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The effects of embryonic experience with predation risk vary across a wave exposure gradient

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Abstract. Gradients in environmental stress can alter the ecological effects of predation risk to create variable landscapes of fear that shape prey antipredator responses. Prey obtain information about their risk environment not only from their immediate experiences with predators, but also from their previous experiences, especially if they occur during particularly sensitive windows in ontogeny. Embryonic development is often a key window when an individual's experiences can have lasting effects on behavior and fitness. The propensity of embryonic experiences with predation risk to affect prey performance, however, may vary across gradients of abiotic stress. Using a rocky intertidal system, we explored whether a dominant abiotic stressor—wave exposure—modifies the influence of embryonic experience with predation risk (from the green crab, *Carcinus maenas*) on prey (the carnivorous snail, *Nucella lapillus*) traits both at emergence and as one-year-olds exposed to current predation risk. We found that snails from wave-exposed, but not sheltered, populations emerged smaller from development and grew less in the absence of current risk as one-year-olds if they experienced risk as embryos. However, exposure to current predation risk reduced the growth and growth efficiency of one-year-old snails from both wave-exposed and sheltered populations. Our results demonstrate that increased environmental stress can modify predator–prey interactions and enhance prey reliance on early life experiences with predation risk, but that direct exposure to risk later in life can strongly affect prey performance across environmental stress gradients.

Key words: abiotic stress; *Carcinus maenas;* developmental plasticity; early life; embryonic effects; *Nucella lapillus;* ontogeny; phenotypic plasticity; predation risk; predator–prey; rocky intertidal; sensitive window.

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INTRODUCTION

Predators can strongly shape a variety of traits and thus the fitness of their prey through nonconsumptive effects (Lima and Dill 1990, Kats and Dill 1998). Nonconsumptive effects can also initiate trophic cascades (Schmitz et al. 2004) and have widespread impacts on community and ecosystem dynamics (Ohgushi et al. 2012). In the presence of predation risk, prey often modify their morphology (i.e., inducible defenses, Tollrian and Harvell 1999) and/or increase their use of safer, refuge habitats (Sih 1980) to reduce their risk of being consumed. However, exposure to predation risk can be highly stressful for prey and result in substantial costs such as reduced foraging (Werner and Hall 1988, Turner and Mittelbach 1990) and enhanced metabolic rates (Slos and Stoks 2008, Hawlena and Schmitz 2010), which can limit somatic growth and reproduction (Havel and Dodson 1987, McPeek 2004).

In systems where predation risk is particularly variable, prey assess their risk of predation through immediate, direct experience with predator cues (Lima and Dill 1990, Kats and Dill 1998). However, prey are also likely to rely on their historical experiences with predators, whether their own or those of their parents or grandparents (Sheriff et al. 2010, Stein et al. 2018), to inform their response to risk in heterogeneous environments. The embryonic phase of life can be particularly sensitive to environmental cues, including those from predators, which may influence an individual's current and future phenotype (Dufty et al. 2002, English et al. 2016). Indeed, embryonic exposure to predation risk can have strong effects on prey development time and size at emergence (Stoks et al. 2006, Dalesman et al. 2015) and continue to impact prey performance, both positively and negatively, throughout ontogeny (Relyea 2001, Orizaola and Braña 2005). For example, red-eyed tree frogs emerge earlier and smaller from development when they are exposed to egg predators (Touchon et al. 2013) and subsequently show maladaptive responses (via reduced antipredator behavior) in response to predators as larvae (Warkentin 1999). Hence, attention to the effects of previous risk exposure, particularly during sensitive periods such as embryonic development, will be crucial to a better understanding of how prey will respond to predation risk.

The role and importance of biological stressors such as predation risk can vary across abiotic environmental stress gradients (Menge and Sutherland 1976, Odum 1985). Both theoretical (Menge and Sutherland 1987) and empirical (Malmqvist and Sackmann 1996, Leonard et al. 1999) work suggest that predators are less active and efficient in habitats where abiotic stressors are particularly harsh. In contrast, mobile predators are likely more abundant and effective hunters in habitats where abiotic stress is relatively benign. Because predation risk is often more predictable in these benign abiotic environments, prey may be less sensitive to, or flexible in, their response to predator cues throughout their lives (West-Eberhard 2003). In contrast, under relatively harsh abiotic conditions where predation risk is more variable, prey may exhibit greater flexibility and sensitivity in both their responses to cues indicating predation risk and the information they require to deploy them. This enhanced flexibility, however, should increase the expression of both beneficial and costly traits among prey when they are exposed to predators. Of course, prey must balance the need to respond to predators with other selective forces (e.g., the abiotic stressor itself, Schmitz and Trussell 2016), thereby constraining their ability to express phenotypes that maximize survival against predators alone.

