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Primary Research Paper

The behavioural response of mayfly nymphs (*Stenonema* sp.) to chemical cues from crayfish (*Orconectes rusticus*)

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Abstract

This study was conducted to determine whether mayfly nymphs (*Stenonema* sp.) have the ability to detect and respond to potential chemical cues from crayfish (*Orconectes rusticus*) by adopting anti-predator behaviours, and to investigate whether any potential responses would differ under exposure to different light conditions. The average number of mayfly nymphs displaying 'scorpion' posture, and the average duration of this behaviour were significantly greater during exposure to crayfish conditioned water than during exposure to unconditioned water. The results also suggested that there was a decrease in drift behaviour and horizontal movement in conditioned water trials relative to controls, as well as an increase in refuge use. However, with the exception of refuge use, differing light intensities did not have a significant effect on the observed prey reactions, although responses did appear to be slightly stronger during exposure to lower light levels relative to higher light conditions. This research provides new insight into the role of invertebrate predators and chemical cues and their influence on the behaviour of an important benthic prey species.

Introduction

The habitat and amount of time available for any species to engage in foraging, courting, or mating behaviours can be strongly affected by the risk of predation (Peckarsky & Dodson, 1980). As a result, many species in the aquatic environment have developed early warning systems for predator detection, some of which include the ability to detect visual, chemical, hydrodynamic and auditory cues (Abjornsson et al., 1997). It has been fairly well established that some aquatic invertebrates, especially pelagic species, can respond to chemical cues exuded by visually foraging piscivorous predators in the water column (Abjornsson et al., 1997; Dahl et al., 1998; Spaak & Boersma, 2001). Observed anti-predator responses include alterations in drift behaviour (Huhta et al., 2000; Miyasaka & Nakano, 2001), feeding behaviour (McIntosh et al., 2004), morphology (Riessen, 1999), life-history traits (Peckarsky et al., 2002; Caudill & Peckarsky, 2003; Dahl & Peckarsky, 2003), colonization and distribution patterns (Resetarits, 2001), and magnitude of vertical migration (Loose & Dawidowicz, 1994). However, considerably less is known about the ability of aquatic invertebrates to use chemoreception to detect invertebrate predators, especially within benthic ecosystems.

In benthic stream communities a common response to invertebrate predators is the exhibition of 'scorpion posture' displays similar to those exhibited by mayfly nymphs in the genus *Ephemerella* when in the presence of stonefly predators (Peckarsky, 1987). During 'scorpion posture' displays, *Ephemerella* nymphs raise their cerci from a horizontal position, up over backs in a 180° arc, and then bring them back down to their original position (Peckarsky, 1980). These displays have also been observed in Trinidad mantids, various types of marine invertebrates, and in freshwater crayfish (reviewed in Peckarsky, 1980). However, very little conclusive information is available on the adaptive significance of scorpion displays, or the mechanisms behind them.

Previous studies have demonstrated differential responses in some mayfly nymphs to morphologically similar but functionally different stonefly species, suggesting that responses may be partially initiated by chemotactile as well as hydrodynamic, visual, and tactile signals (Peckarsky, 1980; Peckarsky & Dodson, 1980; Peckarsky & Penton, 1989). There is also some behavioural evidence which suggests that in a natural environment some species of mayfly nymphs may avoid colonization of available habitat patches in response to chemical cues exuded by certain stonefly predators (Peckarsky & Dodson, 1980). However, while these studies suggest that some mayfly species can use chemoreception to detect certain stonefly predators, the results are often species specific with respect to both predator and prey species, making predictions about mayfly responses to other invertebrate or vertebrate predators hard to determine. Mayfly nymphs have been shown to increase their use of refuges in response to the presence of chemical cues from European minnows (Tikkanen et al., 1996). However, little is known about whether mayfly nymphs can use chemoreception alone to detect the presence of other benthic macroinvertebrate predators, whether they exhibit similar reactions to those displayed in response to stonefly predators, or whether the reactions of these primarily nocturnal nymphs are affected by different light intensities.

