RESEARCH ARTICLE

Functional Ecology | BRITISH ECOLOGICAL SOCIETY

Sex-specific differences in the response of prey to predation risk

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Abstract

1. The non-consumptive effects of predation risk can strongly affect prey behaviour and fitness with emergent effects on community structure and ecosystem functioning. Prey may respond differently to predation risk based on key traits such as sex, but the influence of sex-specific variation is typically explored in species with strong sexual dimorphism. However, sex-specific responses to predation risk may arise even in prey species lacking sexual dimorphisms based on differences in the relative cost of reproduction.

2. Using a rocky intertidal food chain, we conducted a laboratory mesocosm experiment to explore sex-specific responses of morphologically similar, reproductively mature prey (the snail *Nucella lapillus*) to predation risk and whether risk affected female fecundity.

3. We found that predation risk suppressed prey growth only in males via effects on growth efficiency, suggesting that sex-specific disparities may arise due to differences in the energy required for reproduction and/or the costs of mounting a physiological stress response. Moreover, while risk did not affect overall female fecundity, it eliminated the positive relationship between female size and fecundity observed in the absence of risk.

4. We hypothesize that these sex-specific disparities arise due to differences in the energy required for reproduction and/or the costs of mounting a physiological stress response. Reproduction is likely more energetically costly for females than males, so females may display weaker antipredator responses in order to maintain energetic reserves needed for reproduction. Our results suggest that sex-specific responses may be an important component of inter-individual differences in prey responses to risk and influence prey population growth and demography even in species lacking sexual dimorphism.

KEYWORDS
antipredator, fecundity, inter-individual variability, intertidal, non-consumptive effects, *Nucella lapillus*, physiology, plasticity

1 | INTRODUCTION

The non-consumptive effects of predation risk, where predators scare rather than consume their prey, can dramatically affect the behaviour and fitness of prey individuals (Lima & Dill, 1990; Peckarsky et al., 2008). When exposed to visual, auditory or chemical cues signalling the presence of predators, prey often retreat to refuge habitats (Mangel & Clark, 1986; Sih, 1980) and reduce

their foraging activity (Brown & Kotler, 2004; Kats & Dill, 1998) to minimize their risk of being consumed. These behavioural shifts can reduce prey growth rates (Donelan, Grabowski, & Trussell, 2017; McPeek, 2004) and reproductive output (Candolin, 1998; Scheuerlein, Van't Hof, & Gwinner, 2001) as well as decrease metabolic efficiency as prey divert energy away from somatic growth to fuel metabolic stress responses (McPeek, Grace, & Richardson, 2001; Sheriff & Thaler, 2014). Importantly, the non-consumptive effects of predators on prey can scale up to impact prey demography (Nelson, Matthews, & Rosenheim, 2004), community structure (Ford et al., 2014) and ecosystem functioning (Schmitz, Hawlena, & Trussell, 2010).

While non-consumptive effects are common, there is often high inter-individual variability in the antipredator responses of prey based on traits such as sex (Magnhagen, 1991; Mirza, Scott, & Chivers, 2001; Sih, Krupa, & Travers, 1990). Sex-based differences in prey responses to predators have been well documented in sexually dimorphic species, where strong differences in size (Shine, Olsson, Lemaster, Moore, & Mason, 2000), ornamentation (Martín & López, 2001) or mating behaviour (Nonacs & Blumstein, 2010) can result in sex-specific differences in the susceptibility of prey to predators (Husak, Macedonia, Fox, & Sauceda, 2006; Møller & Nielsen, 2006). These disparities in the susceptibility of prey based on sex can in turn favour distinct antipredator phenotypes among males and females (Meuthen, Baldauf, Bakker, & Thünken, 2018; Välimäki & Herczeg, 2012). For example, in water striders, mating is more dangerous for females, and females are more cautious in the presence of predation risk than males (Han, Jablonski, & Brooks, 2015).

