

CONTRASTING BEHAVIORAL RESPONSES BY
DETRITIVOROUS AND PREDATORY MAYFLIES
TO CHEMICALS RELEASED BY INJURED
CONSPECIFICS AND THEIR PREDATORS

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Abstract—Larvae of the mayfly *Siphonisca* are predators of the detritivorous mayfly *Siphonurus* in floodplain wetlands in Maine (USA). Both mayflies are natural prey of brook trout (*Salvelinus fontinalis*). We exposed larvae of *Siphonurus* and *Siphonisca* to chemicals from injured conspecifics and their predators. Significant decreases in movement activity by *Siphonurus* were elicited by chemicals released from *Siphonisca*, chemicals released from brook trout fed conspecifics, and by chemicals released from injured conspecifics. A significant decrease in movement activity by *Siphonisca* was elicited by chemicals released from brook trout fed either conspecifics or *Siphonurus*. Movement activity by either *Siphonurus* or *Siphonisca* was not significantly affected by chemicals released from trout feeding on brine shrimp (*Artemia*). Both *Siphonurus* and *Siphonisca* were able to detect chemicals that provided information about past feeding behaviour by brook trout. However, their response to the chemicals used in this study was context-specific. A reduction in movement activity, a behavior that presumably reduces the probability of being consumed by visual predators, occurred only when mayflies were exposed to chemicals released by brook trout feeding on conspecific (*Siphonurus*) or confamilial (*Siphonisca*) prey.

Key Words—*Siphonisca*, *Siphonurus*, Ephemeroptera, predator avoidance behavior, semiochemicals, alarm pheromones, kairomones, *Salvelinus fontinalis*, wetlands, temporary habitats.

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INTRODUCTION

Modifications of the behavior of freshwater animals in response to chemicals released by their predators or from injured conspecifics have been documented for many taxa, including amphibians, fishes, gastropods, and pelagic and benthic crustaceans and insects (Peckarsky, 1980; Williams and Moore, 1985; Holomuzki and Short, 1988; Dawidowicz et al., 1990; Crowl and Covich, 1990; Covich et al., 1994; Scrimgeour et al., 1994a; Ball and Baker, 1996; Wudkevich et al., 1997; Chivers and Smith, 1998; Kats and Dill, 1998; Van Buskirk and Yurewicz, 1998). When exposed to chemicals released by their predators or from injured conspecifics, benthic insects may show reduced movement activity, sheltering behavior (Peckarsky et al., 1993; Scrimgeour et al., 1994a,b), or increased nocturnal activity relative to daytime activity (McIntosh and Townsend, 1995; McIntosh and Peckarsky, 1996). The chemicals involved have not been identified, but appear to be relatively specific. In some cases prey may react only to predators actively feeding on conspecifics (see review by Chivers and Smith, 1998). In other cases, avoidance behavior is elicited only by suites of cues such as predator odor combined with chemicals released from injured conspecifics (Scrimgeour et al., 1994a). The potential for reaction only to predators that are actively feeding on nearby conspecifics indicates that costs of such avoidance behavior may be reduced by using a relatively fine-tuned mechanism of risk assessment (cf. Ode and Wissinger, 1993).

What are the costs of avoidance behavior? Avoidance behavior usually results in a reduction in time spent feeding, with consequences for rates of growth and development (Feltmate and Williams, 1991; Peckarsky et al., 1993; Ball and Baker, 1996; McPeck and Peckarsky, 1998). Behavior that results in reduced rates of growth may be particularly important for semelparous insects such as mayflies. Mayflies do not feed as adults, and all somatic tissues allocated for reproduction are determined by the size of the larva upon metamorphosis (McPeck and Peckarsky, 1998). Since fecundity of female mayflies is closely correlated with their size, behavior that results in reduction of growth rate and smaller ultimate size upon emergence may have significant consequences for population demographics and viability (McPeck and Peckarsky, 1998). Nonlethal effects of predator avoidance behavior also will have consequences at the ecosystem level because any reduction in growth or feeding activity will ultimately affect levels of secondary production by prey populations. This in turn will influence production dynamics of adjacent trophic levels (McIntosh and Townsend, 1995, 1996; Peckarsky and McIntosh, 1998).