Crayfish (*Orconectes rusticus*) are a common invertebrate predator in the freshwater lakes and streams of North America. They are most active at night, which is when they emerge from their refuges to forage along the bottom for macrophytes, decomposing organic material, and macroinvertebrates (Crocker & Barr, 1968). Crayfish are opportunistic omnivores who have been reported to feed on mayfly nymphs (Hollows et al., 2002). In addition, preliminary research indicated that *O. rusticus* will readily consume *Stenonema* nymphs.

The objectives of this study were to experimentally test whether mayfly nymphs (*Stenonema* sp.) have the ability to detect and respond to potential chemical cues from crayfish (*Orconectes rusticus*) by adopting anti-predator behaviours, and to investigate whether any potential responses would differ under exposure to different light conditions. It was predicted that if mayfly nymphs could detect the presence of chemical cues from crayfish they would exhibit some or all of the following behaviours as part of their anti-predator strategy: either the ‘scorpion’ posture observed in previous studies (Peckarsky, 1987; Peckarsky & Penton, 1989), directional movement away from the source of the chemical cues (horizontal and/or vertical), and an increase in refuge use. In addition, it was predicted that since the organisms involved in the tests were primarily nocturnal (Bouwma & Hazlett, 2001), predation pressure would be stronger at night and that any potential responses would therefore be stronger or different under exposure to a low light intensity relative to a high light intensity.

Methods

Specimen collection

Mayfly nymphs (*Stenonema* sp.) were collected from Thompson’s Creek (78° 18′ W; 44° 20′ 40″ N), a small first-order southern Ontario stream. Nymphs were maintained at 17 °C under natural light in an aquarium filled with unfiltered water from the Otonabee River which feeds the stream, and several large, flat stones collected from the stream. Crayfish (*Orconectes rusticus*) were obtained from the Otonabee River and maintained at room temperature in a flow-through tank. Previous research has shown that prey will respond differently to predators who are satiated relative to those who are hungry (Abjornsson et al., 1997), so crayfish were starved for 24 h prior to the start of each trial in order to standardize hunger levels.

Experimental apparatus

Mayfly nymphs were exposed to crayfish conditioned water and to unconditioned water under two light intensities (less than 0.01 μE m^{-2} s^{-1} and

14.7 μE m^{-2} s^{-1}). Conditions for the lower light intensity treatment were achieved by means of indirect white light provided by a small handheld flashlight in a windowless room. This set-up provided the minimum light required for observations to be made with the naked eye. Both of these intensities are low compared to full sunlight, which falls in the range of approximately 2000 μE m^{-2} s^{-1} (Horne & Goldman, 1994). Trials were conducted in a flow-through chamber consisting of a 1.5 l treatment reservoir, a 1.2 l holding reservoir, and a 1.5 l departure reservoir joined by Plexiglass tubing (3 cm inside diameter, 5 cm length). During experimental trials in which scorpion posture display behaviour, drift behaviour, and directional movement were observed, river water from a 5 l carboy was pumped from the treatment reservoir, through the holding reservoir, to the departure reservoir at a rate of 20 ml min^{-1} using a peristaltic pump. During all trials ten mayfly nymphs, measuring 8–12 mm in length were gently poured into the holding reservoir, while the treatment reservoir was left empty. To expose the mayfly nymphs to conditioned water, two adult crayfish measuring 9–12 cm in length were placed in the treatment reservoir fifteen minutes before commencement of the trial. The bottom of the treatment reservoir was located 3 cm below the opening of the connective tubing, placing the crayfish out of sight and out of the water current entering the holding reservoir. Observation of mayfly nymph behaviour commenced immediately after the nymphs were placed into the holding reservoir. The exit from the treatment reservoir was covered with a 500 μm mesh screen to ensure that the crayfish did not enter the tube connecting the treatment reservoir to the holding reservoir and consume the prey. During control trials no crayfish were added to the treatment reservoir. The bottoms of the holding reservoir and the departure reservoir were covered with coarse nylon mesh to create a substrate on which the mayfly nymphs could obtain a foothold.

During experimental trials in which short-term refuge use was observed, one small, flat stone from Thompson's Creek was placed in the treatment reservoir along with five mayfly nymphs. All refuge stones were thoroughly scrubbed in order to ensure that refuge use was not unduly influenced by differences in the shelters provided. River water was pumped through the treatment reservoir at a rate of 20 ml min^{-1} from a 5 l bucket, starting 15 min prior to the commencement of each trial. During conditioned water trials two crayfish were placed in the 5 l bucket for the duration of the trial.

