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Determinate growth and variable size at maturity in the marine gastropod *Amphissa columbiana*

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Abstract: Individuals of *Amphissa columbiana* from the intertidal zone of San Juan Island, Washington, U.S.A., typically have either shells with very thin, delicate apertural lips, or shells with thick, robust lips. In laboratory observations, thin-lipped snails grew rapidly but were not sexually mature, while thick-lipped snails grew very slowly or not at all and were sexually mature. These observations are consistent with the hypothesis that *A. columbiana* displays determinate growth, as has been inferred for many columbellids on the basis of intraspecific variation in shell form. Sizes of mature snails were very variable, with the largest individuals weighing 4.5 times more than the smallest (wet weight, excluding shell). I tested the hypothesis that maturation and associated shell thickening are phenotypically plastic responses to the presence of predators. Exposure to effluent from the predatory crab *Cancer productus* in the laboratory had no effect on shell form or relative shell weight (an index of shell thickness), suggesting that this is not the case.

Key words: Columbellidae, shell form, growth, maturation, reproduction

Determinate growth, a pattern of ontogeny in which sexual maturation is accompanied by the cessation of growth, is common among many lineages of animals. In shelled gastropods that display determinate growth, maturation may also be accompanied by changes in the form of the shell aperture (*e.g.*, thickening of the outer lip and formation of a callus on the inner lip; Vermeij and Signor 1992). Many members of the gastropod family Columbellidae display such variation in apertural form within populations, which suggests that they display determinate growth (McLean 1978, Jung 1989, Vermeij and Signor 1992). However, in the absence of data on relationships between reproductive maturity, growth rate, and shell form in any columbellid, other interpretations of variable shell form are plausible. For example, shell form might vary in response to environmental cues like wave force, crowding, food availability, or the presence of predators, and so might not be directly related to maturation (*e.g.*, Wellington and Kuris 1983, Kemp and Bertness 1984, Appleton and Palmer 1988, Trussell 1996). Here I provide data on reproduction and growth that are consistent with the hypothesis of determinate growth in an intertidal population of the columbellid *Amphissa columbiana* Dall, 1916. Shell form thus appears to be a reliable indicator of reproductive status in this species.

The sizes of mature *Amphissa columbiana* in this population were very variable, with the largest mature snails having 4.5 times the body wet weight (excluding shell) of the smallest mature snails. Maturation at small size likely imposes a cost in terms of fecundity per reproductive bout in these snails, and thus requires explanation. I present the results of a laboratory experiment aimed at testing the hypothesis that maturation and associated shell thickening is a phenotypically plastic response to the presence of predators. In this case, the potential reduction in fecundity associated with maturation at small size might be balanced by increased resistance to predation. Exposure to effluent from the predatory crab *Cancer productus* had no effect on shell form or relative shell weight (an index of shell thickness) in *A. columbiana*, suggesting that this is not the case. Determining the causes of variable size at maturity in gastropods with determinate growth, like *A. columbiana*, remains an important problem whose solution will be useful in exploring hypotheses on life history evolution, as well as in interpreting ecological and evolutionary patterns in body size in both fossil and recent assemblages (*e.g.*, Budd and Johnson 1991, Roy 2002).

MATERIALS AND METHODS

Shell form

I studied a population of *Amphissa columbiana* from the intertidal zone of Deadman's Bay, on the west side of San Juan Island, Washington, U.S.A. Identifications were verified by comparison with specimens of *Amphissa* spp. in the collections of the Natural History Museum of Los Angeles County in February 2003, with the assistance of J. McLean.

Shell height (from the apex to the tip of the siphonal canal) was measured with calipers to 0.1 mm. Shell and body weights were estimated in living snails using the method of Palmer (1982). Living snails were weighed while immersed in seawater, blotted dry, and then weighed in air. Twelve

thin-lipped and 12 thick-lipped individuals of a wide range of shell heights were measured and weighed as above, then frozen and dissected to separate shell from body tissues. Shell and body tissues were rinsed in fresh water, dried at 65°C for three days, and weighed. Shell weight was related to submerged weight using the ordinary least squares regression: shell weight (g)=1.494* submerged weight (g) −0.002 (r^2=0.999). This regression was used to predict shell weight throughout this study. Body wet weight was calculated by subtracting estimated shell weight from the weight of a snail in air. For this sample of 24 individuals, body wet weight was well correlated with body dry weight (dry weight [g]=0.19* estimated wet weight [g] + 0.001, r^2=0.945), suggesting that body wet weight calculated in this way is a good estimator of body mass.