Rocky intertidal shores provide a model system to explore the effects of abiotic stress on species interactions because similar communities of prey species exist along gradients of wave exposure (Menge 1978*a*,*b*) while predator abundances can vary greatly. On rocky intertidal shores in New England, the snail *Nucella lapillus* (hereafter *Nucella*) is an important intermediate consumer that impacts community dynamics by consuming barnacles and mussels (Menge 1978*a*,*b*) that often dominate space in these habitats. *Nucella* is also a key prey item for a common rocky intertidal predator, the green crab *Carcinus maenas* (Kitching et al. 1966). Importantly, *Nucella* lack planktonic larvae and are relatively immobile as adults (Hughes 1972), which may enhance local adaptation. Empirical evidence suggests that green crabs are more abundant on sheltered shores throughout the Gulf of Maine (Bryson et al. 2014) and that *Nucella* from wave-exposed and sheltered populations respond differently to direct exposure to green crab risk cues. *Nucella* from wave-exposed populations respond strongly to green crab predation risk, often increasing their antipredator behavior while incurring substantial fitness costs (e.g., reduced foraging and growth, Trussell et al. 2006, Matassa et al. 2016). Moreover, *Nucella* from wave-exposed populations are strongly affected by parental and embryonic experiences with predation risk both early (Donelan and Trussell 2018*a*) and later (Donelan and Trussell 2018*b*) in life, suggesting that these sources of information are highly influential to prey in heterogeneous risk environments. In contrast, *Nucella* from sheltered populations produce thicker shells (which should limit the effectiveness of shell-crushing predators such as *Carcinus*) than those from wave-exposed populations regardless of green crab risk exposure (Hughes and Elner 1979, Palmer 1990, Freeman and Hamer 2009), suggesting that selection has favored more fixed versus plastic shell defenses in

habitats where predation risk is more predictable. Despite evidence that prey differ in their response to predation risk across a wave exposure gradient, it is unknown whether such abiotic gradients modify the influence of embryonic experience with predation risk in prey.

We conducted a series of experiments to explore the effects of embryonic experience with predation risk from the green crab *Carcinus maenas* on *Nucella lapillus* prey that emerged from egg capsules collected from wave-exposed and sheltered populations. We examined these effects on *Nucella* traits at emergence and the response of one-year-old *Nucella* to contemporary (hereafter, current) risk exposure. We hypothesized that *Nucella* from sheltered populations would not respond to either embryonic or current risk exposure, but that *Nucella* from wave-exposed populations would be negatively affected (reduced foraging, growth, and growth efficiency) by risk experience at both life stages.

Materials and Methods

We explored whether wave exposure and embryonic experience with predation risk from the green crab *Carcinus maenas* affected the traits of *Nucella lapillus* snails at emergence from egg capsules. We also tested the effects of current experience with green crab predation risk on the performance of one-year-old *Nucella*. Experiments were conducted in the running seawater facilities at Northeastern University's Marine Science Center in Nahant, Massachusetts, USA, with snails that emerged from egg capsules collected from wave-exposed and sheltered populations (Fig. 1; Appendix S1: Table S1). Hence, our wave exposure treatment defines the environment from which each population originated. We categorized populations as wave-exposed or sheltered based on the dissolution rate of plaster clod cards deployed at their collection site (Lindegarth and Gamfeldt 2005, Bryson et al. 2014). Clod cards deployed at sites where we collected exposed populations lost significantly more mass per tide than those where we collected sheltered populations ($F_{1,7.4} = 22.86$, $P = 0.002$; Appendix S1: Table S1). Moreover, green crabs are more abundant at sheltered versus wave-exposed sites in our study region (G. C. Trussell, *unpublished data*).

Nucella lapillus deposit their egg capsules (~1 cm long) on rock surfaces in the intertidal zone and each capsule contains 3–35 developing embryos. Approximately six weeks after deposition, juveniles emerge as crawl-away snails that immediately begin foraging (Donelan and Trussell 2018*a*). Egg capsules that produced snails for the one-year-old experiment were collected in June 2015, and egg capsules that produced snails for the traits at emergence experiment were collected in June 2016. Egg capsules were collected from a relatively small area (~25 m^2) on all shores to minimize any differences in the environmental experiences of embryos prior to collection. Egg capsule collection and embryonic risk exposure protocols were generally similar across years, with some minor exceptions as described below.

Embryonic experience with risk manipulation for the traits at emergence experiment

Egg capsules that produced snails for the traits at emergence experiment were collected over the course of three days in June 2016 from five wave-exposed and four sheltered populations in the Cape Ann region of Massachusetts (Fig. 1; Appendix S1: Table S1). From each population, we collected four newly laid egg capsules from four spatially independent (separated by at least 2 m) egg capsule aggregations where adult *Nucella* were actively laying ($n = 16$ egg capsules per population) for a total of 36 aggregations across the nine populations. We distinguished newly laid egg capsules from older egg capsules by the opacity of their capsule walls and the lack of epiphytic growth on the egg capsule surface. All egg capsule aggregations were at similar tide heights (0.5 m above MLLW) on vertical rock walls. *Nucella lapillus* adults are not highly mobile: Estimates suggest that they move only 4 meters within a year's time (Hughes 1972). Hence, because we collected newly laid egg capsules, it is highly unlikely that egg capsules from the different aggregations were laid by the same parents.