Control and conditioned water treatments were carried out alternately in the chamber. In addition, control and conditioned water replicate trials were alternately conducted during the morning and afternoon to ensure that possible diurnal movement patterns associated with the mayfly nymphs did not bias the results. The experimental apparatus was washed out after each use with hot water and allowed to dry as per Borowsky (1984). New sets of both predator and prey individuals were selected for each trial to ensure that results were independent.

Data collection and analysis

Behavioural reactions were measured in terms of the number of individuals exhibiting 'scorpion' posture displays, the duration of these displays, and the number of individuals exhibiting drift behaviour. The duration of the scorpion posture displays was defined as the interval between the time when the first mayfly in the group began displaying and the time when the last mayfly nymph in the group stopped exhibiting the response. Individual nymphs tended to display fairly constantly during the response interval, and the duration of the behaviour tended to be fairly well synchronized between individuals within a group. However, if display behaviour of individual nymphs was not continuous during the interval, the recorded duration included short gaps in the behaviour. Drift behaviour was defined as any swimming or floating movement that occurred in the water column.

The number of mayfly nymphs exhibiting each of the three behaviours was observed simultaneously during 15 min trials. Seven replicates of each experimental treatment were conducted. The data were tested for normality using the Kolmogorov–Smironov test and the square root transformation was used to convert data that did not conform to a normal distribution. Comparisons were made between lighting conditions and between treatments using two-factor analysis of variance.

Directional movement was measured in terms of the number of mayfly nymphs that moved downstream out of the holding reservoir into which they were initially placed. The number of mayfly nymphs that remained in the reservoir where they were initially placed was counted once every 30 min over a period of 3 h. Five replicates of each treatment were conducted under each light condition. Data were tested for normality using the Kolmogorov–Smironov test, and comparisons between treatments and between lighting conditions were made using either the two-way repeated measures ANOVA, or the Kruskal–Wallis ANOVA and median tests as non-parametric equivalents (Table 1) .

Refuge use was determined by placing five mayfly nymphs and one small, flat, rock collected from Thompson's Creek into the treatment reservoir. The number of mayfly nymphs remaining on top of the rock was counted after a 3 h period of exposure to either unconditioned or conditioned river water. Five replicates of each treatment were made under reduced lighting conditions. Data were tested for normality using the Kolmogorov–Smironov test, and between treatment differences were compared using the Student's *t*-test or the non-parametric equivalent.

Results

Scorpion posture displays

The mayfly nymphs responded to the crayfish conditioned water by displaying 'scorpion' posture behaviour, which involved using their legs to slightly raise themselves up off the substrate, and arching their cerci and the ends of their abdomens up over their backs. Some individuals performed the behaviour only once, while others repeated it, waving their tails up and down in a fanning motion for several minutes. Both prior to and during experimental trials all mayfly nymphs, whether displaying or not, appeared to be randomly oriented with respect to the direction of the water current.

Table 1. Test statistics obtained for Kruskal–Wallis ANOVA and median tests for movement trials

Time (min)	Light: control vs. conditioned water		Dark: control vs. conditioned water	
	χ^2	*p*-value	χ^2	*p*-value
30	3.60	0.06	0	1.00
60	1.11	0.29	0	1.00
90	3.60	0.06	0.40	0.53
120	1.11	0.29	0.40	0.53
150	1.11	0.29	0.48	0.49
180	1.11	0.29	0.48	0.49

The number of individuals engaged in scorpion posture behaviour was significantly greater during trials in which the mayfly nymphs were exposed to crayfish conditioned water than during control trials ($F_{1,22} = 80.48$, $p < 0.001$) (Fig. 1). Light condition did not have a significant effect on the number of mayfly nymphs engaged in scorpion posture behaviour ($F_{1,22} = 2.29$, $p = 0.14$). The interaction term was non-significant as well, indicating that light condition and treatment acted independently on scorpion posture behaviour ($F_{1,22} = 0.66$, $p = 0.42$).

