Predation risk suppresses mating success and offspring production in the coastal marine copepod, *Eurytemora herdmani*

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Abstract

We investigated the effects of a common mysid predator, *Neomysis americana* on the mating success of an estuarine copepod, *Eurytemora herdmani*. The presence of a mysid predator, or only a predator cue, reduced copulation frequency and spermatophore transfer success of *E. herdmani*, and led to a substantial decrease in *E. herdmani* nauplius production. Thus, mysid predators can influence copepod population growth through nonconsumptive processes by reducing the frequency and success of mating events. This highlights the need to look beyond population-level demographic factors (i.e., sex ratio and population density) and consider community-level ecological factors (such as predation risk) when modeling population growth rates of prey species critical to marine food webs.

Predation has long been documented as a key structuring process in aquatic ecosystems, demonstrated as a loss due to direct consumption by the predator of its prey (Paine 1974; Carpenter et al. 1985). More recent empirical studies demonstrated that predators also produce visual, physical, or chemical cues that confer a 'predation risk' to surrounding prey; these nonconsumptive effects generate significant changes in prey populations that cascade through entire ecosystems, and often equal or exceed the effects of predation alone (Peacor and Werner 2001; Werner and Peacor 2003; Preisser et al. 2005). Often, the threat of predation causes prey to reduce activities that make them vulnerable to predators, such as altering the timing and spatial extent of their migration (Ohman et al. 1983; Neill 1990), foraging (Trussell et al. 2002), refuge use (Lima and Dill 1990), or mating behavior (Sih et al. 1990; Koga et al. 1998). Mating and mating-related behaviors are particularly influenced by perceived predation risk because these behaviors are often highly conspicuous and leave prey vulnerable to predators (Magnhagen 1991). As a result, animals may reduce the frequency or duration of their mate-searching (Maier et al. 2000), mate-signaling (Ryan et al. 1982), and copulation behavior (Sih et al. 1990) to avoid detection by predators. Thus, when predation is intense, individual shifts in prey behavior may scale to affect the reproductive success and growth of an entire prey population (Lima 1998). It is especially important to understand these behavioral effects on the population dynamics of species that occupy basal trophic positions in food webs.

Marine copepods play a vital role in coastal food webs as food for a diverse array of predators (e.g., whales, juvenile fish, bivalves, shrimp, etc.), many of which are commercially important species (Runge 1988; Mauchline 1998). Consequently, researchers have identified important factors that influence the productivity of copepod populations (Mauchline 1998). Traditionally, population growth experiments have centered on the effects that environmental factors such as temperature and food concentration have on copepod egg production rate (Checkley 1980; Huntley and Lopez 1992; Mauchline 1998). However, more recent theoretical and experimental studies indicate that demographic factors, such as population density and sex ratio, also strongly affect population growth rates for copepods (Choi and Kimmerer 2008; Kiørboe 2008; Kramer et al. 2008).

Field surveys of zooplankton communities indicate that predators mediate the density and species diversity of copepods (Ohman 1986; Hirst and Kiørboe 2002). However, these field surveys primarily assessed the consumptive effects of predators on copepod prey, in terms of reducing population size (Ohman 1986; Hirst and Kiørboe 2002) or skewing copepod sex ratio (Hirst et al. 2010). Recent studies indicate that changes in copepod sex ratio and density can decrease mate-encounter rates and, thus, successful mating events (Choi and Kimmerer 2008, 2009; Kiørboe 2008). However, the potential for predators to affect copepod-mating behavior via nonconsumptive effects and, thus, alter subsequent population growth, has received little attention.

Here, we investigate the role of predation risk on the mating success of *Eurytemora herdmani*. Using a series of laboratory and field experiments, we asked the following questions: (1) Does the presence of a mysid predator or predator cue interfere with the mating success of *E. herdmani*? (2) What is the nature of the cue responsible for eliciting this effect? (3) Does the presence of a predator cue influence copepod population growth via reduced mating success?

