0.0025)	0.880	−4.70
I-115	HH2	40	24.1	44.0	1.505	0.854 (0.0261)	0.983	1.323 (0.0023)	0.869	−5.03
I-116	HH3	45	15.8	45.5	1.494	0.896 (0.0182)	0.991	1.328 (0.0020)	0.904	−5.27
I-117	HH4	20	16.5	36.3	1.382	0.946 (0.0258)	0.993	1.238 (0.0025)	0.953	−1.83
I-118	PC1	40	12.8	34.3	1.384	0.850 (0.0287)	0.979	1.256 (0.0030)	0.868	−4.59
I-119	PC2	11	15.6	23.9	1.274	0.897 (0.0714)	0.973	1.151 (0.0035)	0.922	−1.09
I-120	CD1	40	18.6	30.8	1.373	0.819 (0.0410)	0.956	1.260 (0.0020)	0.857	−3.50
I-121	CD2	55	10.8	31.6	1.342	0.836 (0.0226)	0.981	1.201 (0.0025)	0.852	−6.54
X = log (Shell length, mm), Y = log (Body dry wt., mg)										
I-132	ALL	369	10.8	45.5	1.415	2.700 (0.0418)	0.959	2.268 (0.0045)	2.815	−4.42
I-133	HS1	38	20.8	38.5	1.459	3.104 (0.1507)	0.960	2.396 (0.0100)	3.233	1.55
I-134	HS2	40	20.0	38.2	1.452	3.077 (0.0883)	0.985	2.401 (0.0063)	3.124	1.40
I-135	HH1	40	13.0	34.7	1.382	2.489 (0.1240)	0.956	2.113 (0.0128)	2.604	−3.20
I-136	HH2	40	24.1	44.0	1.505	3.526 (0.1013)	0.985	2.423 (0.0080)	3.580	5.72
I-137	HH3	45	15.8	45.5	1.494	3.154 (0.0841)	0.985	2.464 (0.0090)	3.202	2.40
I-138	HH4	20	16.5	36.3	1.382	3.191 (0.1548)	0.979	2.158 (0.0150)	3.259	1.68
I-139	PC1	40	12.8	34.3	1.384	2.874 (0.1094)	0.974	2.186 (0.0115)	2.951	−0.45
I-140	PC2	11	15.6	23.9	1.274	2.943 (0.3151)	0.952	1.963 (0.0158)	3.091	0.29
I-141	CD1	40	18.6	30.8	1.373	2.661 (0.1327)	0.956	2.272 (0.0070)	2.783	−1.63
I-142	CD2	55	10.8	31.6	1.342	2.544 (0.0689)	0.981	2.081 (0.0078)	2.593	−5.90

X = log (Shell length, mm), Y = log (Projected area, mm^2)									
I-143	ALL	369	10.8	45.5	1.415	1.878 (0.0107)	0.994	2.326 (0.0013)	1.889	–10.34
X = log (Shell length, mm), Y = log (Shell capacity, mg)									
I-144	ALL	369	10.8	45.5	1.415	2.785 (0.0306)	0.979	3.016 (0.0033)	2.845	–5.07
I-145	HS1	38	20.8	38.5	1.459	3.069 (0.1002)	0.981	3.147 (0.0068)	3.128	1.28
I-146	HS2	40	20.0	38.2	1.452	3.200 (0.0696)	0.991	3.138 (0.0053)	3.229	3.29
I-147	HH1	40	13.0	34.7	1.382	2.613 (0.0999)	0.973	2.890 (0.0100)	2.686	–3.15
I-148	HH2	40	24.1	44.0	1.505	3.113 (0.0809)	0.987	3.207 (0.0068)	3.154	1.90
I-149	HH3	45	15.8	45.5	1.494	3.032 (0.0606)	0.991	3.217 (0.0065)	3.060	0.98
I-150	HH4	20	16.5	36.3	1.382	2.963 (0.0853)	0.993	2.943 (0.0083)	2.984	–0.19
I-151	PC1	40	12.8	34.3	1.384	2.867 (0.1034)	0.976	2.941 (0.0108)	2.938	–0.60
I-152	PC2	11	15.6	23.9	1.274	3.135 (0.2408)	0.974	2.644 (0.0123)	3.219	0.91
I-153	CD1	40	18.6	30.8	1.373	2.752 (0.1051)	0.973	2.986 (0.0055)	2.828	–1.63
