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Prey responses to the presence of a native and nonnative predator

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ABSTRACT

Phenotypically plastic responses to different environmental stimuli are very common across taxa and systems. For example, increased predation risk can induce a variety of defenses in gastropods including thicker shells, shells of different shapes, and development of apertural teeth. However, the role of coevolution between species that produce these defense responses and their consumers is not well known. This study examined the responses of an ovoviviparous gastropod (*Littorina saxatilis*) with low dispersal potential from three different habitats (marsh habitat, rocky/barnacle habitat, and cobble stone habitat) to the presence of chemical cues from a native (*Dyspanopeus sayi*) and nonnative (*Hemigrapsus sanguineus*) crab predator. This work tested the potential role of coevolution in shaping phenotypically plastic responses and whether responses to both a native and a nonnative predator differed for snails from different source sites. The morphological responses tested included shell axial growth, width growth, whorl growth, and changes in total mass. Because different traits displayed different responses, many measures of growth were examined. Overall there was a similar response to cues from native predators and the reduced diet treatment for measurements of growth, indicating a behavioral response of reduced feeding in the presence of the native predator. Snails from the marsh and barnacle habitats displayed a reduced response to cues from the nonnative predator, suggesting that they recognized this predator as a risk, but did not show as strong of a response as to the native predator. Although snails from the cobble habitat had reduced growth in the presence of the native predator, they did not have this same reduced response in the presence of the nonnative predator. This result suggests that snails from this source site do not recognize the non-native predator as a risk. Snails in the rocky/barnacle habitat, which live in barnacle tests, also had a slower growth rate than snails from the other two source sites. These results suggest the possibility of local adaptation and genetic differences among snails from these different source sites.

1. Introduction

Phenotypically plastic responses, where different phenotypes are produced by a single genotype under different environmental conditions, have been observed in a wide range of vertebrate and invertebrate animals, algae, fungi, and plants (reviewed in Miner et al., 2005; Padilla and Savedo, 2013) and can include changes in any trait including morphology, life history, physiology, or behavior (Clark and Harvell, 1992; Fisher et al., 2009; Fisk et al., 2007; Hoverman et al., 2005). Phenotypically plastic responses triggered by predators, or inducible defenses, have received particular attention because of the importance of predation risk and especially when predator risk varies in both time and space (reviewed in Adler and Harvell, 1990; Fordyce, 2006; Tollrian and Harvell, 1999).

Novel predators pose a challenge for prey because of the lack of a co-evolutionary history. As a result, prey may not recognize the introduced predator as a risk. Whether prey can recognize a novel predator may depend on the duration of time (number of generations) they have co-occurred. For example, several studies have shown that prey that have co-existed with introduced predators for >30 generations recognize the nonnative predator as a threat (Anson and Dickman, 2013; Fisk et al., 2007; Trussell and Nicklin, 2002), while prey that have co-existed with an introduced predator for <2 generations do not respond to the introduced predator (Edgell and Neufeld, 2008).

Gastropods have proven to provide good systems for studies of inducible defenses and predator recognition. They show a high degree of behavioral and morphological plasticity, are abundant and easy to collect, have small body sizes, and are very amenable to laboratory experiments. Gastropods have been shown to have a range of predator induced morphological responses, including changes in shell thickness (Appleton and Palmer, 1988; Trussell and Nicklin, 2002), reduction in both somatic and shell growth (Bourdeau, 2010; Edgell and Neufeld, 2008), and changes in shell shape corresponding to the mode of feeding of their predator (Bourdeau, 2009). In most cases, these morphological changes are due to a behavioral response of reduced foraging in response to predators (reviewed in Bourdeau and Johansson, 2012).

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This study focused on responses of the ovoviviparous gastropod *Littorina saxatilis* (Olivi, 1792) to the presence of chemical cues from a native predator, the mud crab *Dyspanopeus sayi* (Smith, 1869), and from the introduced predatory crab, *Hemigrapsus sanguineus* (De Haan, 1835), with which it has coexisted with for approximately 20 years (20 generations). This study tested whether these snails showed predator-induced responses to the native predator and whether they recognized the introduced predator as a similar risk. *L. saxatilis* has a short generation time and low dispersal, increasing the likelihood of developing local differences among populations in response to changes in the environment. Due to the possibility of local differences among snails from different locations, *L. saxatilis* were collected from three different sites with different habitat types to test whether there were differences in response to the two predators among snails from different sites.

2. Material and methods

2.1. Study system

L. saxatilis is a small bodied (1–9 mm) herbivorous snail found high on the shore along Atlantic coastlines in North America and Europe (Reid, 1996). *L. saxatilis* is ovoviviparous with newly born juveniles ~1 mm, is thought to live approximately one year, and is reproductive year round (Reid, 1996). It can be found in a wide range of habitats including rocky and cobble shores (Reid, 1996), as well as in salt marshes (personal observation). *D. sayi* is a native predatory crab that is abundant on the east coast of the United States and is common on Long Island, NY (Strieb et al., 1995). It is found on shores with *L. saxatilis* and is a known predator of molluscs (Strieb et al., 1995). *H. sanguineus* was introduced to North America from Asia in 1988 and was first found on Long Island in the early 1990s (McDermott, 1998). It is now a common predator of molluscs, especially littorinid snails, where it has been introduced (Bourdeau and O'Connor, 2003; Kraemer et al., 2007).