Growth of thin-lipped and thick-lipped snails

Growth was examined in two sets of laboratory observations made in the winter (during the reproductive season) and spring (after the reproductive season) of 2003. In the first, started in January 2003, 6 thin-lipped (heights 13.2-16.4 mm) and 10 thick-lipped (14.5-16.6 mm) snails were marked by attaching numbered beetags to their shells with cyanoacrylate glue. The snails were measured and weighed as described above, then placed in a plastic container (15 × 15 × 4 cm) with mesh sides submerged in flowing seawater (8-10°C) in a laboratory seatable. The snails were fed muscle tissue from scallops (*Chlamys* spp.) weekly for 10 weeks, after which they were measured and weighed again. The second set of growth observations, started in April 2003, included 11 thin-lipped (heights 12.3-16.4 mm) and 9 thick-lipped (11.1-16.0 mm) snails. After being marked, measured, and weighed, the snails were placed in a mesh-sided container (30 × 18 × 10 cm) submerged in flowing seawater (10-14°C). Snails were fed muscle from *Chlamys* spp. or *Nuttalia obscurata* (Reeve, 1857) 1-2 times weekly for the next 11 weeks, after which they were measured and weighed again. In both sets of observations, food was always present in excess.

Sexual maturity

Maturity of field-collected snails was assessed in two ways. First, I compared lengths of the penises of thin-lipped and thick-lipped snails in a collection of snails made in December 2002 and January 2003 (during the reproductive season). Snails were relaxed in a mixture of equal volumes of seawater and 7.5% $MgCl_2 \cdot 6H_2O$, then fixed in 10% formalin in seawater. Their shells were later removed. Penises were removed from six thick-lipped males, pinned out straight, and measured to the nearest 0.5 mm with a ruler. Penises of the five thin-lipped snails examined were too small to pin out, and were measured without removing them from adults.

Second, I looked for evidence of deposition of egg capsules by snails maintained in the laboratory during the reproductive season. I collected 17 thin-lipped snails and 26 thick-lipped snails in Dec 2002 and sexed them by holding them off the substratum by their shells with forceps and looking for a penis as they extended their bodies from their shells. Most individuals of both groups lacked penises and were assumed to be females. I divided the thin-lipped snails into two separate mesh-walled containers (making sure to include several males in each container), and did the same for the thick-lipped snails. All four containers were submerged in flowing seawater and the snails were fed scallop muscle weekly until March 2003. Containers were examined for the presence of egg capsules at every feeding.

Causes of variation in size at maturity

In a laboratory experiment, I tested the hypothesis that odor cues associated with the presence of crushing predators induce changes in shell form associated with maturation. Because food level has been linked to changes in shell thickness in several snails (*e.g.*, Kemp and Bertness 1984, Boulding and Hay 1993), I also manipulated this variable. In May 1999, I collected 50 thin-lipped *Amphissa columbiana* (shell height 10.5-18.8 mm) from the intertidal zone about 1 km south of Deadman's Bay. These were marked, measured, and weighed. Groups of four or five snails selected to span the size range of collected snails were placed into each of 12 small, mesh-sided containers. Two of these containers were placed in each of six plastic aquaria (20 × 13 × 13 cm). Each aquarium had a separate source of inflowing seawater. Three of the aquaria, "crab" treatments, contained a single individual of *Cancer productus* Randall, 1839 (59-66 mm carapace width). The crab was restricted to the bottom half of the aquarium (away from the snail containers) with rigid plastic mesh. Thus, in the three "crab" aquaria, snails shared a common pool of water with a potential predator. The remaining three "no crab" aquaria were identical to "crab" aquaria except that no crab was included. In each of the six aquaria, snails in one container received food (1/4 of the adductor muscle from a *Chlamys*) weekly (fed treatment); snails in the other container received no food (starved treatment). Containers were cleaned at each feeding. Each crab was fed a single individual of *Chlamys* spp. weekly. When crabs molted, they were replaced with newly collected crabs 55-66 mm in carapace width. Snails were maintained in this experiment for two months, after which they were measured and weighed. During the experiment 8 snails (of the total of 50) died, all of these in fed treatments; these were excluded from analyses. Because of this mortality, the number of snails in each container varied from 3-5, except for one

container in which all the snails died. Effects of predator (crab vs. no crab) and food level (starved vs. fed) on relative shell weight (shell dry weight/total weight of the snail) were assessed in a factorial ANOVA.

RESULTS

Shell form

Most individuals of *Amphissa columbiana* exhibited one of two distinct shell morphologies, with a few individuals displaying intermediate forms. In thin-lipped individuals (Fig. 1A), the outer lip of the aperture was extremely thin (50-70 μm) and very delicate, frequently breaking when snails were handled. The outer lip of the aperture was continuously curved, with no straight portions. No denticles were present on either the columellar or outer lips of the aperture, and there was no callus on the columellar lip of the aperture. The remainder of the shell was usually relatively free of epibionts, and the apical whorls were not eroded. Thin-lipped snails were most common deep in crevices and overhangs, and especially under large cobbles at low tide levels. In these habitats, they often occurred in aggregations of up to 20-30 individuals of a variety of sizes. On occasion they were also found singly on exposed rock surfaces.

