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Should I stay or should I go: predator- and conspecific-induced hatching in a marine snail

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Abstract Predator-induced hatching plasticity has been demonstrated in many species of amphibians. However, animals from other clades (e.g., marine species of molluscs and annelids) also place their embryos in capsules or gelatinous masses and might also exhibit hatching plasticity to predators. To date there is no evidence of predator-induced hatching plasticity from any marine species or a major clade of bilateria animals, the Lophotrochozoa. We studied predator-induced hatching plasticity of *Nucella lamellosa*, a carnivorous marine snail that deposits embryos in capsules. We used two experiments to investigate the effects of two types of predator, crabs and isopods, on developing embryos. In the first experiment, we quantified proportion of hatched embryos from capsules through time exposed to water-borne chemicals of crabs and isopods. Crabs delayed time-to-hatching, and the effects of predators were additive. In the second experiment, we quantified proportion of hatched embryos from capsules through time, developmental stage, and size of embryos in capsules exposed to water-borne chemicals of crabs and conspecifics. With this experiment, we wanted to answer: (1) whether a delay in hatching corresponded to embryos developing slower, and (2) whether the general products of metabolic waste from organisms can delay hatching. We unexpectedly observed that adult conspecific snails accelerated hatching but not developmental rate—the few past studies on the effects of conspecifics have all demonstrated that conspecifics delay time-to-hatching and rate of development. The results were also inconsistent with metabolic waste in general causing a delay in hatching, although the effect of conspecifics does weaken this inference. This study demonstrates that predators delay time-to-hatching in a marine mollusc, and suggests that predator-induced hatching plasticity is widespread among animals and likely evolved multiple times within the bilateria. In addition, conspecifics accelerated time-to-hatching in a marine mollusc, which suggests that conspecifics, like predators, might commonly influence when embryos hatch.

Keywords *Hemigrapsus oregonensis* · *Idotea* · Larva · Life history · *Nucella lamellosa*

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Introduction

Organisms with complex life histories often spend part of their lives in different habitats, and the timing of switching from one habitat to another or to a subsequent life history stage has important ecological and evolutionary consequences. Researchers have long been aware of this and life history models often focus on the effects of when organisms switch habitats or the factors that predict when organisms should switch (e.g., Benoît et al. 2000; Levitan 2000; Pechenik 1990; Peckarsky et al. 2001; Vance 1973; Werner 1986; Wilbur 1997). Altering a switch point can influence the traits, abundance, and distribution of organisms (Roff 2002) by changing time to maturity (e.g., Havenhand 1993), body size (e.g., Vonesh and Bolker 2005), or dispersal time (e.g., Levin 1984).

There is a large body of research that demonstrates local environmental conditions can influence when an organism switches between habitats or stages. Theory predicts that individuals should transition between stages or habitats to

maximize the balance between survivorship and growth (or developmental rate; Hentschel 1999; Krug 2009; Ludwig and Rowe 1990; Nussbaum and Schultz 1989; Rowe and Ludwig 1991; Sargent et al. 1987; Shine 1978; Werner 1986). Consistent with theory, biotic and abiotic conditions can alter when organisms metamorphose, switch from larval to juvenile habitats, and sexually mature (e.g., Crowl and Covich 1990; Krug 2009; Newman 1992; Reznick 1990). Coupled with the evolutionary and ecological consequences of shifts in the duration or timing of switch points, plasticity in switch points are an important biological phenomenon.

Despite this large body of research on plasticity of switch points, there are relatively few examples of predator-induced hatching plasticity. Of the limited groups investigated, amphibians, particularly treefrogs, are the best studied. For example, in Costa Rica the red-eyed treefrog *Agalychnis callidryas* deposits embryos in gelatinous masses on leaves above ponds. When treefrog embryos detect a predatory snake via vibrations, they hatch earlier from the mass and fall into the pond below (Warkentin 1995; Warkentin 2005). Hatching early, however, comes at a cost. Treefrogs embryos that hatch early because of a snake enter the pond at a smaller size and are more susceptible to predators that prey upon free-living larvae (Warkentin 1995). To date, predators are known to alter, either accelerate or delay, time-to-hatching in 14 species of frog (reviewed by Warkentin 2007), a species of salamander (Moore et al. 1996; Sih and Moore 1993), a species of fish (Kusch and Chivers 2004), a species of spider (Li 2002), and a species of fairy shrimp (De Roeck et al. 2005). Evidence suggests that the presence of predators also affects when a mosquito and some crustaceans hatch (Blaustein 1997; Livdahl et al. 1984). All of these species occur in terrestrial and freshwater habitats.

