Evolutionary Ecology Research, 2001, **3**: 15–25

Food and environmental cues trigger an inducible offence

Dianna K. Padilla

Department of Ecology and Evolution, State University of New York, Stony Brook, NY 11794-5245, USA

ABSTRACT

Polyphenisms, in particular inducible defences, have been the focus of much research on the ecological and evolutionary importance of functional morphologies. Less attention has been paid to inducible offences, traits that enhance competitive ability or feeding ability of consumers, particularly those that are capable of changing during the lifetime of an individual. For most taxa with phenotypically plastic feeding morphologies, changes are usually use-induced, due to direct mechanical feedback to the feeding apparatus created by consumption of a particular food. I tested whether the direct consumption of food or chemical cues associated with feeding habitat were sufficient to trigger a new morphology in two species of snails in the genus *Lacuna*. I found that although diet had an influence on the shape of teeth induced, environmental cues were also important induction cues. *L. variegata* produced blunt teeth when fed epiphytes on eelgrass, independent of their feeding environment. They also produced blunt teeth when fed kelp, but were exposed to an eelgrass environment. If, however, they were fed kelp in a kelp bed environment, *L. variegata* produced pointed teeth. For *L. vincta* the pattern was not as extreme, but there was a significant effect of both diet and environment type on the shapes of teeth produced. There was variability among individuals of both species in the propensity to change morphology under different circumstances. This variability could be due to differences in experience, recent feeding or environmental history, or genetic differences among individuals. This inducible offence is not just a simple use-induced morphological change. Induction patterns are similar to those of inducible defences assumed to be adaptive.

Keywords: feeding morphology, inducible offence, inducible morphology, phenotypic plasticity.

INTRODUCTION

Phenotypically plastic morphologies, or polyphenisms, have attracted the attention of ecologists and have been used as strong evidence for the ecological and evolutionary importance of specific morphologies (for reviews, see West-Eberhard, 1989; Moran, 1992; Padilla and Adolph, 1996; Schmitt, 1999; Tollrian and Harvell, 1999; Emlen and Nijhout, 2000). In many cases, particularly with insects, polyphenisms are expressed across generations. Although a given genotype will produce different phenotypes under different

circumstances, an individual will express only a single morphology. In contrast, some phenotypically plastic morphologies can be expressed during the lifetime of a single individual. Inducible defences (for reviews, see Havel, 1987; Stearns, 1989; Harvell, 1990; Tollrian and Harvell, 1999) are often associated with morphological shifts within the lifetime of a single individual. For many cases of inducible defences, research has focused on the cues and consequences of defensive morphologies. However, much less attention has been paid to inducible offences, traits that enhance competitive ability, such as the stolons of bryozoans (Harvell and Padilla, 1990; Padilla *et al*., 1996b), or traits that enhance feeding ability of consumers, which are also expressed during the lifetime of a single individual.

Most documented cases of inducible feeding morphologies that shift during the lifetime of an individual are considered to be use-induced changes. In these cases, there is direct feedback during feeding to the feeding apparatus that stimulates morphological modifications due to forces required to consume alternative prey. For example, jaw remodelling in fish is associated with consuming harder prey (Meyer, 1987, 1990; Wainwright *et al*., 1991; Wimberger, 1991). Consuming prey with hardened structures, such as shells, stimulates hypertrophy of muscles associated with the jaw apparatus. This stimulates remodelling and enlargement of the bones of the jaw, allowing the generation of higher forces for feeding on harder prey. Similar modifications have been observed in arthropods, including the jaws of insects (Bernays, 1986; Greene, 1989; Thompson, 1992) and chelae of crustaceans (Smith and Palmer, 1994). The muscles associated with feeding and their associated skeletal elements increase disproportionately in size and change shape with successive moults when animals consume harder prey. These use-induced morphological changes tend to show continuous variation, displaying what Smith-Gill (1983) called 'phenotypic modulation'. Smith-Gill suggested that, although phenotypic modulation may be adaptive, it should not be *assumed* to be adaptive. Continuous phenotypic variation may result from a lack of physiological regulation rather than an adaptive response.

An alternative to this model is the head polyphenism of amphibian tadpoles. In some species, tadpoles either develop a small, slender head and consume invertebrate prey, or they develop a cannibalistic phenotype, with a large broad head, and consume other tadpoles; intermediate forms are not found (Collins and Cheek, 1983; Loeb *et al*., 1994).