I-154	CD2	55	10.8	31.6	1.342	2.780 (0.0704)	0.983	2.800 (0.0078)	2.828	–2.44
X = log (Shell length, mm), Y = log (Shell dry wt., mg)									
I-155	HS1	38	20.8	38.5	1.459	2.400 (0.1005)	0.970	3.392 (0.0067)	2.474	–5.23
I-156	HS2	40	20.0	38.2	1.452	2.894 (0.0887)	0.983	3.315 (0.0065)	2.944	–0.63
I-157	HH1	40	13.0	34.7	1.382	3.292 (0.1002)	0.983	3.272 (0.0103)	3.349	3.48
I-158	HH2	40	24.1	44.0	1.505	2.963 (0.1028)	0.978	3.502 (0.0085)	3.030	0.29
I-159	HH3	45	15.8	45.5	1.494	3.016 (0.0645)	0.990	3.509 (0.0070)	3.046	0.72
I-160	HH4	20	16.5	36.3	1.382	3.464 (0.1298)	0.988	3.094 (0.0125)	3.506	3.90
I-161	PC1	40	12.8	34.3	1.384	3.148 (0.0783)	0.989	3.264 (0.0080)	3.183	2.34
I-162	PC2	11	15.6	23.9	1.274	3.229 (0.3745)	0.944	2.904 (0.0188)	3.421	1.12
I-163	CD1	40	18.6	30.8	1.373	3.084 (0.1497)	0.958	3.236 (0.0077)	3.219	1.46
I-164	CD2	55	10.8	31.6	1.342	3.107 (0.0738)	0.985	3.112 (0.0080)	3.154	2.09

APPENDIX II

Thais leuteostoma.

Regr.			X-Axis			Least Sq. Linear Regr.		Expected Y @	RMA	Ts
#	Site	N	Min.	Max.	Mean	Slope (SEM)	r	Mean X (SEM)	Slope	Allom.
X = log (Aperture length, mm), Y = log (Aperture area, mm^2)										
II-01	PC1	23	16.5	28.2	1.337	1.868 (0.0838)	0.979	2.258 (0.0065)	1.908	−1.10
II-02	PC2	15	12.4	23.3	1.229	2.202 (0.0595)	0.995	2.021 (0.0055)	2.213	3.58
II-03	CD1	22	14.1	28.6	1.315	2.069 (0.0488)	0.995	2.229 (0.0043)	2.079	1.63
II-04	CD2	21	12.1	32.3	1.292	2.042 (0.0340)	0.997	2.185 (0.0048)	2.048	1.42
X = log (Aperture length, mm), Y = log (Aperture width, mm)										
II-05	PC1	23	16.5	28.2	1.337	0.967 (0.0739)	0.944	1.052 (0.0058)	1.024	0.33
II-06	PC2	15	12.4	23.3	1.229	1.186 (0.0449)	0.991	0.895 (0.0043)	1.197	4.38
II-07	CD1	22	14.1	28.6	1.315	1.075 (0.0520)	0.977	1.046 (0.0048)	1.100	1.93
II-08	CD2	21	12.1	32.3	1.292	1.105 (0.0250)	0.995	1.030 (0.0035)	1.111	4.42
X = log (Aperture length, mm), Y = log (Knob height, mm)										
II-09	PC1	23	16.5	28.2	1.337	0.747 (0.2596)	0.532	0.197 (0.0205)	1.404	1.56
II-10	PC2	15	12.4	23.3	1.229	1.292 (0.1449)	0.927	0.374 (0.0133)	1.394	2.72
II-11	CD1	22	14.1	28.6	1.315	1.468 (0.3333)	0.702	0.238 (0.0295)	2.091	3.27
II-12	CD2	21	12.1	32.3	1.292	0.979 (0.2204)	0.714	0.224 (0.0315)	1.371	1.68
X = log (Aperture length, mm), Y = log (Lip thickness, mm)										
II-13	PC1	23	16.5	28.2	1.337	1.106 (0.2367)	0.714	−0.030 (0.0188)	1.549	2.32
II-14	PC2	15	12.4	23.3	1.229	0.949 (0.1733)	0.835	−0.316 (0.0158)	1.137	0.79
