

# Seasonal Differences in Predator-prey Behavior in Experimental Streams

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**ABSTRACT.**—Invertebrate prey have been shown to select suboptimal resource patches in the face of predation (the food-predation risk trade-off). The foraging strategy used by a predator and the environmental context under which an interaction occurs potentially mediates prey responses to predators. Here, I determined whether season, predator presence or alternative prey availability affected prey patch use when faced with a sit-and-wait predator from streams in southern Maine. In addition, instantaneous mortality rates and predator movement behavior were assessed as possible mechanisms explaining patch use by prey in different seasons. In the absence of predators, prey did not show any preference for substrate patches based on particle size. But, depending on prey type and season, substrate position in streams had a significant effect on prey survival. Mayflies survived most in summer when pebble substrates were located upstream whereas caddisfly survival was highest when pebble substrates were located downstream in winter. Season and taxa significantly affected instantaneous mortality rates, suggesting this predator responded differently to available prey in each season. Predators changed ambush positions in the streams significantly more during winter than during summer, both with and without prey present. The presence of caddisflies in mixed-prey trials reduced consumption of mayflies in summer, but increased their mortality in winter. Increased movement behavior of predators in winter may have led to greater encounters with prey, thus increasing winter mortality. Collectively, these data reveal season can influence the outcome of predator-prey interactions. Environmental context, as well as predation mode, is critical to predicting predation effects in macroinvertebrate communities. Further studies of the seasonal changes in organism-specific behavior are needed to evaluate the importance of biotic interactions in structuring stream communities.

## INTRODUCTION

Organism behavior changes seasonally. Whereas evidence of this is pervasive for long-lived vertebrates (*e.g.*, Krebs and Davies, 1991), relatively little attention has been devoted to investigating seasonal changes in stream insect behavior. This, in part, is due to the short duration of most insect life cycles and the harsh nature of winter conditions in temperate zone streams where much research is conducted. In some temperate streams, winter conditions (*e.g.*, water temperature <5 C, low flow, reduced light conditions under ice/snow cover) persist for several months, accounting for a substantial portion of the life span of many stream organisms and warrant further investigation. Accordingly, we require more knowledge of seasonal changes in habitat condition, species behaviors and behavioral interactions to formulate a more accurate picture of the key forces structuring stream insect communities and to better understand the selective forces acting on populations (*e.g.*, Peckarsky *et al.*, 1997).

Because stream insects generally are ectothermic, their life history, productivity and behavioral patterns often are mediated by changes in environmental conditions, especially

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temperature (Huryn and Wallace, 2000). Substrate use and predator-prey interactions are two significant, and related, behaviors influenced by environmental conditions. For example, Minshall (1984) and Robertson *et al.* (1995) showed that changes in discharge led to altered substrate use by invertebrates and Lancaster *et al.* (1988) showed that season was a strong determinant of microsite selection by caddisfly larvae under different predation and food availability regimes. Temperature is a cue for emergence and diapause in a variety of taxa with both events leading to a search for specific microhabitats (*e.g.*, Sweeney, 1984). Biotic interactions, like predator-prey or intraspecific dynamics, also can be affected by changing temperature (*e.g.*, Peckarsky, 1984; Pennuto, 2000). Collectively, these observations suggest seasonal observations or repeated testing of biotic interactions are important to gain a fuller understanding of annual patterns in prey mortality and patch use.

Predation and competition influence prey microdistribution in streams (Peckarsky, 1979; McAuliffe, 1984; Michael and Culver, 1987; Lancaster *et al.*, 1988; Moutka, 1993; Scrimgeour *et al.*, 1994a, b). Recently, patch use by prey has been examined in the context of predation risk trade-offs (*i.e.*, predator avoidance) where prey balance foraging and growth against predation risk in an optimal fashion (*e.g.*, Fraser and Huntingford, 1986; Abrahams and Dill, 1989; Culp and Scrimgeour, 1993; Holomuzki and Messier, 1993; Turner, 1997; Heithaus and Dill, 2002). Optimal patch use decisions can be modified by prey size (Culp and Scrimgeour, 1993; Scrimgeour *et al.*, 1994b) or hunger levels (Kohler and McPeck, 1989; Dill and Fraser, 1997). Abiotic conditions like current velocity (Lancaster and Hildrew, 1993; Johnson and Brown, 1997), substrate composition (Hildrew and Townsend, 1976; Feltmate *et al.*, 1986), and water chemistry (Pennuto and deNoyelles, 1993; Panis *et al.*, 1996; Moore and Townsend, 1998) also have been correlated with prey patch use. Few studies of prey patch use in streams have examined seasonal changes in predator and prey behavior or incorporated multiple prey species responses to predators. In addition, most studies on prey response to predators have focused on mobile predators and prey, not ambush predators.