Upon returning to the laboratory, we split the four egg capsules from each aggregation into two tea infusers ($n = 2$ egg capsules per tea infuser; 5.5 × 6 cm, dia × h, Upton Tea Imports, Holliston, Massachusetts, USA). Each tea infuser was then placed individually in its own larger

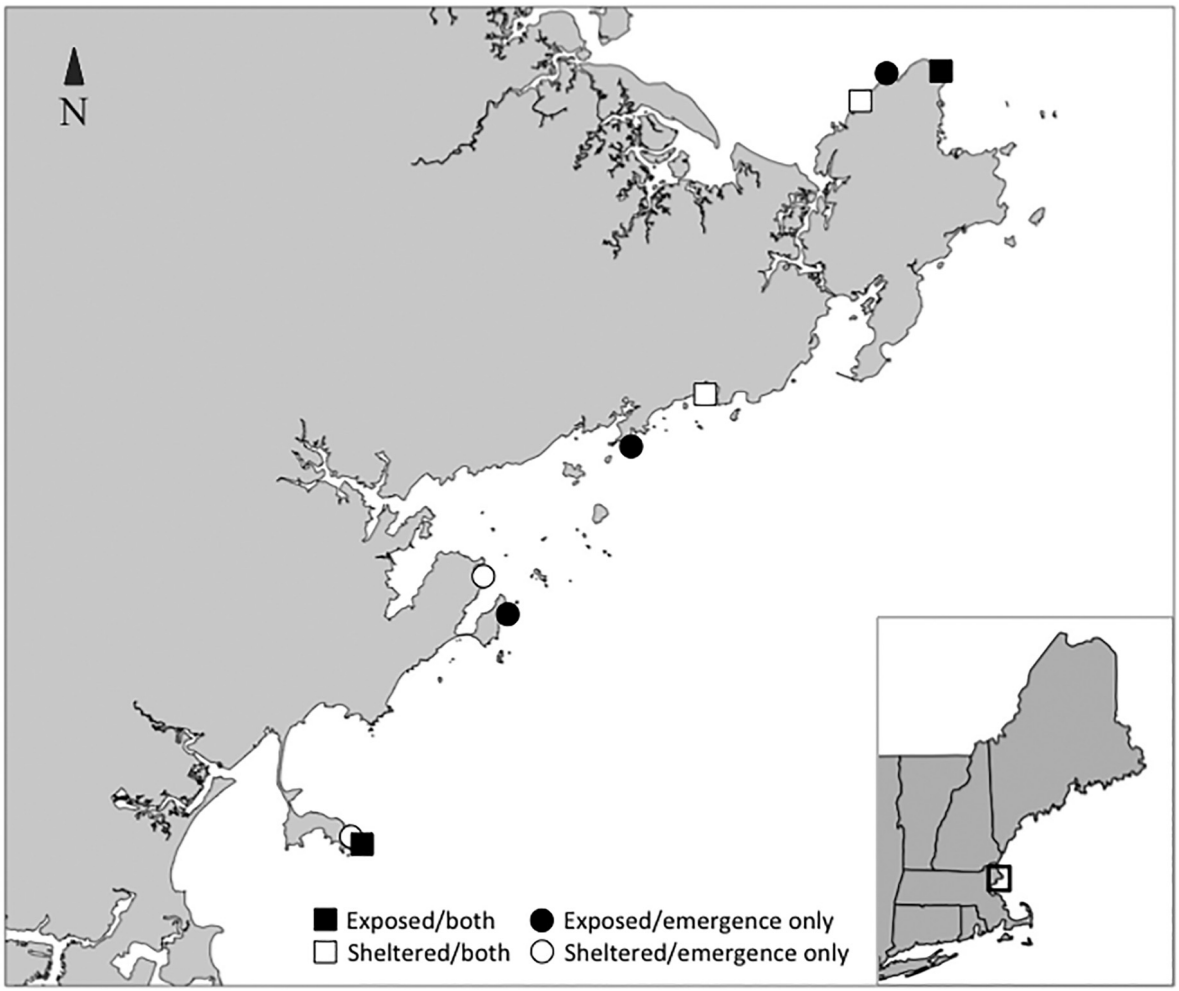

Fig. 1. Map of experimental wave-exposed (filled symbols) and sheltered (open symbols) study populations in the Cape Ann region of Massachusetts, USA. Squares indicate populations used in both the traits at emergence and one-year-old experiments, while circles indicate populations that were used in the traits at emergence experiment only. Population coordinates are given in Appendix S1: Table S1.