Methods

Study site and organisms—Eurytemora herdmani were collected in the Damariscotta River estuary, Walpole, Maine (43°56'N, 69°35'W) using a plankton net with a mesh size of 250 μ m, towed obliquely by boat at ~ 30-m depth. Upon collection, animals were immediately transferred into 20-liter containers of surface seawater and

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transported to the lab. Eurytemora herdmani was chosen as our target species because of its high abundance in our study site, reaching peak densities > 1000 individuals per m³ (R. S. Lasley-Rasher and J. Yen, unpubl.). Eurytemora herdmani were sorted from mixed samples under a dissecting microscope and placed in containers filled with filtered seawater at densities < 25 individuals L⁻¹. Containers were gently aerated and placed in a temperature-controlled room set to match ambient water temperature (15°C). Copepods were fed mixtures of Rhodomonas lens and Tetraselmis sp. and provided a 14:10-h light: dark cycle. To ensure virgin status for mating experiments, copepodite stage V (CV) females were reared in the absence of males until they reached sexual maturity (1-4 d). Prior to experiments, females were visually inspected under a microscope to be sure that only mature females (i.e., possessing dark oocytes) were used in experiments. Males were held in aerated containers of filtered seawater, separated from females for 1-2 d to allow enough time for spermatophore generation and increase their eagerness to mate during experiments.

To assess consumptive and nonconsumptive predator effects on copepod mating success, mating experiments were conducted in the presence of a mysid shrimp, Neomysis americana. Neomysis americana were used in these assays because they are common in our study area. can achieve high swarm densities up to 10⁵ m⁻³ in some areas (Jumars 2007), and readily feed on adult Eurytemora herdmani (R. S. Lasley-Rasher and J. Yen, unpubl.). Furthermore, mysids are important copepod predators in many systems (Takahashi 2004). Neomysis americana were collected at night via vertical plankton tows from the dock at the Darling Marine Center in Walpole, Maine, (43°56'N, $69^{\circ}35'$ W). A plankton net with 250-µm mesh size was lowered into the water column and kept in the middle of the water column for several minutes and then pulled to the surface. Mysids were kept in aerated 20-liter buckets and fed mixed zooplankton and mixtures of *Rhodomonas lens* and Tetraselmis sp. phytoplankton. Mysids were measured under a microscope and only individuals between 8 mm and 10 mm were used for experiments.

Laboratory: Mating behavior in the presence of a predator and predator cue-To determine the effects of predation and predation risk on the mating success of Eurytemora herdmani, one male and one virgin female were incubated in either (1) the presence of a Neomysis americana, (2) a physical predator mimic, (3) a chemical predator cue, or (4)a combined physical and chemical predator cue. To mimic the physical cue of a mysid predator, Artemia salina (8-10 mm) were used because they swim around the experimental vessel frenetically and create a feeding current (Barlow and Sleigh 1980), thus producing fluid shear that copepods will escape from. Supplemental experiments confirmed that there was no difference between the frequency of copepod escapes from physical cues generated by A. salina and the actual predator, N. americana (t =0.53, df = 30, p = 0.9, n = 16, *t*-test). To apply a chemical cue generated by N. americana to appropriate treatments, N. americana were incubated with male and female Eurytemora herdmani (at a density of 10 mysids + 20 copepods L⁻¹) in filtered, autoclaved seawater for 24 h, allowing *N. americana* to hunt and feed on *E. herdmani*. Seawater was then filtered through a 100- μ m sieve to remove animals, and further vacuum-filtered with a 0.4- μ m filter paper to remove particulates. This conditioned seawater was stored at 4°C and used in experiments in an undiluted form within 12 h.

Trials were conducted in small volumes (20 mL) to facilitate high encounter rates and because this volume is comparable to volumes that yielded maximum mating success in a previous study on the congeneric Eurytemora affinis (Choi and Kimmerer 2009). A consumptive predator treatment (predator present), nonconsumptive predator treatments (physical predator mimic, chemical predator cue, combined physical + chemical predator cue) and a control (predator absent) were randomly assigned to containers (n = 30 per treatment) and copepods were randomly assigned to each treatment. Experiments were run in the dark at 15°C for 2 h. Animals were inspected under a dissecting scope every 20 min and males and females were scored as alive and healthy (i.e., swimming normally), dead, or missing. Females were further inspected for the presence of a spermatophore attached to their urosome, indicating a successful mating event.

