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Inducible Phenotypic Plasticity of the Radula in *Lacuna* (Gastropoda: Littorinidae)

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Abstract. The radula is the major feeding organ of most gastropods and is a key taxonomic feature for many species. I demonstrate that two species of snail in the genus *Lacuna* Turton, 1827 (Gastropoda: Littorinidae) produce differently shaped radular teeth when fed different foods, displaying intraspecific variability as extreme as would usually be considered to define different species. The new tooth morphology is produced on the non-feeding end of the constantly regenerating radula, and is thus different from use-induced feeding morphologies seen in arthropods or vertebrates. Tooth shape in *Lacuna* is phenotypically plastic, inducible with different food conditions, and reversible within an individual's lifetime, allowing rapid response to new environmental conditions.

INTRODUCTION

Gastropod species identity and taxonomy traditionally has been based on a wide variety of soft body and shell characteristics. The shell is used for taxonomic purposes both in extant and extinct species as it preserves well and is abundant in fossil deposits. However, many aspects of the shell shape and decoration are variable within species, and several have been shown to be phenotypically plastic (Appleton & Palmer, 1988). The gastropod radula is widely regarded as being a reliable character for species identity, and is commonly considered to be species specific. For example, Fretter & Graham (1994: 162) state, regarding the radula, that "the ribbon bears teeth placed regularly along side one another . . . and the number of these and the shape of the teeth differ from species to species, though remaining fairly constant within one species. As a consequence of this and the fact that they are imperishable and may be extracted from dried bodies, the radula is an important organ from the taxonomic view." Because the radula is a major feeding organ of most gastropods, we might predict close associations between diet and radular form (Padilla, 1985, 1989). In fact, ontogenetic changes in diets of some species of *Conus* have been shown to be correlated with ontogenetic changes in radular morphology (Nybakken, 1990).

In the northeastern Pacific, snails in the genus *Lacuna* Turton, 1827, are important grazers of macroalgae, including kelp, and are the dominant grazers in many eelgrass communities (Martel, 1990; Martel & Chia, 1991a, b). These snails readily move between these two habitats as planktonic larvae (> 4 weeks as planktotrophic larvae) or as juveniles and adults which use mucus threads to parachute in water currents (Martel & Chia, 1991b, c). The shapes of radular teeth most effective at grazing on these two different types of foods will be very different

(Padilla, 1985, 1989). *Lacuna* feeding on kelps and other macrophytes excavate the algal tissue itself. Pointed teeth are more effective at gouging this type of surface due to mechanical factors such as stress concentration at tooth tips as compared to broad tooth cusps (Padilla, 1985). In eelgrass beds, however, *Lacuna* graze on the epiphytic micro and filamentous algae growing on the surface of the grass blades without damaging the tissues of the grass beneath. Blunt teeth would be more effective at scraping epiphytes from a surface. Feeding efficiency on these two very different substrata may therefore be a strong selective force on radular tooth morphology (Hickman, 1980; Padilla 1985, 1989).

In initial observations, I found individuals of *Lacuna vincta* (Montagu, 1803) and *L. variegata* Carpenter, 1864, collected from kelp had pointed radular teeth, whereas those collected in eelgrass possessed blunt teeth. These differences could be due to several factors: (1) animals could change their diet ontogenetically and have an ontogenetic shift in radular tooth shape as is seen in *Conus*; (2) *Lacuna vincta* and *L. variegata* populations could be polymorphic for tooth shape—different individuals could have different radular morphologies, and move to habitats that match their tooth shape; or (3) tooth shape could be phenotypically plastic, and inducible by cues from the animal's food or environment (Bradshaw, 1965; Smith-Gill, 1983). I conducted experiments to test whether tooth morphology in an adult snail could change in response to the diet of these snails.

MATERIALS AND METHODS

Lacuna variegata and *L. vincta* (males and females, 2.5–9 mm shell length) were collected from several different kelp beds and eelgrass beds near the Friday Harbor Laboratories, San Juan Island, Washington. Flow-through

Table 1

Radular tooth shape of snails reared on kelp or epiphyte covered eelgrass for 8 weeks. The results of a 3-way G test showed that for *Lacuna vincta* and *L. variegata* food had a significant effect on tooth form ($P < 0.001$), and the two species did not differ in their response.

Food	Epiphytes	Kelp
<i>Lacuna vincta</i>		
Pointed Teeth	0%	100%
Blunt Teeth	100%	0%
<i>Lacuna variegata</i>		
Pointed Teeth	0%	100%
Blunt Teeth	100%	0%

seawater tanks were filled with either epiphyte-covered eelgrass (*Zostera marina*) or kelp (*Laminaria groenlandica*). The snails from each species were randomly assigned to one of two environment/food conditions, kelp or epiphyte-covered eelgrass. Snails were housed in plastic cages with 1 mm plastic screening replacing four sides (eight different cages for each food/habitat type), and fed fresh food every 3 to 4 days, before all of the kelp or epiphytes provided were consumed. After 8 weeks, I sacrificed one animal of each species from each cage, dissected their radulae, and cleaned them in a mild chlorine solution with very gentle sonication without heat (Norelco Razormate). The cleaned radulae were dehydrated with 2,2, Dimethoxy-propane and mounted flat with dual adhesive tape on aluminum stubs.

