

## EVOLUTION OF ADAPTATION THROUGH ALLOMETRIC SHIFTS IN A MARINE SNAIL

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**Abstract.**—Variation in ontogenetic development among individuals may be a major contributor to morphological variation within species. Evolution of different growth trajectories might, for example, evolve as a response to varying ecological contexts of individuals living in different environments, or by life-stage or gender differences. The intertidal periwinkle *Littorina saxatilis* is strongly polymorphic in shell shape. We compared ontogenetic trajectories between life stages, local populations, and sexes to understand how different morphological end points are reached during ontogeny and what might cause these differences. Applying landmark-based geometric morphometrics, we captured shell shape variation for four Swedish populations of this species. We also derived a method to visualize ontogenetic trajectories described by the relationship of size to the multivariate shape space. We found that growth trajectories differed between individuals living in different habitats, as well as between sexes and maturity stages. Males living on rocky cliffs grew isometrically throughout life, whereas females from the same habitat switched from isometric growth as juveniles to allometric growth as adults. In contrast, males and females living on boulders grew allometrically as juveniles but changed to isometric growth at sexual maturity. Thus, in this species, ontogenetic growth seems influenced by habitat-associated selection as well as by gender and age-specific selection. These differing selection regimes result in ontogenetic shifts in allometry in three of the four groups examined.

**Key words.**—Allometric growth, biphasic shape allometry, geometric morphometrics, isometric growth, *Littorina saxatilis*, local adaptation, ontogeny, rocky shore.

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Intraspecific morphological diversity is substantial in many species and fundamental to lineage evolution, yet we still have only a minimal understanding of how and why such intraspecific variation exists. Considerable morphological diversity is generated through spatially varying natural selection, producing differences between groups of individuals living in different environments (Futuyma 2005). However, additional variation within species may be generated by selection that changes the pattern of ontogenetic growth of individuals throughout their lifetime (Peters 1983; McKinney and McNamara 1991). In many taxa, the optimal morphological shape for a particular environmental condition may vary throughout the course of the organism's growth and development. Therefore, stage-specific or size-specific selective components will be expected to promote additional phenotypic variation in a population. Changes in optimal size and shape over an individual's lifetime may also differ between males and females, given their differing roles in mating and reproduction (Fairbairn 1997). Under this scenario, gender-specific ontogenetic growth patterns would be expected. Finally, ontogenetic growth patterns may differ among individuals of a species that live in different ecological habitats.

Ontogenetic growth patterns that change across developmental stages (biphasic allometry) can significantly contribute to population variability in morphology (Callery et al. 2001). It is well established that many organisms grow allometrically (Huxley 1932; Thompson 1942; Loy et al. 1998; Birch 1999; Tokeshi et al. 2000; Rosas and Bastir 2002; Cardini and Tongiorgi 2003), whereas lifetime proportionality through isometric growth is rarely found (Schmidt-Nielsen 1984; McKinney and McNamara 1991; Klingenberg

1998). On the other hand, allometric shifts during ontogeny and how these shifts link to life history have not been extensively investigated in species with indeterminate growth. In particular, the role of stage-specific selection in promoting allometric shifts needs to be explored to understand how ontogenetic variation contributes to total phenotypic variation in these species.

The marine gastropod *Littorina saxatilis* is strongly polymorphic in shell traits, which is a consequence of a poor dispersal (<3 m in three months; Janson 1983) and living in a habitat with strong and variable selection, the rocky shore (Vermeij 1972; Janson 1983; Denny et al. 1985; Tissot 1988; Reid 1996; Gaylord 1999). Indeed, there is extensive experimental data showing that this species, as well as other rocky shore gastropods with low dispersal of various life stages (e.g., hatchlings, juveniles, and adults), achieve considerable morphological divergence as a result of heavy and site-specific selection on size and shape (Seeley 1986; Palmer 1990; Johannesson et al. 1993; Johannesson and Johannesson 1996; Reid 1996; Rolán-Alvarez et al. 1997; Johnson and Black 2000; Tokeshi et al. 2000; Johannesson 2003). Field experiments have shown that this polymorphism is essential to local survival: snails of *L. saxatilis* from one type of microhabitat released in a similar microhabitat survive approximately 10 times better than released snails from another microhabitat (Janson 1983; Rolán-Alvarez et al. 1997).

