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Larval feeding structure plasticity during pre-feeding stages of echinoids: Not all species respond to the same cues

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Abstract

Much of the work on phenotypic plasticity has focused on inducible defenses. As a result, little is known about induced phenotypes that improve the acquisition of resources (i.e. inducible offenses). Feeding larvae of several marine invertebrate species, gastropods and echinoderms, have inducible offenses, and produce larger feeding structures when given less food. To better understand inducible offenses, I investigated when in development sea urchin and sand dollar larvae can first alter their feeding morphology in response to different concentrations of food. Food induced feeding structure changes in both sea urchin and sand dollar larvae before larvae were able to ingest food. This suggests that the nervous system and a regulator gene, orthopedia, play a mechanistic role. In addition, larvae of the two species, *Strongylocentrotus purpuratus* and *Dendraster excentricus*, responded to different cues. Pre-feeding larvae of both species developed relatively shorter arms when given algal cells (i.e. chemical and physical stimuli), whereas only pre-feeding larvae of *D. excentricus* developed shorter arms when exposed to algal exudates (i.e. chemical stimuli). Larvae of neither species responded morphologically to the presence of polystyrene beads (i.e. physical stimuli).

Keywords: Development; Echinodermata; Feeding; Larvae; Morphology; Phenotypic plasticity

1. Introduction

Many organisms are challenged with surviving in environments that vary both spatially and temporally. Some organisms have met this challenge by producing different phenotypes that are specific to different environmental conditions (phenotypic plasticity) (Bradshaw, 1965; Karban and Baldwin, 1997; Tollrian and Harvell, 1998; Pigliucci, 2001; West-Eberhard, 2003; DeWitt and Scheiner, 2004). To evolve phenotypic plasticity, an organism must be able to gain information about environmental conditions via cues (Harvell, 1990). In aquatic species with inducible defenses, individuals typically respond to either chemicals emitted from predators or contact with a predator (e.g., Gilbert, 1966; Krueger and Dodson, 1981; Harvell, 1986; Lively, 1986; Appleton and Palmer, 1988; Bronmark and Pettersson, 1994; McCollum and Leimberger, 1997; Leonard et al., 1999; Langerhans and DeWitt, 2002). In contrast to inducible defenses, there is not much information on the cues that elicit another common type of phenotypic change, inducible offenses, in aquatic organisms (Walls et al., 1993; Padilla, 2001; Karban and Agrawal, 2002; Kopp and Tollrian, 2003). Inducible offenses are defined as plasticity that improves the acquisition of resources (Padilla, 2001).

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Larvae of several marine taxa posses the ability to change the size of their feeding structure in response to the amount of food (unicellular algae) — bipinnaria of asteroids (George, 1994, 1999), ophioplutei of ophiuroids (Podolsky and McAlister, 2005), echinoplutei of echinoids (Boidron-Metairon, 1988; Hart et al., 1988; Hart and Strathmann, 1994), and veligers of gastropods (Strathmann et al., 1993; Estrella Klinzing and Pechenik, 2000). These larvae all use ciliary bands to swim and capture particles (Strathmann, 1971, 1987b; Gallager, 1988; Hart, 1991), and produce a longer band of cilia when food is scarce. To date, only one author has investigated the cues that elicit a change in the size of larval feeding structures, and concluded that plutei use dissolved organic compounds, like amino acids and glucose, to detect food conditions (Shilling, 1995). However, it is difficult to interpret these results because the experiment was psuedoreplicated and larval size was not measured (making it unclear whether larvae just grew more or produced different sized feeding structures).

Another aspect of inducible responses (both offenses and defenses) that can affect the evolution of plasticity is the age or stage at which individuals can first morphologically respond. In the case of inducible offenses in larvae, this question seems particularly relevant because larvae are exposed to food before they can actually feed. Although a pre-feeding response might allow larvae to produce different morphologies at the onset of feeding, it prohibits larvae from using several cues that likely accurately indicate food concentrations—such as, the amount of food ingested or energy assimilated to initially detect food concentrations.

In this study, I investigated whether nutritive and non-nutritive cues can induce shorter feeding structures in pre-feeding stages of echinoid larvae. Blastulae of two species, *Strongylocentrotus purpuratus* and *Dendraster excentricus*, were reared with either (1) seawater conditioned with algae but with the algal cells removed, (2) plastic beads of similar size to algal cells, (3) algal cells, or (4) no additive, for several days, and the size of larval feeding structures of four-armed pre-feeding larvae were compared among the different treatments.

2. Materials and methods

I performed four experiments, two for each species, to determine whether individuals can alter their feeding morphology before they are able to feed, and whether different cues elicit a phenotypic response in pre-feeding stages of echinoid larvae. This was because different results were obtained for each species in the first experiments and it was difficult to interpret these differences as species-specific because the experiments differed in several ways. Thus, I conducted a second experiment for each species to verify the results of the first experiments. See Table 1 for general experimental information for each of the four experiments.

All four experiments began with 1 d old hatched blastulae, and ended before larvae were able to feed. Although larvae of both *S. purpuratus* and *D. excentricus* are reported to begin ingesting particles when they are approximately 5 d old at the temperatures of these experiments (≈11–13 °C) (Strathmann, 1987a; Miner,

Table 1
Experimental details

	S. purpuratus		*D. excentricus*	
	First experiment	Second experiment	First experiment	Second experiment
Location of collected adults	Subtidal, Santa Barbara, CA	Subtidal, Friday Harbor, WA	Intertidal, Crescent Beach, Orcas Island, WA	Intertidal, Crescent Beach, Orcas Island, WA
Supplemented diet of adults	*Macrocystis pyrifera*	*Nereocystic luetkeana*	None	None
Location of experiment	Bodega Marine Laboratory, CA	Friday Harbor Laboratories, WA	Friday Harbor Laboratories, WA	Friday Harbor Laboratories, WA
Date of experiment	March 1999	July 1999	June 1999	July 1999
Duration of experiment	4 d	3.5 d	4 d	3.5 d
Treatments [a]	C, AC, CC, PC	C, AC, CC	C, AC, CC, PC	C, AC, CC
Algae used	*D. tertiolecta*	*D. tertiolecta*	*D. tertiolecta, R. lens*	*D. tertiolecta*
Number of replicate containers per treatment	4	4	3	4
Number of larvae measured per container	15	6	6	6

[a] C = Control, AC = Algal contact, CC = chemical contact, PC = Physical contact.