Both species replace their radula at a rate of around three rows per day, and completely replace their radula in around 3 to 4 weeks (Padilla et al., 1996). Therefore, all individuals would have completely replaced the teeth on the radula at least once during the experiment. Radulae of eight individuals for each species in each treatment were examined with a scanning electron microscope to determine the shapes of the teeth. The shapes of the main feeding teeth are always correlated with the shape of the central rachidian tooth (personal observation). The central tooth is the easiest to mount in a consistent orientation, so it was used as the primary tooth to determine tooth shape. Only teeth on the youngest half of the radula were examined. No teeth that had been used for feeding (the first five to six rows) were used to determine tooth shape.

RESULTS

All *Lacuna vincta* and *L. variegata* fed epiphytes on eelgrass and kept in a tank containing eelgrass produced blunt teeth (Table 1; Figure 1). Similarly, all *L. vincta* and *L. variegata* fed kelp and kept in a tank containing kelp produced pointed teeth (Table 1; Figure 1). No intermediate-shaped teeth were found in any individuals.

Within each treatment, no differences were found as a function of size or sex of snails. The results of a 3-way G test showed that for both *L. vincta* and *L. variegata*, food had a significant effect on tooth form ($P < 0.001$), and the two species did not differ in this respect.

DISCUSSION

Although radular morphology is generally considered stereotypic within species, and is frequently used as a taxonomic character and for species identification (Fretter & Graham, 1994), I found that radular morphology is plastic for both of these species (Table 1). Animals fed kelp and kept in a kelp environment produced pointed teeth, whereas those fed epiphytes and kept in an eelgrass environment produced blunt teeth (Figure 1). Radular variability within gastropod species is often considered anomalous or unexplained (Howe, 1930; Langan, 1984; Reid, 1988, 1996). In *Peristernia*, tooth number and cusp length vary greatly among and within rows of teeth, and may be an extreme case of fluctuating asymmetry (Taylor & Lewis, 1995). In some cases, tooth shape may change ontogenetically (Nybakken, 1990), or tooth size may be different for animals found on different host plants (Bleakney, 1990). Variation in radular tooth form in species of *Lacuna* has caused some question in regard to species identifications (King, 1965; Langan, 1984; Langan-Cranford & Pearse, 1995). This is the first demonstration that radular tooth form can be phenotypically plastic and inducible in adult snails.

The inducible plasticity of the *Lacuna* radula is remarkable, not only because it occurs in what is traditionally thought of as a species-specific character, but also because this is the first case of non use-induced plasticity in a feeding structure for any invertebrate. Plasticity in the feeding apparatus has been demonstrated in a wide array of taxa including fishes, insects, arachnids, and crabs (Bernays, 1986; Meyer, 1987; Wimberger, 1991; Thompson, 1992; Smith & Palmer, 1994). In all of the previous studies, the mechanical use of the apparatus controls the remodeling of the structure. The nature of the morphogenesis of the radula precludes this type of remodeling. Once a tooth has developed, its morphology cannot be changed. Instead, the induced morphology is found only on new teeth produced in the new environment, physically distant from the teeth in use. The morphological induction seen in *Lacuna* is much more similar to that seen in anti-predator induced morphologies such as in bryozoans (Harvell, 1990).

Although variability in radular morphology frequently has been viewed as anomalous, if inducible morphological plasticity is heritable, it is the raw material on which natural selection will act, and could be adaptive (Stearns, 1989; West-Eberhard, 1989; Thompson, 1991; Padilla & Adolph, 1996). The fact that radular morphology can be phenotypically plastic is a major finding, and has impor-