In many areas the phenotypic polymorphism of *L. saxatilis* is extensive, and microhabitat-specific ecotypes or ecomorphs are produced (Reid 1996; Johannesson 2003). In the intervening regions between different microhabitats, populations of distinct ecotypes are connected through hybrid

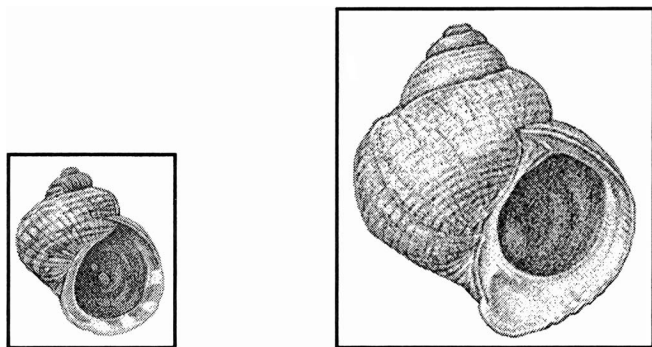


FIG. 1. Swedish ecotypes of *Littorina saxatilis*. The E morph (left) is small and thin-shelled, and has a rounded and large aperture. The S morph (right) is larger, with a robust shell and a relatively smaller aperture and a higher spire.

zones that include both pure ecotype snails and snails of intermediate phenotype (Janson and Sundberg 1983; Johannesson et al. 1993; Panova et al. 2006). In rocky parts of the Swedish west coast, for example, two ecotypes are present, the ‘E’ morph of exposed rocky cliffs and the ‘S’ morph of boulder shores (Janson 1982a). E-morph snails have low spires, thin shells, and are small in size (Janson 1982a) (Fig. 1). These characters are believed to reduce drag forces from waves and allow the snails to better fit into cracks and cavities in the rock (Emson and Faller-Fritsch 1976; Raffaelli and Hughes 1978; Hart and Begon 1982). S-morph snails are two to four times as large as E snails and have a thick shell and a small aperture (Janson 1982a). These traits show resistance to crab crushing and winking (pulling the soft parts of the snail out of the shell through the aperture; Johannesson 1986). The trait differences between the two ecotypes are largely genetically fixed ontogenetic differences (Johannesson and Johannesson 1996), although some environmentally induced phenotypic differences are expressed during development (Hollander et al. 2006). As a result of these observations, we hypothesized that growth patterns might differ in this species. From this we formulated three predictions: (1) individuals from different environments may show different ontogenetic growth as a result of different habitat-specific selection regimes, (2) males and females may reveal different growth trajectories owing to gender-specific reproductive demands, and (3) different selection regimes for juvenile and adult individuals may promote ontogenetic shifts in growth trajectories at size of maturity.

## MATERIALS AND METHODS

### *Phenotypic Data*

We performed a descriptive cross-sectional allometric analysis (Cock 1966; Klingenberg 1998) to examine size-specific development. With this approach we separately analyzed four groups; females of the E and S morph and males of the E and S morph from two islands. Representative samples of individuals of all sizes (>2 mm) of E- and S-morph *Littorina saxatilis* were collected in the area around Tjärnö Marine Biological Laboratory, on the Swedish west coast, during the summer 2003. Snails of S morph and E morph were sampled (50 m apart) from the island Jutholmen

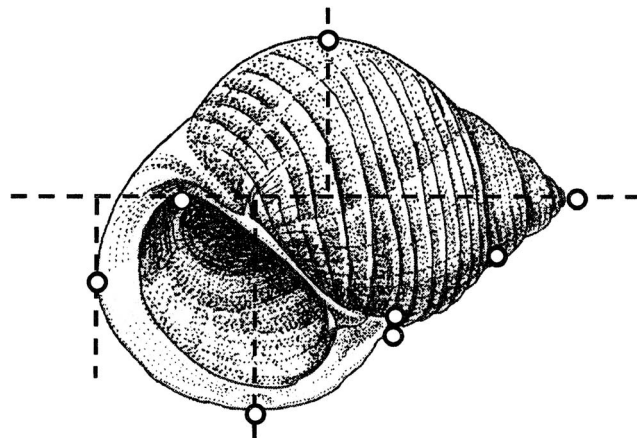


FIG. 2. Eight anatomical landmarks used in the morphometric analysis.