bucket (17 × 14 cm, dia × h) that received an independent supply of flowing seawater so that there were two independent buckets per aggregation (N = 72 buckets). Each bucket also contained a perforated chamber (10 × 10 × 7 cm, l × w × h) for the manipulation of predation risk. In one bucket from each aggregation, we placed one adult male green crab (70.8 ± 2.8 mm, mean carapace width ± SD) in the risk manipulation chamber along with two adult *Nucella* for food (presence of risk), while the other bucket from an aggregation contained a risk manipulation chamber that remained empty except for two adult *Nucella* (absence of risk). Hence, half of the egg capsules from each aggregation were in the presence of embryonic risk and half were in the absence of embryonic risk. *Nucella* are highly responsive to green crab risk cues both with and without the presence of conspecific alarm cues (Donelan et al. 2017). After one week in the presence or absence of embryonic risk, we removed each tea infuser from its risk manipulation bucket and placed it into its own plastic jar (8 × 10 cm, dia × h) that received risk-free flowing seawater. We also removed one egg capsule from each tea infuser

(so that only one remained) and counted the number of nurse eggs it contained. *Nucella lapillus* egg capsules each contain hundreds of nurse eggs (Donelan and Trussell 2018*a*) that nourish embryos during development. However, nurse eggs are consumed within the first 10 d of development when it is difficult to differentiate developing snails from nurse eggs (Costello and Henley 1971). Therefore, to quantify the approximate number of nurse eggs, we counted the total number of particles (nurse eggs + snails) present within a dissected egg capsule and subtracted the average number of snails to emerge from the remaining egg capsule that was collected from the same aggregation and population and subjected to the same embryonic conditions (Spight 1976). We then divided this value by the average number of snails to emerge from the remaining egg capsule to determine the number of nurse eggs available per capita (Donelan and Trussell 2018*a*).

After four weeks in risk-free conditions, we checked the tea infusers for newly emerged *Nucella* every 2–3 d. We measured the shell length (mm) and shell width (mm) of each newly emerged snail using an AZ100 Nikon Stereomicroscope and NIS Elements Basic Research microscope imaging software (v. 4.30; Nikon, Tokyo, Japan). We measured 608 snails from 64 egg capsules at approximately equal numbers across treatment combinations (152 ± 20, mean no. individuals ± SD). We also counted the number of snails to emerge from each egg capsule. Finally, we sacrificed a subset of newly emerged snails (n = 2 per egg capsule, N = 96) to determine their shell (inorganic content) and tissue (organic content) weights using an ash-free dry mass technique (Moran and Emlet 2001). While *Nucella* shell contains some organic content (~1.5% in other *Nucella* species, Palmer 1983), the allocation of energy to organic growth by *Nucella* should mainly reflect the investment in soft tissue mass. Snails were frozen individually in micropipette tubes in a −20°C freezer. They were then thawed, rinsed five times with deionized water, and dried in a drying oven (60°C) for five days. We then weighed them individually on a microbalance (Mettler Toledo MX5, Columbus, Ohio, USA) in pre-ashed and pre-weighed aluminum micro weighing tins (VWR, Radnor, Pennsylvania, USA). Snails were then ashed in their tins at 450°C for four hours in a muffle furnace and weighed again once they returned to room temperature. We calculated tissue mass (mg) by subtracting the mass that remained after ashing from the initial mass. We calculated shell mass (mg) by subtracting the mass that remained after ashing from the mass of the weighing tin alone.

Embryonic experience with risk manipulation for the one-year-old experiment

Egg capsules that produced *Nucella* for the one-year-old experiment were collected over the course of three days in June 2015 from two wave-exposed and two sheltered populations that were also used for the traits at emergence experiment (Fig. 1; Appendix S1: Table S1). From each population, we collected eight newly laid egg capsules from four spatially independent egg capsule aggregations as described above (n = 32 egg capsules per population) for a total of 16 aggregations across the four populations.

Upon returning to the laboratory, we divided the eight egg capsules from each aggregation into four mesh-lined tea infusers (n = 2 egg capsules per tea infuser). We manipulated embryonic experience with predation risk as described above, but two tea infusers from each aggregation were placed in the presence of embryonic risk and two in the absence of embryonic risk (N = 64 buckets) for one week. After one week, we removed each tea infuser from its risk manipulation bucket and placed it into its own plastic jar that received risk-free flowing seawater. After four weeks under these conditions, we began checking tea infusers every 2–3 d for the emergence of new snails. After emergence, snails were immediately given ~300 juvenile blue mussels (1.1 ± 0.2 mm, mean shell length ± SD) for food. This procedure continued each week until *Nucella* were large enough to consume larger mussels (4.6 ± 1.9 mm, mean shell length ± SD). Before the onset of winter, *Nucella* from each tea infuser were transferred to a larger perforated jar (8 × 10 cm, dia × h) to accommodate their larger size. Due to logistical constraints, these jars were placed into plastic buckets (3.4 L, 19 × 14 × 21 cm, l × w × h) that contained three additional jars from the same population × embryonic risk experience treatment combination. There was no effect of winter bucket on initial *Nucella* shell length or weight the following June

(both $P > 0.14$), so this factor was not included in our analyses of one-year-old *Nucella* performance. Snails were fed an ad libitum supply of blue mussels every two weeks throughout the winter until their use in the one-year-old experiment the following summer, described below.