Despite these few documented cases, predator-induced hatching plasticity might be very common and phylogenetically widespread among bilateral animals. Many animals lay embryos in capsules or gelatinous masses, and these structures are often thought to protect organisms from environmental conditions, including predators (Pechenik 1986). This is especially true for animals that live in the ocean. Many species of molluscs and annelids place embryos in masses, and this developmental mode has likely evolved numerous times given the phylogenetic distribution of species that exhibit this reproductive trait (Collin 2004; Goddard 2004; Rousset et al. 2007; Strathmann 1987). This raises the possibility that predator-induced hatching occurs in the ocean, and has evolved many times in the bilateria.

If marine organisms exhibit predator-induced hatching plasticity, then we can greatly expand our ability to understand the ecology and evolution of predator-induced hatching plasticity. A range of reproductive and developmental strategies occur in marine animals that place embryos in masses: gelatinous masses versus tough capsules, benthic versus pelagic masses, and partial versus complete development in masses. All of these strategies occur in the gastropods alone. This diversity allows for testing current and future hypotheses about predator-induced hatching plasticity.

In this paper, we present the first test of predator-induced hatching plasticity in a marine mollusc, *Nucella lamellosa*. In particular, we wanted to answer the following questions:

1. Do two types of predator, crabs and isopods, alter time-to-hatching in *N. lamellosa*?
2. Are the effects of each type of predator additive?

In our initial experiment, we observed that predators can delay hatching, and posed two additional questions to follow up on this result:

3. Is delayed hatching in response to predators a general response of embryos to metabolic waste?
4. Is delayed hatching in response to predators a result of reduced rate or size of developing embryos of *N. lamellosa*?

Materials and methods

We performed two laboratory experiments to determine whether predators can affect larval development and time-to-hatching of *Nucella lamellosa*. In the first experiment, we tested whether two types of predators altered time-to-hatching, and whether there was an interaction between the two types of predator. In the second experiment, we tested whether metabolic waste in general could have caused the results we observed in the first experiment, and whether delayed hatching corresponded to delayed development.

N. lamellosa is a predatory marine snail that lives in the intertidal and shallow subtidal zones. This species forms breeding aggregations from November to April, and lays encapsulated eggs on rocks in the mid-low intertidal zone (Strathmann 1987). Each capsule contains about 20 embryos (Spight and Emlen 1976), and is encased in a tough, thin, proteinaceous capsule that looks like a little American-style football with biomechanical properties similar to keratin (Rapoport and Shadwick 2002; Rapoport and Shadwick 2007). Unlike several related species, there are no reports of nurse eggs or intra-capsule cannibalism for *N. lamellosa*. A single female will lay about 50 capsules on average (Spight and Emlen 1976). However, because this species aggregates when spawning, it is often difficult to determine which capsules are from which mother. The benefit of snails aggregating is that many snails synchronize their spawning, so many capsules are produced at

approximately the same time. This makes it easy to collect many capsules of the same age for experiments. Additionally, encapsulated embryos are hardy and easily reared in the laboratory, likely due to evolving in variable intertidal conditions. The offspring hatch as juveniles between 29 and 140 days in the lab and field (Strathmann 1987). Snails escape from a capsule when a small plug at the end of the capsule is dislodged, which makes it is easy to determine when capsules hatch.

General experimental design

Both experiments had a similar design. Developing snails in capsules were exposed to water-borne chemicals from predators in the first experiment, and predators and conspecific adult snails in the second experiment. We placed capsules in tea strainers to ensure that developing snails could detect water-borne chemicals from predators or adult snails, but predators could not consume the developing snails. An independent experimental unit was a 9.5-l aquarium with a filter (without charcoal), tea strainers with developing snails in capsules, and a rock with green algae and barnacles. In the appropriate treatments, predators and conspecific adult snails were also included. Aquaria were filled with seawater (32‰) from the Shannon Point Marine Center in Anacortes, Washington, and water in the aquaria was replaced approximately every 2 weeks during an experiment. To replace the water in each tank, we siphoned off about 75% of the water in each tank, rinsing the siphons well after finishing each tank, and then refilled the tanks with new seawater. Treatments were randomly assigned to each aquarium, and all aquaria were kept in a cold room at 10°C.