Females without attached spermatophores were individually incubated for 24 h to see whether they developed an egg sac. If these females did develop an egg sac, we assumed that they received a spermatophore during the mating trial and that the spermatophore fell off. To test this assumption, we conducted supplementary experiments to determine whether virgin females would develop an egg sac without first receiving a spermatophore. The behavior of 50 couples (one male + one virgin female) was observed under infrared light; virgin females that did not receive a spermatophore during the trial (n = 15) were subsequently incubated for 24 h to determine whether or not they would develop an egg sac. No females developed an egg sac without receiving a spermatophore first.

To determine at what stage mating success was interrupted by predation or perceived predation risk, a subset of the mating trials for each treatment (n = 15 per)treatment) were observed in a darkened room using an infrared light to illuminate the animals and score their mating behavior. No more than three pairs were observed at once so that the observer could carefully score the following mating behaviors: mate captures (i.e., male grasps female with his antennule), mating pair formations (male and female assume copulatory position), and spermatophore transfer (male attaches a spermatophore to female's urosome; Buskey 1998). During the trial, males were allowed to capture their female multiple times. In contrast, we only allowed copepods to form copulatory pairs once during the trial. After observing pair formation, copulation, and separation, we immediately scored females for the presence or absence of an attached spermatophore. Therefore, trials in which pair formation occurred were inherently shorter in duration. We calculated capture frequency by dividing the number of captures by the number of minutes observed to facilitate comparison across trials of different durations.

Field: Effects of predator cues on copepod fitness—To examine the effects of a mysid-predator cue on Eurytemora herdmani mating success under conditions more closely resembling those in the field, three male and three female E. herdmani were placed in 1-liter polyethylene bottles containing either (1) 10 mysid predators, (2) a combined chemical + physical cue consisting of 10 predator mimics swimming in mysid exudates, or (3) a filtered-seawater control (n = 15 per treatment). We chose this copepod density, (6 individuals L^{-1}) to be high enough to facilitate adequate mate-encounter rates during trials and to increase the odds that some copepods would survive in treatments containing predators. We chose this predator density, 10 mysids L^{-1} , to represent a medium density swarm of Neomysis americana (Jumars 2007). As with all other experiments, Neomysis americana between 8 mm and 10 mm were used as the predator and Artemia salina 8-10 mm were used to mimic the physical cue given off by the predator. However, to create a chemical cue matching the amount of exudates created during this experiment, the cue was created by allowing 10 mysids to forage on six E. herdmani for 2 h in 1 liter of seawater; this conditioned water was filtered as described above and added in full to appropriate treatments. Containers were sealed and placed in individual mesh bags that were suspended from the dock at the Darling Marine Center during ebb or flood tide to subject the bottles to natural water motion. These larger (1-liter) floating containers were used to more closely replicate natural conditions for encounter rates that may be constrained in the small (20-mL) vessels containing still water. All experiments were conducted at night. After 2 h, animals were carefully removed from experimental bottles. For each container, we noted the number of animals missing (presumed eaten) from predator treatments. All copepods were recovered from our control and predatorcue treatments.

All females were individually incubated in 20-mL containers until their eggs hatched (2–3 d). Females that never developed an egg sac were incubated for 3 d. On day three, all females were removed from their container and 2 mL of acetic acid was added to the container to stain and fix the nauplii (Maps et al. 2005). All nauplii were counted.

Statistical analyses—For binomial data (i.e., mating success, pair formation, and spermatophore transfer), we fit generalized linear models (GLM) with binomial distribution (i.e., success = 1, failure = 0) and logit-link function followed by post hoc contrasts using SAS software v.9.1 (SAS Institute Inc. 2007). To estimate the magnitude of our treatment effects, we calculated odds ratios (OR) with corresponding 95% confidence intervals (CI). Odds ratios that fall between 3.2 and 10 indicate substantial evidence, and between 10 and 100 indicate strong evidence (Jeffreys 1961).