II-15	CD1	22	14.1	28.6	1.315	1.014 (0.2236)	0.712	−0.079 (0.0198)	1.424	1.90
II-16	CD2	21	12.1	32.3	1.292	1.407 (0.0729)	0.975	−0.047 (0.0105)	1.443	6.08
X = log (Body dry wt., mg), Y = log (Shell dry wt., mg)										
II-17	PC1	23	132	795	2.528	1.049 (0.0852)	0.940	3.462 (0.0210)	1.116	1.36
II-18	PC2	15	47	423	2.163	1.122 (0.1235)	0.929	3.058 (0.0338)	1.208	1.68
II-19	CD2	22	59	1352	2.420	1.109 (0.0387)	0.988	3.285 (0.0178)	1.122	3.16
X = log (Projected area, mm^2), Y = log (Aperture area,mm^2)										
II-20	PC1	23	157	583	2.462	0.861 (0.0427)	0.975	2.259 (0.0073)	0.883	−2.74
II-21	PC2	15	80	378	2.233	0.949 (0.0322)	0.993	2.021 (0.0070)	0.956	−1.38
II-22	CD1	22	113	471	2.419	0.961 (0.0475)	0.976	2.229 (0.0090)	0.985	−0.32
II-23	CD2	21	76	691	2.382	0.897 (0.0196)	0.995	2.185 (0.0063)	0.902	−5.03
X = log (Shell capacity, mg), Y = log (Aperture area, mm^2)										
II-24	PC1	21	706	4016	3.260	0.603 (0.0275)	0.981	2.262 (0.0073)	0.615	−1.89

II-25	PC2	13	229	1864	2.898	0.651 (0.0388)	0.981	2.017 (0.0108)	0.664	–0.08
II-26	CD2	21	274	6925	3.151	0.630 (0.0100)	0.998	2.185 (0.0045)	0.631	–3.54
X = log (Shell capacity, mg), Y = log (Occupied volume, mg)										
II-27	PC1	21	706	4016	3.260	0.995 (0.0378)	0.987	3.042 (0.0098)	1.008	0.21
II-28	PC2	13	229	1864	2.898	0.921 (0.0692)	0.970	2.649 (0.0193)	0.949	–0.73
II-29	CD2	22	274	6925	3.132	1.036 (0.0190)	0.997	2.921 (0.0088)	1.039	2.06
X = log (Shell capacity, mg), Y = log (Shell dry wt., mg)										
II-30	PC1	21	706	4016	3.260	1.047 (0.0745)	0.955	3.471 (0.0193)	1.096	1.29
II-31	PC2	13	229	1864	2.898	1.062 (0.0913)	0.962	3.047 (0.0253)	1.104	1.14
II-32	CD2	22	274	6925	3.132	1.107 (0.0350)	0.990	3.284 (0.0160)	1.118	3.38
X = log (Shell length, mm), Y = log (Aperture area, mm^2)										
II-33	PC1	23	21.4	42.8	1.481	1.653 (0.1029)	0.962	2.258 (0.0090)	1.718	–2.74
II-34	PC2	15	16.4	35.5	1.365	1.847 (0.0963)	0.983	2.021 (0.0105)	1.879	–1.26
II-35	CD1	22	19.2	38.6	1.459	1.984 (0.0873)	0.981	2.229 (0.0080)	2.022	0.26
II-36	CD2	21	15.8	47.4	1.442	1.758 (0.0479)	0.993	2.185 (0.0080)	1.770	–4.79
X = log (Shell length, mm), Y = log (Aperture length, mm)										
II-37	ALL	83	15.8	47.4	1.447	0.875 (0.0147)	0.989	1.302 (0.0018)	0.885	–7.84
II-38	PC1	23	21.4	42.8	1.481	0.886 (0.0361)	0.983	1.338 (0.0033)	0.901	–2.73
II-39	PC2	15	16.4	35.5	1.365	0.839 (0.0366)	0.988	1.229 (0.0040)	0.849	–4.12
II-40	CD1	22	19.2	38.6	1.459	0.961 (0.0320)	0.989	1.316 (0.0028)	0.972	–0.88