We began an experiment when enough capsules had accumulated in the tank in which we held adults, and ended it after at least half the capsules had hatched on average from a treatment. The first experiment ended after 36 days of exposing capsules to experimental treatments, and the second experiment ended after 65 days. However, these times do not represent the absolute time to hatching. To allow enough capsules to accumulate before starting the experiment, we waited several weeks after capsules first appeared in the tank in which we held spawning adults in the first experiment, but less than a week in the second experiment. In the literature, there is a wide range of values reported for time-to-hatching for *N. lamellosa*, and rough estimates of time-to-hatching in our experiments are within this range (Strathmann 1987).

Study species and collection

Adult snails, *Nucella lamellosa*, and the predators *Hemigrapsus oregonensis* (a crab) and *Idotea* sp. (an isopod) were collected by hand from a beach with cobble at Marine Park in Bellingham, Washington during a low tide. Adult snails were collected while aggregating to spawn in April 2007 for the first experiment and in December 2008 for the second experiment. Snails and predators were transported in separate coolers to a cold room in the Biology Department at Western Washington University, and placed in separate aquaria. Snails were fed the barnacles *Balanus glandula* and *Chthamalus dalli*, and predators were fed green algae and heterospecific snails, *Littorina* spp. Because many species induce greater defenses to cues from injured conspecifics (e.g., Li 2002; Schoeppner and Relyea 2009), feeding crabs heterospecific snails is likely a conservative test and rules out the possibility that embryos are sensing injured conspecifics. The aquaria were kept at 10°C and 32‰, and the water was filtered with a standard aquarium filter.

For both experiments, snails began spawning within a week after being collected and laid capsules for several weeks, during which a few large clusters of capsules appeared. It was not possible to keep track of when a capsule was laid, but clusters of capsules typically appeared in a few days—the result of multiple individuals producing capsules. Capsules in recently laid clusters were gently removed from the rocks and sides of aquaria, and separated from each other. Capsules were placed into tea strainers and placed in experimental aquaria.

Experiment 1

In the first experiment, we used the crab *H. oregonensis* and isopod *Idotea* sp. as predators because both consume capsules of *Nucella emarginata* (Rawlings 1990), a closely related species of *N. lamellosa*. The experiment had two factors, crab and isopod, and each factor had two levels, the presence and absence of a predator. The two factors were fully crossed, which resulted in four treatment combinations. The control treatment had neither crabs nor isopods; the crab treatment had crabs but not isopods; the isopod treatment had isopods but not crabs, and the both treatment had crabs and isopods. Each treatment combination was replicated with four experimental aquaria. Three tea strainers, each containing three capsules, were placed into each experimental aquarium. In this design the capsules in each tea strainer in an aquarium were not independent, but aquaria were independent—we used the total number of capsules hatched from an aquarium as our response variable, and did not test for differences among aquarium with a nested design. Four crabs were included in each tank assigned to the crab and both treatments, and five isopods were added to each aquaria assigned to the isopod and both treatments.

The capsules were monitored for hatching during the following weeks. The capsules of *N. lamellosa* have plugs at

one end that likely dissolve and are detached by osmotic pressure inside the capsule prior to hatching, which allows the juveniles to crawl out of the capsule (Hawkins and Hutchinson 1988; Pechenik 1975; Sullivan and Bonar 1985). As snails began to hatch, the capsules were observed every 2 days and each capsule was scored as either plug intact or missing. Observations continued until a majority of capsules were missing their plugs.

Experiment 2

The second experiment was conducted to follow up on the results of the first experiment, in which we observed that predators delayed hatching. We were interested in testing whether the delay was due to a general response to metabolic waste from organisms in an aquarium—in the first experiment, we observed that the delay in hatching corresponded with the number of predators. We also wanted to test whether a delay in hatching corresponded with a decreased developmental rate. We hypothesized that if metabolic waste in general can cause snails to delay hatching, then conspecific adult snails should also cause developing snails to delay hatching and slow development. To test this hypothesis, we used the same species of crab and snail as in the first experiment, and included three treatments in the experiment. The control treatment had neither crabs nor conspecific adult snails, the snail treatment had conspecific adult snails, and the snail and crab treatment had crabs and conspecific adult snails. To include more replicates per treatment and improve the power of this experiment, we focused only on a single species of predator, and did not fully cross the presence and absence of crabs and snails. Each treatment was replicated 6 times.

We estimated metabolic rates of crabs (*H. oregonensis*) and conspecific adult snails (*N. lamellosa*) to determine the numbers of individuals to add to a treatment. Scaling relationships between oxygen consumption and mass were determined for a range of crab and snail masses. The oxygen consumption of crabs was determined using a Gilson respirometer and the oxygen consumption of the snails was determined using polarographic oxygen electrodes. Based on metabolism, 1 g of crab is metabolically equivalent to 10 g of snail. We added an equivalent metabolic mass of animal to each aquarium. Ten adult snails were added to the snail treatment, and four crab and two snails were added to the snail and crab treatment.