For data sets comprised of continuous response variables with normal error distributions (i.e., capture frequency and clutch size), we compared treatments using a one-way ANOVA. The total number of nauplii produced per replicate failed to meet normality assumptions even after transformation attempts. This is a typical problem for count data



Fig. 1. Effects of predator cues on mating success. Percentage of individual *Eurytemora herdmani* females that successfully mated during a 2-h incubation with one conspecific male in the presence of a mysid predator *Neomysis americana*, a chemical predator cue, a physical predator cue, or combined physical + chemical predator cues, relative to controls (n = 30 for all treatments). Percentages were analyzed using a generalized linear model with a binomial distribution and logit-link function with post hoc contrasts ($\chi^2 = 25.98$, df = 4, p < 0.001). Different lowercase letters indicate differences at the 0.05 α level.

containing many zeros (Crawley 2005), so these data were analyzed with a generalized linear model using R (R Development Core Team, 2009) with a logarithmic link function and a quasi-Poisson distribution to compensate for overdispersion (Crawley 2005), followed by post hoc contrasts. To estimate the effect sizes of our treatments with continuous data, we calculated Cohen's d (d). Cohen's d is commonly used in meta-analyses to depict the relative magnitude of treatment effects. Cohen's d values greater than 0.8 or less than -0.8 are indicative of strong effects (Cohen 1988).

Results

The presence of a mysid predator significantly reduced *Eurytemora herdmani* mating success (Fig. 1; control vs. predator OR = 16.0, 95% CI = 4.5–56.7, χ^2 = 18.45, df = 1, p < 0.0001 [GLM binomial distribution]). *Neomysis americana* consumed at least one of the two copepods in 30% of the predator treatments and did not differentially prey on males or females (d = 0, 95% CI = -0.69-0.71, U = 97.0, df = 28, p = 0.9 [Mann–Whitney *U*-test]). In the absence of an actual predator, *E. herdmani* mating success was significantly reduced by combined (chemical + physical) treatments (Fig. 1; control vs. combined cue OR = 8.0, 95% CI = $2.5-25.9, \chi^2 = 12.07, df = 1, p = 0.0005$ [GLM binomial distribution]), indicating that this effect is not simply due to consumption or injury caused by predatory attacks.

Visual observations in a subset of experiments revealed that there was no significant difference in the number of mate captures min⁻¹ (i.e., male grasps female with his antennae; d = 0.69, 95% CI = -0.13-1.25, $F_{4,70} = 1.83$, p = 0.1 [ANOVA]). However, male and female *Eurytemora*



А



Fig. 2. Effects of predator cues on mating behavior. Percentage of *Eurytemora herdmani* couples that formed mating pairs (A) and successfully transferred spermatophores (B) in the presence of a mysid predator *Neomysis americana*, a chemical predator cue, a physical predator cue, or combined physical + chemical predator cues, relative to controls (n = 15 for all treatments). Percentages were analyzed using a generalized linear model with a binomial distribution and logit-link function with post hoc contrasts ($\chi^2 = 12.48$, df = 4, p < 0.05) and ($\chi^2 = 23.15$, df = 4, p < 0.001) for (A) and (B), respectively. Different lowercase letters indicate a significant difference at an α level of p < 0.05.

herdmani formed copulatory pairs significantly less often in the presence of a combined (chemical + physical cue), relative to predator-free controls (Fig. 2A; control vs. combined cue OR = 17.9, 95% CI = 2.7–116.9, χ^2 = 9.06, df = 1, p = 0.003 [GLM binomial distribution]). Furthermore, the chemical cue alone also reduced the frequency of *E. herdmani* pair formations (Fig. 2A; control vs. chemical cue OR = 7.4, 95% CI = 1.2–45.1, χ^2 = 4.76, df = 1, p = 0.03 [GLM binomial distribution]). In contrast,



Fig. 3. Effects of predator cues on mating duration. The time spent mating (mean $\pm 95\%$ CI) between male and female *Eurytemora herdmani* in the presence of a mysid predator *Neomysis americana*, a chemical predator cue, a physical predator cue, or combined physical + chemical predator cues, relative to controls (n = 15 per treatment). Analyzed by ANOVA ($F_{4,34} = 1.82, p = 0.9$).