II-41	CD2	21	15.8	47.4	1.442	0.860 (0.0200)	0.995	1.292 (0.0033)	0.864	–6.78
X = log (Shell length, mm), Y = log (Body dry wt., mg)										
II-46	ALL	63	15.8	47.4	1.436	2.702 (0.0761)	0.977	2.393 (0.0097)	2.766	–3.08
II-47	PC1	22	21.4	42.8	1.481	2.627 (0.1913)	0.951	2.528 (0.0173)	2.762	–1.24
II-48	PC2	15	16.4	35.5	1.365	2.443 (0.2090)	0.956	2.163 (0.0225)	2.555	–2.13
II-49	CD2	22	15.8	47.4	1.435	2.761 (0.0702)	0.994	2.420 (0.0115)	2.778	–3.17
X = log (Shell length, mm), Y = log (Projected area, mm^2)										
II-50	ALL	83	15.8	47.4	1.447	1.962 (0.0193)	0.996	2.393 (0.0023)	1.970	–1.56
X = log (Shell length, mm), Y = log (Shell capacity, mg)										
II-51	ALL	60	15.8	47.4	1.437	2.762 (0.0577)	0.988	3.125 (0.0075)	2.796	–3.54
II-52	PC1	21	21.4	42.8	1.482	2.722 (0.1381)	0.976	3.261 (0.0128)	2.789	–1.53
II-53	PC2	13	16.4	31.5	1.361	2.841 (0.2058)	0.972	2.898 (0.0195)	2.923	–0.37
II-54	CD2	22	15.8	47.4	1.435	2.777 (0.0619)	0.995	3.133 (0.0103)	2.791	–3.38
X = log (Shell length, mm), Y = log (Shell dry wt., mg)										
II-55	PC1	23	21.4	42.8	1.481	3.016 (0.1399)	0.978	3.461 (0.0123)	3.084	0.60
II-56	PC2	15	16.4	35.5	1.365	3.041 (0.1460)	0.985	3.058 (0.0155)	3.087	0.60
II-57	CD1	22	19.2	38.6	1.459	3.348 (0.1749)	0.974	3.347 (0.0160)	3.437	2.50
II-58	CD2	22	15.8	47.4	1.435	3.109 (0.0579)	0.996	3.284 (0.0095)	3.121	2.10

APPENDIX III

Monodonta labio.

Regr. #	Site	N	X-Axis Min.	X-Axis Max.	X-Axis Mean	Least Sq. Linear Regr. Slope (SEM)	Least Sq. Linear Regr. *r*	Expected Y @ Mean X (SEM)	RMA Slope	Ts Allom.
X = log (Aperture length, mm), Y = log (Aperture area, mm^2)										
III-01	TT	20	7.0	12.7	0.981	2.148 (0.0604)	0.993	1.796 (0.0053)	2.163	2.70
III-02	HS1	24	8.0	14.5	1.045	2.136 (0.0352)	0.997	1.936 (0.0030)	2.142	4.05
III-03	HS2	24	7.3	14.9	1.017	2.043 (0.0560)	0.992	1.879 (0.0050)	2.059	1.06
III-04	HH1	30	8.5	17.8	1.117	2.039 (0.0305)	0.997	2.091 (0.0023)	2.045	1.48
III-05	HH2	30	8.1	16.9	1.103	2.136 (0.0458)	0.994	2.059 (0.0037)	2.149	3.25
III-06	HH3	29	9.0	16.7	1.110	2.168 (0.0620)	0.989	2.076 (0.0050)	2.192	3.10
III-07	HH4	30	8.2	15.4	1.076	1.994 (0.0525)	0.990	2.003 (0.0035)	2.014	0.27
III-08	PC2	9	8.1	15.5	1.043	2.123 (0.0702)	0.996	1.928 (0.0060)	2.132	1.87
III-09	CD2	40	9.2	15.7	1.108	2.145 (0.0479)	0.991	2.066 (0.0033)	2.164	3.43
X = log (Aperture length, mm), Y = log (Aperture width, mm)										
III-10	TT	20	7.0	12.7	0.981	1.012 (0.0448)	0.983	0.909 (0.0040)	1.030	0.66