(58°52.3'N, 10°59.3'E) and from a replicate population (again S and E morph 50 m apart) from the island Burholmen (58°51.0'N, 10°59.4'E) 3 km away. Earlier studies using molecular genetic markers showed that populations separated on different islands are genetically isolated and can be considered independent populations, but samples of different ecotypes from the same island are connected by a gene flow and less differentiated in neutral loci than samples from distinct islands (Johannesson and Tatarenkov 1997; Johannesson et al. 2004; Panova et al. 2006).

A total of 556 specimens was used in this study; 70 males and 70 females of each morph from each of the two islands including both juveniles and adults (four outliers were removed). To quantify phenotypic diversity in shape we used landmark-based geometric morphometrics (Rohlf and Marcus 1993; Adams et al. 2004; Hollander et al. 2005). Snail species with indeterminate growth (such as *Littorina saxatilis*) continually accrete shell material throughout life, which poses challenges for capturing the complete ontogenetic trajectory and all aspects of ontogenetic shape change (Guralnick and Kurpius 2001). However, for size-specific allometric patterns, shapes can be consistently quantified between individuals to allow comparisons of a snapshot of ontogenetic variation, and therefore such challenges are alleviated. In this study, our aim was to analyze size-specific allometry of different life stages using size at sexual reproduction as the reference. For this purpose, the anatomical landmarks described below provide useful means of capturing size-specific shape variation.

We used a side view to capture shape changes in ecologically relevant traits such as aperture size and spiral volume (although for other hypotheses, a top view might be preferable; see Guralnick and Kurpius 2001). Images of each individual with the aperture facing upward were projected through a camera lucida onto a digitizing tablet (Summasketch III, GTCO Calcomp, Inc., Columbia, MD), and the  $x,y$  coordinates of eight anatomical landmarks at the surface of the shell (Fig. 2) were recorded using DS-DIGIT (Slice 1994). The effects of nonshape information (position, orientation, and scale) were mathematically eliminated from these landmark configurations using a generalized Procrustes analysis

(GPA; Rohlf and Slice 1990) which aligns all specimens and superimposes them to a common coordinate system. From the aligned specimens, shape variables were generated as partial warp scores from the thin-plate spline (Bookstein 1991) and from the two standard uniform components (Bookstein 1996; Rohlf and Bookstein 2003). Together, these variables (called the weight matrix) capture all aspects of shape variation, and can be used to test hypotheses of shape variation and covariation within and among groups using standard multivariate statistical procedures (Adams and Rohlf 2000; Adams 2004; Collyer et al. 2005). Because we were interested in examining allometric effects on shape, we retained the size of each individual as represented by centroid size (CSize), which is the squared root of the sum of squared distance from each landmark to their centroid (Bookstein 1991). Finally, an additional 133 females of the S morph (length 3.15–13.53 mm) from both of the boulder sites and 125 females of E morph (1.16–10.77 mm) from both of the rocky sites were dissected to determine size at sexual maturation. E-morph females carrying embryos were 4 mm in length or larger, and S-morph females were 10 mm or larger. We used these sizes to separate juvenile and adult females, and we also defined males as being sexually mature at these sizes, although earlier reports sometimes indicate that males might mature at somewhat smaller sizes than females (Reid 1996).

#### Statistical Analyses

To understand patterns of phenotypic diversity and patterns of allometry, we first examined overall shape variation using a principal component analysis (PCA) and thereafter assessed the degree to which size influenced shell shape through allometric growth using several analyses. First, overall allometry was examined using a multivariate analysis of covariance (MANCOVA). In this analysis, males and females of both ecotypes (E and S) were treated as separate groups and compared, and variation in shell shape was explained in terms of the allometric effects of body size, as well as group effects. Data were separated by island to investigate concordance of morphological signal among groups. We also examined patterns of allometry in different developmental stages (juveniles and adults) for each sex, morph, and island using a multivariate regression performed on each group separately; and each dataset was assessed for significance through a randomization procedure. Where concordances of allometric patterns were identified between islands, island groups were pooled to increase statistical power. Finally, pairwise multiple comparisons of allometric regression vectors were performed to identify possible biphasic allometry (i.e., differences between developmental stages), and to determine whether allometric patterns differed between ecotypes or between sexes. All analyses were performed in JMP (SAS Institute 2003), TPSRegr (Rohlf 2003), and NTSYSpc (Rohlf 2000).