The duration of the scorpion posture response was significantly longer during exposure to crayfish conditioned water than to controls ($F_{1,22} = 35.77$, $p < 0.0005$) (Fig. 2). Light condition did not have a significant effect on the duration of the scorpion posture displays ($F_{1,22} = 2.74$, $p = 0.11$), and the interaction term was non-significant as well ($F_{1,22} = 0.001$, $p = 0.97$).

Swimming and drift behaviour

The number of mayfly nymphs observed actively swimming or drifting upward in the water column was significantly greater during control trials than during crayfish conditioned water trials ($F_{1,22} = 9.01$, $p = 0.007$) (Fig. 3). The number of mayfly nymphs moving vertically through the water column was also significantly greater during trials conducted under low light than under high light conditions ($F_{1,22} = 8.45$, $p = 0.008$). The interaction term between light condition and treatment was not significant ($F_{1,22} = 0.67$, $p = 0.42$).

Directional movement

Underlying trends in the data suggest that, on average, more individuals remained in the reser-

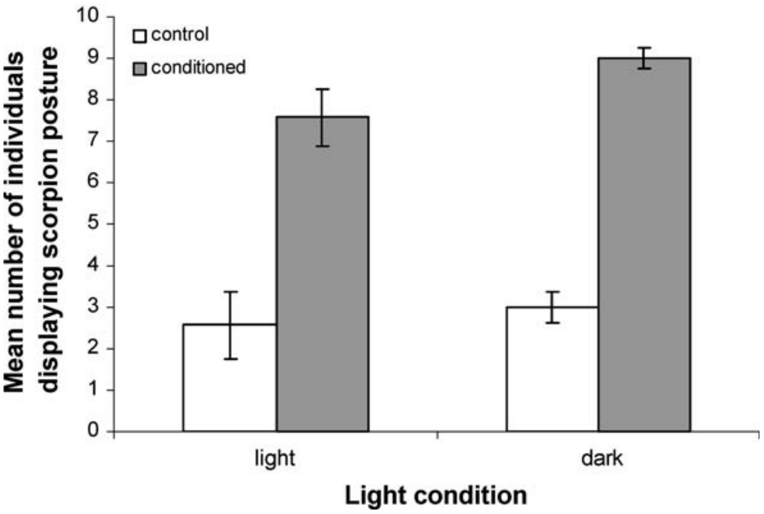

Figure 1. Mean number of mayfly nymphs exhibiting scorpion posture response (±SE) in conditioned and control water under low and high light.

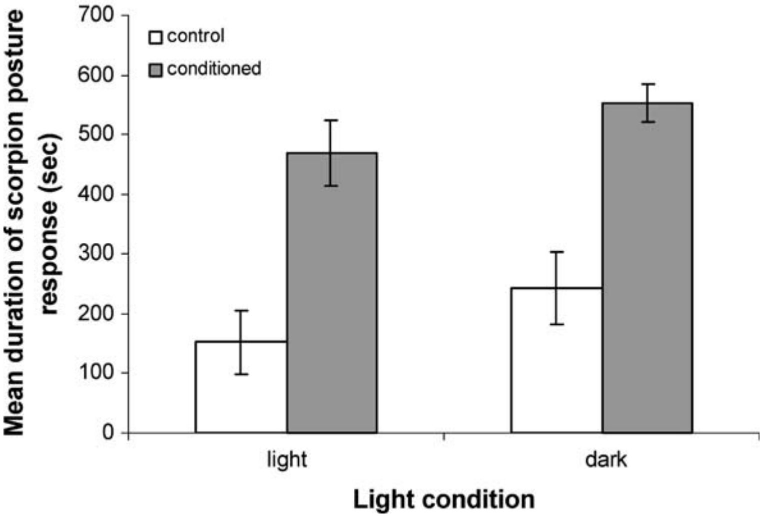

Figure 2. Mean duration of scorpion posture response (±SE) (defined as interval between when first individual commences behaviour and last individual stops behaviour) in conditioned and control water under low and high light.

voir where they were initially placed during exposure to conditioned water than during control trials under both high and low light (Fig. 4 and 5). However, although this relationship remained consistent over the duration of each trial, treatment did not have a significant effect on horizontal movement ($F_{6,24} = 1.40$, $p = 0.25$). Light condition did not have a significant effect on the number of individuals remaining in the reservoir where they were initially placed either ($F_{6,24} = 3.94$, $p = 0.06$). The interaction term was non-significant as well ($F_{6,24} = 0.71$, $p = 0.41$).