III-11	HS1	24	8.0	14.5	1.045	1.066 (0.0278)	0.993	0.985 (0.0023)	1.074	2.64
III-12	HS2	24	7.3	14.9	1.017	1.094 (0.0324)	0.990	0.961 (0.0028)	1.105	3.24
III-13	HH1	30	8.5	17.8	1.117	1.003 (0.0300)	0.988	1.057 (0.0023)	1.015	0.51
III-14	HH2	30	8.1	16.9	1.103	1.113 (0.0360)	0.986	1.047 (0.0030)	1.129	3.58
III-15	HH3	29	9.0	16.7	1.110	1.070 (0.0464)	0.975	1.054 (0.0038)	1.097	2.10
III-16	HH4	30	8.2	15.4	1.076	0.994 (0.0423)	0.976	1.018 (0.0028)	1.018	0.44
III-17	PC2	9	8.1	15.5	1.043	1.111 (0.0905)	0.978	0.976 (0.0073)	1.136	1.50
III-18	CD2	40	9.2	15.7	1.108	1.076 (0.0393)	0.976	1.045 (0.0028)	1.102	2.61
X = log (Aperture length, mm), Y = log (Lip thickness, mm)										
III-19	TT	20	7.0	12.7	0.981	0.703 (0.1115)	0.830	0.105 (0.0098)	0.847	−1.37
III-20	HS1	24	8.0	14.5	1.045	1.204 (0.1206)	0.905	0.084 (0.0103)	1.330	2.74
III-21	HS2	24	7.3	14.9	1.017	0.984 (0.0936)	0.913	0.140 (0.0083)	1.078	0.83
III-22	HH1	30	8.5	17.8	1.117	1.603 (0.1317)	0.917	0.143 (0.0105)	1.748	5.68
III-23	HH2	30	8.1	16.9	1.103	0.840 (0.1698)	0.683	0.192 (0.0138)	1.230	1.35
III-24	HH3	29	9.0	16.7	1.110	1.547 (0.1036)	0.944	0.185 (0.0083)	1.639	6.17
III-25	HH4	30	8.2	15.4	1.076	0.762 (0.1234)	0.760	0.211 (0.0083)	1.003	0.02
III-26	PC2	9	8.1	15.5	1.043	1.094 (0.1362)	0.950	0.122 (0.0113)	1.152	1.11
III-27	CD2	40	9.2	15.7	1.108	1.149 (0.1045)	0.872	0.089 (0.0073)	1.318	12.61
X = log (Body dry wt., mg), Y = log (Shell dry wt., mg)										
III-28	TT	20	14	107	1.651	0.793 (0.0269)	0.990	2.830 (0.0083)	0.801	−7.40
III-29	HS1	24	22	172	1.837	0.909 (0.0292)	0.989	2.896 (0.0087)	0.919	−2.77

III-30	HS2	24	22	268	1.843	0.960 (0.0276)	0.991	2.902 (0.0090)	0.969	−1.13
III-31	HH1	30	26	339	2.084	1.135 (0.0366)	0.986	3.164 (0.0100)	1.151	4.13
III-32	HH2	30	27	280	2.051	0.930 (0.0345)	0.983	3.149 (0.0103)	0.946	−1.56
III-33	HH3	29	29	353	2.097	1.049 (0.0264)	0.992	3.158 (0.0083)	1.057	2.18
III-34	HH4	30	30	263	2.030	0.851 (0.0417)	0.968	3.138 (0.0095)	0.879	−2.90
III-35	PC2	6	24	233	1.780	0.988 (0.0559)	0.994	2.866 (0.0230)	0.994	−0.11
III-36	CD2	40	27	187	1.952	0.855 (0.0290)	0.979	3.085 (0.0070)	0.873	−4.37
X = log (Projected area, mm^2), Y = log (Aperture area, mm^2)										
III-37	TT	20	51	168	1.995	1.047 (0.0364)	0.989	1.796 (0.0063)	1.059	1.61
III-38	HS1	24	55	202	2.061	0.931 (0.0371)	0.983	1.936 (0.0070)	0.947	−1.43
III-39	HS2	24	54	290	2.079	0.876 (0.0188)	0.995	1.879 (0.0040)	0.880	−6.36