The radula, a chitinous ribbon with repeated rows of teeth, is the feeding apparatus of herbivorous snails. Tooth shape is phenotypically plastic in snails in the genus *Lacuna*, and tooth shape is induced by some aspect of diet or feeding environment. Rather than having continuous variation in tooth shape, *Lacuna* produce one of two alternative morphologies, either blunt or pointed teeth (Padilla, 1998). In addition, individual teeth cannot be remodelled once fabricated. Smith-Gill (1983) has considered this pattern of plasticity to be a developmental conversion. Different environmental conditions trigger alternative developmental programs, producing alternative morphologies. This pattern of induction is very common for inducible defences. Smith-Gill (1983) suggested that developmental conversion should be indicative of adaptive inducible morphologies.

Lacuna are small, generalist marine herbivores (3–12 mm) that feed on macro- and micro-algae in the low intertidal to subtidal zone. They live only on macrophytes – either macro-algae or seagrasses – never on benthic substrata. When on macro-algae, they feed directly on algal tissue. When on eelgrass, *Zostera marina*, they feed on the micro-algal epiphytes, mostly diatoms, rather than consuming seagrass tissue. The radular apparatus can be likened to the tools used as abrasives (Padilla, 1985). Different shaped teeth have

different effectiveness when rasping against different substrata. Padilla (1985, 1987, 1989) found that pointed radular teeth are most effective at puncturing fleshy algae, such as kelp, and blunt radular teeth are most effective at scraping surfaces. In *Lacuna*, pointed teeth are induced when feeding on kelp in kelp bed environments; blunt teeth are induced when feeding on epiphytes in an eelgrass bed environment (Padilla, 1998). Because *Lacuna* are small, their habitat and food are confounded, making it difficult to determine the cues that induce this morphological shift.

I designed experiments to determine whether feeding on a given food induced a specific morphology or environmental cues associated with feeding environment were sufficient for induction. If the plastic induction of shape of radular teeth is a form of use-induced offence, diet alone should determine the shape stimulated. However, if environmental cues can stimulate the production of a given morphology independent of food, then this system would more closely resemble inducible defences, where remote stimuli such as odours produced by predators can trigger a morphological switch.

MATERIALS AND METHODS

Study species

Lacuna variegata and *L. vincta* are closely related species in the same subgenus (Reid, 1996). They are common gastropods in the low intertidal and shallow subtidal zones of the north-eastern Pacific from northern British Columbia to Oregon. Both species are reproductive throughout the year and have indirect development. Females lay egg masses on the surface of macrophytes. Veliger larvae hatch from egg masses in 5–7 days, and spend from 4 to 12 weeks in the plankton before they metamorphose (Martel and Chia, 1991a; D.K. Padilla, unpublished data). Both species co-occur on a variety of macroalgae and seagrasses, especially eelgrass. *L. vincta* is often more abundant than *L. variegata* on macro-algae, particularly on kelp. *L. variegata* is usually more abundant in eelgrass beds. Both species of *Lacuna* readily move among host plants and environments as juveniles and adults. They may be dislodged by water motion or actively drift on mucus threads (Martel and Chia, 1991b,c; Martel and Diefenbach, 1993).

The main feeding organ of herbivorous gastropods is the radula, a long ribbon of tissue with numerous, usually identical, rows of teeth. In *Lacuna*, the teeth are chitinous, and radulae generally range from 65 to 100 rows long (Padilla *et al*., 1996a). Only the anterior-most 5–6 rows of teeth are used during feeding. Worn teeth are constantly shed anteriorly, whereas new teeth are produced posteriorly in a dynamic equilibrium (Isarankura and Runham, 1968). Both species of *Lacuna* produce approximately three rows of teeth per day and, on average, it takes 23 (*L. vincta*) to 27 days (*L. variegata*) to replace all of the teeth along the entire ribbon (Padilla *et al*., 1996a). Therefore, at any point in time, the radula contains the previous 3-week history of tooth production. Once fabricated, radular teeth are not remodelled; the odontoblast (the cell producing the tooth) sets the template for tooth fabrication. Because the inter-individual variation in tooth production is low (Padilla *et al*., 1996a), and the number of tooth rows along the ribbon is constant within an individual over time (Isarankura and Runham, 1968), it is possible to determine the approximate day that a given tooth-row was produced.