In species that lack overt behavioural or morphological sexual dimorphism, however, disparity in the energetic cost of reproduction between males and females may itself drive variation in antipredator responses (Christianson & Creel, 2008; Lima & Dill, 1990; Sih, 1994). Reproduction is often especially energetically costly for females because eggs require more energy to be produced than sperm (Hayward & Gillooly, 2011; Trivers, 1972). If females require more energy to build and maintain gonad than males, then the reductions in energetic intake that are often associated with antipredator behaviour may be especially costly for females through effects on reduced fecundity. Females may therefore exhibit weaker antipredator responses than males in order to maintain fecundity despite the high potential costs, as has been shown in guppies (Abrahams & Dill, 1989), or sacrifice fecundity in order to maintain their own body condition (Ghalambor & Martin, 2001). Alternatively, the relatively high energetic investment in reproduction by females may enhance cautious behaviour in the presence of predation risk (the asset protection principle, Clark, 1994), especially if reproductive events coincide with predator encounters to make the costs of being consumed particularly high. For example, in viviparous or ovoviviparous species, females (or the sex bearing offspring) exert considerable caution while they are gravid (Brown & Shine, 2004).

Exposure to predation risk can also drive changes in prey reproductive output (Öst, Lindén, Karell, Ramula, & Kilpi, 2018; Reznick, Callahan, & Llaured, 1996; Zanette, White, Allen, & Clinchy, 2011).

Because predation risk often limits prey foraging and/or increases their production of energetically costly stress molecules, risk exposure can reduce the total energy available for reproduction, thereby influencing overall reproductive success. For example, female hares produce more glucocorticoids and give birth to smaller offspring in the presence of risk compared to unstressed females (Sheriff, Krebs, & Boonstra, 2009). Moreover, reproductively mature prey must choose between allocating energy to somatic growth or reproduction (Lima & Dill, 1990; Magnhagen, 1991). In extreme cases, prey may choose to delay reproduction in predator-rich environments and instead allocate energy into somatic growth while waiting until risk subsides (Scheuerlein et al., 2001; Shaw & Levin, 2013). This calculus will further depend on an individual's assessment of their future reproductive potential, as predicted by life-history theory (Magnhagen, 1991; Stearns, 1992), and therefore vary across an individual's life stage (Grégoir et al., 2018; Meuthen et al., 2018) or between species based on differences in life history (e.g. Ghalambor & Martin, 2001). Despite the potential for male and female prey to exhibit variable responses to predation risk, sex-specific patterns of prey antipredator responses have been primarily explored in species with strong behavioural or morphological sexual dimorphism. How male and female prey differ in their responses to risk based on other factors, such as sex-based differences in the energy required for reproduction, remains poorly understood.

On rocky intertidal shores in New England, *Nucella lapillus*, a carnivorous snail, alters its behaviour, growth and physiology in response to predation risk from the green crab *Carcinus maenas* (Matassa, Donelan, Luttbeg, & Trussell, 2016; Trussell, Ewanchuk, & Matassa, 2006). *Nucella* are dioecious, morphologically similar across sex (Crothers, 1985), and behave similarly throughout their life history, including during mating (Crothers, 1985). Hence, this is an ideal system for exploring potential sex-specific differences in the response of prey to predation risk based solely on energetic disparities in reproduction. Male *Nucella* fertilize females internally and after mating, females lay egg capsules by attaching them to the rocky substratum (Crothers, 1985). Egg capsules contain hundreds of nutritious nurse eggs and multiple, directly developing embryos. There is no parental care (Spight, 1976) and juveniles emerge from egg capsules and begin feeding. Because the energetic cost of producing such egg capsules is likely higher than that of producing sperm, as is the case for other gastropods (Kideys, Nash, & Hartnoll, 1993), reproduction is expected to be more costly for *Nucella* females than males.