III-40	HH1	30	56	321	2.228	0.809 (0.0214)	0.990	2.091 (0.0043)	0.817	−8.54
III-41	HH2	30	67	306	2.208	0.873 (0.0341)	0.979	2.058 (0.0065)	0.892	−3.18
III-42	HH3	29	64	363	2.236	0.816 (0.0208)	0.991	2.076 (0.0045)	0.823	−8.49
III-43	HH4	30	71	272	2.215	0.921 (0.0356)	0.980	2.003 (0.0050)	0.940	−1.69
III-44	PC2	9	51	259	2.022	0.852 (0.0477)	0.989	1.928 (0.0095)	0.861	−2.90
III-45	CD2	40	68	227	2.153	1.009 (0.0248)	0.989	2.066 (0.0035)	1.020	0.82
X = log (Shell capacity, mg), Y = log (Aperture area, mm^2)										
III-46	TT	20	141	1063	2.642	0.639 (0.0177)	0.993	1.796 (0.0053)	0.644	−1.31
III-47	HS1	24	221	1521	2.817	0.633 (0.0203)	0.989	1.936 (0.0058)	0.640	−1.31
III-48	HS2	24	198	2256	2.797	0.594 (0.0102)	0.997	1.879 (0.0030)	0.596	−6.95
III-49	HH1	30	210	2934	3.050	0.598 (0.0130)	0.994	2.091 (0.0035)	0.602	−5.00
III-50	HH2	22	593	2519	3.119	0.603 (0.0345)	0.969	2.136 (0.0060)	0.622	−1.29
III-51	HH3	29	292	3108	3.059	0.585 (0.0130)	0.993	2.076 (0.0040)	0.589	−5.96
III-52	HH4	30	279	2220	2.995	0.587 (0.0151)	0.991	2.003 (0.0033)	0.592	−4.92
III-53	PC2	6	187	2085	2.728	0.570 (0.0178)	0.998	1.908 (0.0075)	0.571	−5.37
III-54	CD2	40	260	1718	2.929	0.637 (0.0122)	0.993	2.066 (0.0028)	0.641	−2.06
X = log (Shell capacity, mg), Y = log (Occupied volume, mg)										
III-55	TT	20	141	1063	2.642	1.116 (0.0240)	0.996	2.365 (0.0070)	1.120	5.02
III-56	HS1	24	221	1521	2.817	1.076 (0.0160)	0.998	2.562 (0.0045)	1.078	4.88
III-57	HS2	24	198	2256	2.797	1.061 (0.0113)	0.999	2.568 (0.0035)	1.062	5.49
III-58	HH1	30	210	2934	3.050	1.016 (0.0160)	0.996	2.815 (0.0043)	1.020	1.26
III-59	HH2	22	593	2519	3.119	1.066 (0.0387)	0.987	2.902 (0.0068)	1.080	2.07
III-60	HH3	29	292	3108	3.059	1.071 (0.0115)	0.998	2.826 (0.0035)	1.073	6.36
III-61	HH4	30	279	2220	2.995	1.031 (0.0228)	0.993	2.761 (0.0050)	1.038	1.68
III-62	PC2	6	187	2085	2.728	0.985 (0.0473)	0.995	2.504 (0.0200)	0.990	−0.21
III-63	CD2	40	260	1718	2.929	1.052 (0.0110)	0.998	2.682 (0.0025)	1.054	4.92
X = log (Shell capacity, mg), Y = log (Shell dry wt., mg)										
III-64	TT	20	141	1063	2.642	0.827 (0.0213)	0.994	2.830 (0.0063)	0.832	−7.89
III-65	HS1	24	221	1521	2.817	0.946 (0.0282)	0.990	2.896 (0.0083)	0.956	−1.58
III-66	HS2	24	198	2256	2.797	0.995 (0.0254)	0.993	2.902 (0.0080)	1.002	0.08

Appendix III (cont.)

Regr. #	Site	N	X-Axis Min.	X-Axis Max.	X-Axis Mean	Least Sq. Linear Regr. Slope (SEM)	Least Sq. Linear Regr. *r*	Expected Y @ Mean X (SEM)	RMA Slope	Ts Allom.