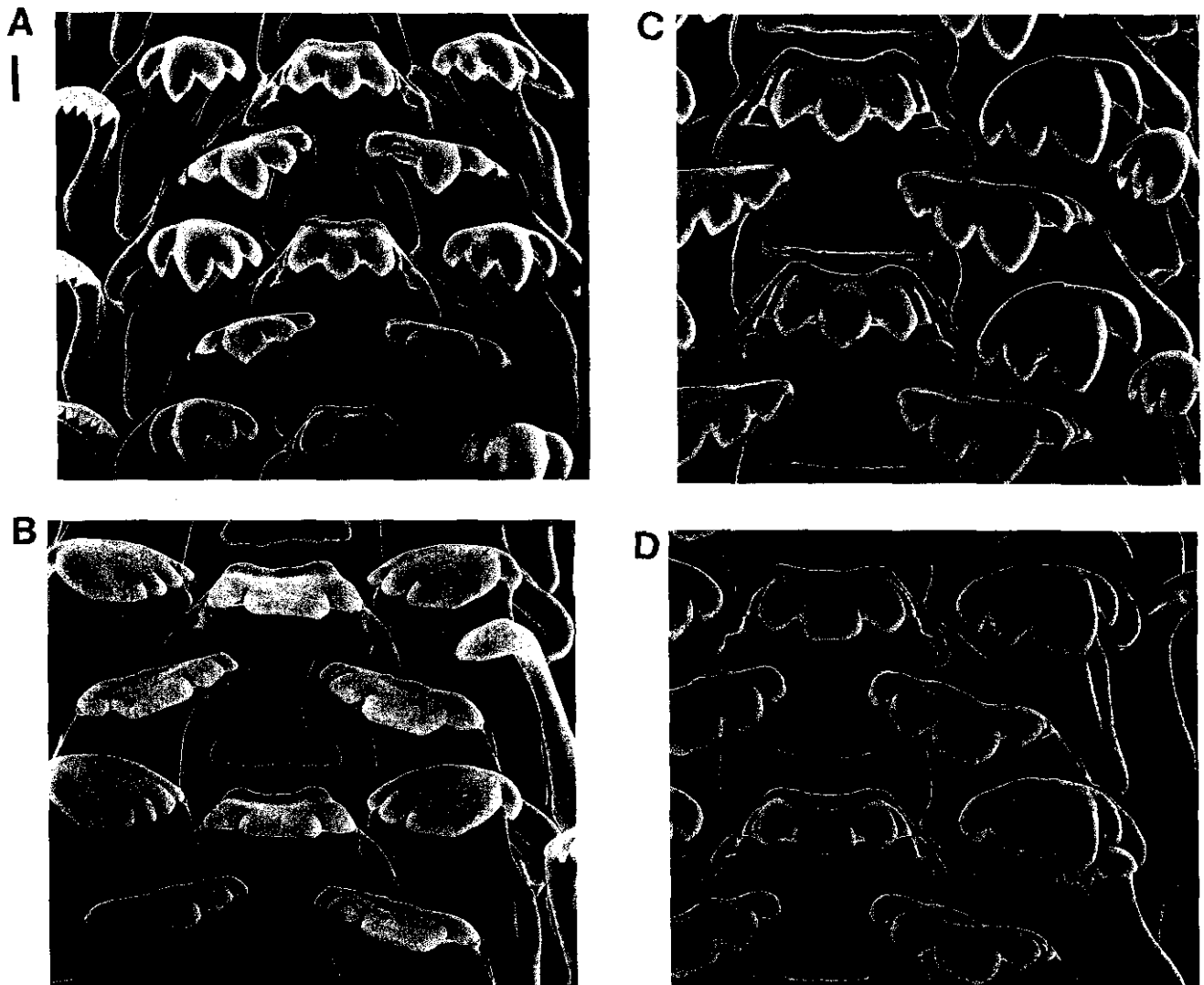


Figure 1

Scanning electron micrographs of the radulae of *Lacuna variegata* (A, B) and *L. vincta* (C, D). Animals held in a kelp bed environment and fed kelp produced pointed teeth (A, C), whereas those held in an eelgrass environment and fed epiphytes produced blunt teeth (B, D). Scale bar = 10 μm .

tant implications not only for ecology, but for molluscan taxonomy and systematics. Clearly radular tooth shape can be a labile trait and sensitive to natural selection. Using radular form for taxonomic and systematic purposes therefore must be approached with caution. Ecologically, we might expect other species living in highly variable habitats in which different morphologies have advantage to display similar plasticities. If a species occurs in a wide range of habitats, moves from habitat to habitat, or if habitat conditions change during the lifetime of an individual, a single optimal phenotype may not exist. For species of *Lacuna* in the northeastern Pacific, pelagic larval dispersal of 4 to 12 weeks is common, and

juveniles and adults regularly move among habitats by drifting on mucus threads (Martel & Chia, 1991b, c). Therefore, individuals with a fixed phenotype may be at a disadvantage, and the ability of individuals to change their phenotype to best take advantage of current environmental conditions could be adaptive (Padilla & Adolph, 1996). Many gastropods, especially those in the intertidal and shallow subtidal zones, may be subject to such environmental changes. Other species of *Lacuna* have been found to have variable radular tooth morphologies similar to those studied here (Langan, 1984; Langan-Cranford & Pearse 1995), and six of 19 species of *Littorina* show intraspecific radular shape variability par-

alleling that seen in *Lacuna* (Padilla & Dittman, unpublished data). By examining more species where unexplained intraspecific variability has been noted, we may find many more examples of phenotypically plastic inducible radular morphologies.

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