In contrast, in thick-lipped individuals (Fig. 1C) the outer lip of the aperture was 750-1000 μm thick and very robust. Further, a segment of the outer lip of the aperture—from about 1/3 of the aperture back from the anterior end to about 1/4 of the aperture forward from the posterior end of the aperture—was usually straight and approximately parallel to the coiling axis of the shell. The outer apertural lip bore 15-20 short denticles on its inner surface and several denticles were usually found on the columellar apertural lip as well. A raised callus was present on the columellar lip of the aperture, although it was frequently obscured by encrusting epibionts. At Deadman's Bay, thick-lipped snails were often found in crevices and overhangs and were also relatively common on exposed rocks at low tide. Thick-lipped snails were usually found singly, not in aggregations.

Snails of intermediate shell form (Fig. 1B) were much less common than either thin-lipped or thick-lipped snails. Intermediates had apertures of intermediate thickness, with or without a straight portion of the outer lip of the aperture.

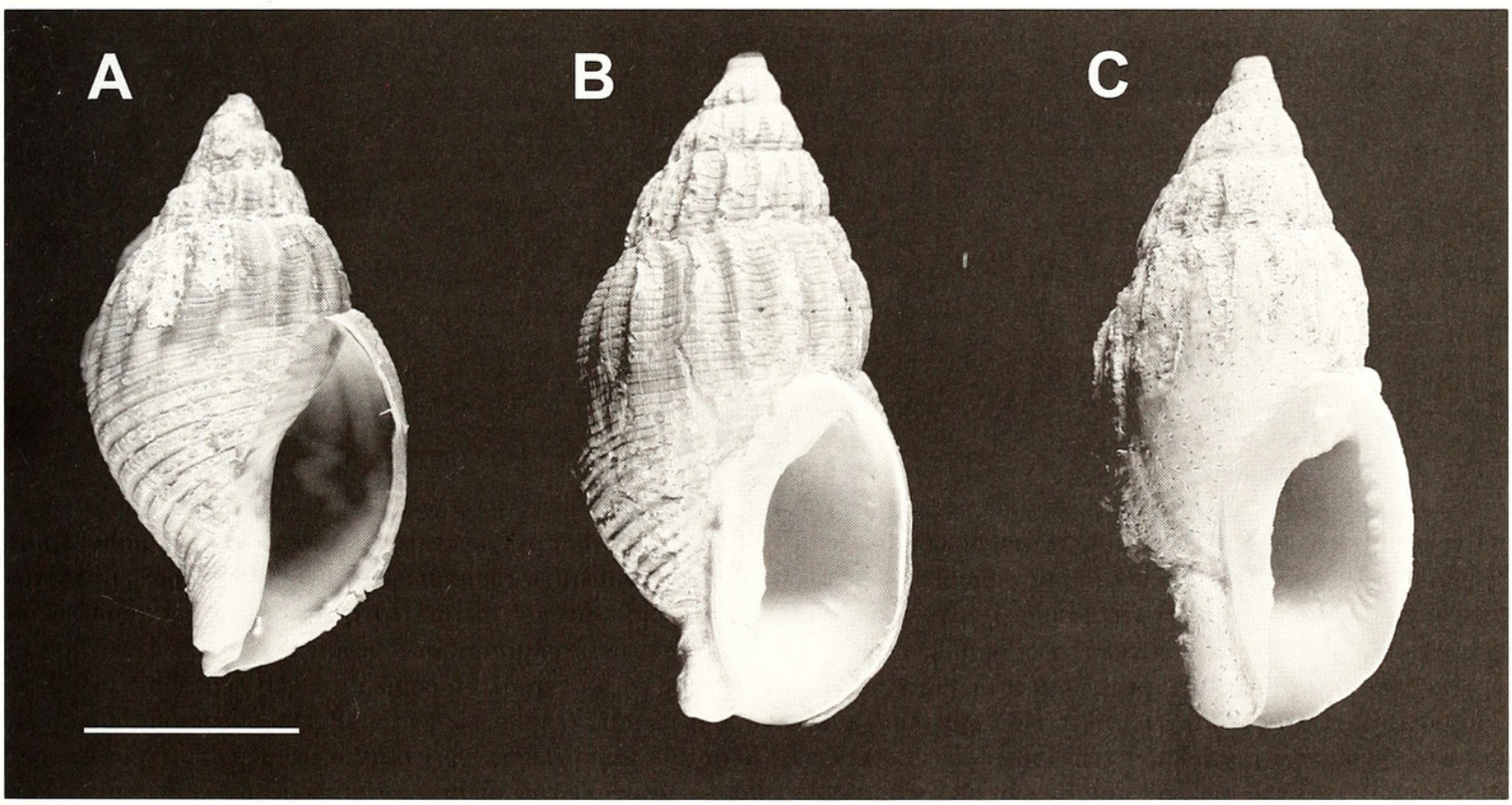

Figure 1. Shells of *Amphissa columbiana* from the intertidal zone of Deadman's Bay, San Juan Island, Washington, U.S.A. A, Thin-lipped individual. Note the continuously curved outer lip of the aperture and the lack of apertural teeth. B, Individual with intermediate shell form. Note the presence of a callus on the columellar lip of the aperture. C, Thick-lipped individual. Note the well-developed teeth, especially on the outer lip of the aperture, the callus on the columellar lip of the aperture, and the greatly thickened outer apertural lip (compare to A). Scale bar=5 mm.