We measured hatching in the same way as in the first experiment, with a few exceptions. We placed ten capsules in one tea strainer per aquarium. We also measured larval development and growth in this experiment. A second tea strainer was added to each aquarium with 24 capsules. Each week during the experiment, three capsules were haphazardly selected from the tea strainer that initially had 24 capsules. Each of these capsules was cut open, and the embryos were deposited onto a depression slide. A digital camera attached to a dissecting microscope was used to photograph the embryos. We were careful to include at least six embryos in a photograph. The lengths of six developing snails from each capsule were measured using ImageJ 1.41 (http://rsb.info.nih.gov/ij). The selection of the six snails was haphazard, but treatments were unknown to the measurer. In addition, we rated the developmental stage of an entire capsule as follows: 0, egg or blastula; 1, preveliger (gastrula or trochophore); 2, early veliger (small shell, small velar lobes, no foot); 3, veliger (shell, large velar lobes, no foot); 4, late veliger (shell, losing velar lobes, foot); and 5, unhatched juvenile. Typically all healthy embryos in a capsule were at the same developmental stage.

Data analyses

All data were analyzed with a generalized linear mixed effects model. Mixed effects models were used because the data at different days in a tank are not independent (Pinheiro and Bates 2000). We accounted for this by specifying tank as a random factor. We tested for the significance of interactions between factors, and main effects of factors with more than two levels by comparing the fits of fully crossed and reduced models. The best-fit model was identified with the Akaike information criterion (AIC). Specific contrasts were used to test for differences between treatments and controls (i.e., treatment contrasts).

Hatching data from both experiments were analyzed with a logit link function and a binomial error structure. This analysis is most appropriate because the response variable is binary, and therefore the error term is best modeled with a binomial distribution (Bolker 2008; Quinn and Keough 2002). Size and developmental stage data from the second experiment were analyzed with a normal error structure. We used a log link function for the size data because size appeared to increase exponentially with time, and an identify link function for the developmental stage data because the relationship between developmental stage and time appeared linear.

Results

For the hatching data in both experiments, there was no evidence for interactions between main factors. In the first experiment, the model with the main factors time, isopod, and crab, but not interactions among these factors had the lowest AIC value indicating that it fit the data best given the number of parameters (Table 1). The lack of significant interactions suggests that the effects of crab and isopod

Table 1 Model comparison of hatching data for each experiment

Model	Log likelihood	*df*	AIC[a]
Experiment 1			
Time × Crab × Isopod	−58.59	11	139.17
Time × Crab + Isopod	−61.13	8	138.26
Time + Crab + Isopod	−61.706	7	137.41
Experiment 2			
Time × Treatment	−107.48	9	232.96
Time + Treatment	−109.16	7	232.33
Time	−112.11	5	234.23

Generalized linear mixed-effect models were used to test for interactions among fixed factors and the main effects of factors with more than two levels. Tank was a random factor for all models

[a] The smallest Akaike information criterion (*AIC*) value indicates the most appropriate model given the number of parameters

were additive, and predators had little or no effect on the shape of the logistic curve. In the second experiment, the model with the main factors time and treatment, but no interaction between these factors had the lowest AIC value (Table 1). The inclusion of treatment in the best-fit model indicates that the presence of adult snails or adult snails and crabs affected time-to-hatching. The lack of an interaction between treatment and time suggests again that adult snails or crabs had little or no affect on the shape of the logistic curve.

For the hatching data in both experiments, there were significant effects for the main factors. In the first experiment, predators reduced the proportion of hatching capsules (Fig. 1a). This decrease in the proportion hatching was significant for crabs, but not isopods (Table 2), and translates into a delay in hatching (Fig. 1b). On average, the crab treatment delayed hatching by 3.4 days, the isopod treatment delayed it by 3.1 days, and the crabs and isopod treatment delayed it by 6.1 days compared to the control treatment. In the second experiment, adult snails increased the proportion of hatching capsules (Fig. 2). This increase in the proportion of hatching capsules was significantly different between the control and snail treatment, but was not significantly different between the control and snail and crab treatments (Table 2), and translates into an acceleration in hatching (Fig. 2b). On average, the snail treatment accelerated hatching by 6.3 days, and the snail and crab treatment accelerated it by 3.5 days compared with the control treatment.