Juvenile *L. saxatilis* were collected from three different habitats in June 2012 on Long Island, NY: a rocky shore with barnacles, which are used for refugia (Crane Neck Point, 40° 58′ 4.1″N and 73° 9′ 29.5″W), a beach with cobble (Crab Meadow, 40° 55′ 47.7″N and 73° 19′ 44.3″W), and a salt marsh (Flax Pond, 40° 57′ 41.7″N and 73° 8′ 17.1″W) (Fig. 1). These three sites were within 1.8–21 km of each other along the north shore of Long Island. Absolute densities of crabs at each site were not assessed, but the relative abundance of different species of crabs was determined by visual inspection, relative trapping success, and number of crabs collected per unit time spent searching at each site. *H. sanguineus* is the most abundant crab predator at the rocky/barnacle shore site, but is also common at the other two sites. *D. sayi* and other species of mud crabs are abundant at both the marsh and cobble site, but not at the barnacle (rocky) site where *H. sanguineus* dominates. Overall, crab predator abundance is low at the cobble site compared to the other source sites where snails were collected. Due to their relatively low abundance at the cobble site, *H. sanguineus* and *D. sayi* were collected from the marsh and barnacle site.

2.2. Experimental design

An experiment with four treatments and five replicate aquaria (30.5 cm long × 19.1 cm wide × 20.3 cm high) of each treatment was used to test whether *L. saxatilis* responded to cues associated with predator risk from a native and a nonnative predator. The treatments were: 1) chemical cues from *H. sanguineus*, the nonnative predator, 2) chemical cues from *D. sayi*, the native predator, 3) a control with no predator chemical cues, and 4) a reduced diet treatment for the snails with no predator cues present to test whether responses to predators were likely due to the behavioral response of reduced foraging (reviewed in Bourdeau and Johansson, 2012).

Prior to experimentation, snails were weighed and photographed with their aperture up (Fig. 2A), and the initial total damp mass of each snail was determined. Due to their small size, it was not possible to use techniques common for gastropods that allow separation of somatic and shell mass (Palmer, 1982), thus it was not possible to

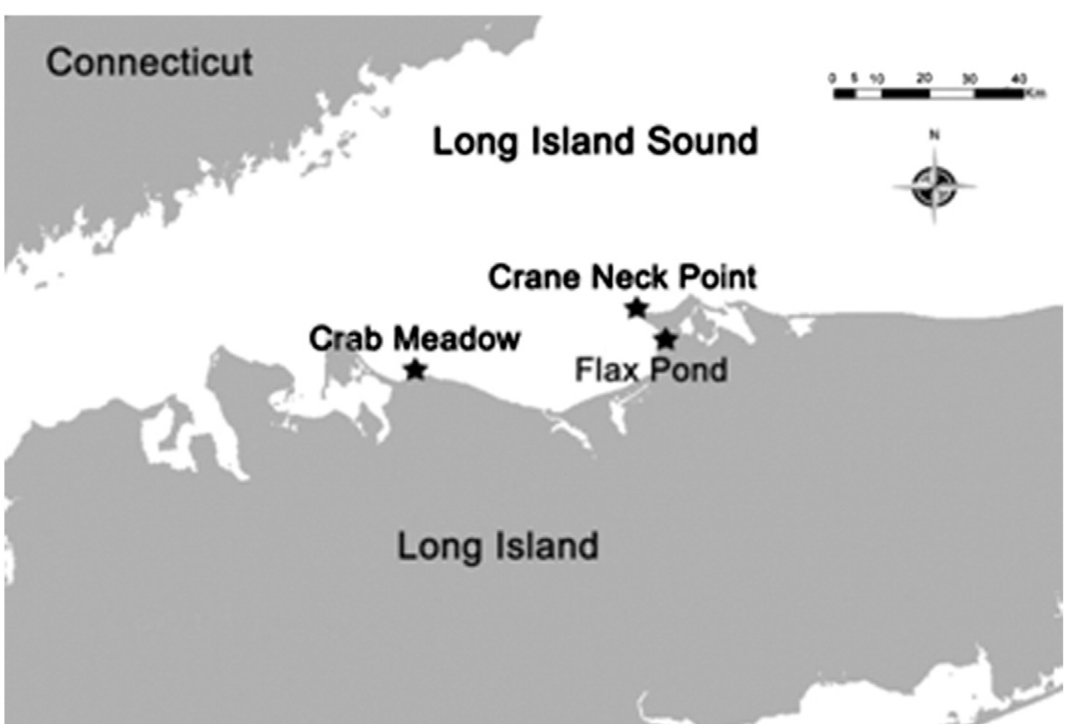

Fig. 1. Collection sites on the north shore of Long Island, NY. Sites included Crane Neck Point ('Barnacle' source site), Flax Pond ('Marsh' source site), and Crab Meadow ('Cobble' source site).