Short-term refuge use

There was no significant difference between the average number of mayfly nymphs observed on the top of each flat stream rock during control trials or

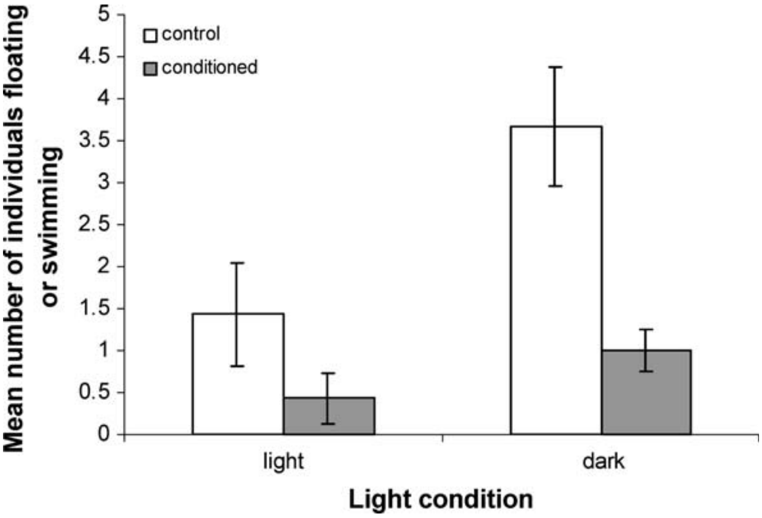

Figure 3. Mean number of mayflies (± SE) observed either swimming or drifting in conditioned and control water under low and high light.

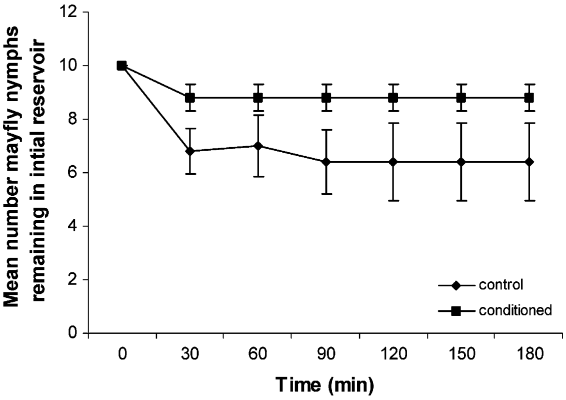

Figure 4. Mean number of mayfly nymphs (± SE) remaining in the reservoir where they were initially placed over time during trials conducted under high light conditions.

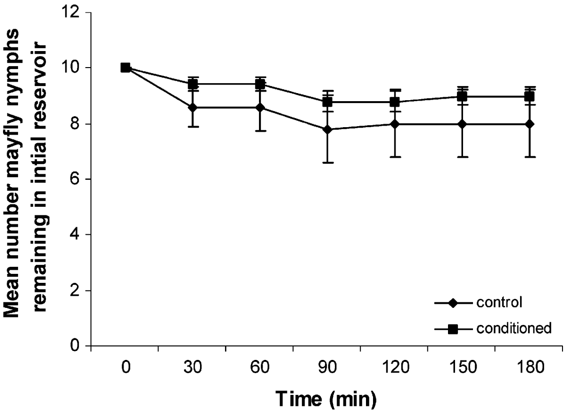

Figure 5. Mean number of mayfly nymphs (± SE) remaining in the reservoir where they were initially placed over time during trials conducted under low light conditions.

conditioned water trials ($t_{(1)19} = 2.83$, $p = 0.07$, Fig. 6).