The size and developmental stage of snails in capsules was very similar among treatments throughout development in the second experiment (Fig. 3). The difference in size was <1% among the treatments at the end of the experiment (Fig. 3). The model without treatment had the lowest AIC value and fit the data very similarly to the two models that included treatment (Table 3). There was also little

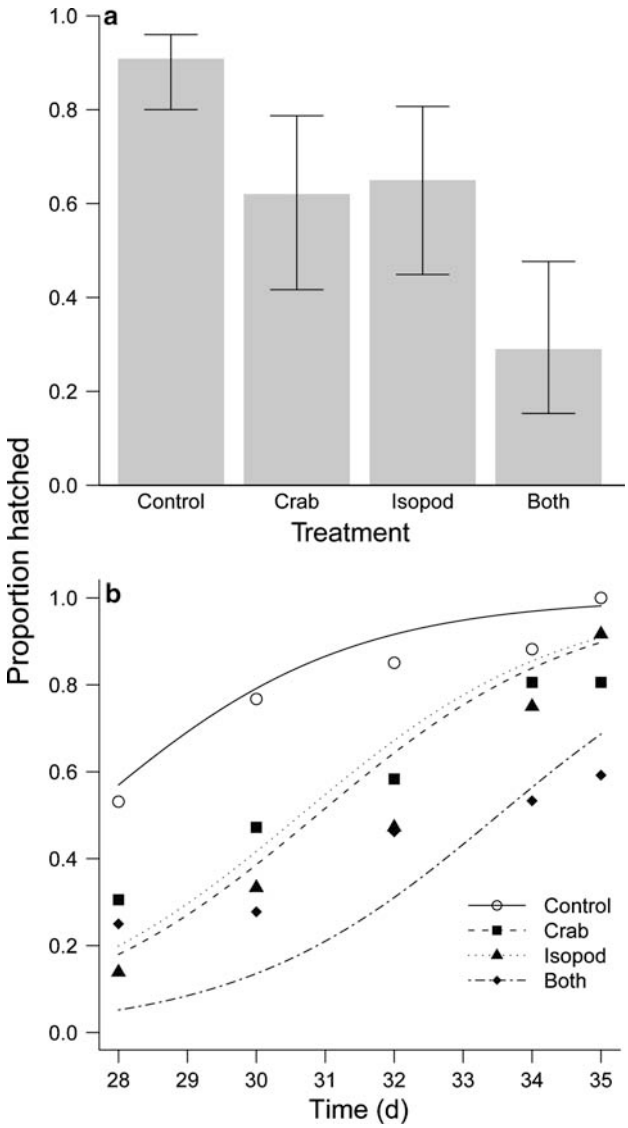

Fig. 1 Proportion of *Nucella lamellosa* capsules hatched (mean ± SE) **a** at 31.5 days (*d*) from the start of the experiment, the middle of the sampling period, and **b** throughout the experiment when alone (*Control*) or exposed to *Hemigrapsus oregonensis* (*Crab*) or *Idotea* sp. (*Isopod*). Lines show best-fit logistic regressions for each treatment, $n = 4$

difference in developmental stage among treatments. As with size, the model without treatment had the lowest AIC value (Table 4).

Discussion

Our results demonstrate that predators delay hatching in a marine snail, and we unexpectedly discovered that adult conspecific snails accelerated hatching. In the first experiment, crabs delayed hatching of snails (isopods delayed hatching by a similar magnitude to crabs but the delay was not significant). Furthermore, we found that the effects of

Table 2 Treatment contrasts of the main effects for hatching data in the reduced models for each experiment

Fixed effect	Estimate	SE	*Z* value	*P* value
Experiment 1				
Time	0.526	0.077	6.80	<0.0001
Control and Crab vs. Isopod and Both	−1.677	0.818	−1.83	0.067
Control and Isopod vs. Crab and Both	−1.497	0.818	−2.05	0.041
Experiment 2				
Time	0.181	0.024	7.30	<0.0001
Control vs. Snail	1.123	0.394	2.85	0.004
Control vs. Snail and crab	0.630	0.397	1.61	0.108

crabs and isopods were additive. Ireland et al. (2007) also reported additive effects between predators for time-to-hatching. In the second experiment, conspecific adult snails accelerated hatching, but did not affect developmental rate or size compared to the control. In contrast, the treatment with snails and crabs was more similar to the control, which is probably due to conspecific adults accelerating hatching while crabs delayed hatching, so that the combined effects resulted in a hatching time which was shorter than when only adult snails were present but longer than in the control. This highlights that if conspecifics and predators have opposite effects, then feeding conspecifics to predators will suppress a predator effect, not enhance it.