E. herdmani did not significantly reduce pair formation frequency in response to a physical cue alone (Fig. 2A; control vs. physical cue OR = 4.3, 95% CI = 0.7–26.5, χ^2 = 2.52, df = 1, p = 0.1 [GLM binomial distribution]). The presence of an actual predator did not significantly reduce copulatory pair formation (Fig. 2A; control vs. predator OR = 5.7, 95% CI = 0.9–34.5, χ^2 = 3.58, df = 1, p = 0.06 [GLM binomial distribution]), but did decrease the number of successful spermatophore transfers among copulating pairs (Fig. 2B; control vs. predator OR = 56.0, 95% CI = 5.1–611.7, $\chi^2 = 10.89$, df = 1, p = 0.001 [GLM binomial distribution]), indicating that the predator interferes with the process of spermatophore transfer. Neomysis americana consumed at least one copepod in 7% of the predator treatments. We did not detect a statistical difference in the duration of mating events across any treatment (Fig. 3; d =0.47, 95% CI = -0.35-1.25, $F_{4,34}$ = 1.82, p = 0.9 [ANOVA]).

In field incubation experiments, the total number of offspring produced per replicate was suppressed by the presence of both predator and predator cue treatments (Fig. 4A; control vs. predator d = 1.45, 95% CI = 0.78– 2.12, $t_{43} = 3.73$, df = 1, p < 0.001; control vs. cue d = 0.76, 95% CI = 0.05–1.59, t_{43} = 2.04, df = 1, p < 0.05 [GLM quasi-Poisson distribution]). Neomysis americana consumed one of six copepods in 21% of the replicates, consumed two of six copepods in 14% of the replicates, and consumed more than two of six copepods in 7% of the replicates. In summary, actual predation on E. herdmani adults during the experiment contributed to the subsequent reduction in offspring in 43% of the predator replicates. We did not detect a difference in the number of nauplii per clutch (Fig. 4B; d = 0.22, 95% CI = -0.57-0.96, $F_{2,34} =$ 0.51, p = 0.61 [ANOVA]).

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Fig. 4. Effects of predator cues on offspring production. The (A) total number of nauplii and (B) number of nauplii per clutch, (mean $\pm 95\%$ CI) produced by female *Eurytemora herdmani* after a 2-h incubation with equivalent densities of males in containers incubated in the field housing either a mysid predator *Neomysis americana*, a chemical predator cue, or a predator-free control. Copepods were removed postincubation and kept in isolation until eggs hatched (2–3 d) in laboratory containers. Total number of nauplii (A) analyzed by generalized linear model with quasi-Poisson distribution and logarithmic link function and post hoc contrasts, ($F_{2,42} = 6.43$, p = 0.003). Number of nauplii per clutch (B) analyzed by a one-way ANOVA ($F_{2,34} = 0.51$, p = 0.3). Different lowercase letters indicate a significant difference at α level p < 0.05.

Discussion

The presence of a combined predator cue (chemical exudates + physical cue mimic), considerably reduced the mating success and subsequent offspring production of Eurytemora herdmani (Figs. 1, 2, 4). These effects were observed in the absence of an actual predator, indicating that a reduction in copepod mating success can occur by nonconsumptive mechanisms, and need not involve attacks from predators or predator-induced changes in mate density or sex ratio. These results suggest that nonconsumptive effects of N. americana on its prey generate a significant proportion of the overall patterns we observed in our study. Our findings corroborate a growing number of studies demonstrating that nonconsumptive effects of predators have large effects on prey population growth (Peacor and Werner 2001; Werner and Peacor 2003; Preisser et al. 2005) and highlight the importance of perceived risk in reducing offspring production and subsequent population growth.