Discussion

The results of this study support the hypothesis that mayfly nymphs can detect chemical cues associated with the presence of crayfish. The observed increase in scorpion posture behaviour, combined with the observed reduction in activity levels strongly suggests that mayfly nymphs have the ability to detect and respond to chemical cues by altering their behaviours and activity levels in ways that could be interpreted as predator avoidance strategies. However, with the exception of refuge use, differing light intensities did not have a significant effect on the observed prey reactions, although responses did appear to be slightly stronger during exposure to lower light levels.

Exhibition of the ‘scorpion’ posture was the most obvious response of the mayfly nymphs to the presence of chemical cues from the crayfish predators. This response has also been observed in the presence of other invertebrate predators (reviewed in Peckarsky, 1980), suggesting that it

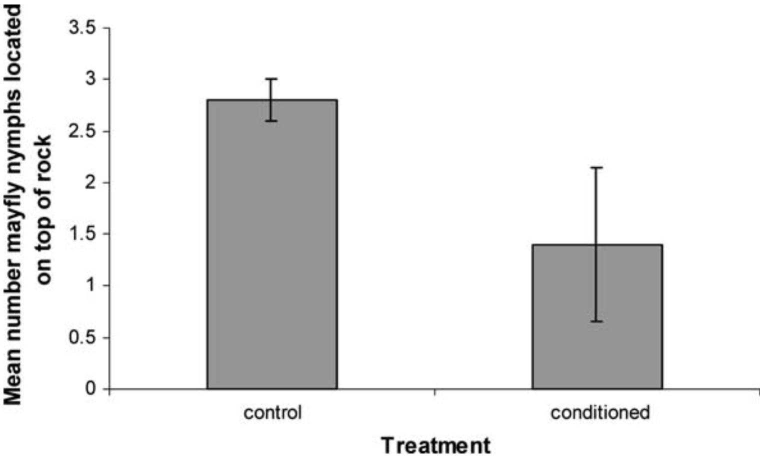

Figure 6. Mean number of mayfly nymphs (±SE) on top of the rock after a 3 h time period under low light conditions.

may be a generalized response. *Orconectes rusticus* is not native to the study area, and is thought to have been unintentionally introduced to the region during the last fifty years (Berrill, 1978). However, two other species of *Orconectes, O. propinquus* and *O. virilis* are native to this area, and have been observed in similar habitats along with *Orconectes rusticus*. This suggests that mayfly prey in this region would likely have co-evolved in the presence of a similar predator to *O. rusticus*. It could then be expected that any responses exhibited by *Stenonema* sp. to cues from crayfish predators would represent adaptive anti-predator strategies. However, very little conclusive information is available on the adaptive significance of these displays or the mechanisms behind them.

A statistically significant decrease in the number of mayfly nymphs actively swimming during conditioned water trials suggests that *Stenonema* nymphs can detect and respond to the presence of crayfish chemical cues. Since these nymphs are awkward and conspicuous swimmers (Edmunds et al., 1976), decreasing the level of highly visible behaviours is likely an adaptive anti-predator response. This explanation is consistent with the hypothesis suggested by Scrimgeour & Culp (1994), who found that in the presence of predatory stonefly nymphs and longnose dace, *Beatis* nymphs, who are good swimmers that can move rapidly through the water, will significantly increase their swimming and drifting behaviour. While it may be advantageous for *Beatis* nymphs to adopt a flight strategy in the presence of a predator, it is likely more beneficial for the mayfly nymphs used in this study to avoid detection and/or attempt to appear indigestible. The observed increase in scorpion posturing, combined with the decrease in swimming and drifting behaviour lend support to the hypothesis that mayfly nymphs can detect and respond to chemical cues from invertebrate predators by adopting behaviours and activities that could be interpreted as predator avoidance strategies.

Previous studies involving predator-prey relationships have not provided conclusive evidence that mayfly nymphs can detect chemical cues from invertebrate predators or initiate anti-predator strategies in response to chemical cues alone. Peckarsky (1980) observed the ‘scorpion’ posture exhibited by *Stenonema* nymphs in this study in several species of *Ephemerella* in the presence of stonefly nymphs. Increases in the frequency of this behaviour were usually observed following direct contact with stonefly predators, and not in the presence of chemical cues alone, suggesting that tactile rather than chemical cues were the initiator of the response (Peckarsky, 1987). Mayflies avoid colonization of cages containing a predatory stonefly species, but readily inhabit cages containing a morphologically similar but detritivorous stonefly species, suggesting that these nymphs may be able to use chemical cues to distinguish between different types of predators (Peckarsky & Dodson, 1980). However, the observed avoidance of predatory stonefly nymphs only occurred in two of four species tests, suggesting that other factors may have come into play. The results of our research provide support for the speculation in these studies that mayfly nymphs can detect and respond to chemicals associated with some invertebrate predators.