The results from the second experiment are inconsistent with the hypotheses that metabolic waste in general can delay hatching, and that shifts in hatching correspond with changes in developmental rates. However, because of the effects of adult conspecifics, this conclusion that metabolic waste in general does not cause the delayed hatching in response to predators is weak. It is possible that metabolic waste did delay hatching, but was undetected because the delay was relatively small compared to the acceleration in hatching due to conspecific adults. However, past studies, which have demonstrated that metabolites do not delay hatching (Beladjal et al. 2007; De Roeck et al. 2005; Kaha et al. 1988; Sih and Moore 1993; Voronezhskaya et al. 2004), argue against this. We can confidently conclude that the accelerated hatching due to conspecific adults is not due to a general response to metabolic waste.

Our study suggests that predator-induced hatching plasticity is widespread among animals. Studies have demonstrated that predators can alter when vertebrates and arthropods hatch, but they only tested species from freshwater or terrestrial habitats (Fig. 4). Vertebrates and arthropods represent two of the three major clades in the bilateria, the deuterostomes and ecdysozoans. Our results show for the first time that predator-induced hatching plasticity has

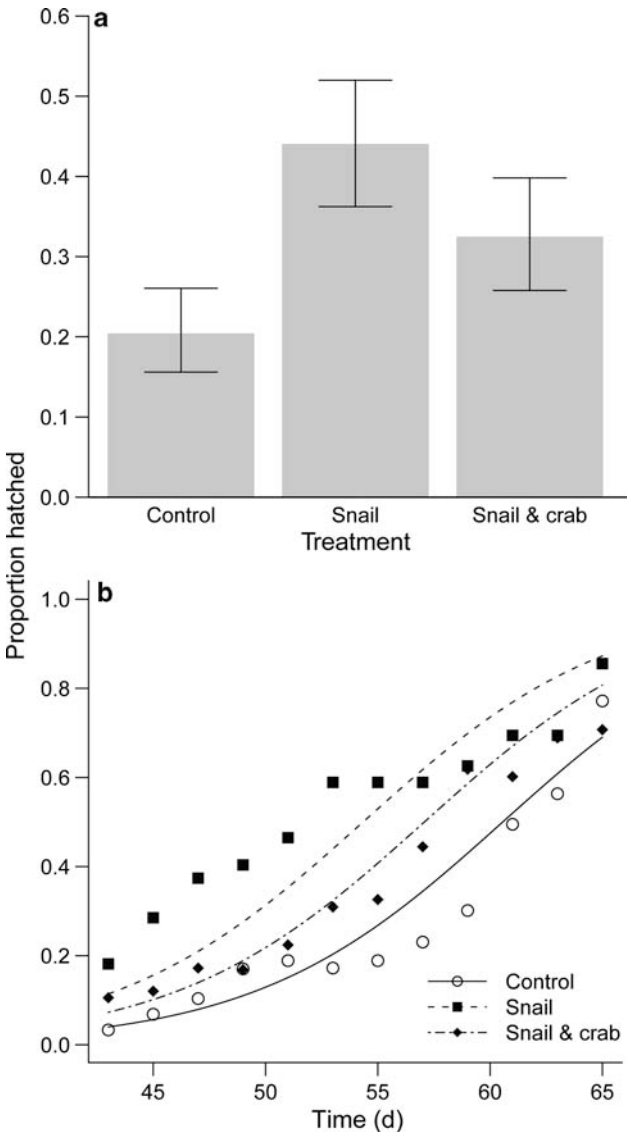

Fig. 2 Proportion of *N. lamellosa* capsules hatched (mean ± SE) **a** at 54 days from the start of the experiment, the middle of the sampling period, and **b** throughout the experiment when alone (*Control*) or exposed to conspecific adults (*Snail*) or both *Hemigrapsus oregonensis* and conspecific adults (*Snail and crab*). *Lines* show best-fit logistic regressions for each treatment, $n = 6$

evolved in the marine environment and in the third major clade of the bilateria, the lophotrochozoans. The evolution of predator-induced hatching plasticity in molluscs, arthropods, and vertebrates is almost certainly convergent. The ancestral condition for these clades is likely planktonic development of unencapsulated embryos, while encapsulating embryos is derived (Jägersten 1972; Strathmann 1978). Thus, predator-induced hatching plasticity should also be derived in these groups. Given the number of marine species that place their offspring in capsules or gelatinous masses and the phylogenetic distribution of these species,