Because of the potential for interactive effects of multiple predators that operate at multiple trophic levels, consequences of predator avoidance behavior in most food webs will be difficult both to predict and detect (Peckarsky et al., 1997). This scenario becomes even more complex in view of the appar-

ent specificity of predator avoidance behavior with respect to the diet of the predator (e.g., Crowl and Covich, 1990; Mathis and Smith, 1993; Wilson and Lefcort, 1993; Chivers et al., 1996; Mathis and Hoback, 1997; Wisenden et al., 1997). The objective of this study is to use laboratory experiments to examine the behavioral responses of several members of the macroinvertebrate community of a sedge-meadow wetland in eastern Maine (USA) to chemical cues released by their predators. This macroinvertebrate community is unusual in that it is dominated by mayflies of the families Leptophlebiidae (*Leptophlebia*) and Siphonuridae (*Siphonurus*, *Siphonisca*), and because one of these, *Siphonisca aerodromia* is a predator of the other mayflies (Gibbs and Mingo, 1986; Gibbs and Siebenmann, 1996; Hury and Gibbs, 1998). Larvae of *Siphonurus* spp. are largely detritivorous. Larvae of *Siphonisca* feed primarily on *Siphonurus* (Gibbs and Mingo, 1986). The brook trout (*Salvelinus fontinalis*), a predator of both *Siphonurus* and *Siphonisca*, enters the wetland from adjacent streams to feed during spring floods.

We report the results of laboratory experiments that test four specific predictions: (1) larvae of *Siphonurus* show predator avoidance behavior (reduced movement activity) in the presence of chemicals released by *Siphonisca*; (2) larvae of *Siphonurus* and *Siphonisca* show predator avoidance behavior in the presence of chemicals released by brook trout actively feeding on conspecifics, (3) larvae of *Siphonurus* and *Siphonisca* do not show predator avoidance behavior when in the presence of chemicals produced by brook trout that are not actively feeding on conspecifics, and (4) larvae of *Siphonurus* and *Siphonisca* show predator avoidance behavior in the presence of chemicals released by injured conspecifics.

METHODS AND MATERIALS

Study Site and Source of Experimental Animals. The source of mayfly larvae used in this study was a seasonally inundated floodplain north of the confluence of Tomah Stream and Beaver Creek (Washington County, Maine, 45°26'42"N, and 67°34'50"W). Tomah Stream, is a fourth-order tributary of the St. Croix River. During much of the year (June-March), Tomah Stream is confined to its channel. During March-April, melting snowpack causes the river to inundate the floodplain. The inundated area gradually decreases from April to May and the floodplain is generally dry by June. Tussock sedge (*Carex* spp.) is the dominant plant species on the floodplain. Following inundation until the floodplain dries in June, mayflies are abundant within the dense meshwork of sedge detritus that characterizes the habitat. Species of mayflies documented from the Tomah Stream floodplain include the siphonurids *Siphonisca aerodromia* and *Siphonurus mirus*, *S. alternatus*, and *S. quebecensis*, and the

leptophlebiids *Leptophlebia cupida*, *L. nebulosa*, and *L. johnsoni* (Burian and Gibbs, 1991). Together these mayflies contribute 73–94% of the total micro-invertebrate biomass on the floodplain (Huryn and Gibbs, 1998). The life history of *Siphonisca* has been intensively studied (Gibbs and Mingo, 1986; Gibbs and Siebenmann, 1996), and provides a general example of the life cycle of river–floodplain fauna (Huryn and Gibbs, 1998). Larvae first appear beneath the ice of the stream channel during November and remain in the stream until snowmelt during March or April. At this time larvae migrate onto the inundated floodplain. Most larval growth and development occurs here, and adults emerge in late May and early June. After mating flights, females return to the stream and oviposit. Eggs hatch in the stream the following November. The life cycles of the dominant species of *Siphonurus* from the Tomah floodplain follow a similar pattern (Huryn and Gibbs, 1998).

Siphonisca is the major macroinvertebrate predator on the floodplain during inundation, where it contributes 80% to total biomass of predacious invertebrates (Huryn and Gibbs, 1998). The most common prey are larvae of *Siphonurus*, but *Leptophlebia*, *Eurylophella* (Ephemeroptera: Ephemerellidae), and midge larvae are also consumed (Gibbs and Mingo, 1986). *Siphonurus* is primarily detritivorous and herbivorous, but may consume animal material in later instars. The relative importance of animal prey compared to biofilm and organic particles is unknown (Edmunds et al., 1976). Vertebrates that prey on aquatic macroinvertebrates are conspicuous during floodplain inundation at Tomah Stream. The common shiner (*Notropis cornutus*), three-spine stickleback (*Gasterosteus aculeatus*), chain pickerel (*Esox niger*), common white sucker (*Catostomus commersoni*), and brook trout all have been reported from the floodplain during inundation. While on the floodplain, these fish feed heavily on macroinvertebrates, particularly mayflies (Gibbs and Mingo, 1986). Their quantitative and qualitative effects on the floodplain macroinvertebrate fauna, however, are unknown.