#### RESULTS

Although snails of E and S morph were largely distinct in shell shape, variation within ecotype revealed considerable shape overlap between males and females and between ju-

veniles and adults, such that differences between these groups were not at all obvious (Fig. 3). However, examining the allometric relationships we found noticeable differences in ontogenetic growth between the groups, and these patterns were largely similar between snails of the same ecotype from different populations (islands). Indeed, the MANCOVA revealed significant effects of morph, sex, and size (CSize) and their interactions, except for the highest level of interaction term in one population (Jutholmen), indicating that all factors and most interactions were important to the allometric shape of a snail (Table 1). Furthermore, rank order of importance of main effects was morph > CSize > sex in both islands, implying that the phenotypic signal tended to be concordant between independent populations.

When multivariate regressions of shape versus size were performed for each island and for each group of morph-sex-developmental stage separately, we found that some groups displayed significant shell shape allometry, whereas others showed nonsignificant allometry, that is, isometric growth (Table 2). In six of eight comparisons these results were consistent between islands. Therefore, we pooled data from the two islands to increase statistical power. For adult and juvenile females of the E morph, separate analyses of the two islands suggested different results. However, this seemed to be a statistical artifact rather than a description of biologically distinct allometric patterns (see below).

Analyzing the pooled data indicated that E-morph juveniles of both sexes and adult males grew isometrically, whereas adult females of the E morph grew allometrically (Table 3). Although the separate statistical analysis of each island suggested different growth patterns among E-morph females, the deformation grids displayed highly similar patterns between islands for both juveniles and adults, strongly supporting the overall result of the pooled data (Fig. 4). Thus, growth of E-morph males followed an isometric trajectory throughout life whereas female E morphs switched from juvenile isometric growth to adult allometric growth (Fig. 5). Indeed, pairwise comparisons revealed differences in growth patterns between E-morph female juvenile and female adult snails ( $F = 4.93$ ,  $df = 12,537$ ,  $P < 0.0001$ ), while no significant difference was found between male and female juvenile growth patterns ( $F = 0.53$ ,  $df = 12,529$ ,  $P = NS$ ).

S-morph snails showed another allometric pattern: both males and females displayed significant allometric growth during the juvenile stage but switched to isometric growth at size of maturation (Table 3). Similar to the E morph, juvenile S-morph allometry was not significantly different between sexes ( $F = 1.67$ ,  $df = 12,529$ ,  $P = NS$ ), whereas in both sexes adult and juvenile growth patterns differed ( $F = 34.91$ ,  $df = 12,529$ ,  $P < 0.0001$ ). Thus both females and males of the S morph exhibited biphasic growth trajectories with size at sexual maturation (Fig. 5). Moreover, in both morphs juvenile development did not differ between sexes. Notably, only E-morph males grew isometrically throughout life.

Examining the thin-plate spline deformation grids of shape revealed that most of the allometric changes occurred near the aperture and at the apex of the shell (Fig. 5). Among the adult E-morph females the most prominent change was an extended spire volume and a somewhat decreased aperture