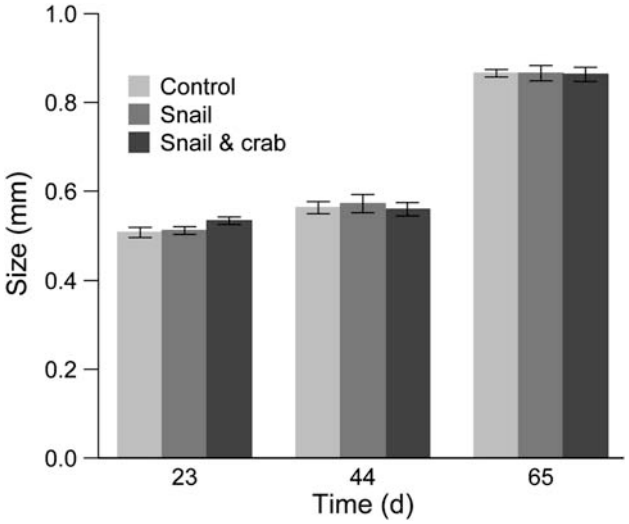

Fig. 3 Size (longest diameter, mm; mean ± SE) of *N. lamellosa* during development in capsules in control, snail, or snail and crab treatments. Days represent time from the start of the experiment, $n = 6$. For treatments, see Fig. 2

Table 3 Model comparison of size data for the second experiment on the effects of metabolic waste

Model	Log likelihood	*df*	AIC[a]
Time × Treatment	−5.30	10	30.61
Time + Treatment	−5.30	8	26.61
Time	−5.30	6	22.61

Generalized linear mixed-effect models were used to test for an interaction between time and treatment and the main effect of treatment. Tank was a random factor for all models

[a] The smallest AIC value indicates the most appropriate model given the number of parameters

Table 4 Model comparison of developmental stage data for the second experiment on the effects of metabolic waste

Model	Log likelihood	*df*	AIC[a]
Time × Treatment	−11.09	10	42.187
Time + Treatment	−12.59	8	41.18
Time	−13.026	6	38.05

Generalized linear mixed-effect models were used to test for an interaction between time and treatment and the main effect of treatment. Tank was a random factor for all models

[a] The smallest AIC value indicates the most appropriate model given the number of parameters

predator-induced hatching plasticity might be common and evolved many more times than 3 (Collin 2004; Goddard 2004; McEdward and Miner 2001; Rousset et al. 2007).

Among organisms with predator-induced hatching plasticity, a delay in hatching has been documented only a few times (De Roeck et al. 2005; Ireland et al. 2007; Laurila et al. 2002; Schalk et al. 2002; Sih and Moore 1993; Warkentin 2007). More commonly, predators accelerate hatching (Warkentin 2007). Theory predicts that individuals should maximize the balance between survivorship and growth (or developmental rate) among stages (Hentschel 1999; Krug 2009; Ludwig and Rowe 1990; Nussbaum and Schultz 1989; Rowe and Ludwig 1991; Sargent et al. 1987; Shine 1978; Werner 1986). Therefore, a delay in hatching in response to predators is predicted when pre-hatching stages are safer from predators than post-hatching stages. However, delaying hatching likely has a cost because pre-hatching individuals typically do not eat, whereas post-hatching individuals do eat. So, delaying hatching might increase survivorship but slow growth. This might be the situation for *N. lamellosa*. The capsules of *N. lamellosa* are tough structures (Rapoport and Shadwick 2002; Rapoport and Shadwick 2007), and studies of other species suggest that capsules protect individuals from predators (Pechenik 1999); however, the two species of predators used in our experiment can consume capsules and their contents (personal observation). In addition, *N. lamellosa* do not eat