One-year-old experiment: current risk manipulation and snail performance

We conducted a fully factorial laboratory mesocosm experiment in June 2016 using one-year-old *Nucella* that had been collected and exposed to the embryonic risk treatments the previous summer to explore whether snails from wave-exposed and sheltered populations performed differently in response to embryonic experience with green crab predation risk (present/absent) and current experience with green crab predation risk (present/absent). We selected snails that were the same initial size regardless of their prior treatments (initial shell length: 12.78 ± 0.20, mean ± SE, $P = 0.9$). Three *Nucella* from the same population x embryonic experience with risk treatment combination were placed in a perforated container (12 × 8.5 × 6.5 cm, l × w × h) that held a raised (1 cm) granite tile (7.5 × 7.5 × 1 cm, l × w × h) substratum and 50 blue mussels (12.91 ± 2.05 mm, mean shell length ± SD) for food. This container sat downstream of another perforated risk container (10 × 10 × 7 cm, l × w × h) that housed either one male green crab (presence of current risk) or remained empty (absence of current risk) for the manipulation of current risk. The snail and risk manipulation chambers were placed together in a larger plastic bucket (14 × 14 × 16 cm, l × w × h) that received an independent supply of flowing seawater. There were 10 replicates of each treatment combination (N = 80), and the experiment ran for 35 d.

Nucella were individually marked prior to the experiment and weighed at the start and end of the experiment using a non-destructive buoyant weighing technique (Palmer 1982). We estimated individual *Nucella* tissue growth (final–initial, Joules, J) by converting tissue mass (mg) into its energetic equivalent (J) using empirically derived equations that convert wet tissue mass into dry tissue mass (Matassa and Trussell 2014, Donelan and Trussell 2018*a*) and dry tissue mass into energy (Hughes 1972). We quantified the total amount of energy consumed by *Nucella* in a given replicate by measuring the maximum shell length of each mussel consumed during the experiment (indicated by a drill hole on the remaining shell) and using this shell length to calculate mussel dry mass and energetic content using empirically derived equations (Elner and Hughes 1978, Burrows and Hughes 1990). We calculated *Nucella* per capita foraging activity by dividing the total amount of energy consumed by all *Nucella* in each replicate by the average number of *Nucella* present in that replicate over the course of the experiment ($n = 3$ for all but one replicate, where one snail died on day 32). Finally, we measured *Nucella* growth efficiency (the ability to convert ingested energy into body mass, which can be reduced by exposure to predation risk, Trussell et al. 2006) by dividing individual *Nucella* tissue growth (J) by the per capita energy consumed (J) in that replicate.

Statistical analyses

We analyzed *Nucella* shell length, shell width, tissue and shell mass at emergence, the number of snails emerging per egg capsule, and the per capita number of nurse eggs using separate type III mixed-model ANOVAs that considered wave exposure and embryonic experience with risk as fixed effects. Population was nested within wave exposure and considered a random effect. We also included the aggregation from which an egg capsule originated as a random block effect to account for potential effects of relatedness among individuals. Analyses for traits at emergence were conducted on egg capsule averages.

For one-year-old snails, we analyzed individual tissue growth and growth efficiency using separate type III mixed-model ANOVAs that considered wave exposure, embryonic experience with risk, and current experience with risk as fixed effects. Population was nested within wave exposure and considered a random effect, and embryonic bucket was included as a random block effect. Because we could not determine individual foraging rates, we analyzed per capita foraging rates using replicate averages (N = 80) and a type III mixed-model ANOVA with wave exposure, embryonic experience with risk, and current experience with risk as fixed effects and population nested within wave exposure as a random effect.

All analyses on *Nucella* traits were conducted in JMP 11 using REML-weighted variance estimates to account for unequal variances among treatment combinations (Zuur et al. 2009). When we found a significant interaction among factors, we conducted least square (ls) contrasts to compare group means. Complete ANOVA tables are provided in Appendix S1: Tables S2, S4. We also assessed the significance of population as a random effect using likelihood ratio tests (Zuur et al. 2009, see Appendix S1) in R (v. 3.4.3; R Core Team 2017) using the nlme package (Pinheiro et al. 2018).

Results

Embryonic experience with predation risk negatively affected *Nucella* shell length (wave exposure × embryonic experience: $F_{1,32.2} = 9.4$, $P = 0.004$, Fig. 2A), shell width (wave exposure × embryonic experience: $F_{1,31.9} = 11.3$, $P = 0.002$, Fig. 2B), and tissue mass (wave exposure × embryonic experience: $F_{1,31.8} = 5.6$, $P = 0.02$, Fig. 2C) at emergence, but only among snails from wave-exposed populations. After experiencing predation risk as embryos, wave-exposed *Nucella* emerged with shells that were 15% shorter (ls contrast: $P = 0.0001$) and 14% narrower (ls contrast: $P < 0.0001$) and also had 36% less tissue (ls contrast: $P = 0.003$) than snails from sheltered populations. There was no effect of population on shell length, shell width, or tissue mass at emergence (Appendix S1: Table S3). There were no additive or interactive effects of the wave exposure or embryonic risk experience on shell mass (all $P > 0.25$; Appendix S1: Fig. S2, Table S2), the number of snails emerging per egg capsule (all $P > 0.15$; Appendix S1: Fig. S1a, Table S2), or the number of nurse eggs per emerging snail (all $P > 0.24$; Appendix S1: Fig. S1b, Table S2).