We conducted a laboratory mesocosm experiment to explore potential differences in the response of male and female *Nucella* to green crab predation risk. Our results revealed that predation risk strongly affected male, but not female, *Nucella* growth despite males and females consuming similar amounts of energy. Moreover, while exposure to predation risk did not directly affect female fecundity, exposure to risk eliminated the positive relationship between female size and reproductive effort that was evident in the absence of risk. Our results suggest that sex-specific responses to predation risk by prey may be driven by differences in both the energetic cost of

reproduction and the physiological response of male and female prey to risk. Hence, quantifying the effects of sex on prey responses to predation risk may be equally important in species lacking strong sexual dimorphism.

2 | MATERIALS AND METHODS

Our experiment explored the effects of predation risk (presence or absence of cues from the green crab *Carcinus maenas*) and the sex of prey (male/female *Nucella lapillus* snails) on prey growth, foraging and growth efficiency. We also quantified the impact of predation risk on prey fecundity. Snails (N = 48) were collected from a wave-exposed rocky headland (Donelan & Trussell, 2019) in Nahant, Massachusetts and held in the running seawater facilities at the Marine Science Center in Nahant, Massachusetts for 3 months prior to the start of the experiment. During this time, males and females were kept separately and given ad libitum food (blue mussels *Mytilus edulis*).

After 3 months of acclimation, we randomly created 24 mating pairs of *Nucella* snails. Each pair consisted of one male and one female adult snail (24.0 ± 1.6 mm, mean shell length ± SD). The male and female snail in a given pair were placed into two separate perforated jars (8 cm × 10 cm, diameter × height) with four blue mussels each (16.6 ± 3.0 mm, mean shell length ± SD) as food (Figure 1). These two jars were placed side-by-side in a larger plastic bucket (24 cm × 24 cm, diameter × height) that received an independent supply of flowing seawater and also housed another perforated chamber (11.5 cm × 10 cm, diameter × height) for the manipulation of predation risk. This 'risk manipulation' chamber contained either one male green crab (73.7 ± 2.2 mm, mean carapace width ± SD) with two *Nucella* for food (presence of risk) or two *Nucella* alone (absence of risk). The 'food snails' in each risk manipulation chamber were placed at random and replaced weekly. Moreover, *Nucella* respond to green crab risk cues regardless of green crab diet (Large & Smee, 2010), suggesting that the experimental *Nucella* are responding to cues from the green crab rather than cues from injured conspecifics alone.

Male and female snails remained in the risk/no risk conditions for 3 days before they were transferred to separate mesocosms for mating (Figure 1). All pairs mated in the absence of predation risk. The male and female in a given pair were removed from their individual jars and placed together in a perforated jar (8 cm × 10 cm, diameter × height) that was housed in a plastic bucket that received its own supply of flowing seawater. Male *Nucella* deposit sperm directly into the female; the female then lays ~1 cm tall, stalked egg capsules affixed to hard substratum (Crothers, 1985). A male and female remained together for 4 days so they could mate and deposit egg capsules, after which time they were placed back into the risk manipulation mesocosm set-up described above. Egg capsules were counted and removed at the end of each mating stage.

This week-long cycle of 3 days of risk exposure or 4 days of mating occurred for 12 weeks over the summer of 2015. There were 24 total pairs of snails (n = 12 per treatment combination, N = 48), so there were 24 independent buckets in the risk manipulation stage and 24 independent buckets in the mating stage. Snails began the experiment at the same size (initial tissue mass: risk: $p = 0.63$, sex: $p = 0.12$). Mussels and food snails were replenished weekly so that snails and crabs had access to four mussels and two food snails respectively. We removed all consumed mussels from the male and female jars when the snails were moved to their mating chambers. We quantified the per capita energy consumed by each snail by measuring the maximum shell length of each consumed mussel (indicated by a drill hole on the remaining shell), which can be used to calculate dry tissue weight and tissue energetic value using empirically derived equations (Burrows & Hughes, 1990; Elner & Hughes, 1978).

