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Carryover effects of predation risk on postembryonic life-history stages in a freshwater shrimp

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ABSTRACT

For organisms with complex life histories it is well known that risk experienced early in life, as embryos or larvae, may have effects throughout the life cycle. Although carryover effects have been well documented in invertebrates with different levels of parental care, there are few examples of predator-induced responses in externally brooded embryos. Here, we studied the effects of nonlethal predation risk throughout the embryonic development of newly spawned eggs carried by female shrimp on the timing of egg hatching, hatchling morphology, larval development and juvenile morphology. We also determined maternal body mass at the end of the embryonic period. Exposure to predation risk cues during embryonic development led to larger larvae which also had longer rostra but reached the juvenile stage sooner, at a smaller size and with shorter rostra. There was no difference in hatching timing, but changes in larval morphology and developmental timing showed that the embryos had perceived waterborne substances indicative of predation risk. In addition to carryover effects on larval and juvenile stages, predation threat provoked a decrease of body mass in mothers exposed to predator cues while brooding. Our results suggest that risk-exposed embryos were able to recognize the same infochemicals as their mothers, manifesting a response in the free-living larval stage. Thus, future studies assessing anti-predator phenotypes should include embryonic development, which seems to determine the morphology and developmental time of subsequent life-history stages according to perceived environmental conditions.
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1. Introduction

Many organisms change foraging behavior, morphological traits and the timing of life-history events in response to the risk of predation (see, e.g., Lima, 1998; Benard, 2004). Predator-induced plasticity can reduce predation risk, but it often entails other fitness costs (e.g., slow growth or development; Relyea, 2002; Benard, 2004). Theory developed for organisms with complex life histories predicts that organisms should switch between two life stages when their mortality/growth ratio is lower in the following stage than in the previous one (Benard, 2004 and references therein). For instance, embryonic exposure to egg predators may favor early hatching at a smaller size and less developed stage. Such effects have been widely demonstrated in amphibians, the best-studied taxa with regard to predator-induced hatching plasticity (Warkentin, 2011; Touchon et al., 2013). Plasticity in hatching can also adjust risks of benthic and planktonic development in benthic marine invertebrates. For instance, if a particular egg mass or brooding parent is frequently attacked, then plasticity at hatching may evolve, because the probability of survival in the benthic zone is greatly reduced and planktonic life may be a relatively better option (Oyarzun and Strathmann, 2011).

Variations in early life experience can lead to delayed effects later in life, which in turn may influence individual fitness, population dynamics, and even the course of evolution (Touchon and Warkentin, 2010 and references therein; Sih, 2011). It is well known that stage-specific effects of predation risk (as well as of other factors such as temperature, food quality and habitat selection) can propagate throughout the life cycle of benthic invertebrates (reviewed in Pechenik, 2006). Predator-induced changes in the defensive morphology of planktonic larvae have been demonstrated in benthic invertebrates that lack parental care: some larvae, for instance, can adjust their size based on experience in the plankton (Vaughn and Allen, 2010 and references therein). Such developmental responses may eventually affect subsequent life-history stages. Species that release eggs (or gametes) directly into

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the plankton, however, have less scope for plasticity at hatching (Oyarzun and Strathmann, 2011). Therefore, the carryover effects of hatching plasticity on larval traits are expected to be greater for benthic invertebrates that are able to brood or to encapsulate offspring until hatching (Oyarzun and Strathmann, 2011). Predation risk delays time-to-hatching but does not alter developmental rate in the marine snail *Nucella lamellosa* which lays encapsulated eggs in the benthos (Miner et al., 2010). This form of post-fertilization parental care (egg attendance) differs from egg brooding, a form of parental care where parents carry the eggs after laying (Smiseth et al., 2012). Until now, there have been few documented cases of predator-induced responses and their consequences in brooded embryos. For instance, predation risk experienced by the embryos of the viviparid snail *Bellamya chinensis* affects the phenotypes of the juvenile and adult phases (Prezant et al., 2006). Some other species carry eggs externally. This may render parents and offspring vulnerable to predators due to reduced mobility, increased conspicuousness (Magnhagen, 1991; Reguera and Gomendio, 1999) or prey choice behavior of predators (Li and Jackson, 2003). As far as we know, there have been no documented cases of predator-induced responses (and their consequences) in externally brooded eggs of marine invertebrates.

Predation risk in aquatic ecosystems is indicated by specific forms of chemical information. Predation events entail a series of steps beginning with initial detection leading to attack, capture, and finally prey ingestion (Wisenden, 2000). In this sequence, chemical cues released at each step can be used by prey to assess and avoid predation risk (Wisenden, 2000; reviewed in Ferrari et al., 2010a). Prey may initially detect predators through the predator's signature odor, a kairomone. This is a chemical released by the predator and received by a prey; it is adaptively favorable to the receiver, but not to the source species. A second class of pre-attack chemical signals comes from startled or disturbed prey and usually involves pulses of ammonia in urine; these are referred to as disturbance cues. Alarm cues are a third class of signals that come from damaged prey during attack and handling prior to ingestion; these chemical compounds leak from the prey epidermis and provoke strong behavioral responses from conspecifics. Dietary cues, which are related to alarm cues, may be released from the predator's digestive system during digestion and defecation (Ferrari et al., 2010a and references therein).