The experimental design used in this study eliminates the possibility of visual or hydrodynamic cues being transported between the predator and the prey organisms. However, it is possible that previously undetected mechanisms, such auditory or bacterial cues, could play a role in these experiments. While we consider this unlikely, future experiments could be conducted in which prey were exposed only to water which had contained the predator. These tests could be supplemented by trials in which mayfly prey were stimulated with additional cues, such as sight or touch, to further describe the roles of different detection modalities.

The lack of a significant difference in horizontal movement between conditioned water and control treatments could be a result of the mayfly nymphs' ability to use chemoreception to assess the risk associated with a specific predator. If this were the case, the presence of chemical cues alone might not signal an immediate threat, and therefore would not elicit a strong directional response. Previous research has indicated that when *Beatis* nymphs were exposed to non-contact encounters with stonefly nymphs they showed a decrease in crawling, swimming, and drifting movement, but when they were exposed to contact encounters with the same predator they showed a significant increase in movement (Peckarsky & Penton, 1989). These findings appear to be consistent with the results of the present study, and could indicate that *Stenonema* sp. can use chemoreception to detect and assess the level of risk associated with invertebrate predators. In the absence of immediate threats they will reduce movements that may be attractive to predators, or attempt to create the illusion of ingestibility instead.

Alternatively, the lack of a significant response during the horizontal movement trials could be the result of the potential chemical cues being more dilute than in other trials. Response of aquatic invertebrates to predators has been shown to depend on the concentration of the chemical cue in the water (Loose & Dawidowicz, 1994). It is also possible that the lack of a significant response was the result of small sample sizes, low statistical power, or other factors associated with the experimental set-up or design. Further research could be done to explore the effects of different flow-through rates, chemical cue concentrations, or test apparatuses.

The lack of a significant increase in refuge use in the presence of chemical cues from crayfish is consistent with the results of Tikkanen et al. (1996) which indicated that chemical cues from a predatory minnow alone were not sufficient to increase short-term refuge use in *Baetis*. However, short-term refuge use was increased in the presence of live minnows, and in the presence of a combination of a fish model and fish kairomones, suggesting that tactile, hydrodynamic, or visual cues are required in order to initiate a response (Tikkanen et al., 1996). Once again, these observations are consistent with the hypothesis that mayfly nymphs can use chemoreception, not only to distinguish between different predators, but also to assess the level of imminent danger associated with them.

Exposure to high light versus low light conditions did not appear to have a significant effect on the mayfly nymphs' response to the presence of conditioned water. However, in the absence of chemical cues mayfly nymphs appear to be more active under reduced light conditions than under brighter light conditions. During control trials significantly more mayfly nymphs were observed swimming in the low light conditions than in the higher light, no mayfly nymphs were observed outside their refuges under high light conditions, and horizontal movement appeared to taper off much earlier in trials conducted in the light than in those conducted under reduced lighting conditions (Fig. 4 and 5). Both light intensities used in this study would be considered low, as they fall below the light compensation point for aquatic plants (15–85 μmol m^{-2} s^{-1}) (Horne & Goldman, 1994). Further research using a wider range of lighting conditions that correspond more closely to those observed in nature is needed to determine whether mayfly nymph responses are affected by differing light intensities.

Conclusion

In conclusion, the results of this study suggest that mayfly nymphs can detect chemical cues associated with crayfish predators and alter their behaviour and activity levels in response to these signals. However, with the exception of refuge use, observed responses do not differ between higher and lower light intensities. As predator-prey relationships govern the abundance, distribution, and behaviour of many prey species, information regarding the mechanisms driving these interactions is important for understanding food web dynamics. This research contributes to our understanding of prey responses to invertebrate predators in benthic stream communities and some of the mechanisms involved in these interactions.

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