Before initiating the experiment, snails were individually tagged using plastic bee tags, which allowed individual measurement of growth. We measured snail tissue production (final – initial tissue, Joules, J) by buoyant weighing (Palmer, 1982) each snail at the beginning and end of the experiment and converting tissue growth (g) into dry tissue mass and its energetic equivalent (J) using empirically derived equations (Supporting Information: Appendix 1; Hughes, 1972; Matassa & Trussell, 2014). We also explored the effect of predation
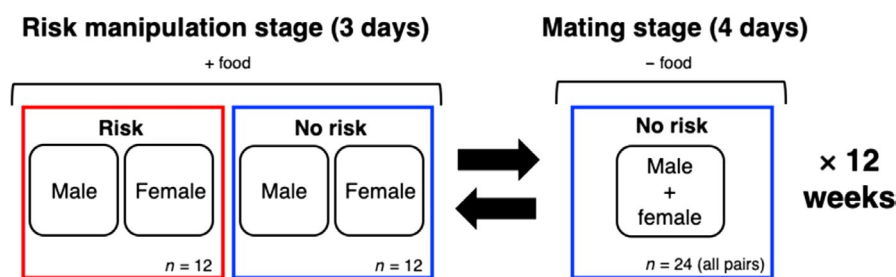

FIGURE 1 Schematic of the experimental design. Adult *Nucella lapillus* snails were collected from a wave-exposed shore and acclimated in running seawater laboratory facilities for 3 months prior to the start of the experiment. We then randomly paired 24 male and 24 female snails. We manipulated exposure to predation risk by placing snails in a week-long cycle that consisted of two stages: (1) a risk manipulation stage (3 days), where the male and female in a pair were placed in separate containers held in the same bucket and exposed to the presence or absence of green crab (*Carcinus maenas*) predation risk followed by (2) a mating stage (4 days), where the male and female in a pair were placed together in the same container in the absence of risk to mate and lay egg capsules. We repeated this cycle for 12 weeks. Snails were given four blue mussels for food during the risk manipulation stage only

risk on snail growth efficiency, which is a measure of how well an individual converts ingested energy into body mass. Predation risk is known to reduce prey growth efficiency in this and other systems (Trussell et al., 2006). We calculated individual growth efficiency by dividing the tissue produced (J) by each snail by the amount of energy (J) it consumed from mussels over the course of the experiment. We measured fecundity by adding up the total number of egg capsules produced by each female over the experiment (i.e. one total number of egg capsules per female).

We analysed snail tissue growth (J), foraging (J), and growth efficiency using separate two-way ANCOVAs (with REML variance estimates) that considered Risk and Sex as fixed effects and initial tissue mass (J) as a covariate. Because male–female pairs were housed in the same risk manipulation bucket, replicate units were nested within risk and considered a random effect. We conducted these analyses in JMP 11 and performed least squares (ls) contrasts on group means to explore any significant interactions.

We analysed the total number of egg capsules laid by each female in the presence and absence of risk using a negative binomial GLM to account for the high number of zeros. Risk was considered a fixed effect, initial tissue mass (J) was included as a covariate and their interaction was included as a slope term. We then ran a Type II ANCOVA to determine if the overall interaction (slope) was significant. We conducted these analyses in R (v.3.4.3) using the MASS (Venables & Ripley, 2002) and CAR (Fox & Weisburg, 2019) packages. Data are available in the Dryad Digital Repository.

3 | RESULTS

Sex significantly affected *Nucella* snail tissue production under predation risk (Sex × Risk: $F_{1,41.0} = 6.8$, $p = 0.01$, Figure 2a). In the presence of risk, male snails lost 10% of their initial tissue mass, while female snails gained 5% relative to their initial tissue (ls contrast: $p = 0.0004$). Female snails that were exposed to predation risk grew similarly to all snails in the absence of risk (ls contrast: $p = 0.5$). In contrast, while sex did not affect snail foraging rates ($F_{1,41.0} = 1.4$, $p = 0.3$, Figure 2b), both male and female snails foraged less in the presence of risk ($F_{1,41.5} = 22.4$, $p < 0.0001$, Figure 2b). However, the effects of predation risk on snail growth efficiency varied by sex (Sex × Risk: $F_{1,41.1} = 12.5$, $p = 0.001$, Figure 2c): in the presence of risk, male snails had significantly lower growth efficiency than female snails (ls contrast: $p < 0.0001$). In contrast, males grew as efficiently as females in the absence of risk (ls contrast: $p = 0.8$).