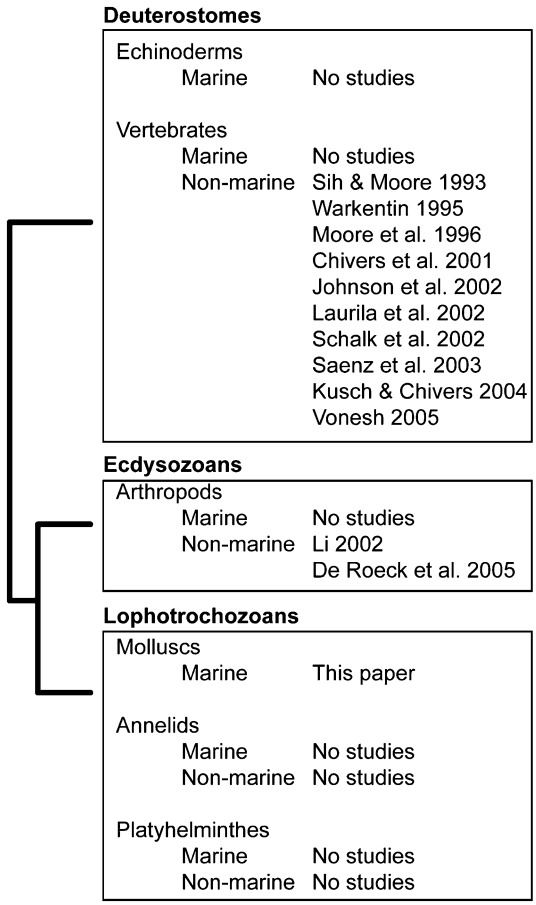

Fig. 4 Summary of published studies on predator-induced hatching plasticity. Non-marine vertebrates are the best-studied group. Our study is the first to demonstrate that predators can affect time-to-hatching in marine organisms and in the lophotrochozoan clade

before they hatch, but can presumably feed immediately after hatching when they crawl out of capsules as juveniles (Strathmann 1987). Therefore, if delayed hatching in *N. lamellosa* is adaptive, we would predict that post-hatching juveniles have (or had) a much greater risk of morality from crabs and isopods than pre-hatching individuals to offset the cost of delayed feeding. Adaptive tests of delayed hatching should measure how delaying hatching affects both survivorship and growth, and might shed light on why it appears that more species decrease than increase their time-to-hatching in response to predators (Warkentin 2007).

In addition, our data demonstrate that conspecifics can alter when individuals hatch. There are only a few examples of conspecifics altering time-to-hatching (Beladjal et al. 2007; Kaha et al. 1988; Voronezhskaya et al. 2004). In all of these studies conspecifics delayed hatching and slowed developmental rate, which is opposite to what we found. We found that conspecifics accelerate hatching, but did not affect developmental rate. We propose several hypotheses for the response to conspecifics that we observed. First, the presence of conspecifics could inform larvae about levels of competition. Presumably when there are more adult snails, there are more juveniles hatching and increased competition. This might be especially important for *N. lamellosa* because adults aggregate when spawning, and the number of adults likely correlates with the number of capsules and juveniles that will hatch. It might therefore be beneficial to hatch early and start feeding to gain a competitive advantage when there are more adult conspecifics and therefore presumably more juveniles and less food (e.g., Krug 2009). Alternatively, the response to conspecifics could have evolved in an ancestor with larvae that hatched from capsules and then resided in the plankton until they settled and metamorphosed into benthic juveniles, and has not been lost in *N. lamellosa*. Hatching early when adult densities are high might allow the larvae to spend more time in the plankton and disperse farther from their parental site where intra-specific competition might be high (Scheltema 1971). These two hypotheses could be tested by studying several groups of related species and mapping which species display hatching plasticity to conspecifics onto a phylogeny. Lastly, responding to conspecifics might have evolved in an ancestor with planktonic larvae as a cue for settlement. Planktonic larvae of some marine species can slow development and alter when they metamorphose and settle after they become competent to metamorphose (Pechenik 1990). While competent to metamorphose, chemical cues from adults can trigger settlement and metamorphosis in larvae of some marine species (e.g., Pearce and Scheibling 1990). Larvae of *N. lamellosa* might still possess this ability, and use cues from conspecifics to trigger hatching and metamorphosis. This last hypothesis is not mutually exclusive with the two above, and might represent an exadaptation.

Our results suggest that when snails hatch is not fixed to their rate of development. Conspecfic snails accelerated time-to-hatching but did not alter developmental rate or size of encapsulated snails. Therefore, when snails hatched was independent of a particular size or developmental rate. The mechanism of hatching in *N. lamellosa* is unknown. However, other related species of neogastropods produce proteolytic substances that break down the plug and increase the osmotic pressure inside a capsule allowing snails to hatch (Hawkins and Hutchinson 1988; Pechenik 1975; Sullivan and Bonar 1985; Sullivan and Maugel 1984). Our results suggest that selection can modify when encapsulated snails release these proteolytic substances independent of developmental rate, which could explain how different modes of development evolved in animals. For example, if selection favors accelerated hatching, then hatching might occur before larvae metamorphose into juveniles. This would result in a switch from juveniles hatching to larvae hatching. Furthermore, we hypothesize that modifying when snails release these enzymes is the physiological mechanism that is altered by the chemical cues from conspecifics snails and predators.

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