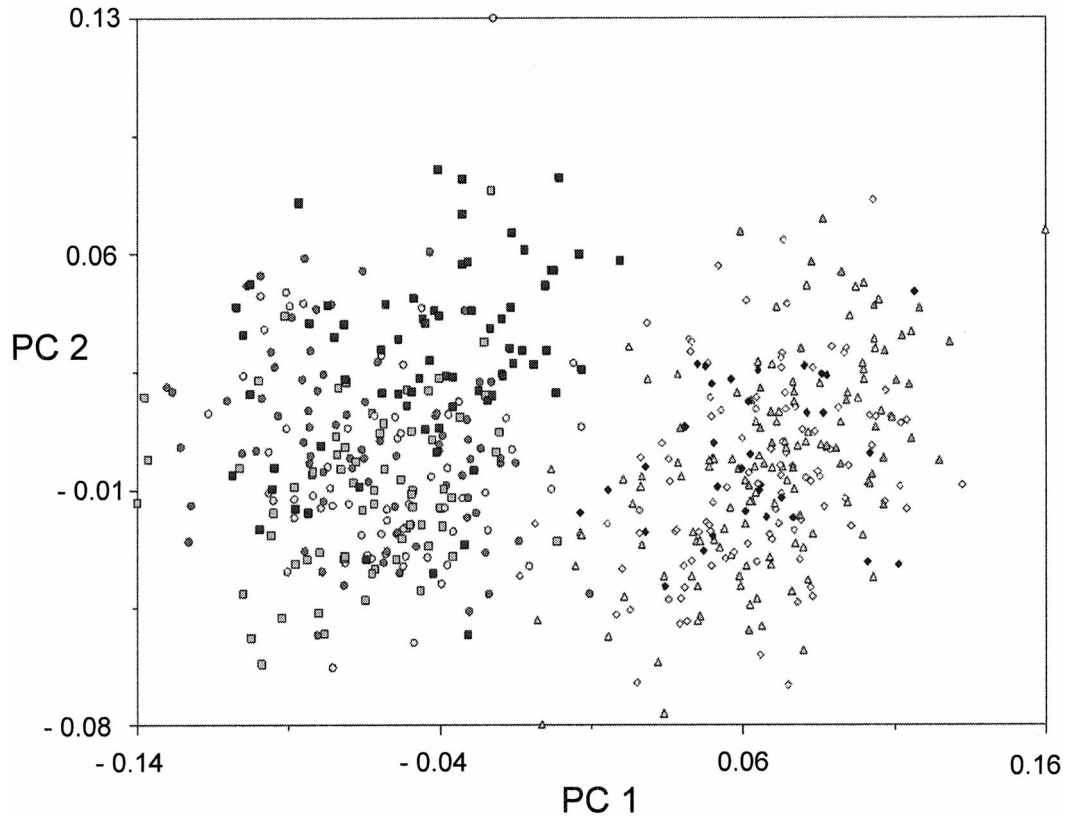


FIG. 3. Principal component analysis of variation in shell shape; 69% of the variation is expressed in the first two axes of the data space. Light symbols represent juveniles and darker symbols represent adults. Form of datapoints indicates sex-ecotype combinations (circle: E-morph male, square: E-morph female, diamond: S-morph male, triangle: S-morph female).

area. Similar shape deformations occurred during the juvenile stage of S-morph development (Fig. 5). At size of maturation, both males and females of the S morph thus attained a relatively small aperture and a voluminous spire, and these char-

acteristics were maintained by isometric growth during the adult stage (Fig. 5).

#### DISCUSSION

Allometric growth has previously been reported in *L. saxatilis*, as well as in other gastropod species (Vermeij 1980; Johannesson and Johannesson 1996; Reid 1996). Here we show that snails of *L. saxatilis* show both allometric and isometric growth and that ontogenetic growth patterns are strongly related to microhabitat, sex, and life stage of individuals. Notably, juvenile and adult individuals may differ in developmental patterns that result in biphasic growth trajectories. Although biphasic allometry is commonly reported for metabolic traits (Post and Lee 1996; Glazier 2005), morphological shifts in growth trajectories are most often associated with early metamorphosis from larval to postlarval stages in many animal species (for gastropod examples see Vermeij 1980; Reid 1996). Additionally, shifts in the allometric growth of morphological traits at sexual maturity have rarely been reported. Furthermore, sustained isometric growth during an organism's lifetime is seldom observed in nature (Schmidt-Nielsen 1984; McKinney and McNamara 1991; Klingenberg 1998). Our result supports this generalization, as we found only periods of isometric growth in three of four groups of *L. saxatilis* (male and female S-morph and female E-morph). Interestingly, though, males of E morph revealed isometric growth throughout life.

TABLE 1. Multivariate analysis of covariance analyzing the phenotypic effects of morph, sex, and CSize (centroid size) for each island separately. The phenotypic signal was similar between the two islands, and all terms were significant except the interaction morph  $\times$  sex  $\times$  CSize at Jutholmen.

Island	Source	F	df	P
Burholmen	morph	58.7	12, 258	<0.0001
	sex	5.98	12, 258	<0.0001
	CSize	6.74	12, 258	<0.0001
	morph $\times$ sex	5.53	12, 258	<0.0001
	morph $\times$ CSize	2.08	12, 258	0.02
	sex $\times$ CSize	4.86	12, 258	<0.0001
	morph $\times$ sex $\times$ CSize	3.05	12, 258	0.0005
Jutholmen	morph	97.07	12, 261	<0.0001
	sex	2.59	12, 261	0.003
	CSize	7.08	12, 261	<0.0001
	morph $\times$ sex	2.01	12, 261	0.02
	morph $\times$ CSize	1.94	12, 261	0.03
	sex $\times$ CSize	3.28	12, 261	0.0002
	morph $\times$ sex $\times$ CSize	0.57	12, 261	NS

TABLE 2. The results of multivariate regression analyses indicating allometric ( $P < 0.05$ ) or isometric (nonsignificant) development. Data is analyzed separately for each of the different morph-sex-developmental stages, and for each island separately. Bold numbers indicate significant regression. A dash denotes no value, as sample size was too small for a meaningful statistical test.