For both species of *Lacuna,* the shapes of newly produced radular teeth are determined by cues associated with their food or environment (Padilla, 1998). Snails fed the kelp

Laminaria groenlandica in a tank filled with kelp produced pointed rachidian, lateral and inner marginal teeth, whereas those fed epiphytes on eelgrass in a tank filled with eelgrass produced blunt teeth (Padilla, 1998). I performed controlled experiments to determine whether the food the snail was eating triggered the new morphology, or whether some cue in the environment could control the induction of this offence.

Experimental design

I used a complete factorial design to test the importance of food and habitat for producing cues that control the induction of radular tooth shape. I collected *L. variegata* and *L. vincta* 4–10 mm in size from several different kelp beds, intertidal macro-algal beds and eelgrass beds near the Friday Harbor Laboratories, San Juan Island, Washington. A range of sizes of snails from each species was randomly assigned to one of four conditions: kelp bed environment, fed kelp; kelp bed environment, fed epiphytes; eelgrass bed environment, fed kelp; eelgrass bed environment, fed epiphytes. The mean size of snails did not differ among treatments. I simulated kelp bed and eelgrass bed environments by filling flow through seawater tanks either with kelp or with epiphyte-covered eelgrass. It was impractical to house snails individually; therefore, groups of 20 snails were housed in plastic cages ($10 \times 10 \times 8$ cm) with 1-mm plastic screening replacing four sides. Snails were fed one of two diets, kelp or epiphytes on eelgrass. Replicate boxes of each diet type were placed in each environment type. Eight boxes of snails fed a diet of kelp and eight boxes of snails fed a diet of epiphytes were placed in a simulated kelp bed environment, and eight boxes of snails fed a diet of kelp and eight boxes of snails fed a diet of epiphytes were placed in a simulated eelgrass bed environment for each species. Food was changed every 3–4 days, well before all of the kelp or epiphytes provided were consumed. The tanks and the snail cages were cleaned regularly to prevent the growth of epiphytes, especially diatoms, in the kelp bed environment. All containers of snails fed kelp were regularly replaced with clean containers to prevent diatom accumulation.

This experimental design was repeated twice. In the first experiment, snails were sacrificed after 14 days, before all of the teeth along their radular ribbon were replaced; in the second experiment, snails were sacrificed after 35 days, when all of the teeth on the radula would have been completely replaced in most individuals (Padilla *et al*., 1996a). At the end of each experiment, all snails were frozen until they were dissected. Dissected radulae were cleaned in a mild sodium hypochlorite solution (commercial bleach) with very gentle sonication without heat, rinsed in distilled water, and then mounted on glass slides with a water-soluble mounting medium (polyvinyl lactophenol). The slides were examined at 400× with a phase contrast compound microscope and a green filter to enhance contrast, or with Hoffman optics to enhance the shapes of mature teeth. The shapes of the main feeding teeth (rachidian, lateral and inner marginal teeth) were always correlated. The central, rachidian tooth is the easiest to mount in a consistent orientation and thus was used as the primary tooth to determine tooth shape. For each radula, I determined the total number of tooth rows, the shape of the teeth and the number of rows from the posterior (youngest) end of the radula to any change in shape. No teeth that had been used for feeding (the first 5–6 rows) were used to determine tooth shape. When the shapes of the teeth differed along the length of the radula, I calculated the approximate number of days from the initiation of the experiment until the row of teeth with the new shape was produced (assuming a production rate of 3 rows per day).

Analysis

Although initial sample sizes were the same for all treatments in each experiment, random mortality, loss of snails and damage to radulae during dissection and mounting resulted in unequal sample sizes for analysis. Because the data were categorical, three-way contingency table analyses, using the *G*-test, were used to test whether diet and environmental conditions affected tooth morphology (Fienberg, 1970). Two methods were used to assess the significance of interaction terms (the effect of diet on tooth shape and the effect of environment on tooth shape). First, all possible goodness-of-fit models were examined sequentially to determine the simplest model with the best fit. Second, I compared the *G*-value of models that contained an interaction term to those lacking it (Fienberg, 1970).

RESULTS

The two experiments of different duration provided complementary information regarding the range of time required for the induction of a morphological change. However, because one experiment was long enough for all snails to completely replace their radula at least once (eliminating evidence of a morphological response during that early time period), it was impossible to estimate the real time to a morphological switch for individuals that did not display a change in tooth morphology along the radula at the time of dissection. Given this limitation, and combining information from both experiments, I found that some snails responded to treatments very quickly (1–10 days), others very slowly (> 30 days), or not at all within the maximum time frame of the experiment.