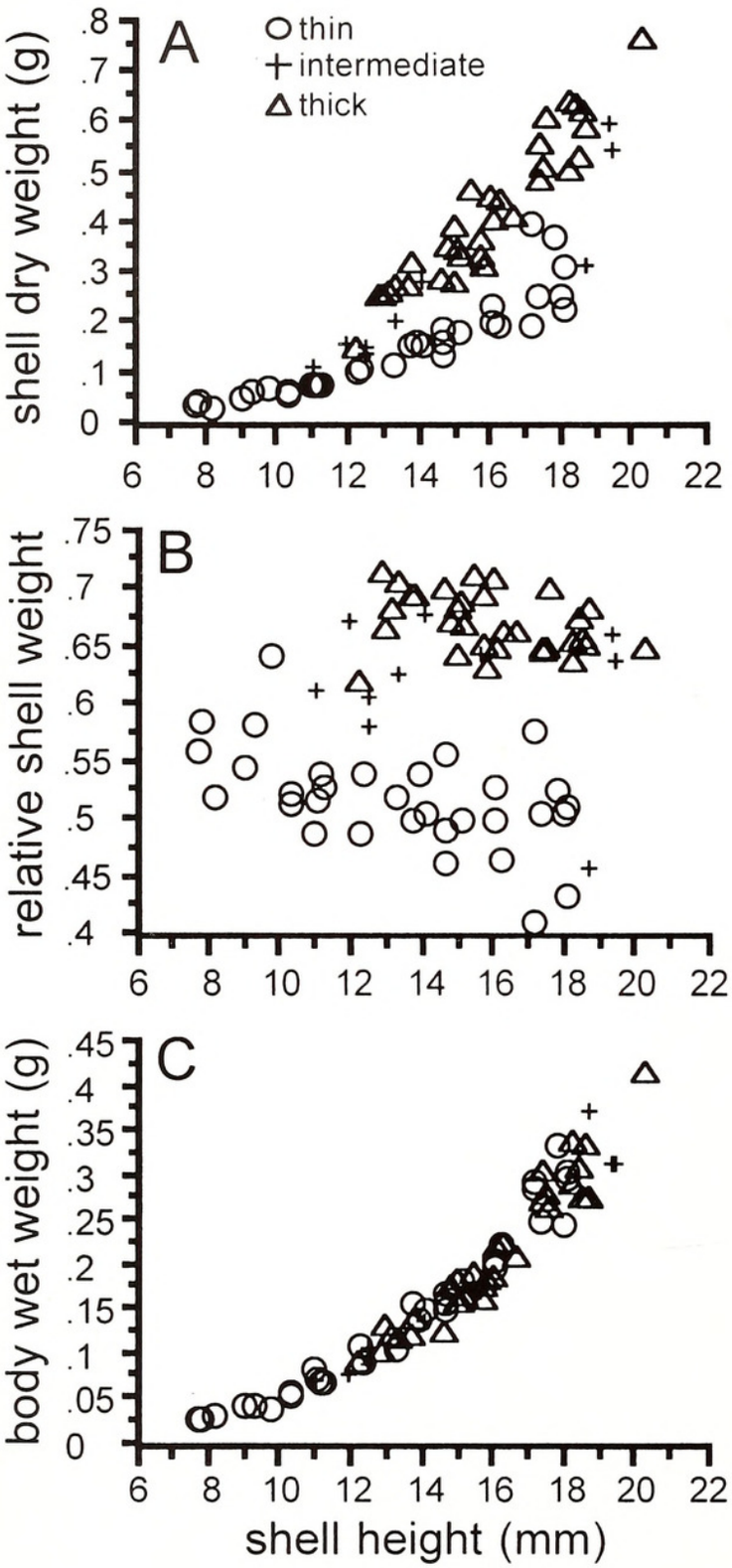

Figure 2. Relationships of shell height with (A) shell dry weight, (B) relative shell weight, and (C) body wet weight for thin-lipped, intermediate, and thick-lipped individuals of *Amphissa columbiana*. Ordinary least squares regressions of log-transformed data showed the following relationships: In (A), for n=32 thin-lipped snails, log (dry shell weight) =2.454 (±0.106) * log (shell height) −3.626 (±0.118), r^2=.947; for n=32 thick-lipped snails, log (dry shell weight) =2.653 (±0.173) * log (shell height) −3.591 (±0.207), r^2=.887 (adjusted means significantly different by ANCOVA, p<0.0001). In (B), for n=32 thin-lipped snails, log (tissue wet weight) =2.818 (±0.069) * log (shell height) −4.064 (±0.077), r^2=.983; for n=32 thick-lipped snails, log (tissue wet weight) =2.945 (±0.134) * log (shell height) −4.247 (±0.161), r^2=.941 (adjusted means significantly different by ANCOVA, p=0.0038). In (C), regression of relative shell weight on shell height is not significant for intermediate and thick-lipped snails (p=0.54 and 0.06, respectively), but it is significant for thin-lipped snails (n=32, relative shell weight =0.614 −0.007 * height, r^2=.266).