Island	Group	F	df	P
<b>Burholmen</b>				
	E female juvenile	3.27	12, 22	<b>0.008</b>
	E female adult	2.29	12, 22	<b>0.04</b>
	E male juvenile	1.76	12, 21	0.12
	E male adult	1.866	12, 23	0.09
	S female juvenile	4.58	12, 44	<b>0.0001</b>
	S female adult	—	—	—
	S male juvenile	3.8	12, 45	<b>0.0005</b>
	S male adult	—	—	—
<b>Jutholmen</b>				
	E female juvenile	0.978	12, 20	0.49
	E female adult	1.42	12, 24	0.22
	E male juvenile	2.3	12, 17	0.06
	E male adult	0.756	12, 27	0.68
	S female juvenile	5.06	12, 35	<b>0.0001</b>
	S female adult	1.3	12, 9	0.35
	S male juvenile	2.64	12, 36	<b>0.01</b>
	S male adult	2.04	12, 8	0.16

A variety of factors may influence ontogenetic shell growth. For example, ontogenetic growth may be under genetic control, environmentally induced, or, most likely, influenced by both factors. Common-garden and transplant studies have shown that genetic variation is a dominant component of differences in shell shape and size between ecotypes of *L. saxatilis* (Janson 1982b; Johannesson and Johannesson 1996; Johannesson et al. 1997). From these results we infer that differences in developmental patterns between the two Swedish ecotypes of *L. saxatilis* is largely inherited and molded by local selection to increase individual fitness of snails of different sex and age living in different microhabitats. Viewed from a biomechanical perspective, the distinct ontogenetic patterns among snail groups that we identified may be explained in terms of specific and differing evolutionary forces inferred from knowledge about the relationships between physical and biotic forces and shell shape and size. For instance, in shores where wave action is a dominating selective factor for snail survival, shell morphologies are formed to minimize drag (small size, low spire) and maximize attachment (a large aperture and foot; Reid 1996; Trussell and Etter 2001; Johannesson 2003). Here, drag force generated by the moving water can be expressed as;

$$F_{Hyd} = A_1 \times U^2 \times h, \tag{1}$$

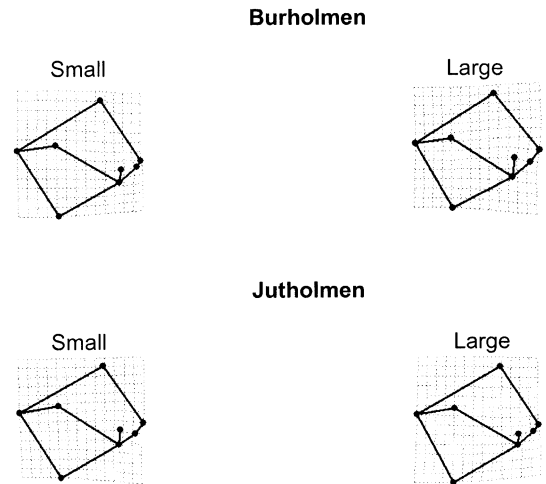
where  $F_{Hyd}$  is the drag,  $A_1$  is the cross-sectional area exposed by the organism against the flow,  $U^2$  is the velocity of the moving fluid, and  $h$  is the drag coefficient (Denny 1988). Thus the force acting on the snail is simply proportional to the cross-sectional area of the snail. Furthermore, the strength with which an organism is able to attach to the substratum depends on the area against the substratum. For a snail, this strength is proportional to the area of the foot, rendering a capacity of adhesion of:

$$F_{Add} = h \times A_2, \tag{2}$$

TABLE 3. Multivariate tests of allometry of pooled data for each group of sex, ecotype, and developmental stage in *Littorina saxatilis*. Nonsignificant tests (NS) indicate isometric growth.