For both species in both experiments, tooth shape was affected by food type and by environmental conditions (Table 1, Fig. 1). For *L. variegata*, blunt teeth were produced when snails fed on epiphytes 90–100% of the time, even when they were in a kelp environment. Only 12 of 315 individuals were found to produce pointed teeth when exposed to epiphyte-covered eelgrass either as their food or in their environment when their food was kelp. Nine individuals were found to have a pointed tooth morphology along the entire length of their radulae, and three individuals were found with a blunt morphology anteriorly and a pointed morphology in the newest produced teeth when fed kelp in an epiphyte environment. Two snails switched their morphology rapidly (within 3 days) and one switched after 28 days.

Pointed teeth were produced when *L. variegata* were fed kelp and were kept in a kelp bed environment (where there were no cues associated with eelgrass) 91% of the time. No individuals were found in the process of changing from a pointed to a blunt tooth morphology. Animals that changed from producing blunt teeth to pointed teeth initiated the change 1–26 days after the experiment began.

The patterns of morphological change were somewhat different for *L. vincta*. As with *L. variegata*, tooth shape was affected by both food and environmental conditions (Table 1). Blunt teeth were produced 80–97% of the time when snails were fed epiphytes in an eelgrass environment, and pointed teeth were produced 96–97% of the time when snails were fed kelp in a kelp bed environment (Fig. 1). None of the snails fed epiphytes in an eelgrass bed environment had blunt anterior, older teeth and pointed posterior, newer teeth. For animals that changed from the pointed tooth form to a blunt form, the change occurred after 6–31 days. *L. vincta* fed kelp in a kelp bed environment never changed their tooth morphology

Table 1. Three-way contingency table analysis presenting the *G*-statistic for all possible models for associations (interaction terms) between all pairs of variables, for two species (*Lacuna variegata*, *L. vincta*), for differences in association between tooth shape (C = blunt or pointed), environmental conditions (A = kelp or eelgrass) and diet (B = kelp or epiphytes) for two experiments of different duration (14 or 35 days)

	Lacuna variegata (14 days)			*Lacuna variegata* (35 days)		
Model	*G*	d.f.	*P*	*G*	d.f.	*P*
1. A, B, C	112.9	4	<0.001	224.1	4	<0.001
2. A, B, C, A × B	111.2	3	<0.001	224.0	3	<0.001
3. A, B, C, A × C	71.7	3	<0.001	112.3	3	<0.001
4. A, B, C, B × C	52.3	3	<0.001	153.4	3	<0.001
5. A, B, C, A × B, A × C	70.0	2	<0.001	112.3	2	<0.001
6. A, B, C, A × B, B × C	50.6	2	<0.001	153.4	2	<0.001
7. A, B, C, A × C, B × C	11.1	2	<0.01	41.6	2	<0.001
8. A, B, C, A × B, A × C, B × C	0.0	1	1	4.2	1	<0.05
Significance of interaction terms based on differences between models						
A × B (Model 1–Model 2)	1.72	1	$0.1 < P < 0.5$	0.01	1	$0.9 < P < 0.95$
A × B (Model 7–Model 8)	11.13	1	<0.001	37.42	1	<0.001
A × C (Model 1–Model 3)	41.18	1	<0.001	111.78	1	<0.001
A × C (Model 6–Model 8)	50.59	1	<0.001	149.20	1	<0.001
B × C (Model 1–Model 4)	60.56	1	<0.001	70.63	1	<0.001
B × C (Model 5–Model 8)	69.97	1	<0.001	108.05	1	<0.001
	Lacuna vincta (14 days)			*Lacuna vincta* (35 days)		
Model	*G*	d.f.	*P*	*G*	d.f.	*P*
1. A, B, C	39.0	4	<0.001	180.1	4	<0.001
2. A, B, C, A × B	39.0	3	<0.001	179.0	3	<0.001
3. A, B, C, A × C	30.6	3	<0.001	171.8	3	<0.001
4. A, B, C, B × C	11.2	3	<0.001	15.1	3	<0.005
5. A, B, C, A × B, A × C	30.5	2	<0.001	170.8	2	<0.001
6. A, B, C, A × B, B × C	11.2	2	<0.005	14.0	2	<0.001
7. A, B, C, A × C, B × C	2.8	2	$0.25 < P < 0.5$	6.8	2	<0.025
8. A, B, C, A × B, A × C, B × C	0.0	1	1	0.6	1	$0.25 < P < 0.5$
Significance of interaction terms based on differences between models						
A × B (Model 1–Model 2)	0.02	1	>0.75	1.05	1	$0.10 < P < 0.25$
A × B (Model 7–Model 8)	2.77	1	>0.10	6.23	1	<0.25
A × C (Model 1–Model 3)	8.47	1	<0.005	8.21	1	>0.005
A × C (Model 6–Model 8)	11.23	1	<0.001	13.39	1	>0.001
B × C (Model 1–Model 4)	27.78	1	<0.001	165.00	1	<0.001
B × C (Model 5–Model 8)	30.53	1	<0.001	170.19	1	<0.001

