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Effects of a patchy food environment across life history stages

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ABSTRACT

Many animals experience periods of feast or famine, which can have major consequences for growth, survival, and reproductive fitness. For animals with complex life histories, the question remains whether a major ontogenetic transition, such as metamorphosis, removes the legacy of early diet variability, or if early stressors persist into later stages. This study examined the effect of constant versus variable food availability and average food concentration during the larval stage on the performance of the marine gastropod *Crepidula fornicata* (L.) before and after metamorphosis. There was no detectable effect of variable food availability on larval growth, energy stores, survival, and metamorphic competence, or juvenile growth rate and survival. Instead, the average amount of food available during the larval period had the greatest impact on larval size and metamorphic competence. Surprisingly, there were no impacts of larval diet on growth or survival during the juvenile stage. Differences that originated during the larval stage were removed post-metamorphosis. These results suggest that some organisms may be resilient to variations in food availability and that not all early life experiences produce legacy effects. Heterogeneous environments, including variable food availability, should favor flexibility in the timing of ontogenetic transitions that allow individuals to be robust in later life stages.

1. Introduction

Many plants and animals have complex life cycles, where discrete life history stages are linked by major transitions in morphology, physiology, and behavior (Wilbur, 1980). For many animals, a major transition in the life history is metamorphosis from a larva to a juvenile, which is often accompanied by changes in habitat. Despite a radical re-organization of the body, distinct life stages can be linked by legacy effects (also known as latent effects or carryover effects, Padilla and Miner, 2006; Pechenik, 2006; Pechenik et al., 1998). Legacies occur when experiences of one life history stage affect the next stage. Legacy effects have been identified in numerous taxa including amphibians (e.g., Altwegg and Reyer, 2003), birds (e.g., Merilä and Svensson, 1997), fish (e.g., McCormick and Gagliano, 2008), insects (e.g., Colasurdo et al., 2009), plants (e.g., Van Zandt and Mopper, 2002), and a variety of taxa of marine invertebrates (reviewed by Marshall and Morgan, 2011; Pechenik et al., 1998). Many organisms experience a variety of stressors throughout their lives, including periods of low food quality or quantity. These periods of diet restriction or starvation during early life stages can have a legacy effect on organismal physiology, morphology, or growth later in life in a variety of taxa (Johnson et al., 2014; Le Galliard et al., 2005; Noguera et al., 2011).

Many benthic, marine invertebrates have complex life histories with a planktonic larval stage that can disperse to new environments. Across species, the duration of the larval phase varies from hours to months depending on maternal resource allocation, and whether the larvae are feeding (planktotrophic) or not (lecithotrophic) (Mileikosvky, 1971; Strathmann, 1987; Thorson, 1950). During their time in the water column, invertebrate larvae experience temporal and spatial fluctuations in temperature, pH, and salinity among other factors. For marine invertebrate larvae, legacy effects have been documented for maternal provisioning (Marshall et al., 2003a), food quantity (Chiu et al., 2007; Paulay et al., 1985), food quality (Twombly and Burns, 1996), food variability (Miner and Vonesh, 2006), pH (Hettinger et al., 2012), salinity (Diederich et al., 2011), delays in metamorphosis (Marshall et al., 2003b; Thiyagarajan and Qian, 2003), exposure to contaminants (Ng and Keough, 2003), and natural variation in development (Przelawski and Webb, 2009).

The quality and concentration of food available can vary greatly as larvae develop (Cowles et al., 1993; Davis et al., 1991; Seuront et al., 2011). Field estimates indicate that patches of low food can be insufficient to meet metabolic demands or reach maximum growth rates (Bos et al., 2006; Mullin and Brooks, 1976). In laboratory experiments, variable food availability and starvation have consequences for larvae, including changes to morphology, decreased growth and survival, and increased time to metamorphosis (Anger et al., 1981; Fenaux et al., 1994; Howard and Hentschel, 2005; Miner and Vonesh, 2006; Zhao et al., 2003). The effects of low food or starvation during the larval stage can persist past metamorphosis and decrease the short term growth (up to 6 days) and survival of juveniles (Pechenik et al, 1996a,

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b, 2002; Phillips, 2004; Qian and Pechnik, 1998), as well as their ability to withstand future nutritional stress (Calado et al., 2010). In most studies on the legacy effects of variable food, larvae are starved for a period of time, and then returned to a high food availability environment (e.g., Pechenik et al., 1996a,b, 2002; Qian and Pechnik, 1998) or experience a temporary change in food concentration (e.g., moved once from a high food concentration to a low food concentration and back, Pechenik et al., 1996a, 2002). Other studies (e.g., Howard and Hentschel, 2005; Phillips, 2004; Twombly and Tisch, 2002) make a single switch in feeding rations (e.g., low to high) at various stages in larval development. In nature, many organisms experience repeated fluctuations between favorable and unfavorable conditions. Whether or not repeated transitions between high and low food availability for larvae can cause a lasting legacy effect on later life stages is unknown.