A raised callus was present on the columellar lip of the aperture and apertural denticles were sometimes present (but weakly developed). The shell was usually neither very eroded nor covered with epibionts.

Snails classified according to these criteria also differed quantitatively in allocation to shell and body weight. This is illustrated by data on 74 snails collected in January 2003 (snails collected in 1999 and 2002 showed very similar patterns). Thin-lipped and thick-lipped snails overlapped broadly in shell height (thin 8-18 mm, thick 12-20 mm). ANCOVA of log-transformed data showed that thick-lipped snails had significantly higher shell weight than did thin-lipped snails when shell height was considered as a covariate (Fig 2A; see figure legend for regression parameters). Snails of intermediate shell form fell between thin-lipped and thick-lipped snails. Relative shell weight (shell dry weight/ total weight of the snail) was much higher in thick-lipped snails (67%±2.6% standard deviation) than in thin-lipped snails (52%±4.5%), with snails of intermediate shell form falling in between (62%±6.4%; differences among all three classes of snails significant by ANOVA followed by Fisher's PLSD post-hoc tests, p<0.001). Relative shell weight was unrelated to shell height in intermediate and thick-lipped snails, but negatively correlated with shell height in thin-lipped snails (Fig. 2B). Thus, in addition to qualitative characters, a quantitative index (relative shell weight) could be used to distinguish thin-lipped and thick-lipped snails.

Thin-lipped and thick-lipped snails also differed in relationships between body weight and shell height. ANCOVA of log-transformed data showed that thin-lipped snails had very slightly (but significantly) higher body wet weight than did thick-lipped forms (Fig. 2C). Body weight of the largest thick-lipped snails (0.41 g) was about 4.5 times that of the smallest thick-lipped snails (0.09 g).

Growth of thin and thick-lipped snails

Thick-lipped snails added very little shell or tissue on average (Table 1). Because results from the two observation periods were very similar, I pooled data for thick-lipped snails to test for differences from hypothesized means of zero. In thick-lipped snails, the mean growth increment in shell height was not significantly different from zero (t-test,

Table 1. Initial sizes and changes in size of thin-lipped and thick-lipped individuals of *Amphissa columbiana* held in a common laboratory environment. Two sets of observations of growth increment were made, the first starting in January 2003 (during the reproductive season) and the second in April 2003 (after the reproductive season). Changes in size are reported as means (standard deviation).

January-March observations (10 weeks)					
Shell form	n	Initial height (mm)	Change in height (mm)	Change in shell weight (g)	Change in body weight (g)
Thin-lipped	6	14.48 (1.187)	4.8 (1.58)	0.128 (0.021)	0.225 (0.093)
Thick-lipped	10	15.47 (0.785)	0.06 (0.18)	0.004 (0.004)	0.007 (0.007)
April-July observations (11 weeks)					
Shell form	n	Initial height (mm)	Change in height (mm)	Change in shell weight (g)	Change in body weight (g)
Thin-lipped	11	13.49 (0.686)	5.9 (1.87)	0.197 (0.043)	0.238 (0.105)
Thick-lipped	9	14.32 (1.672)	0.0 (0.15)	0.007 (0.007)	0.009 (0.008)

$p=0.16$), but mean growth increments for shell mass and body mass growth were very slightly greater than zero (t-tests, $p<0.001$). Thin-lipped snails grew very rapidly (Table 1), with many individuals adding more than a whorl of new shell during these observations. There were no obvious differences between growth increments of thin-lipped snails measured during the reproductive season versus those measured after the reproductive season. Growth increments for all three parameters were significantly greater in thin-lipped snails than in thick-lipped snails in both sets of observations (t-tests, $p<0.005$).

Sexual maturity

Penises of six thick-lipped snails (shell heights 19.0-22.1 mm) ranged from 10-12 mm in length (mean 11.2 mm), while penises of five thin-lipped snails (shell heights 14.1-20.3 mm) ranged from 1-3 mm in length (mean 1.7 mm). Thus, penises of thick-lipped snails were on average about seven fold longer than those of thin-lipped snails (difference significant by t-test, $p<0.001$).

None of the 17 thin-lipped snails observed in the laboratory during the reproductive season of 2002-2003 deposited egg capsules. In contrast, many egg capsules (indicating deposition by multiple females) were observed in both of the chambers containing thick-lipped snails.

Causes of variation in size at maturity

Food availability had clear effects on growth (expressed as percent change) in shell height, shell weight, and body weight (Fig. 3A). These effects were in the expected direction—fed snails grew much more than did starved snails. In contrast, presence or absence of crabs had no obvious effects on snail growth.

By the qualitative criteria described above, shell form in experimental snails did not change during the experiment—no snails obviously switched from the thin-lipped to the thick-lipped morph. Predator treatment had a nearly significant effect on an index of shell thickness, relative shell weight, when raw data were used in the analysis ($F=3.84$, degrees of freedom 1, 38; $p=0.057$; Fig. 3B). When container means were used in place of raw data (a modification of the analysis that reduces its power, but also reduces the chances of Type I error), predator treatment had no significant effect on relative shell weight ($F=1.46$, d.f. 1, 7; $p=0.267$).