In the present study, we address whether predation risk alters the timing of hatching in externally brooded embryos and whether embryonic response has implications for the life cycle by affecting early postembryonic stages. We used freshwater shrimp, *Palaemonetes argentinus* (Crustacea: Decapoda: Palaemonidae), as study animal. As in most decapod crustaceans with indirect development, only the embryos of this shrimp are protected by females, which incubate eggs on the ventral surface of their abdomen prior to their release into the plankton as larvae. Developing embryos are attached to ovigerous setae by the funiculus and egg coat. As they have no vascular or nervous connection with the female, they could be essentially autonomous (e.g., Ituarte et al., 2005). However, a maternal–embryo interaction might be involved in the control of hatching time in *P. argentinus* (Giovagnoli, 2011), as is the case in several other species (Ikeda et al., 2006; Christy, 2011). In the present study we examined the hypothesis that embryos of *P. argentinus* are able to acquire information about potential predators. If embryos are sensitive to substances indicating predation risk, we expect that this information will be propagated throughout the life cycle. We also expect that risk of predation on eggs will alter the timing of hatching and, in turn, risk-induced plasticity in hatching will affect the phenotype of early postembryonic stages. We specifically predict that if risk of predation on eggs causes early hatching, small hatchling size will occur, and as a result, small juveniles, too. Otherwise, if it causes late hatching, we expect large size at hatching and large juveniles.

Our laboratory experiment involved the direct exposure of female *P. argentinus* with newly spawned eggs to the presence/absence of nonlethal predation risk throughout embryonic development. We simulated an imminent but nonlethal threat of predation by allowing developing embryos to be constantly exposed to chemical signals from a predator cichlid (*Australoheros facetus*) and an attacked prey (ovigerous females of the shrimp). Since most predation chemical cues are organic compounds that degrade over time (Forward and Rittschof, 2000; Peacor, 2006; Ferrari et al., 2010a), this experimental design allowed us to ensure that waterborne substances indicative of predation risk were present and active throughout embryonic development. We measured the period of embryonic and larval development as well as larval and juvenile morphology for animals hatched from unexposed and risk-exposed embryos. To determine whether predator-induced responses of embryos affect postembryonic life-history stages, we raised newly hatched larvae in water free of chemical cues, and compared larval period, number of larval instars and juvenile morphology for animals hatched from unexposed and risk-exposed embryos.

2. Materials and methods

2.1. Study species

The freshwater shrimp *P. argentinus* inhabits shallow lakes and streams in southeastern South America, breeds in spring and summer and is found sympatrically with predator fishes such as cichlids, characins, poecilids and cyprinodonts (Ringuelet, 1975; González Sagrario and Balseiro, 2003; Ituarte et al., 2007). This shrimp has a complex life cycle with benthic adult and juvenile stages, and a planktonic phase that includes at least seven larval instars (Menú-Marque, 1973; Magiera, 2009). The newly hatched larvae of *P. argentinus* grow by gradual addition of appendages after every molt, but go through major changes in morphology and swimming behavior when they enter the benthic adult habitat. The last larval stage (decapodid) still has vestiges of larval characters and becomes a juvenile after one or two molts (Anger, 2001; Bauer, 2004). The juvenile is similar to the adult in structure, though without reproductive organs, and has lost all traces of larval morphology.

2.2. Animal collection and maintenance

We collected shrimp and fish from Lake Mogotes (38°03′43″ S/57°32′39″ W), Mar del Plata (Argentina). This small, shallow lake covers an area of 0.0764 km^2 and has an extended vegetated littoral zone which hosts small to medium-sized fish species, birds and a rich assemblage of predatory macroinvertebrates, as do most of the temperate lakes of central Argentina (González Sagrario et al., 2009). The littoral fish assemblage, generally omnivorous, preys on zooplankton and macroinvertebrates. In turn, the macroinvertebrate assemblage is strongly associated with macrophyte stands and is composed of high abundances of insect larvae, flatworms, water mites and the shrimp *P. argentinus* (González Sagrario and Balseiro, 2003; González Sagrario et al., 2009). Juvenile and adult individuals of *P. argentinus* dwell predominantly in stands of submerged macrophytes associated with the inner parts and/or edges of vegetated patches (González Sagrario et al., 2009).

On October 15, 2011, we collected females (with fully developed ovaries) and males of *P. argentinus*, as well as juveniles of the cichlid *A. facetus*. Specimens were obtained from the littoral zone using a hand net (45 cm width, 30 cm deep and 1 mm mesh size). Shrimp

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