Overall, females produced the same number of egg capsules in the presence and absence of risk ($F_{1,20} = 0.06$, $p = 0.8$, Figure 3a). However, the relationship between female size (initial tissue mass) and the number of egg capsules produced depended on risk (Risk × Initial Tissue Mass: $F_{1,20} = 10.1$, $p = 0.005$, Figure 3b). In the presence of risk, females laid the same number of egg capsules
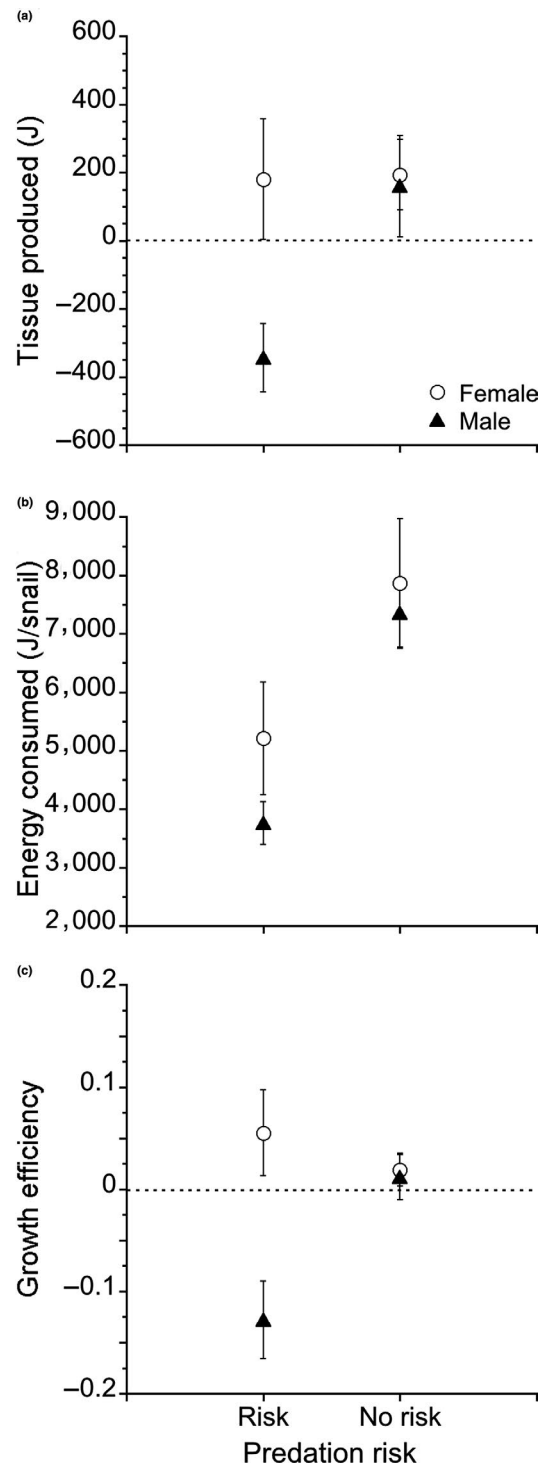

FIGURE 2 (a) Energy produced (Joules, J), (b) per capita energy consumed and (c) growth efficiency of male (filled triangles) and female (open circles) *Nucella lapillus* snails exposed to the presence and absence of predation risk from the green crab *Carcinus maenas*. Values are means ± *SE*

regardless of their initial mass (GLM: $p > 0.05$), while in the absence of risk, females that were initially larger laid more egg capsules (GLM: coefficient = 7.8, $p = 0.001$). Full results are presented in Supporting Information: Appendix 2.