[a] The biologically important interactions are A × C and B × C. In all cases, both diet and environment significantly influence tooth shape.

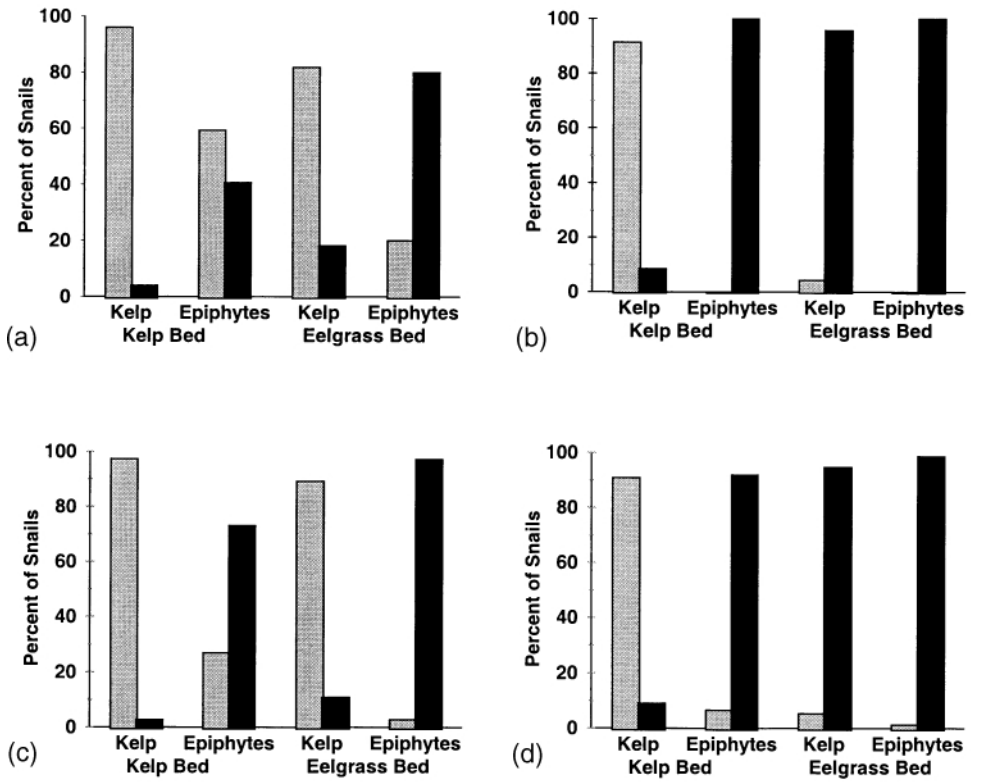

Fig. 1. Frequencies of snails that produced pointed radular teeth (grey bars) or blunt radular teeth (black bars) when they were fed kelp or epiphytes and were exposed to a kelp bed or eelgrass bed environment. (a) *L. vincta*, 14-day experiment (kelp bed environment: kelp diet, $n = 25$; epiphyte diet, $n = 27$; eelgrass bed environment: kelp diet, $n = 22$; epiphyte diet, $n = 25$). (b) *L. variegata*, 14-day experiment (kelp bed environment: kelp diet, $n = 35$; epiphyte diet, $n = 29$; eelgrass bed environment: kelp diet, $n = 23$; epiphyte diet, $n = 31$). (c) *L. vincta*, 35-day experiment (kelp bed environment: kelp diet, $n = 37$; epiphyte diet, $n = 26$; eelgrass bed environment: kelp diet, $n = 74$; epiphyte diet, $n = 77$). (d) *L. variegata*, 35-day experiment (kelp bed environment: kelp diet, $n = 77$; epiphyte diet, $n = 62$; eelgrass bed environment: kelp diet, $n = 95$; epiphyte diet, $n = 75$).

from pointed to blunt. For animals that changed their tooth morphology to the blunt form from a pointed form, the change occurred between 1 and 7 days after the experiment began.