For one-year-old *Nucella*, there was a three-way interaction between wave exposure, embryonic experience with risk, and current experience with risk on tissue growth ($F_{1,67.9} = 8.4$, $P = 0.005$, Fig. 3A). In the absence of current risk, *Nucella* from wave-exposed populations grew 16% less tissue if they experienced risk as embryos (ls contrast: $P = 0.01$), while embryonic experience with risk did not affect *Nucella* from sheltered shores (ls contrast: $P = 0.06$). There was no effect of embryonic experience with risk on either wave-exposed or sheltered snails in the presence of current risk (ls contrasts: wave-exposed, $P = 0.16$, sheltered, $P = 0.38$). However,

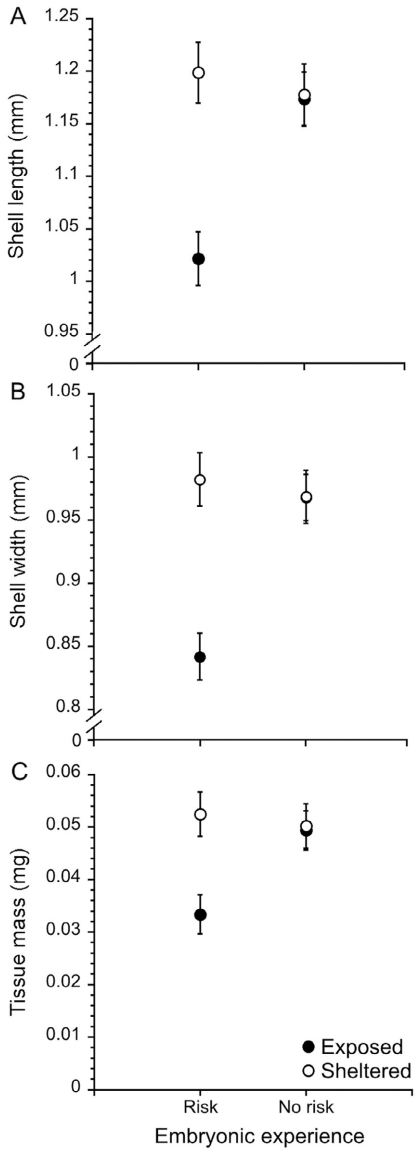

Fig. 2. Mean (± SE) (A) shell length (mm), (B) shell width (mm), and (C) tissue mass (mg) at emergence of *Nucella lapillus* that experienced the presence or absence of predation risk from the green crab *Carcinus maenas* as embryos. *Nucella* emerged from egg capsules collected from wave-exposed (filled circles) or sheltered (open circles) rocky intertidal populations. Note the y-axes break in (A) and (B). Data for snail traits at emergence were collected in 2015.

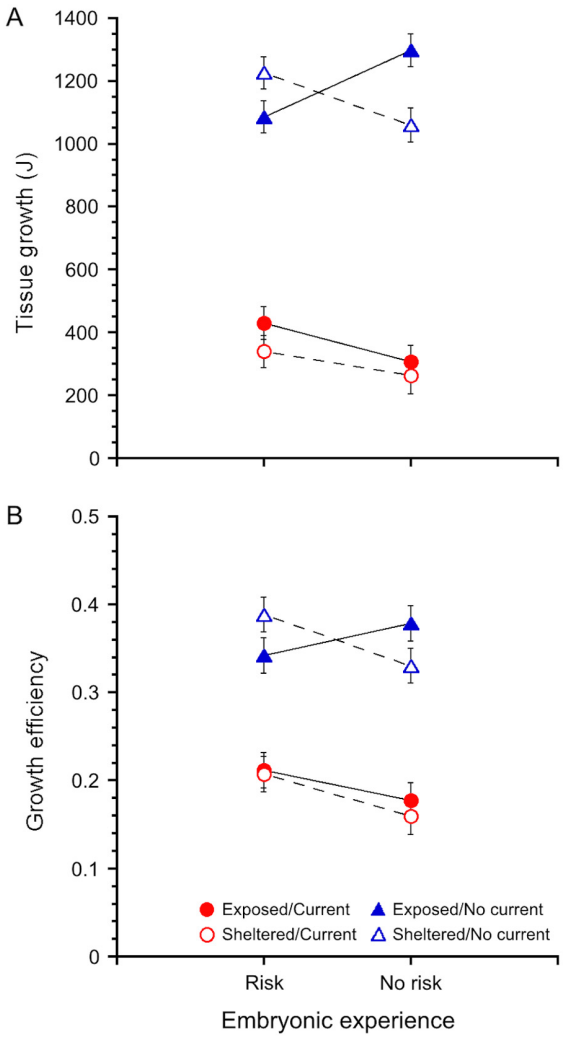

Fig. 3. Mean (± SE) (A) tissue growth (Joules, J) and (B) growth efficiency of *Nucella lapillus* in the presence (red circles) and absence (blue triangles) of current predation risk from the green crab *Carcinus maenas*. *Nucella* experienced the presence and absence of green crab predation risk as embryos and emerged from egg capsules collected from wave-exposed (filled symbols) and sheltered (open symbols) rocky intertidal populations. The three-way interaction is not significant in (B), but is shown for ease of comparison to (A). Data on the response of one-year-old *Nucella* to current predation risk were collected in 2016.