FIGURE 3 Number of egg capsules laid per female *Nucella lapillus* (a) in each risk treatment (means ± *SE*) and (b) by initial tissue mass (J) for female snails in the presence (filled squares) and absence (open squares) of predation risk from the green crab *Carcinus maenas*. For (b), lines show relationships between initial tissue mass and number of egg capsules per female *Nucella* in the absence and presence of risk as determined by a negative binomial GLM
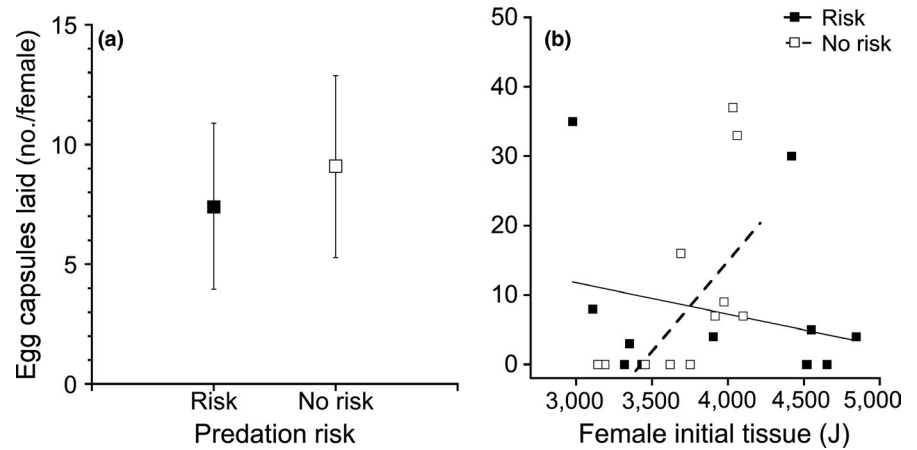
4 | DISCUSSION

The non-consumptive effects of predation risk can influence prey behaviour, growth, fecundity and survival in numerous systems (Peckarsky et al., 2008). But how these effects vary among individual prey based on traits such as sex is less understood, especially in systems where males and females are morphologically and behaviourally similar. However, sex-specific differences in the cost of reproduction are common even among organisms that lack sexual dimorphism (Hayward & Gillooly, 2011), and may drive sex-specific differences in how prey respond to predation risk, particularly when they are actively engaged in reproduction. Hence, sex-specific differences in prey responses to predation risk may have important impacts on prey demography and population dynamics.

Our results show that exposure to predation risk substantially altered the growth of male, but not female, snails during their reproductive season. In the presence of risk, males lost 10% of their initial tissue mass over the 12-week experiment, but in the absence of risk, grew 5% relative to their initial size (Figure 2a). In contrast, female snails grew similarly in the presence and absence of predation risk, adding 5% to their initial tissue mass and thus producing ~600 J more tissue than males in the presence of risk (Figure 2a). This higher growth in females occurred despite their need to also devote energy to egg capsule production, which was similar in both the risk and no-risk treatments ($\bar{x}$ = 8.25 egg capsules per female, Figure 3a). While the relative energetic costs of reproduction are not known for male and female *Nucella lapillus*, female *Buccinum undatum*, another carnivorous gastropod, invest 14 times more energy in reproduction than males over one season (Kideys et al., 1993). Interestingly, the strong sex-specific differences in tissue growth were not caused by sex-specific differences in foraging rates, as both male and female snails consumed similarly less energy in the presence versus absence of risk (Figure 2b). Prey often respond to predation risk by decreasing their foraging effort (Grabowski & Kimbro, 2005; Matassa et al., 2016), and our results suggest that these patterns hold regardless of sex in a system where males and females are similarly vulnerable to predation risk.