Experimental Animals. Larvae of *Siphonurus* and *Siphonisca* and conditioned sedge detritus were collected by dip net on April 29 and May 14, 1998. Larvae were placed in plastic bags containing water and stored on ice during transport. In the laboratory, larvae and sedge detritus were placed in 37-liter glass aquaria containing 25-liters of aerated well water (water temperature: 17°C, light–dark cycle 14:10 hr). Three aquaria each were used to house *Siphonurus* and *Siphonisca*. *Siphonurus* were fed ad libitum on the biofilm associated with sedge detritus. *Siphonisca* fed upon *Siphonurus* larvae that were continually provided as a source of prey. Except for several individuals that died while molting and instances of cannibalism by *Siphonisca*, mortality did not appear to be significant. Larval growth during the experiments was readily apparent as an increase in size by both taxa. Brook trout were collected from a stream in central Maine. One brook trout was placed in each of three separate 37-liter glass aquaria containing 25-liters of well water and was fed either *Siphonurus*,

Siphonisca, or brine shrimp (*Artemia*) for the duration of the experiments (April 29–May 18, 1998). For logistical reasons and because of the low variability in semiochemicals produced by members of a given fish population (Mathis et al., 1993; Brown et al., 1995), single fish were used for each predator–prey combination. The trout were selected so that they were as close to the same size as practicable. The total lengths of all fish used in the experiments ranged from 126 to 133 mm.

Preparation of Stimuli. Eight stimuli were produced: (1) brook trout fed *Siphonurus*, (2) brook trout fed *Siphonisca*, (3) brook trout fed brine shrimp, (4) *Siphonisca* fed *Siphonurus*, (5) *Siphonisca* fed *Siphonurus* + injured *Siphonurus* chemicals, (6) injured *Siphonurus*, (7) injured *Siphonisca*, and (8) unadulterated well water (base stimulus or control).

Trout-based stimuli were prepared by the following protocol. Trout were allowed to feed ad libitum on appropriate diets (e.g., *Siphonurus*, *Siphonisca*, brine shrimp) from April 29–May 18, 1998, except for 24-hr periods prior to experiments. At the beginning of this 24-hr period, tanks were cleaned and drained and the water was replaced with aerated well water. No additional prey were introduced during this period. At the end of this 24-hr period, water containing chemicals released by the fish was removed from the tanks and immediately used as a stimulus. The *Siphonisca* stimulus was prepared by placing four individuals, without prey, in a 300-ml glass bowl containing ~200 ml of well water for a 24-hr period prior to experiments. A stimulus combining *Siphonisca* chemicals with injured *Siphonurus* chemicals was also prepared by placing 16 *Siphonurus* and 4 *Siphonisca* in a 300-ml glass bowl containing ~200 ml of well water for 24 hr before experiments. On each occasion all *Siphonurus* were consumed prior to the experiment. Stimuli from injured mayflies were prepared by grinding either two *Siphonurus* or one *Siphonisca* larvae in 10 ml of well water using a mortar and pestle. The resulting solutions were filtered through a fine mesh net. All stimuli were used immediately following preparation.

Behavioral Assays. Experiments were performed on May 11, 12, and 18, 1998, during daylight hours using 300-ml circular (10.5-cm-ID) glass dishes containing ~200 ml of aerated well water maintained at room temperature. For experiments using *Siphonurus*, five larvae were arbitrarily selected and placed in the dishes (10 dishes were used at a time) and were allowed to acclimate for 5 min. After the acclimation period, each dish was observed at 15-sec intervals and the instantaneous number of individuals swimming was recorded. After 5 min, 5 ml of stimulus was added to the center of each dish using a polyethylene syringe, and the observation procedure was repeated for another 5 min. This resulted in 20 prestimulus and 20 poststimulus observations. Stimuli were randomly assigned to the 10 dishes used in each trial. This procedure was repeated until 20 replicates were obtained for each treatment. Individual larvae were used only once. The mean \pm SD total length (excluding cerci) of a sample of 40 test animals was

8.2 ± 1.3 mm. The treatments consisted of: (1) brook trout fed *Siphonurus*, (2) brook trout fed *Siphlonisca*, (3) brook trout fed brine shrimp, (4) *Siphlonisca* fed *Siphonurus*, (5) *Siphlonisca* fed *Siphonurus* + injured *Siphonurus* chemicals, (6) injured *Siphonurus*, and (7) well water (control).