Crepidula fornicata (Family Calyptraeidae) is a common marine gastropod in intertidal and subtidal habitats, primarily along the Atlantic coast of North America, as well as the Atlantic coast of Europe where it has been introduced (Blanchard, 1997). Like many marine invertebrates, it has a sessile, benthic adult and a planktonic larval stage. The larvae are planktotrophic and remain in the water column for approximately two to eight weeks depending on water temperature (Henry et al., 2010; Pechenik, 1984). Larvae are readily raised in the laboratory, making *C. fornicata* an ideal species for studying factors affecting early life history stages (Henry et al., 2010). As a result, numerous studies have examined the effects of food concentration, temperature, and other conditions on larval development and performance. Studies have found that starvation during the larval stage produces legacy effects of reduced short term juvenile growth and survivorship relative to animals that do not experience periods of starvation. Pechenik et al. (1996a, 1996b, 2002) found that two to three days of starvation as larvae reduced the growth rate of juvenile *C. fornicata* three to four days post-metamorphosis, and occasionally decreased the feeding rates of juveniles. Previous work also suggests that *C. fornicata* may be robust to minor dietary stresses. Periods of low food availability (~95% food reduction for 2–4 days) decreased larval growth rates, but did not cause a legacy effect on juvenile growth (Pechenik et al., 2002). Pechenik et al. (1996a, 1996b) also found that the food concentration must be sufficiently low and the duration of the stress must be sufficiently long in order to produce a detectable legacy effect. Chiu et al. (2007) found that larvae of the congener *Crepidula onyx* fed a food concentration of 20,000 cells larva^{-1} day^{-1} (or 1 larva mL^{-1} fed 10,000 cells mL^{-1} daily) had decreased juvenile growth and survival compared to juveniles from larvae that had been fed 20 times that concentration (400,000 cells larva^{-1} day^{-1} or 1 larva mL^{-1} fed 200,000 cells mL^{-1} daily). These studies suggest that the accumulated nutritional stores during the larval phase are critical for affecting post-metamorphic growth rates and survival.

This study was designed to directly test the effects of variable food availability on larvae and subsequent juveniles, while separating the effects of differences in average food availability, on a range of response variables in both larval and juvenile *C. fornicata*. In particular, this study asked the question: what are the effects of a steady versus a variable (i.e., repeated transitions between high and low food concentrations) diet on larval growth, metamorphic competence, and energy stores at metamorphosis, and then post-metamorphic growth and survival?

2. Methods

Adult *C. fornicata* were collected from three populations on the north shore of Long Island, NY (Northport 40.93002°, −73.33030°; Shoreham 40.96518°, −72.86369°; and Poquott 40.95324°, −73.08195°). Adult snails were then maintained in a recirculating seawater aquarium at 15 °C and a salinity of 28 and fed daily a dilution of concentrated microalgae (Shellfish Diet, Reed Mariculture) dripped into the tank over several hours.

2.1. Larval collection and conditions

To reduce contamination by protozoans, adult female snails that were brooding eggs were washed with filtered sea water to remove epibionts and rinsed with deionized water. The clean females were transferred into 1 L beakers filled with filtered seawater (0.2 μm, here and elsewhere) with a salinity of 28 until larvae hatched. Larvae that hatched on the same day were collected from one female from Northport, three females from Shoreham, and five females from Poquott. To ensure that experimental replicates received individuals from a random mixture of parents (i.e., to include a range of genotypes), and maternal or genetic effects were spread across all replicates of each treatment, newly hatched larvae from all females were transferred via pipette to 4 L containers filled with filtered seawater and were mixed. Individual larvae from this pooled group were pipetted into 1 L beakers filled with clean, filtered seawater. There were six replicates of each experimental treatment with 100 larvae in 930 mL of filtered seawater, providing room for food additions between days when water and beakers were changed. Beakers were covered with a plastic petri dish to keep out contaminants (e.g., dust). Finally, beakers were randomly allocated to experimental diet treatments.

Food concentrations for the experimental treatments were selected to include a range of the food concentrations used in previous studies (because of the wide range of densities of larvae used in different experiments, comparisons of algal food concentrations are reported as cells per larva per day; Chiu et al., 2007 "low" treatment: 20,000; Diederich et al., 2011: 45,000; Taris et al., 2010: 100,000; Gaudette et al., 2001: 150,000; and Penniman et al., 2013: 225,000 cells larva^{-1} day^{-1}). The treatment levels, however, were not as high as some of the highest feeding concentrations for this species reported in the literature (e.g., Pechenik et al., 1996a,b; Chiu et al., 2007 "high" treatment, approximately 300,000 cells larva^{-1} day^{-1} or more).

To test for the legacy effects of variable food environments separate from average food concentration, this experiment had five diet treatments. These diet treatments differed in the average food concentration over the duration of the larval stage and the feeding frequency. Three of the diet treatments received food every day: 1) 200,000 cells larva^{-1} day^{-1}; 2) 100,000 cells larva^{-1} day^{-1}; and 3) 66,667 cells larva^{-1} day^{-1}. The two other diet treatments did not receive daily food: 4) an average of 100,000 cells larva^{-1} day^{-1} with a feeding of 200,000 cells larva^{-1} every second day; and 5) 66,667 cells larva^{-1} day^{-1} with a feeding of 200,000 cells larva^{-1} every third day. These diet treatments are described in Table 1. All larvae were transferred by pipette into clean beakers with filtered seawater two times per week, but only on days that the food was provided. Therefore, some algal cells may have remained in the variable food treatments on days that the replicates were not fed. One beaker in the 200,000 cells larva^{-1} day^{-1} fed daily treatment was spilled on day 12 of the experiment and was excluded from results and analyses.

Table 1
Larval diet treatments providing one of three average food concentrations, by delivering food daily, every second, or every third day.

Treatment	Average food concentration (cells larva^{-1} day^{-1})	Feeding frequency	Feeding concentration (cells mL^{-1})
1	200,000	Daily	20,000
2	100,000	Daily	10,000
3	66,667	Daily	6667
4	100,000	Every 2nd day	20,000
5	66,667	Every 3rd day	20,000

Note: replicates initially had 100 larvae in 930 mL of filtered seawater. Larvae were transferred into clean beakers with filtered seawater two times per week, on days that the food was provided. The same food densities at the beaker level were kept throughout the experiment; they were not reduced with larval mortality or assumed mortality (survivorship was determined as the number of live larvae found each day they were counted. Missing larvae were assumed to have died).