Group	P randomization	Growth pattern
E female juvenile	NS	isometric
E female adult	0.0083	allometric
E male juvenile	NS	isometric
E male adult	NS	isometric
S female juvenile	<0.0001	allometric
S female adult	NS	isometric
S male juvenile	<0.0001	allometric
S male adult	NS	isometric

a) E-morph juveniles (Isometry)



b) E-morph adults (Significant Allometry)

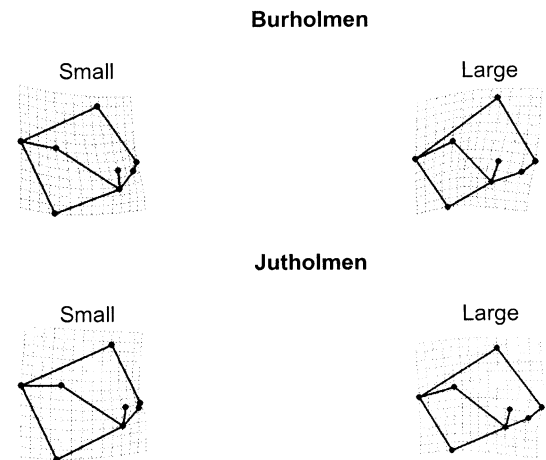


FIG. 4. Deformations grids illustrating E-morph female growth development at each of two islands: Burholmen and Jutholmen. Snail's positions as in Figure 2. Because there was no obvious difference between ontogenetic growth of snails from the two islands, neither at juvenile (a), nor at adult (b) stages we pooled island data also for this group of snails.