exposure to current predation risk reduced tissue growth for snails from both wave-exposed and sheltered populations (current risk: $F_{1,68.3} = 515.5$, $P < 0.0001$).

Current risk experience negatively affected *Nucella* foraging rates ($F_{1,70} = 291.31$, $P < 0.0001$), but no other main effects or their interactions impacted foraging (Appendix S1: Fig. S3, Table S4). Unlike growth, *Nucella* growth efficiency was not affected by the interaction between wave exposure, embryonic risk experience, and current risk, though there were suggestive trends ($F_{1,68.7} = 3.07$, $P = 0.08$, Fig. 3B): In the absence of current risk, *Nucella* from wave-exposed populations tended to have lower growth efficiency if they experienced risk as embryos. However, snails from both wave-exposed and sheltered populations had lower growth efficiency in the presence of current risk ($F_{1,68.7} = 215.07$, $P < 0.0001$). There was no effect of population on one-year-old *Nucella* growth, foraging, or growth efficiency (Appendix S1: Table S5).

Discussion

When exposed to risk as embryos, *Nucella* that emerged from egg capsules collected from wave-exposed populations had shorter, narrower shells and less tissue at emergence than *Nucella* that emerged from egg capsules from sheltered populations. In contrast, *Nucella* from sheltered populations emerged at the same size regardless of embryonic experience with risk (Fig. 2A–C). These results support our hypothesis that because green crab abundance is lower and likely more variable on wave-exposed shores, wave-exposed snails display greater plasticity in response to predation risk, as well as the results of our previous work showing that embryonic experience with risk causes wave-exposed snails to emerge at a smaller size (Donelan and Trussell 2018*a*). Emerging at a smaller size, however, is likely maladaptive (but see Moore et al. 2015) because it can reduce an individual's energetic stores (Rivero and West 2002), increase vulnerability to predators (Janzen et al. 2001), and delay reproduction (Marshall et al. 2003). The fact that wave-exposed, but not sheltered, snails incur these fitness costs suggests that sensitivity to predation risk during development is favored only in environments where uncertainty about risk is high (i.e., wave-exposed shores). While this heightened sensitivity may benefit wave-exposed snails by providing critical information on their potential risk environment, these costs

may negatively affect snail fitness throughout ontogeny.

We also found that embryonic experience with predation risk affected the tissue growth of one-year-old *Nucella* from wave-exposed populations, but these patterns only emerged in the absence of current risk (Fig. 3A). These results are consistent with our previous work on wave-exposed snails: In the absence of current risk, *Nucella* grew less tissue as one-year-olds if they experienced risk as embryos (Donelan and Trussell 2018*b*). In contrast, snails from sheltered populations do not appear to be affected by embryonic risk either at emergence or as one-year-olds. Sheltered snails may lack embryonic sensitivity to risk if the costs of this sensitive window are particularly high (Fawcett and Frankenhuis 2015). Indeed, there appear to be high costs (reduced size) to embryonic sensitivity to risk for wave-exposed snails both early and late in life. These costs would be particularly impactful for snails from sheltered populations because they typically mature at a larger size (Etter 1989), have less food available (Bryson et al. 2014), and require greater morphological defenses against predators (Hughes and Elner 1979) than snails from wave-exposed populations. Moreover, sheltered snails may be less sensitive during development because they have more certainty about the likelihood of risk, reducing the potential benefits of embryonic sensitivity (increased information). In contrast, wave-exposed snails may be more reliant on information they receive at all stages of life to estimate their future risk conditions and thus display sensitivity to risk as embryos.

The impacts of embryonic risk experience on the tissue growth of one-year-old wave-exposed snails may only manifest in the absence of current risk because their effects are subtle and may be masked by exposure to current risk. Indeed, when operating, the magnitude of the embryonic effect was much less than that of current risk exposure (16% vs. 249% change in tissue growth, respectively). Interestingly, we found that in the absence of both current and embryonic risk, *Nucella* from wave-exposed populations grew more than those from sheltered populations despite consuming similar amounts of energy. Snails from wave-exposed populations have been shown to grow slower and terminate growth at a smaller size relative to those from sheltered populations (Etter 1989), but these patterns may exist only in the field where harsh wave action limits foraging rates (Menge 1978*a*, Etter 1996) and maximum body size (Denny et al. 1985). Because our experimental conditions were physically benign (i.e., low flow) compared to those on wave-exposed shores, snail growth was likely not limited by hydrodynamic forces, thus allowing wave-exposed snails to grow larger in the absence of risk. Snails from wave-exposed populations may also be more physiologically efficient in order to compensate for the limited foraging opportunities they experience (Hawlena and Schmitz 2010), thereby enabling them to grow more than snails from sheltered populations when provided with ad libitum food in the experiment.