III-67	HH1	30	210	2934	3.050	1.144 (0.0369)	0.986	3.164 (0.0100)	1.160	4.34
III-68	HH2	22	593	2519	3.119	1.003 (0.0418)	0.983	3.265 (0.0073)	1.020	0.49
III-69	HH3	29	292	3108	3.059	1.117 (0.0292)	0.991	3.157 (0.0085)	1.127	4.35
III-70	HH4	30	279	2220	2.995	0.876 (0.0401)	0.972	3.138 (0.0090)	0.901	–2.46
III-71	PC2	6	187	2085	2.728	0.959 (0.0193)	0.999	2.866 (0.0083)	0.960	–2.07
III-72	CD2	40	260	1718	2.929	0.885 (0.0286)	0.981	3.085 (0.0067)	0.902	–3.42
X = log (Shell length, mm), Y = log (Aperture area, mm^2)										
III-73	TT	20	10.4	19.9	1.172	2.068 (0.0885)	0.984	1.796 (0.0078)	2.102	1.15
III-74	HS1	24	10.1	21.2	1.188	1.653 (0.0850)	0.972	1.936 (0.0090)	1.701	–3.52
III-75	HS2	24	10.5	24.5	1.206	1.695 (0.0543)	0.989	1.879 (0.0060)	1.714	–5.27
III-76	HH1	30	10.5	26.9	1.279	1.426 (0.0557)	0.979	2.091 (0.0063)	1.457	–9.76
III-77	HH2	30	11.5	26.9	1.274	1.529 (0.0873)	0.957	2.058 (0.0095)	1.598	–4.61
III-78	HH3	29	11.3	29.3	1.288	1.499 (0.0473)	0.987	2.076 (0.0055)	1.519	–10.17
III-79	HH4	30	12.0	25.6	1.284	1.604 (0.0934)	0.956	2.003 (0.0073)	1.678	–3.45
III-80	PC2	9	10.1	23.8	1.167	1.605 (0.0997)	0.987	1.928 (0.0108)	1.626	–3.75
III-81	CD2	40	11.8	22.5	1.241	1.939 (0.0619)	0.981	2.066 (0.0045)	1.977	–0.38
X = log (Shell length, mm), Y = log (Aperture length, mm)										
III-82	ALL	236	10.1	29.3	1.244	0.776 (0.0195)	0.933	1.076 (0.0020)	0.832	–8.63
III-83	TT	20	10.4	19.9	1.172	0.952 (0.0460)	0.980	0.981 (0.0040)	0.971	–0.62
III-84	HS1	24	10.1	21.2	1.188	0.774 (0.0381)	0.974	1.045 (0.0040)	0.795	–5.39
III-85	HS2	24	10.5	24.5	1.206	0.816 (0.0350)	0.980	1.017 (0.0035)	0.833	–4.78
III-86	HH1	30	10.5	26.9	1.279	0.696 (0.0280)	0.978	1.117 (0.0030)	0.712	–10.30
III-87	HH2	30	11.5	26.9	1.274	0.701 (0.0466)	0.943	1.103 (0.0050)	0.743	–5.51
III-88	HH3	29	11.3	29.3	1.288	0.687 (0.0177)	0.991	1.111 (0.0023)	0.693	–17.33
III-89	HH4	30	12.0	25.6	1.284	0.801 (0.0440)	0.960	1.077 (0.0033)	0.834	–3.76
III-90	PC2	9	10.1	23.8	1.167	0.749 (0.0560)	0.981	1.043 (0.0060)	0.764	–4.22
III-91	CD2	40	11.8	22.5	1.241	0.883 (0.0372)	0.968	1.109 (0.0028)	0.912	–2.36
X = log (Shell length, mm), Y = log (Body dry wt., mg)										
III-101	ALL	231	10.1	29.3	1.244	2.816 (0.0402)	0.978	1.956 (0.0043)	2.879	–3.00
III-102	TT	20	10.4	19.9	1.172	3.365 (0.1029)	0.992	1.651 (0.0090)	3.392	3.81
III-103	HS1	24	10.1	21.2	1.188	2.735 (0.0805)	0.991	1.837 (0.0085)	2.760	–2.98