Food availability had a significant effect on relative shell weight regardless of whether raw data or container means were used in the analysis (raw data $F=27.06$, d.f. 1, 38; $p<0.0001$; container means $F=14.08$, d.f. 1, 7; $p=0.007$). At the beginning of the experiment, for all snails, shell comprised a mean of 50.3±5.0% of total snail weight. At the end of the experiment, starved snails had a higher mean relative shell weight (54.2±4.5%) than fed snails (47.4±4.5%; Fisher's PLSD post-hoc test for container mean data, $p=0.008$; Fig. 3B).

DISCUSSION

Determinate growth explains striking variation in shell form in the intertidal gastropod *Amphissa columbiana* (Fig. 1). Young snails build thin-lipped shells and grow rapidly, but eventually they alter the shape and thicken the apertures of their shells and grow only very slowly, if at all (Table 1). These differences in shell form and growth rate are correlated with differences in sexual maturity. Male thick-lipped snails have large penises, while the penises of thin-lipped snails are so minute that they are likely not functional in copulation. Thin-lipped snails maintained in the laboratory did not deposit egg capsules, while thick-lipped snails deposited many egg capsules, suggesting that female thin-lipped snails are not sexually mature. However, in these experiments, female thin-lipped snails were only offered thin-lipped males (which have tiny, probably nonfunctional penises) to mate with, so an alternative hypothesis is that female thin-lipped snails were sperm-limited. Although I studied patterns of shell form, growth rate, and maturity in