Recent copepod-population growth models suggest that small population densities (Choi and Kimmerer 2008, 2009) and biased sex ratios (Kiørboe 2007, 2008) decrease copepod mating success and subsequent population growth by reducing mate-encounter rates (Kiørboe and Bagøien 2005; Visser and Kiørboe 2006; Kramer et al. 2011). Here, we show in small (20-mL) vessels, where encounter rates are not limiting, that *E. herdmani* mating success is significantly reduced by the presence of a predator cue. While we acknowledge that changes in encounter rates have obvious and important consequences for copepod mating success, our results suggest that predator cues play an important, but underestimated, role in reducing copepod mating success by reducing the ability or willingness of copepods to mate even when encounter rates are high. Our results highlight the importance of nonconsumptive effects of predators on copepod mating success (Figs. 1, 2, 4). Broadly, there are two possible explanations for this effect. First, predator cues alter the behavior of copepods, leading them to adopt more inconspicuous behaviors and delay reproduction to ensure their own survival. Second, predator cues interfere with the ability of copepods to successfully mate by disrupting mate finding, pair formation, or spermatophore transfer. How we distinguish between these two mechanisms varies depending on the stage of mating being examined (Buskey 1998).

At the earliest stage of mating, we found no significant difference in the frequency of mate captures among any of the treatments, indicating that males are able to locate females equally well in the presence of a predator and are willing to pursue females in the presence of predator cues. Therefore, it does not appear that predators diluted pheromones by mixing the water or masked pheromones with their kairomones in our study. In contrast, once mate capture occurred, there was a reduction in mating pair formation in the presence of a combined (chemical + physical) predator cue as well as a chemical cue alone (Fig. 2A); this could occur because females are less willing to mate, males voluntarily release females, or predators (and mimics) disturb the surrounding water and make it difficult for males to 'hold on.' There was no difference in mating pair formation when copepods were exposed to a physical mimic alone (Fig. 2A), suggesting that they have the ability to mate in the presence of a physical disturbance. Therefore, the reduction in pair formation was likely due to a reduction in the willingness to mate by the male, the female or both.

In the final stage of mating, copepods suffered reduced spermatophore transfer success when exposed to predators and all predator cue types (Fig. 2B). Again, this could be due to females rejecting spermatophores, males voluntarily releasing females before transferring, or predators (and mimics) disturbing the surrounding water and interfering with the male's ability to properly place and fasten his spermatophore. Our data suggest that when copepods are exposed to predator cues they behaviorally reduce their spermatophore transfer rate and when they are exposed to an actual predator these effects are due to both behavior and actual consumption or injury. Therefore, we conclude that at nearly every stage in the mating process, the threat of predation alters mating behavior and hinders mating success.

The risk associated with forming copulatory pairs (i.e., heightened conspicuousness and diminished escape ability) is shared equally by males and females. Therefore, it is plausible that males and females would separate when they perceive elevated predation risk. However, a female incurs an additional cost after mating due to the development of a large egg sac that makes her more visually conspicuous to predators and reduces her escape ability (Magnhagen 1991; Maier et al. 2000). Therefore, females may escape from copulatory pairings more often than males, or reject spermatophores to reduce these extended reproductive costs (Maier et al. 2000).

In our study, copepods did not alter their mating duration in the presence of predators or predator cues (Fig. 3). These results are similar to those found by Maier et al. (2000) for the freshwater cyclopoid Cyclop vicinus, which did not alter mating durations in the presence of a Chaoborus predator. Together, these results suggest that individual copepods do not alter their mating durations in response to proximate predator cues. However, over evolutionary time scales, freshwater copepod populations have adapted to lakes with high predator densities by having shorter mating durations (Jersabek et al. 2007), suggesting that natural selection favors individuals that copulate quickly when predation is intense. In these freshwater systems, there is a trade-off between assured paternity through postcopulatory mate guarding and the elevated risk of predation associated with prolonged copulation (Jersabek et al. 2007). In our study, E. herdmani males always released females shortly after spermatophore transfer, suggesting that mate guarding does not occur in E. herdmani and that copulation duration is set by the amount of time it takes for a male to transfer a spermatophore.