Male and female snails exhibited similar suppression of their foraging in the presence of predation risk, so foraging rates cannot explain the observed sex-specific patterns in tissue growth. Instead, sex-specific differences in growth were driven by the strong, sex-specific effects of predation risk on prey growth efficiency. Females grew with similar efficiency in the presence and absence of predation risk, on average converting 4% of the energy they consumed into body mass. In contrast, males were as efficient as females in the absence of risk, but in the presence of risk lost 15% of the energy they consumed, presumably to support physiological processes other than growth (Figure 2c). Prey often exhibit reduced growth efficiency in the presence of predation risk (McPeek, 2004; Trussell et al., 2006). This response may manifest because energy is allocated away from somatic growth and instead devoted to support physiological components of the stress response, including elevated metabolic rate and the production of stress hormones (Boonstra, Hik, Singleton, & Tinnikov, 1998; Creel, Christianson, Liley, & Winnie, 2007; Pauwels, Stoks, & De Meester, 2005). For example, to mitigate the negative molecular effects of stress imposed by predation risk, damselflies increase their production of heat shock proteins (Slos & Stoks, 2008).

In our system, it may be advantageous for female prey to forego allocating energy to support physiologically based stress responses, particularly during the reproductive season, and instead allocate energy to their own somatic growth. This view is consistent with evidence from many systems, including other gastropod species (Kideys et al., 1993), showing that larger females produce more or better quality offspring than smaller females (Barneche, Robertson, White, & Marshall, 2018; Lim, Senior, & Nakagawa, 2014), whereas this relationship is weaker for males (Hayward & Gillooly, 2011). Indeed, we found a positive relationship between initial size and fecundity for female *Nucella* in the absence of risk (Figure 3b), suggesting that larger body size has a direct, positive effect on female fitness in this system. Hence, in systems where female body size is positively correlated with fecundity, the fitness consequences of achieving or maintaining a larger body size may be under stronger selection in female versus male prey. Again, such divergent selection pressure may be particularly pronounced during the reproductive season. If this is the case, then we hypothesize that male prey may have more latitude in diverting energy to support molecular stress responses at

the cost of reduced growth, whereas the adverse consequences of such diversions on female growth may entail significant costs to their reproduction. This hypothesis assumes that the costs of reproduction are lower for males than females, which is the case for many species (Hayward & Gillooly, 2011), but nevertheless warrants future testing.

The potentially adverse influence of parental effects on their offspring may also explain why females potentially devote less energy to stress responses during reproduction. In many systems, females exposed to predation risk during reproduction can pass stress hormones to their offspring through, for example, the nourishment they provide to their developing embryos (e.g. yolk; McCormick, 1998; Saino et al., 2005). High levels of stress hormones from mothers can influence offspring fitness, sometimes in negative ways. For example, increased egg cortisol reduces the size of larval reef fish at emergence (McCormick, 1999), which can negatively affect their subsequent survival in the presence of some predators (Holmes & McCormick, 2010). Similar negative correlations in maternal stress hormones and offspring size/number have been shown in mammals (Sheriff et al., 2009), birds (Hayward & Wingfield, 2004; Saino et al., 2005) and insects (Silbermann & Tatar, 2000). In contrast, while there is growing evidence that the transmission of stress effects by fathers is also common (Crean, Dwyer, & Marshall, 2013; Hellmann, Bukhari, Deno, & Bell, 2019), such paternal effects may operate through mechanisms other than the direct transfer of stress hormones to their offspring, including reduced paternal care (Bell, McGhee, & Stein, 2016) and lower sperm quality (Sales et al., 2018).