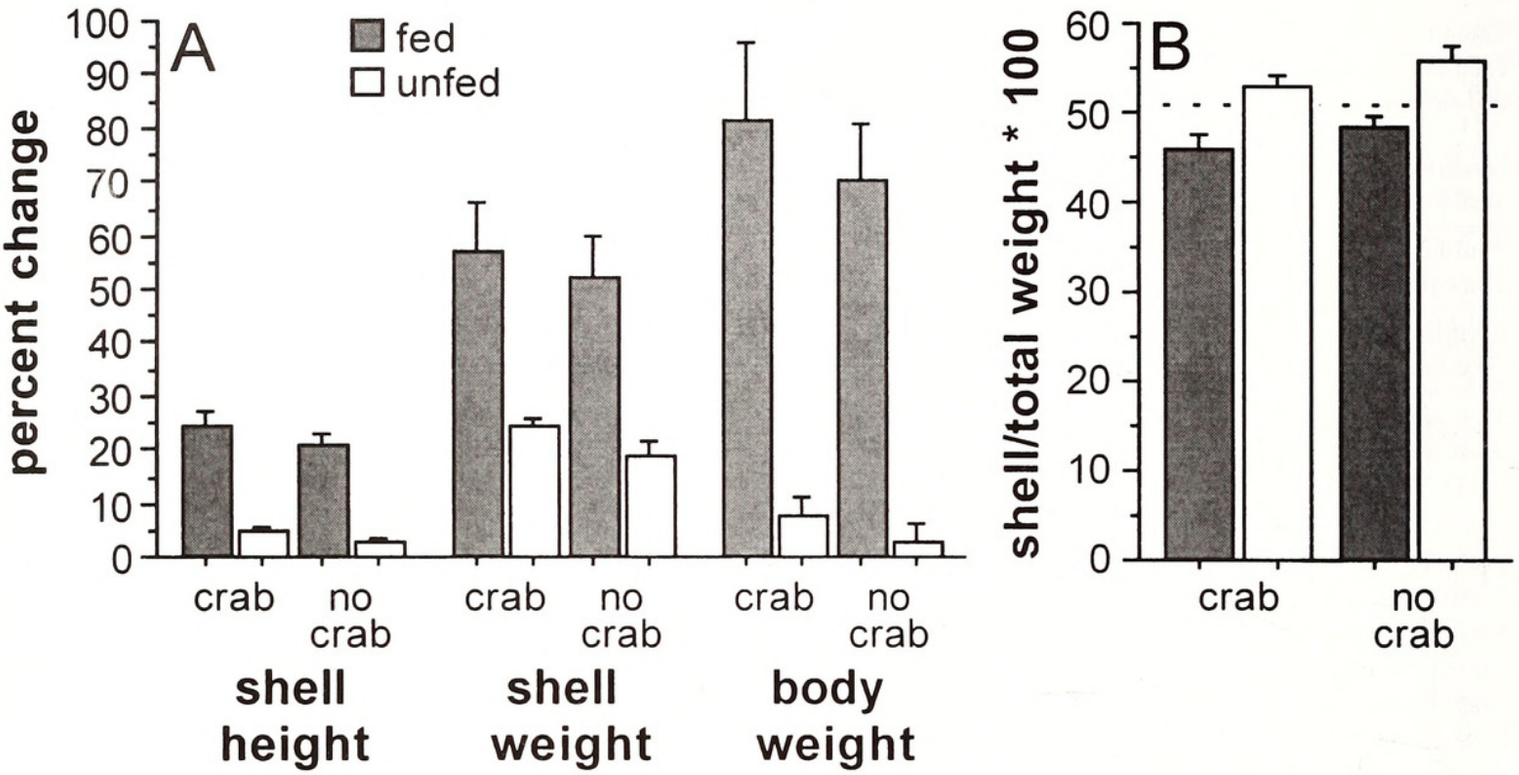

Figure 3. Percent change in (A) shell height, shell weight, and body weight and (B) relative shell weight (shell weight/total weight) in individuals of *Amphissa columbiana* after two months of rearing under different conditions in the laboratory. Means (± standard error) are shown, with n=8-14 replicate snails for each bar. The dashed line in (B) represents the mean relative shell weight of all snails at the beginning of the experiment.

only one intertidal population, both thin-lipped and thick-lipped snails are also present in intertidal populations elsewhere in Washington State and in subtidal populations in the San Juan Islands (personal observation). In these populations as well, similar differences in shell form are likely attributable primarily to determinate growth. To my knowledge, these are the first data on growth and reproduction applied to testing the hypothesis of determinate growth in columbellids. Determinate growth in the family has previously been inferred solely from variation in shell form (McLean 1978, Vermeij and Signor 1992).

In a popular guide to shells, White (1976) mentioned variation in shell thickness in intertidal populations of *Amphissa columbiana*, but interpreted it with the hypothesis that *A. columbiana* "develops thicker shells where exposed to wave action." The variability he mentioned (but did not describe further) may simply have been normal ontogenetic variation in shell form and thickness like that described here. It is possible that shell form in *A. columbiana* varies both ontogenetically and with environmental conditions like wave action, but further studies comparing shell form among populations exposed to different environmental conditions are needed to clarify this issue. Tupen (1999) described substantial site-associated quantitative variation in adult shells of another columbellid, *Alia carinata*. A plausible explanation for such variation is phenotypic plasticity, similar to that suggested by White (1976).

It is interesting to note that collections of post-mortem shells of *Amphissa columbiana* may, depending on their provenance, represent strongly biased samples of life history stages and shell sizes. For example, assemblages of post-mortem shells of *A. columbiana* present on the shore at Deadman's Bay (almost all occupied by hermit crabs) are mostly those of thick-lipped snails greater than 13 mm in height (personal observation). The rarity of thin-lipped shells of juvenile snails in these assemblages may be a result of low mortality among juvenile snails (*e.g.*, because they tend to inhabit protected microhabitats), greater vulnerability of juvenile shells to shell-destroying predators, or rapid post-mortem degradation of thin-lipped shells. Collections made from natural assemblages of dead shells are very likely to reflect a bias towards the shells of larger, mature snails. For similar reasons, the delicate juvenile shells of *A. columbiana* (and perhaps other determinately-growing columbellids) may also be less likely to be preserved as fossils than are robust adult shells. Such potential sampling and taphonomic biases should be taken into consideration when making inferences from shell form in determinately-growing snails.

If, as argued above, thickening of the shell aperture and cessation of growth is correlated with maturation in *Amphissa columbiana*, then size at maturity varied over a range of about 1.7-fold as shell height and 4.5-fold as wet body weight in the Deadman's Bay population. This wide range in size within a single population of a single species represents about 22% of the total range of adult sizes of 144 species of columbellids studied by Roy (2002). (Roy used the geometric mean of shell height and width as an index of size, and I estimated this index for small and large adult individuals of *A. columbiana* for comparison with his data.) Such great variability in adult size appears to be fairly common among determinately-growing gastropods (Vermeij 1980). Although no data are available on the relationship between body size and fecundity in *A. columbiana*, by analogy with other gastropods (*e.g.*, Iyengar 2002, Angeloni 2003) the two are very likely correlated. The fecundity of small *A. columbiana* is thus probably limited relative to that of large individuals. What causes many snails in this population to mature and stop growing at small sizes?

Some component of the observed variation in size at maturity is likely to be genetic (*e.g.*, Richards and Merrit 1975, Brown *et al.* 1985) and might be identified in breeding studies. Size at maturity might also vary as a plastic response to several environmental variables, such as food quantity or quality, or risk of predation or parasitism (*e.g.*, Brown 1985, Brown *et al.* 1985, Lafferty 1993). I examined whether one of these environmental factors, the presence of odor cues associated with a crushing predator, affects the timing of maturation and shell thickening in *Amphissa columbiana*. High risk of predation might induce early maturation in *Amphissa columbiana* because this would improve the chances of reproduction before death, but also because shell thickening, which is associated with maturation, is expected to render shells more resistant to attack by shell-crushing predators (*e.g.*, Palmer 1985, Vermeij and Signor 1992, Trussell 2000). My results suggest that odor cues associated with a potential crushing predator (the crab *Cancer productus*) do not induce maturation and shell thickening in *Amphissa columbiana* (Fig. 3). There were no qualitative changes in the form of thin-lipped snails raised in the presence of crabs. Whether or not *C. productus* was present, thin-lipped fed snails increased in shell weight by a mean of about 55% of their initial shell weight over 8 weeks (Fig. 3A). Because fed snails added even more body weight over the course of the experiment (roughly 75% of initial body weight, Fig. 3A), relative shell weight, an index of shell thickness, decreased slightly over the course of the experiment (Fig. 3B). This index was expected to increase if snails thickened their shells in response to crab-associated odor cues. Addition of 55% of initial shell weight, if allocated primarily to thickening the shell instead of to continued spiral growth, would be nearly sufficient to fully convert a thin-lipped to a thick-lipped snail (Fig. 2).