III-104	HS2	24	10.5	24.5	1.206	2.947 (0.0824)	0.991	1.843 (0.0090)	2.974	–0.32
III-105	HH1	30	10.5	26.9	1.279	2.399 (0.0819)	0.984	2.085 (0.0093)	2.438	–6.86
III-106	HH2	28	11.5	26.9	1.276	2.630 (0.1139)	0.976	2.051 (0.0125)	2.695	–2.68
III-107	HH3	29	11.3	29.3	1.288	2.733 (0.0591)	0.994	2.097 (0.0067)	2.749	–4.24

III-108	HH4	30	12.0	25.6	1.284	2.816 (0.1327)	0.970	2.030 (0.0103)	2.903	−0.73
III-109	PC2	6	10.1	23.8	1.161	2.688 (0.1217)	0.996	1.780 (0.0185)	2.699	−2.47
III-110	CD2	40	11.8	22.5	1.241	3.139 (0.0875)	0.986	1.952 (0.0065)	3.184	2.10
X = log (Shell length, mm), Y = log (Projected area, mm^2)										
III-111	ALL	236	10.1	29.3	1.244	1.848 (0.0128)	0.994	2.153 (0.0013)	1.859	−11.00
X = log (Shell length, mm), Y = log (Shell capacity, mg)										
III-112	ALL	225	10.1	29.3	1.248	2.722 (0.0376)	0.979	2.933 (0.0038)	2.780	−5.84
III-113	TT	20	10.4	19.9	1.172	3.245 (0.0849)	0.994	2.642 (0.0075)	3.265	3.12
III-114	HS1	24	10.1	21.2	1.188	2.637 (0.0686)	0.993	2.817 (0.0075)	2.656	−5.02
III-115	HS2	24	10.5	24.5	1.206	2.851 (0.0793)	0.992	2.797 (0.0085)	2.874	−1.59
III-116	HH1	30	10.5	26.9	1.279	2.379 (0.0821)	0.984	3.051 (0.0093)	2.418	−7.09
III-117	HH2	22	14.6	26.9	1.320	2.283 (0.1377)	0.965	3.120 (0.0103)	2.366	−4.61
III-118	HH3	29	11.3	29.3	1.288	2.562 (0.0568)	0.993	3.059 (0.0065)	2.580	−7.39
III-119	HH4	30	12.0	25.6	1.284	2.766 (0.1136)	0.977	2.995 (0.0090)	2.831	−1.49
III-120	PC2	6	10.1	23.8	1.161	2.793 (0.0583)	0.999	2.728 (0.0090)	2.796	−3.50
III-121	CD2	40	11.8	22.5	1.241	3.043 (0.0799)	0.987	2.929 (0.0060)	3.083	1.04
X = log (Shell length, mm), Y = log (Shell dry wt., mg)										
III-122	TT	20	10.4	19.9	1.172	2.690 (0.0903)	0.990	2.830 (0.0083)	2.717	−3.13
III-123	HS1	24	10.1	21.2	1.188	2.500 (0.0928)	0.985	2.895 (0.0100)	2.538	−4.98
III-124	HS2	24	10.5	24.5	1.206	2.854 (0.0820)	0.991	2.902 (0.0090)	2.880	−1.46
III-125	HH1	30	10.5	26.9	1.279	2.792 (0.0555)	0.995	3.164 (0.0063)	2.806	−3.49
III-126	HH2	30	11.5	26.9	1.274	2.499 (0.0754)	0.988	3.143 (0.0083)	2.529	−6.24
III-127	HH3	29	11.3	29.3	1.288	2.899 (0.0428)	0.997	3.157 (0.0050)	2.908	−2.16
III-128	HH4	30	12.0	25.6	1.284	2.494 (0.1010)	0.978	3.138 (0.0080)	2.550	−4.45
III-129	PC2	9	10.1	23.8	1.167	2.677 (0.0902)	0.996	2.890 (0.0097)	2.688	−3.46
III-130	CD2	40	11.8	22.5	1.241	2.746 (0.0719)	0.987	3.085 (0.0053)	2.782	−3.03