Female *Nucella* produce nurse eggs within their egg capsules to nourish developing embryos, providing a pathway that enhances the likelihood of stress hormone transfer to their offspring relative to males that provide only sperm. Because exposure to elevated levels of stress compounds during development can negatively affect key offspring traits at emergence, the production of these stress compounds during reproduction may be especially costly for female versus male prey in terms of the fitness of their offspring. Importantly, over the long-term, failure to support molecular stress responses may ultimately prove costly for females if the effects of physiological stress reduce survivorship or cumulatively impair lifetime fecundity. For example, in female *Drosophila*, increased production of heat shock proteins reduces overall egg hatching success, but improves survival in older females (Silbermann & Tatar, 2000). Moreover, this reduction in egg hatching success does not affect the first brood that a female lays after she is exposed to stress, but only manifests in subsequent broods (Silbermann & Tatar, 2000), suggesting that in some systems there is a strong trade-off between short-term fecundity and lifetime fitness among females. Whether selection favours sex-specific physiological responses of reproductively mature prey to predation risk remains an important but under-explored questions in this and other systems.

Our measurements of growth efficiency accounted only for the energy expended on somatic growth and did not include the energy expended to produce gametes or egg capsules. Because we did not measure the energetic costs of gamete/egg capsule production, it is possible that sex-specific differences in growth efficiency emerged because males allocated more energy to reproduction than females and thus less energy to somatic growth, thereby leading to the reduced growth efficiency we observed. However, because sex-specific differences in growth efficiency only emerged in the presence of risk, and because reproduction has been shown to be substantially more energetically costly for females than males in similar systems (Kideys et al., 1993), we find this explanation to be unlikely.

In other systems (Creel et al., 2007; Zanette et al., 2011), predation risk is known to adversely affect prey fecundity, but this response did not occur in our experiment (Figure 2a). However, it is likely that the number of egg capsules produced by *Nucella* provides an incomplete measurement of total reproductive output or quality. For example, while females exposed to predation risk may produce the same overall number of offspring as those in risk-free conditions, their offspring may be of poorer quality. Indeed, previous work in this system suggests that offspring of risk-experienced parents tend to emerge with less tissue than those of risk-naive parents (Donelan & Trussell, 2018), which may affect early life fitness and survival. We did, however, find that predation risk modified the relationship between female size and fecundity: larger females (as measured by initial tissue mass) laid more egg capsules, but only in the absence of risk (Figure 3b). These results correspond with others showing that larger females tend to produce more offspring (e.g. Barneche et al., 2018; Roff, 2002). This relationship is central to life-history theory (Stearns, 1992) and is well documented, particularly in ectotherms (Arendt, 2011), so we were surprised that the positive fecundity–size relationship disappeared in the presence of predation risk. However, our experiment only observed the effects of predation risk on female fecundity during one reproductive season. We suggest that in the presence of risk, it may be more advantageous in the short-term for large female *Nucella* to maintain their body mass in order to enhance their future potential reproductive success when threats from predation have subsided. Importantly, females consumed more energy in the absence versus presence of risk, and this additional energy may have allowed large females in the absence of risk to maintain both their large body size and high reproductive output. These results suggest that despite similarities in female growth and fecundity in the presence and absence of risk, exposure to predation risk is nevertheless costly for prey, particularly for larger bodied females that may disproportionally contribute to population growth.

Our results indicate that male and female prey can respond differently to predation risk based on differences in physiological costs that are shaped by potential sex-specific differences in the energetic trade-off between growth and reproduction. Because the majority of studies examining sex-specific differences in prey antipredator responses involve species exhibiting morphological and behavioural dimorphisms that affect their vulnerability to predators, our results provide new insight into other potential mechanisms that shape prey responses to risk. Overall, we suggest that prey sex should be better incorporated into studies of the non-consumptive effects of predation risk, particularly in systems where sexual

dimorphism is subtle or absent. Moreover, increased attention to the reproductive costs of predation risk may provide a more robust understanding of how the foraging-predation risk trade-off governs prey decision-making and its implications for communities.

AUTHORS' CONTRIBUTIONS

Both the authors conceived of the study. S.C.D. designed and co-ordinated the study, carried out the statistical analyses and drafted the manuscript. Both the authors contributed equally to manuscript revisions and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.9s4mw6mbw (Donelan & Trussell, 2020).

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SUPPORTING INFORMATION

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