A similar protocol was followed by *Siphlonisca*, except that only one larva was placed in the observation dishes. The treatments consisted of: (1) brook trout fed *Siphonurus*, (2) brook trout fed *Siphlonisca*, (3) brook trout fed brine shrimp, (4) injured *Siphonurus*, (5) injured *Siphlonisca*, and (6) well water (control). Along with these treatments, a seventh treatment consisting of a mixture of brook trout fed brine shrimp (5 ml) and injured *Siphlonisca* (5 ml), was used as a stimulus. Twenty replicates were obtained for each treatment, except the latter where only 18 replicates were obtained because of limited numbers of *Siphlonisca* larvae. The number of replicates was limited to ≤20 because of constraints in the number of *Siphlonisca* we had legal permission to collect. *Siphlonisca* is protected by the state of Maine (McCullough, 1997). The mean ± SD total length (excluding cerci) of a sample of 11 test animals was 17.1 ± 1.8 mm.

Analysis. For each replicate, the difference of the total number of individuals moving during 20 scans (*Siphonurus*), or the number of scans recording movement (*Siphlonisca*), between the pre- and poststimulus periods was calculated. Positive values indicated increased movement activity following addition of a stimulus; negative values indicated decreased activity. Means of each treatment were compared with the control using a one-tail *t* test. The family-wise error rate was assessed and controlled using the modified Bonferroni test following Keppel (1982). Assuming that comparisons are orthogonal and are based on specific a priori predictions, the modified Bonferroni test specifies that corrections to the family-wise error rate be introduced only when the number of comparisons exceeds $k - 1$, where k is the number of treatments (Keppel, 1982). In this study there were a total of seven treatments (six experimental treatments and one control) for each set of experiments (e.g., *Siphlonisca* is the first set, *Siphonurus* the second set). Since the analysis was restricted to six preplanned orthogonal comparisons that were based on specific a priori predictions for each set of experiments, the rejection probability (P) was set at 0.05 for each comparison (Keppel, 1982).

RESULTS

There was a significant reduction of movement activity by *Siphonurus* when exposed to chemicals released by *Siphlonisca* ($t = -2.5893$, $df = 38$, $P = 0.007$, one-tail *t* test; Figure 1). Both *Siphonurus* ($t = -3.1051$, $df = 38$, $P = 0.002$, one-tail *t* test; Figure 1) and *Siphlonisca* ($t = -2.5152$, $df = 38$, $P = 0.008$, one-tail *t* test; Figure 2) showed significant decreases in movement behav-

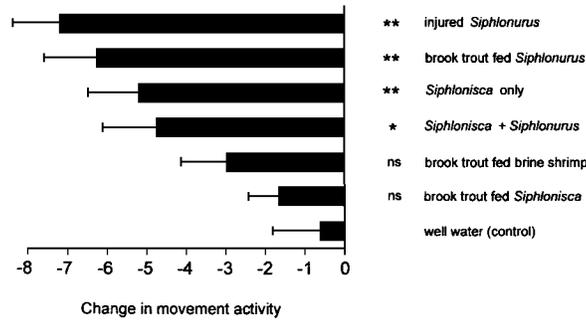


FIG. 1. Graph showing response of *Siphonurus* larvae to chemical cues from injured conspecifics and predators: the mayfly *Siphonisca* and brook trout fed various diets. The x axis indicates change in the average number of observations of the number of individuals swimming out of groups of five before and after being exposed to a chemical stimulus (see text for details). Stimuli are listed on the Y axis. ns = mean not significantly different from control, * $P < 0.05$, ** $P < 0.01$. Error bars are standard errors ($N = 20$).

ior when exposed to stimuli containing chemicals released by brook trout feeding on conspecifics when compared to the control.