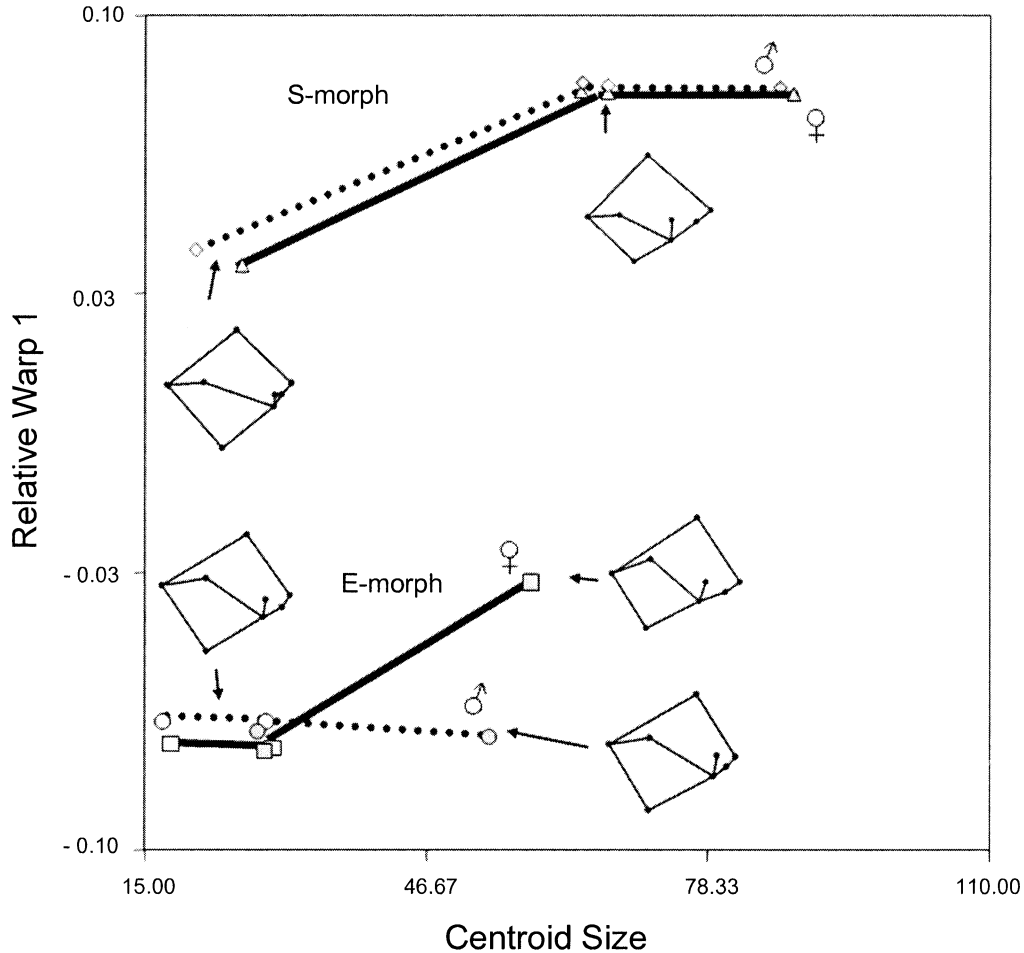


FIG. 5. Pseudo-allometry plot, with centroid size (the squared root of the sum of squared distance from each landmark to their centroid) as the x-axis and relative warp 1 (RW; equivalent to PC) as the y-axis. The minimum and maximum centroid size values are shown for each group, and the average of a subset of small and large specimens for each group generated the y-value. The groups are: E-morph male (circle), E-morph female (square), S-morph male (diamond), S-morph female (triangle). Juveniles are open symbols and adults are shaded gray. Thin-plate spline deformation grids are accentuated by a factor of 3. Snail's positions as in Figure 2.

where  $F_{Add}$  is the force of adhesion,  $A_2$  is the area against the substratum, and  $h$  is the coefficient of adhesion (Denny 1988). Consequently, both drag and adhesion are directly proportional to area (length squared), and an isometric development will maintain a favorable relationship between aperture area and cross-sectional area when snails grow larger, keeping the risk of dislodgement constant over snail sizes.

For E-morph males, wave action is likely to be the dominant ecological selective force, and it may explain their isometric growth throughout life. Interestingly, foot size in the closely related species *Littorina obtusata* has an isometric relationship with size in wave-exposed sites, but not in more protected sites (Trussell 1997).

Although female snails of the E morph live under similar wave-selection conditions, the isometric growth promoting resistance to wave forces is likely counterbalanced by allometric growth promoting increased fecundity in mature females. The observed switch to allometric growth at the size of maturity is consistent with a mechanism to increase reproductive output by expanding spire volume and giving room for more embryos (Reid 1996; Ilano et al. 2004). In-

deed, volume of the shell spire of adult E-morph females was significantly larger than males' spire volume ( $>3\%$ ,  $P < 0.03$ ) for individuals of similar sizes, whereas differences between male and females of the other groups (S adults, S juveniles, E juveniles) were nonsignificant ( $P > 0.05$ ).

In different habitats, boulders protect snails from wave exposure, and thus selection that promotes isometric growth to resist waves is likely weak in boulder-rich habitats. Instead, the high densities of crabs in these environments and increased evidence of crab attacks (as observed by shell-repaired morphology: see Johannesson 1986) indicate that shore crabs exert important selection on shell size and shape on boulder shores (Reid 1996; Trussell and Etter 2001). Boulder shore S-morph snails grow rapidly to attain a large and thick shell (Johannesson and Johannesson 1996), and crab attack success rate appears to decrease with an increase in snail size (Elner and Raffaelli 1980; Johannesson 1986). However, as snails increase their shell size, an alternative attack technique is used by the crabs; instead of breaking the shell they insert a claw through the aperture and pull out the soft parts of the snail (Johannesson 1986). Snails may gain

protection from winking by diminishing aperture size relative to shell size as they grow larger (Johannesson 1986), or by expanding spire height allowing withdrawal of the soft parts into the shell, out of reach of crabs (DeWitt et al. 2000). The allometric growth of juvenile S-morph snails indeed tends to decrease aperture size and expand spire height (Fig. 5), but at size of sexual maturity snails switch to isometric growth. One possible explanation for this switch to isometric growth may be that increased allometric growth results in shell spires that are too high, which consequently increases the risk of crab damage. Support for this is found in *L. obtusata*, where high-spired snails living in crab-free environments on the American east coast lost their spires after shore crabs invaded the area (Seeley 1986).

Although additional experimental studies are needed to sort out the relationship between habitat-related selection and ontogenetic growth patterns of ecotypes, we found that the developmental patterns were largely repeated in independent populations of crabs in similar habitats. Notably, recent studies show that local populations of distinct ecotypes of *L. saxatilis* evolve in situ and that populations of similar ecotype from different areas evolve in parallel (Johannesson 2001; Rolán-Alvarez et al. 2004; Panova et al. 2006). This suggests that the specific allometries have similarly evolved in parallel across these separate populations. If so, this provides additional support for the different ontogenetic developmental pathways being shaped by natural selection. We suggest that researchers have overlooked the importance of developmental shifts in the evolution of species with indeterminate growth, and we recommend further studies be performed to better understand what might be a fundamental component of organic evolution.

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