This result has many possible interpretations. One is that odor cues associated with predators genuinely do not affect the timing of maturation in *Amphissa columbiana*. Alternatively, predator cues may have been too weak to elicit a response in experimental snails; snails may respond to predators other than small *Cancer productus*; or snails may respond to a correlate of predator presence (*e.g.*, the smell of crushed conspecifics) instead of to predator odor itself. However, *C. productus* is known as an important crushing predator of intertidal snails of a wide range of sizes (*A. columbiana* falls within that size range: Palmer 1985, Boulding *et al.* 1999) in similar habitats in the northeast Pacific. *Nucella lamellosa* (Gmelin, 1791) reared under similar conditions to those described here alter shell form in the presence of odor cues from *C. productus* within 2.5 months (Appleton and Palmer 1988), suggesting that sufficient predator cue and time was allowed in my experiments to elicit a response if it existed. In *N. lamellosa*, the effect of crab odor is enhanced when the *C. productus* are fed conspecific snails, but is detectable no matter what the crabs are fed (Appleton and Palmer 1988). These considerations lead me to favor the first interpretation, that size at maturation in *A. columbiana* is genuinely not affected by the presence of cues associated with predators.

Regardless of the presence or absence of predator odor cues, food level had a small but significant effect on relative shell weight in *Amphissa columbiana*. Both fed and starved snails grew during these experiments, but in fed snails, more of the increase in total weight was allocated to the body tissues than the shell, leading to a decline in relative shell weight. In starved snails (which grew much less than fed snails), more of the increase in total weight was due to increased shell weight, leading to a slight increase in relative shell weight (Fig. 3). It seems likely that this increase in allocation to shell is not associated with maturation, but instead is related to slow growth (*e.g.*, Kemp and Bertness 1984; Boulding and Hay 1993). However, habitat quality (of which food quantity and quality is a major part) has been associated with age and size at maturation in several other gastropods (*e.g.*, Vermeij 1980, Brown 1985, Lafferty 1993) and with other changes in shell form in other species (*e.g.*, Appleton and Palmer 1988).

Another way of identifying environmental cues that might affect size at maturation is to examine variation in adult size among habitats. Tupen (1999), for example, found significant differences in shell dimensions among populations of another columbellid, *Alia carinata* (Hinds, 1844), from several different habitats. He argued that these differences might have resulted from phenotypic plasticity or

post-settlement selection on the basis of habitat-specific differences in predation or wave exposure. No comparable studies have been carried out for *Amphissa columbiana*. However, individuals of *A. columbiana* from some subtidal habitats in the San Juan Islands may reach much larger adult sizes than those in the intertidal zone at Deadman's Bay. At the latter site, I have not seen snails larger than 21 mm shell height in five years of observations, but among the 7 subtidally collected specimens in the Friday Harbor Laboratories Synoptic Collections, 4 have shell heights greater than 25 mm, with one snail whose apertural lip is of intermediate thickness measuring 28.7 mm. *A. columbiana* have planktonic, feeding larvae that spend at least two weeks in the plankton (personal observation) so subtidal and intertidal populations are likely well-mixed genetically. These data suggest that environmental differences between intertidal and subtidal habitats affect size at maturation in *A. columbiana*.

Individuals of *Amphissa columbiana* that were kept in the laboratory for two months without food grew substantially, adding on average about 20% to their initial shell weight and about 5% to initial body weight (Fig. 3). It is not clear what fueled the growth of starved snails. Shell growth was not occurring at the expense of body weight, as both increased over the course of the experiment. Similar increases in shell weight in the face of starvation have been recorded previously in *A. columbiana* (and other snails: Palmer 1983), although in that study body weight is not reported. Hatfield (1979) found that another columbellid, *Anachis avara* (Say, 1822), increased in shell height by about 10% over six weeks of starvation, and suggested that particulate or dissolved organic matter present in the seawater fueled this growth. This may be the case for *A. columbiana* as well. My data (Fig. 3) suggest a trend of higher overall growth for snails raised in the presence of crabs versus those raised without crabs. It is possible that some bivalve tissue was torn into small bits by crabs (all of which were fed) and was carried by water into snail containers. However, starved snails reared in the absence of crabs (and in the absence of crab food) also increased in both shell and body weight.

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