Combined (chemical + physical) predator cues interfere with *Eurytemora herdmani* mating success (Figs. 1, 2, 4). In laboratory assays, the presence of N. americana chemical exudates alone reduced copulatory pair formation (Fig. 2A) suggesting that predator kairomones or alarm cues generated by injured conspecifics can alter mating behavior. Predator kairomones and alarm cues are important in eliciting prev behavioral responses in aquatic systems (Brönmark and Hansson 2000). Often, prey show elevated behavioral responses to predator cues if predators are consuming prey conspecifics or closely related prey species, relative to predator exudates generated from starved predators (Schoeppner and Relyea 2005; Smee and Weissburg 2006). It is important to note that the presence of a chemical cue reduced copulatory pair formation, whereas an actual predator did not (Fig. 2A).

We suggest that this may be due to the fact that predator trials were conducted in clean seawater. Therefore, there was no 'scent' of a prior predation event in the water at the beginning of the trial. This may indicate chemical cues from an actual predation event elicit more of a behavioral response than chemical cues from a predator alone. However, in this study, we did not include a starvedpredator treatment or a killed-conspecifics treatment to disentangle these effects. Therefore, we cannot distinguish whether the chemical cue released from the predator, injured conspecifics, or a combination of both is necessary to elicit the changes in copepod mating success.

There is evidence from both marine and freshwater systems that copepods alter their behavior in response to predator exudates by migrating to a depth refuge (Neill 1990), reducing grazing activity (Cieri and Stearns 1999) or reducing swimming speed (Van Duren and Videler 1996). A reduction in swimming activity has important consequences for mating success because it directly affects the probability of encounter between males and females (Gerritsen and Strickler 1977; Kiørboe and Bagøien 2005; Visser and Kiørboe 2006). We did not directly monitor swimming activity in this study. However, a reduction in *E. herdmani* swimming activity in response to *Neomysis americana* exudates would be more important in our larger field containers (1-liter) than in the small vessels used in laboratory studies (20-mL), where encounter rates were inherently high.

To mimic both the hydromechanical and tactile cue of a *Neomysis americana* predator, we exposed *Eurytemora herdmani* couples to an herbivorous brine shrimp. The brine shrimp provided tactile stimulation by swimming up to the copepods and directly touching them (R. S. Lasley-Rasher, unpubl.); their swimming also produced fluid shear, which is known to be the primary hydrodynamic cue responsible for eliciting escape responses in copepods (Yen et al. 1992; Fields and Yen 1997; Fields 2010). The physical cue alone significantly reduced mating success (Figs. 1, 2B) indicating that a physical predator cue can interfere with copepod mating success.

Combined chemical and physical predator cues consistently reduced mating success (Figs. 1, 2, 4) in all field and laboratory experiments, whereas chemical and physical cue treatments produced intermediate responses (in terms of effect sizes). Therefore, E. herdmani may perceive the combined chemical and physical cue treatment as a more risky environment than either cue treatment alone. It is possible that E. herdmani detects predator kairomones, which then heightens its sensitivity to the physical cue of a nearby predator (and vice versa). However, little is known about the ability of copepods to simultaneously process chemical and mechanical information in terms of predatorprey interactions. Nonetheless, prey individuals should be favored by natural selection to alter the magnitude of their behavioral response (i.e., reduce mating frequency) in response to the level of perceived risk so as not to waste valuable mating opportunities (Magnhagen 1991).

Acknowledgments

This work was supported by a National Science Foundation Integrative Graduate Education and Research Traineeship grant (Division of Graduate Education-0114400) and an Addison E. Verrill Award for Marine Biology, Darling Marine Center, University of Maine.

We thank the faculty and staff of the Darling Marine Center who facilitated our work. We thank L. A. Green for guidance in statistical analyses. Finally, we would like to thank D. B. Rasher, D. M. Fields, and two anonymous reviewers for their constructive comments, which greatly improved this manuscript.

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Associate editor: Michael R. Landry

Received: 27 April 2011 Accepted: 09 January 2012 Amended: 23 December 2011