When exposed to chemicals released by trout feeding on prey other than conspecifics, however, differences in movement activity of larvae of *Siphonurus* were not significantly different from controls. For example, the reduction

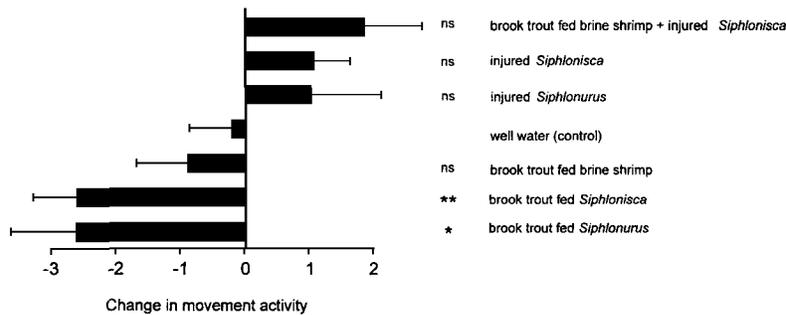


FIG. 2. Graph showing response of *Siphonisca* larvae to chemical cues from injured conspecifics, injured *Siphonurus* (prey) and brook trout fed various diets (predator). The x axis indicates change in the average number of observations of single individuals moving before and after being exposed to a chemical stimulus (see text for details). Stimuli are listed on the y axis. ns = mean not significantly different from control, * $P < 0.05$, ** $P < 0.01$. Error bars are standard errors ($N = 20$ except for "trout fed brine shrimp + injured *Siphonisca*" where $N = 18$).

of movement activity by *Siphonurus* when exposed to chemicals released by brook trout fed either brine shrimp ($t = -1.4046$, $df = 38$, $P = 0.084$, one-tail t test; Figure 1) or brook trout fed *Siphonisca* ($t = -0.7249$, $df = 38$, $P = 0.236$, one-tail t test; Figure 1) was not significantly different from the control. In contrast to *Siphonurus*, movement activity of *Siphonisca* was significantly reduced following exposure to chemicals released by brook trout feeding on either conspecifics ($t = -2.5152$, $df = 38$, $P = 0.008$, one-tail t test, Figure 2) or *Siphonurus* ($t = -1.9494$, $df = 38$, $P = 0.029$, one-tail t test; Figure 2). However, the reduction of movement activity by *Siphonisca* exposed to chemicals from brook trout fed brine shrimp was not significantly different from the control ($t = -0.6715$, $df = 38$, $P = 0.253$, one-tail t test; Figure 2). When exposed to chemicals released by injured conspecifics, *Siphonurus* showed a highly significant reduction in movement activity when compared with controls ($t = -3.7784$, $df = 38$, $P < 0.001$, one-tail t test; Figure 1). In comparison, movement activity by *Siphonisca* did not decrease significantly in the presence of chemicals released by injured conspecifics ($t = 1.4065$, $df = 38$, $P = 0.916$, one-tail t test; Figure 2). It should also be noted that all treatments involving brook trout chemicals without the presence of chemicals released directly from injured mayflies, either conspecifics or *Siphonurus*, elicited a trend toward decreased movement activity by *Siphonisca*, and that all treatments involving the presence of chemicals released directly by injured mayflies elicited a trend toward increased movement activity by *Siphonisca* (Figure 2).

DISCUSSION

The siphonurid mayflies *Siphonisca* and *Siphonurus* showed contrasting behavioral responses to chemicals released by injured conspecifics and their predators. The detritivorous mayfly *Siphonurus* showed a significant decrease in movement activity when exposed to chemicals released by injured conspecifics, as has been shown for other mayflies (e.g., *Baetis*; Scrimgeour et al., 1994a). The response by the predacious mayfly *Siphonisca*, however, was exactly the opposite of *Siphonurus*, its primary prey. *Siphonisca* increased movement activity when exposed to chemicals released by injured conspecifics and *Siphonurus*. The apparent trend toward increases in activity were consistent among all treatments involving chemicals from injured mayflies. Such a behavioral response was not anticipated, contrasted strongly with results from other studies of mayfly antipredator behavior (Scrimgeour et al., 1994a,b; Peckarsky et al., 1993; McIntosh and Peckarsky, 1996; McIntosh and Townsend, 1995), and deserves further interpretation in the context of the specific biology and habitat of *Siphonisca*.