When environmental cues were different than the food type, morphological responses of *L. vincta* were much less predictable. When fed kelp in an eelgrass bed environment, *L. vincta* produced pointed teeth 82% of the time in the short-term experiment and 89% of the time in the longer-term experiment. Two individuals were found in the process of changing from a pointed morphology to a blunt tooth morphology. The change was initiated 29 and 32 days after the experiment began respectively. Individuals found in the process of changing from a blunt to a pointed morphology generally changed very quickly, from 1 to 12 days.

When *L. vincta* were fed epiphytes in a kelp bed environment, snails produced pointed teeth 60% of the time in the short-term experiment and 27% of the time in the longer-term experiment. Seven individuals were found to be in the process of changing from a blunt morphology to a pointed morphology; the change occurred very quickly, from 3 to 9 days. Nine snails were found to be in the process of changing their tooth morphology to the blunt form from a pointed form, the transition occurring 3–31 days after the experiment began.

DISCUSSION

The induction of tooth shape in *Lacuna* is not a simple use-induced phenotypic response, resulting from direct feedback between the feeding apparatus and the food consumed. In general, individuals of both species produced tooth shapes that appear best suited to eating a given food when environmental and food cues were matched. In a kelp bed environment while being fed kelp, most individuals of both species produced pointed teeth within 14–35 days. No individuals were found to change from production of pointed to blunt teeth. Similarly, most individuals of both species produced blunt teeth when fed epiphytes in an eelgrass bed environment, and none were found to change from a blunt morphology to a pointed morphology. For both species, both food and environmental cues affected the production of different tooth morphologies. When environmental and food cues were different, snails did not always produce the shape that corresponded to the best match for their diet. In addition, the responses of the two species differed.

Lacuna variegata produced blunt teeth, independent of food cues, when exposed to an eelgrass bed environment. When exposed to a kelp bed environment, *L. variegata* produced blunt teeth when fed epiphytes and pointed teeth when fed kelp. The morphological response was rapid; the response was the same for the short-term (14 days) and longer-term (35 days) experiment. *L. variegata* is more abundant in eelgrass environments.

Lacuna vincta did not show the same pattern of induction. In the short-term experiment, animals with conflicting diet and environmental cues did not respond in a consistent fashion, particularly those fed epiphytes in a kelp environment. In the longer-term environment, there was a closer match of tooth morphology and diet. Most individuals consuming kelp produced pointed teeth and most individuals consuming epiphytes produced blunt teeth.

In real environments, these two cues will be complementary. Eelgrass beds are in soft-bottom environments and macro-algae, which require hard substrates for attachment, only occasionally drift into this environment. Similarly, in rocky areas dominated by macro-algae, eelgrass cannot live and occasionally appears in the drift. Using more than just diet as a cue for morphological induction could prevent individuals that land on drift algae or eelgrass from prematurely changing their morphology. Surfgrass (*Phyllospadix* spp.) occurs in rocky areas, but it is generally not covered with epiphytes to the same extent as eelgrass. Two more southern species, *Lacuna marmorata* and *Lacuna unifasciata*, are common in surfgrass. These species display different tooth morphologies among individuals (Langan, 1984; Langan-Cranford and Pearse, 1995), and the variability is probably due to phenotypic plasticity (D.K. Padilla, unpublished data). However, no data exist on the relative frequencies of tooth shapes among habitats or induction cues for these species.

There were large inter-individual differences in the timing of the induction of a morphological response in both species of *Lacuna* to different environmental conditions. Some

individuals responded very quickly, others very slowly, and some individuals not at all during the time frame of the experiment. Differences in response among individuals was not associated with gender or size, but may be a consequence of different feeding histories or genetic differences among individuals. Inter-individual variability in morphological transformation is also seen in cannibalistic tadpoles; not all individuals respond when given stimuli that would induce the morphological switch. In the case of tadpoles, only the largest individuals switch. For a cannibal, size is an important factor determining ability to consume other tadpoles (only smaller individuals can be consumed) and success is also frequency-dependent (the greater the proportion of cannibals, the greater the competition among cannibal morphs for a smaller number of normal morph prey) (Loeb *et al.*, 1994). However, size is unlikely to affect the benefits of tooth morphology for a snail. Feeding/environment history probably affects the speed of morphological response. It has been found that food preference in both of these species is affected by the length of time feeding on a given diet (K. Fear and D.K. Padilla, unpublished data). The longer an individual fed on a previous diet, the slower its preference switched to the new food. Similarly, we might expect individuals who have changed environments/food frequently to respond morphologically more quickly than those who rarely change environments.