In contrast to the effects of embryonic experience with risk, exposure to current predation risk reduced the tissue growth of both wave-exposed and sheltered one-year-old snails (Fig. 3A). It is surprising that sheltered snails showed no sensitivity to predation risk as embryos but were highly sensitive as one-year-olds. Theory predicts that individuals should be more sensitive to information received early in life when uncertainty is often greatest (Fawcett and Frankenhuis 2015). However, while snails from sheltered shores may lack embryonic sensitivity to risk because the costs of such sensitivity outweigh its benefits, they may retain the capacity to plastically respond to predation risk as one-year-olds because direct exposure to current risk is such a strong signal of the immediate risk of predation. *Nucella* have relatively little behavioral capacity to escape green crab predators once detected, so exposure to current risk cues may continue to be an acutely stressful event that affects snail growth even in environments with high background levels of risk.

It was also surprising that sheltered snails grew substantially less tissue in the presence of current risk given that others have found that *Nucella* grow similarly thick shells in the presence and absence of risk cues (Hughes and Elner 1979, Palmer 1990, Freeman and Hamer 2009), though Palmer (1990) also found that sheltered snails grow less tissue in the presence of risk cues from another crab (*Cancer pagurus*). Predation risk may have greater impacts on snail tissue (versus shell) growth because tissue is

energetically more costly to produce (Palmer 1992) and thus likely more sensitive to changes in physiological stress caused by predation risk. Because of these energetic differences in shell and tissue production, snails from sheltered shores may be able to grow thick shells regardless of their current risk environment, but unable to produce as much tissue in the presence of current risk because of the high costs of doing so. Indeed, snails from both wave-exposed and sheltered populations consumed substantially less energy from mussels in the presence of current risk (Appendix S1: Fig. S3), which likely contributed to the observed reductions in tissue growth.

Snails from both wave-exposed and sheltered populations had substantially lower growth efficiency when exposed to current risk (Fig. 3B). Predation risk is known to reduce prey growth efficiency in this (Trussell et al. 2006) and other (McPeek 2004, Stoks et al. 2005) systems, likely because prey must allocate energy to support costly stress molecules and physiological pathways rather than allocating energy to growth (Pauwels et al. 2005, Slos and Stoks 2008). The effects of current risk on the growth efficiency of wave-exposed snails are consistent with our previous work (Donelan et al. 2017), but we were surprised to find similarly strong effects for sheltered snails. As suggested above, snails from sheltered shores may be plastic in response to risk as one-year-olds because direct exposure to predators continues to be stressful regardless of prey's expectations for risk. In addition, we found a trend ($P = 0.08$) suggesting the interactive effects of wave exposure, embryonic experience with risk, and current experience with risk on *Nucella* growth efficiency: As with tissue growth, embryonic risk experience negatively affected the growth efficiency of wave-exposed snails in the absence of current risk. Embryonic exposure to risk may activate physiological stress pathways early in life that continue to operate later in life, as has been shown in plants (stress memory, Bruce et al. 2007), and the sensitivity of wave-exposed snails to risk as embryos may have contributed to this trend for lower growth efficiency later in life.

The snails used in our experiments were collected from the field as encapsulated embryos within one week of being laid. Despite this short time in the field, we found persistent effects of wave exposure on the performance of *Nucella* both at emergence and as one-year-olds. We were surprised that we did not find population-specific differences in these responses. *Nucella* are direct developers with a tendency to remain on their natal shores, which should promote local adaptation despite the potential for gene flow between spatially proximate populations (Chu et al. 2014). We are unsure whether local adaptation is operating or we were simply unable to detect it in these experiments. Additionally, it is also possible that the differences we observed between wave-exposed and sheltered snails arose because of variable experiences with predation risk during the weeklong period in the field prior to collection. Regardless of the precise mechanism, the clear and persistent effects of the wave exposure on the response of prey to embryonic risk suggest that abiotic stressors can have important impacts on how prey evaluate and retain information about predation risk across ontogeny.

Our results support a growing body of work demonstrating that previous experiences with predators, either direct or indirect, can impact prey phenotypes and antipredator responses across life history. Moreover, it is clear that early life experiences may be particularly important for organisms in heterogeneous environments. Despite the propensity for abiotic stressors such as wave exposure to mitigate the impacts of biotic stress, it appears that organisms retain the capacity to respond to selectively important biotic stressors. Hence, our results have important implications for our understanding of how prey respond to predation risk across wave exposures and the capacity of prey to integrate information about predation risk across ontogeny.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2676/full