Increased activity by *Siphonisca* in response to chemicals released by

injured mayflies may enhance detection of injured or freshly killed prey nearby. Field and laboratory observations, indicate that *Siphonisca* will feed opportunistically on dead animal tissue (e.g., exuviae; A. D. Huryn, personal observation) and is cannibalistic. Chemicals released by injured or freshly killed invertebrates, including conspecifics, may thus elicit a search response by *Siphonisca* that is similar to those reported for spiny lobsters in marine habitats (Zimmer-Faust, 1993) and predacious stonefly larvae in streams (Dodson et al., 1994). The detection of chemical signals may be particularly important for inhabitants of sedge-meadow wetlands because the dense meshwork provided by sedge detritus obscures clear fields of vision beyond more than a few centimeters.

In comparison to their contrasting responses to injured conspecifics, the responses of *Siphonurus* and *Siphonisca* to chemicals produced by brook trout were similar and highly context specific. Both *Siphonurus* and *Siphonisca* modified their movement activity in response to chemicals released from brook trout. Furthermore, both mayflies were able to use information from these chemicals to assess past feeding behavior by brook trout. *Siphonurus* showed significant reductions of movement activity in response to chemicals released by brook trout only in cases when the trout had fed upon conspecifics. In comparison, *Siphonisca* showed a significant reduction in movement activity when exposed to chemicals released by brook trout fed either conspecifics or *Siphonurus*. Although the response of *Siphonisca* to chemicals released by brook trout was more general than that of *Siphonurus* (e.g., responds to brook trout feeding upon confamilial rather than only conspecific mayflies), neither taxon showed a significant reduction of movement when exposed to chemicals released by brook trout feeding on brine shrimp.

The more general (confamilial) response of *Siphonisca* compared with the more precise (conspecific) response of *Siphonurus* seems to make good evolutionary sense, given the ecology of the two mayflies. First *Siphonisca* is a rare mayfly with a highly localized distribution, being known from fewer than 20 locations worldwide (e.g., McCollough, 1997), whereas *Siphonurus* is widespread throughout much of the Holarctic (Edmunds et al., 1977). Second as expected for a predator, *Siphonisca* is much less abundant than its primary prey, *Siphonurus*, wherever these taxa occur together. For example, benthic samples taken from the study site on May 14, 1998, indicated that the mean abundance of *Siphonisca* was 148 ± 56 individuals/m² (\pm SE, $N = 5$), whereas the mean abundance of *Siphonurus* was 4541 ± 875 individuals/m² (A. D. Huryn, unpublished). Third both mayfly taxa occupy similar habitats, are active swimmers, and presumably are similarly attractive to foraging trout. Assuming that the risk of either *Siphonurus* or *Siphonisca* being detected by a trout is proportional to their relative abundances, and that the risk of being consumed by a trout following detection is similar between taxa, it seems that a response by *Siphonisca* to chemicals produced by predators feeding upon *Siphonurus* would be adaptive.

Siphonisca may simply be too rare in terms of distribution and abundance to elicit a similar response from *Siphonurus*.

Compared with *Siphonurus*, the response of *Siphonisca* to the various stimuli used in the experiments was complex, and indicated the conflicting demands of efficient and simultaneous detection of both predators and prey. The importance of the pattern of response observed in this study becomes particularly clear when considered in the context of the ephemeral floodplain habitat of *Siphonisca*. It has been shown that levels of hunger will influence the amount of risk assumed by *Baetis* mayfly larvae in streams (Scrimgeour et al., 1994b). Because *Siphonisca* inhabits a temporary wetland for a critical period of its life history (Gibbs and Mingo, 1986; Huryn and Gibbs, 1998), risk of mortality from desiccation rather than hunger may have the greatest consequences for fitness. *Siphonisca* completes ~95% of its growth as biomass during a short (two month) period of floodplain inundation during the spring (A. D. Huryn, personal observation). If growth and development are not completed relatively quickly, larvae risk mortality from stranding as the floodplain dries. The risk of stranding and desiccation before completing development also has bearing on the nonlethal consequences of predator avoidance behavior by temporary-wetland species of *Siphonurus* as well. This balance of conflicting risks raises interesting questions about the more subtle nonlethal effects of avoidance behavior on growth and the immediate risk of mortality by predation on the life history strategies of aquatic macroinvertebrates in temporary environments (Crowl, 1990).