It is not known what the specific cues are that trigger different tooth morphologies in *Lacuna*. It may be a chemical that is common only to a given food or environment that triggers a new morphology, or the lack of that chemical that signals the production of the alternate morphology. For example, for *L. variegata* it could be that diatoms in the water signal production of blunt teeth, and that a lack of diatoms signals the production of pointed teeth. Although closely related, *L. vincta* does not respond to the same cues in the same way as *L. variegata*.

For both species, this inducible offence is not a simple use-induced morphology, like other phenotypically plastic feeding morphologies. In most use-induced feeding plasticities there is direct feedback between the feeding process and morphological modification of the feeding structures. This direct feedback can provide a very reliable cue for the induction of an appropriate morphology and can result from a general property of a system that can be co-opted for this new function, for example bone remodelling in vertebrates. Any sort of pressure on a bone (such as that exerted by muscles) will cause the bones to change form and the muscles to readjust. This type of bone remodelling allows fish to develop more robust jaws when they eat snails, which is adaptive. Inducible defences, particularly those in modular species, are more similar to the pattern of induction seen in *Lacuna*. A new phenotype is generated not by direct mechanical feedback but by indirect cues, which are usually chemical signals associated with a high risk of predation. This type of induction of alternative phenotypes has been considered strong evidence for the likelihood that these phenotypic plasticities are adaptive.

ACKNOWLEDGEMENTS

This work could not have been completed without the help of many people, especially D. Dittman and the 21 undergraduates who helped with counting rows of snail teeth and data entry. S. Adolph provided a program for the three-way *G*-test. The manuscript was improved by comments from P. Wainwright and an anonymous reviewer. This research was supported by grants from the NSF (IBN-9317293, IBN-994594) and the University of Wisconsin WARF Fund. I would like to thank the director, staff and library of the University of Washington Friday Harbor Laboratories for support.

REFERENCES

Bernays, E. 1986. Diet-induced head allometry among foliage-chewing insects and its importance for granivores. *Science*, **231**: 495–497.

Collins, J.P. and Cheek, J.E. 1983. Effects of food and density on development of typical and cannibalistic salamander larvae in *Ambystoma tigrinum nebulosum*. *Am. Zool.*, **23**: 77–84.

Emlen, D.J. and Nijhout, H.F. 2000. The development and evolution of exaggerated morphologies in insects. *Ann. Rev. Entomol.*, **45**: 661–708.

Fienberg, S.E. 1970. The analysis of multidimensional contingency tables. *Ecology*, **51**: 419–433

Greene, E. 1989. A diet-induced developmental polymorphism in a caterpillar. *Science*, **243**: 643–646.

Harvell, C.D. 1990. The ecology and evolution of inducible defenses. *Q. Rev. Biol.*, **65**: 323–340.

Harvell, C.D. and Padilla, D.K. 1990. Inducible morphology, heterochrony, and size hierarchies in a colonial invertebrate monoculture. *Proc. Natl Acad. Sci.*, **87**: 508–512.

Havel, J.E. 1987. Predator-induced defenses: A review. In *Predation*: *Direct and Indirect Impacts on Aquatic Communities* (W.C. Kerfoot and A. Sih, eds), pp. 263–278. Hanover, NH: University Press of New England.

Isarankura, K. and Runham, N.W. 1968. Studies on the replacement of the Gastropod radula. *Malacologia*, **7**: 71–91.

Langan, K.M. 1984. The reproductive ecology of two closely related marine snails from central California: *Lacuna marmorata* and *Lacuna unifasciata*. MS thesis, University of California, Santa Cruz, CA.

Langan-Cranford, K.M. and Pearse, J.S. 1995. Breeding experiments confirm species status of two morphologically similar gastropods (*Lacuna* spp.) in central California. *J. Exp. Mar. Biol. Ecol.*, **186**: 17–31.

Loeb, M.L.G., Collins, J.P. and Maret, T.J. 1994. The role of prey in controlling expression of a trophic polymorphism in *Ambystoma tigrinum nebulosum. Funct. Ecol.*, **8**: 151–158.

Martel, A. and Chia, F.S. 1991a. Oviposition, larval abundance, *in situ* larval growth and recruitment of the herbivorous gastropod *Lacuna vincta*, in kelp canopies in Barkley Sound, Vancouver Island. *Mar. Biol.*, **110**: 237–247.

Martel, A. and Chia, F.S. 1991b. Foot-raising behaviour and active participation during the initial phase of post-metamorphic drifting in the gastropod *Lacuna* spp. *Mar. Ecol. Progr. Ser.*, **72**: 247–254.

Martel, A. and Chia, F.S. 1991c. Drifting and dispersal of small bivalves and gastropods with direct development. *J. Exp. Mar. Biol. Ecol.*, **150**: 131–147.

Martel, A. and Diefenbach, T. 1993. Effects of body size, water current and microhabitat on mucous-thread drifting in post-metamorphic gastropods *Lacuna* spp. *Mar. Ecol. Progr. Ser.*, **99**: 215–220

Meyer, A. 1987. Phenotypic plasticity and heterochrony in *Cichlasoma manaquense* (Pisces: Cichlidae) and their implications for speciation in cichlid fishes. *Evolution*, **41**: 1357–1369.

Meyer, A. 1990. Ecological and evolutionary aspects of the trophic polymorphism in *Cichlasoma citrinellum* (Pisces: Cichlidae). *Biol. J. Linn. Soc.*, **39**: 279–299.

Moran, N.A. 1992. The evolutionary maintenance of alternative phenotypes. *Am. Nat.*, **139**: 971–989.

Padilla, D.K. 1985. Structural resistance of algae to herbivores: A biomechanical approach. *Mar. Biol.*, **90**: 103–109.

Padilla, D.K. 1987. Relationships among plant calcification, plant form, and herbivore mode of feeding in marine plant–herbivore interactions. PhD Dissertation, University of Alberta, Edmonton, Alberta.

Padilla, D.K. 1989. Structural defenses of algae: The importance of form and calcification in resistance to tropical limpets. *Ecology*, **70**: 835–842.

Padilla, D.K. 1998. Inducible phenotypic plasticity of the radula in *Lacuna* (Gastropoda: Littorinidae). *Veliger*, **41**: 201–204.

Padilla, D.K. and Adolph, S.C. 1996. Plastic inducible morphologies are not always adaptive: The importance of time delays in a stochastic environment. *Evol. Ecol.*, **10**: 105–117.

Padilla, D.K., Dittman, D.E., Franz, J. and Sladek, R. 1996a. Radular production rates in two species of *Lacuna* (Gastropoda: Littorinidae). *J. Mollusc. Stud.*, **62**: 275–280.

Padilla, D.K., Harvell, C.D., Marks, J. and Helmuth, B. 1996b. Inducible aggression and intraspecific competition for space in a marine bryozoan, *Membranipora membranacea*. *Limnol. Oceanogr.*, **41**: 505–512.

Reid, D.G. 1996. *Systematics and Evolution of* Littorina. London: The Ray Society.

Schmitt, J. 1999. Introduction: Experimental approaches to testing adaptation. *Am. Nat.*, **154**: S1–S3.

Smith, L.D. and Palmer, A.R. 1994. Effects of manipulated diet on size and performance of brachyuran crab claws. *Science*, **264**: 710–712.

Smith-Gill, S.J. 1983. Developmental plasticity: Developmental conversion *versus* phenotypic modulation. *Am. Zool.*, **23**: 47–55.

Stearns, S.C. 1989. The evolutionary significance of phenotypic plasticity. *Bioscience*, **39**: 436–445.

Thompson, D.B. 1992. Consumption rates and the evolution of diet-induced plasticity in the head morphology of *Melanoplus femurrubrum* (Orthoptera: Acridadae). *Oecologia*, **89**: 204–213.

Tollrian, R. and Harvell, C.D., eds. 1999. *The Ecology and Evolution of Inducible Defenses*. Princeton, NJ: Princeton University Press.

Wainwright, P.C., Osenberg, C.W. and Mittelbach, G.G. 1991. Trophic polymorphism in the pumpkinseed sunfish (*Leposmis gibbosus*, Linnaeus): Effects of environment on ontogeny. *Funct. Ecol.*, **5**: 40–55.

West-Eberhard, M.J. 1989. Phenotypic plasticity and the origins of diversity. *Ann. Rev. Ecol. Syst.*, **20**: 249–278.

Wimberger, P. 1991. Plasticity of jaw and skull morphology in the neotropical cichlids *Geophagus brasiliensis* and *G. steindachneri*. *Evolution*, **45**: 1545–1563.