The adaptive significance of the reduction of movement behavior by *Siphonurus* and *Siphonisca* in response to chemicals signaling the presence of a visual predator is presumably to reduce mortality by direct predation. It is probable that nonlethal effects of this behavior will result in reduced food intake, growth, and probably fecundity of adults (McPeck and Peckarsky, 1998). This response is also apparently tuned to specific chemicals released by specific predators, as shown for damselfly larvae by Chivers et al. (1996). In this study, significant reductions in movement activity of both *Siphonurus* and *Siphonisca* in response to brook trout chemicals were observed only for treatments that included an element of direct and active predation on conspecific or confamilial mayflies. This indicates that these mayflies may be able to reduce the nonlethal effects of predator avoidance behavior by detecting active predation on mayflies in their vicinity, rather than the simple presence of a potential predator.

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REFERENCES

- BALL, S. L., and BAKER, R. L. 1996. Predator-induced life history changes: antipredator behavior costs or facultative life history shifts. *Ecology* 77:1116–1124.
- BROWN, G. E., CHIVERS, D. P., and SMITH, R. J. F. 1995. Localized defecation by pike: a response to labelling by cyprinid alarm pheromone? *Behav. Ecol. Sociobiol.* 36:105–110.
- BURIAN, S. K., and GIBBS, K. E. 1991. Mayflies of Maine: An Annotated Faunal List. Maine Agricultural and Forest Experimental Station Technical Bulletin 142, 109 pp.
- CHIVERS, D. P., and SMITH, R. J. F. 1998. Chemical alarm signaling in aquatic predator-prey systems: A review and prospectus. *Ecoscience* 5:338–352.
- CHIVERS, D. P., WISENDEN, B. D., and SMITH, R. J. F. 1996. Damselfly larvae learn to recognize predators from chemical cues in the predator's diet. *Anim. Behav.* 52:315–320.
- COVICH, A. P., CROWL, T. A., ALEXANDER, J. E., and VAUGHN, C. C. 1994. Predator-avoidance responses in freshwater decapod-gastropod interactions mediated by chemical stimuli. *J. North Am. Benthol. Soc.* 13:283–290.
- CROWL, T. A. 1990. Life-history strategies of a freshwater snail in response to stream permanence and predation: balancing conflicting demands. *Oecologia* 84:238–243.
- CROWL, T. A., and COVICH, A. P. 1990. Predator-induced life-history shifts in a freshwater snail. *Science* 247:949–951.
- DAWIDOWICZ, P., PIJANOWSKA, J., and CIECHOMSKI, K. 1990. Vertical migration of *Chaoborus* larvae is induced by the presence of fish. *Limnol. Oceanogr.* 35:1631–1637.
- DODSON, S. I., CROWL, T. A., PECKARSKY, B. L., KATS, L. B., COVICH, A. P., and CULP, J. M. 1994. Non-visual communication in freshwater benthos: An overview. *J. North Am. Benthol. Soc.* 13:268–282.
- EDMUNDS, G. F., JR., JENSEN, S. L., and BERNER, L. 1976. The Mayflies of North and Central America. University of Minnesota Press, Minneapolis, Minnesota.
- FELTMATE, B. W., and WILLIAMS, D. D. 1991. Evaluation of predator-induced stress on field populations of stoneflies (Plecoptera). *Ecology* 72:1800–1806.
- GIBBS, K. E., and MINGO, T. M. 1986. The life history, nymphal growth rates, and feeding habits of *Siphonisca aerodromia* Needham (Ephemeroptera: Siphonuridae) in Maine. *Can. J. Zool.* 64:427–430.
- GIBBS, K. E., and SIEBENMANN, M. 1996. Life history attributes of the rare mayfly *Siphonisca aerodromia* Needham (Ephemeroptera: Siphonuridae). *J. North Am. Benthol. Soc.* 15:95–105.
- HOLOMUZKI, J. R., and SHORT, T. M. 1988. Habitat use and fish avoidance behaviors by the stream-dwelling isopod *Lirceus fontinalis*. *Oikos* 52:79–86.
- HURYN, A. D., and GIBBS, K. E. 1998. Macroinvertebrates of riparian sedge meadows in Maine: A community structured by river-floodplain interaction, pp. 363–382 in D. Batzer, D., Rader, R. B., Wissinger, and S. A. (eds.), Invertebrates in Freshwater Wetlands of North America: Ecology and Management. John Wiley & Sons, New York.
- KATS, L. B., and DILL, L. M. 1998. The scent of death: chemosensory assessment of predation risk by prey animals. *Ecoscience* 5:361–394.
- KEPPEL, G. 1982. Design & Analysis: A Researcher's Handbook. Prentice-Hall, Englewood Cliffs, New Jersey.
- MATHIS, A., and HOBACK, W. W. 1997. The influence of chemical stimuli from predators on precopulatory pairing by the amphipod, *Gammarus pseudolimnaeus*. *Ethology* 103:33–40.
- MATHIS, A., and SMITH, R. J. F. 1993. Fathead minnows (*Pimephales promelas*) learn to recognize pike (*Esox lucius*) as predators on the basis of chemical stimuli from minnows in the pike's diet. *Anim. Behav.* 46:645–656.
- MATHIS, A., CHIVERS, D. P., and SMITH, R. J. F. 1993. Population differences in response of fat-

- head minnows (*Pimephales promelas*) to visual and chemical stimuli from predators. *Ethology* 93:31–40.
- MC COLLOUGH, M. A. 1997. Conservation of invertebrates in Maine and New England: Perspectives and prognoses. *Northeast. Nat.* 4:261–278.
- MCINTOSH, A. R., and PECKARSKY, B. L. 1996. Differential behavioral responses of mayflies from streams with and without fish to trout odour. *Freshwater Biol.* 35:141–148.
- MCINTOSH, A. R., and TOWNSEND, C. R. 1995. Impacts of an introduced predatory fish on mayfly grazing in New Zealand streams. *Limnol. Oceanogr.* 40:1508–1512.
- MCINTOSH, A. R., and TOWNSEND, C. R. 1996. Interactions between fish, grazing invertebrates and algae in a New Zealand stream: A trophic cascade mediated by fish-induced changes to grazer behavior? *Oecologia* 108:174–181.
- MCPEEK, M. A., and PECKARSKY, B. L. 1998. Life histories and the strength of species interactions: Combining mortality, growth, and fecundity effects. *Ecology* 79:867–879.
- ODE, P. R., and WISSINGER, S. A. 1993. Interaction between chemical and tactile cues in mayfly detection of stoneflies. *Freshwater Biol.* 30:351–357.
- PECKARSKY, B. L. 1980. Predator-prey interactions between stoneflies and mayflies: behavioral observations. *Ecology* 61:932–943.
- PECKARSKY, B. L., and MCINTOSH, A. R. 1998. Fitness and community consequences of avoiding multiple predators. *Oecologia* 113:565–576.
- PECKARSKY, B. L., COWAN, C. A., PENTON, M. A., and ANDERSON, C. 1993. Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. *Ecology* 74:1836–1846.
- PECKARSKY, B. L., COOPER, S. D., and MCINTOSH, A. R. 1997. Extrapolating from individual behavior to populations and communities in streams. *J. North Am. Benthol. Soc.* 16:375–390.
- SCRIMGEOUR, G. J., CULP, J. M., and CASH, K. J. 1994a. Anti-predator responses of mayfly larvae to conspecific and predator stimuli. *J. North Am. Benthol. Soc.* 13:299–309.
- SCRIMGEOUR, G. J., CULP, J. M., and WRONA, F. J. 1994b. Feeding while avoiding predators: Evidence for a size-specific trade-off by a lotic mayfly. *J. North Am. Benthol. Soc.* 13:368–378.
- VAN BUSKIRK, J., and YUREWICZ, K. L. 1998. Effects of predators on prey growth rate: relative contributions of thinning and reduced activity. *Oikos* 82:20–28.
- WILLIAMS, D. D., and MOORE, K. A. 1985. The role of semiochemicals in benthic community relationships of the lotic amphipod *Gammarus pseudolimnaeus*: A laboratory analysis. *Oikos* 44:280–286.
- WILSON, D. J., and LEFCORT, H. 1993. The effects of predator diet on the alarm response of red-legged frog, *Rana aurora*, tadpoles. *Anim. Behav.* 46:1017–1019.
- WISENDEN, B. D., CHIVERS, D. P., and SMITH, R. J. F. 1997. Learned recognition of predation risk by *Enallagma* damselfly larvae (Odonata, Zygoptera) on the basis of chemical cues. *J. Chem. Ecol.* 23:137–151.
- WUDKEVICH, K., WISENDEN, B. D., CHIVERS, D. P., and SMITH, R. J. F. 1997. Reactions of *Gammarus lacustris* to chemical stimuli from natural predators and injured conspecifics. *J. Chem. Ecol.* 23:1163–1173.
- ZIMMER-FAUST, R. K. 1993. ATP: a potent prey attractant evoking carnivory. *Limnol. Oceanogr.* 38:1271–1275.