In this study, I examined whether two stream-dwelling prey taxa, an ephemereid mayfly and a hydropsychid caddisfly, altered their substrate use between seasons or in the presence of a sit-and-wait, ambush predator, the fishfly *Nigronia serricornis* Say (Megaloptera: Corydalidae). I also monitored the movement behavior of predators with and without prey in both seasons as a possible mechanism to explain prey patch use patterns. As a result, I anticipated the presence of a fishfly predator would influence prey patch use, causing prey to use stream sections with small substrates because these provided a predation refuge. Alternatively, predators might eliminate prey from large substrates via consumption or by inducing escape responses like drift. I hypothesized that when predators were absent, prey would show a seasonal use of different substrate sizes because of abiotic cues. Lastly, I expected predators to maintain consistent movement patterns between seasons and among prey treatments because they are ambush predators. I anticipated that predator responses to resource conditions were time-dependent, and if anything, movement behavior would be reduced in winter relative to summer.

#### METHODS

*Study organisms.*—All test organisms were collected from a third order reach of the Little River (Cumberland County, Maine 43°41'N, 70°29'W) in June, July, August, November and December 1997–1998. Organisms were collected in kicknets, field-sorted live from debris and immediately placed in buckets containing stream water. Predators were held individually in laboratory tanks and starved for three days to standardize hunger levels. All prey were collected at midday and used on the day of capture to reduce the influence of hunger on movement.

The saw-combed fishfly *N. serricornis* is a common inhabitant of woodland streams in eastern and central U.S. (Evans and Neunzig, 1996) and they are often the largest insect predator found in 2<sup>nd</sup> and 3<sup>rd</sup> order streams in southern Maine. This species readily consumes both prey species in laboratory trials and gut contents of field-collected individuals contain both prey. *Nigronia serricornis* likely has a three year life cycle in the study stream and individuals with head capsule widths of about 3.5 mm represent at least 2 y old larvae (C. Pennuto, pers. obs.).

*Ephemerella invaria* (Walker) (Ephemeroptera: Ephemerellidae) and the net-spinning caddisflies *Hydropsyche venularis* (Banks), *Symphitopsyche walkeri* (Betten and Mosely), and *S. sparna* (Ross) (Trichoptera: Hydropsychidae) were used as prey. About 90% of the caddisflies used were *H. venularis*, with the remainder equally divided among the other two species. Whereas there is evidence that hydropsychid caddisflies exhibit microhabitat preferences based on net mesh size (e.g., Matczak and Mackay, 1990), I have no evidence to suggest that the taxa used here would respond differently to predators.

Both prey types are univoltine; the mayflies emerge in late June and the caddisflies in late May. The species co-occur as larvae in all seasons except early June through July. The prey taxa are not as mobile as other species in their respective orders. Ephemerellid mayflies are poor swimmers compared to other common lotic mayflies (e.g., Baetidae or Leptophlebiidae), making them good candidates for laboratory stream trials. Likewise, hydropsychid caddisflies construct fixed capture nets and retreats that they defend from intruders and are reluctant to abandon (Matczak and Mackay, 1990). Thus, neither are these prey drift prone nor are they likely to accumulate on the downstream retaining nets.

*Experimental streams.*—Experimental streams were similar to Pennuto and deNoyelles (1993) except that water recirculated through a 280-liter, temperature controlled reservoir. Two centrifugal pumps delivered stream water to 24 stream channels (35 × 5 cm length × width, respectively) with an average velocity of 6.1 cm \* s<sup>-1</sup>. Frigid-unit® water chillers maintained water temperature at ambient stream values for all trials. Mesh screens (1 mm) prevented insect escape in either the upstream or downstream direction. Streams were housed in a laboratory with benchtop-to-ceiling windows receiving ambient light and were positioned on raised scaffolding surrounded in black plastic. Each channel had a clear acetate 5 × 5-mm grid affixed to the underside allowing determination of precise coordinates for predator movements when viewed from below. Preliminary observations (2-h intervals for 24 h) indicated that fishflies always remained in pebble (large) substrates regardless of their stream position and moved infrequently after entering the substrate.

Substrate was collected from the Little River, dried and washed prior to use to standardize periphyton levels. Each stream channel had half its length covered with either small particles (gravel = 2–8 mm diam) or large particles (pebble = 16–60 mm diam) arranged in alternating upstream/downstream positions to reduce substrate position effects. The upstream position of gravel was randomly assigned to 12 channels; the other 12 channels had pebble substrate upstream (Fig. 1). Gravel substrates comprised ~15% by weight of field substrates whereas pebble-sized particles represented ~42% of field substrates. Thus gravel substrates in the lab streams were about 2× more common than gravel substrates in the field. Substrate conditions in the field differed from the substrate configuration in laboratory streams in two important ways: 1) laboratory substrates were uniformly-sized habitat patches whereas substrate in the Little River was more heterogeneous at the scale of these lab streams, and 2) laboratory substrates were periphyton-free. Although food levels have been shown to influence prey substrate use (Vaughn, 1986), laboratory trials were of short duration and prey were always used the day of capture, standardizing hunger levels among prey and reducing the likelihood that hunger levels influenced substrate use. The

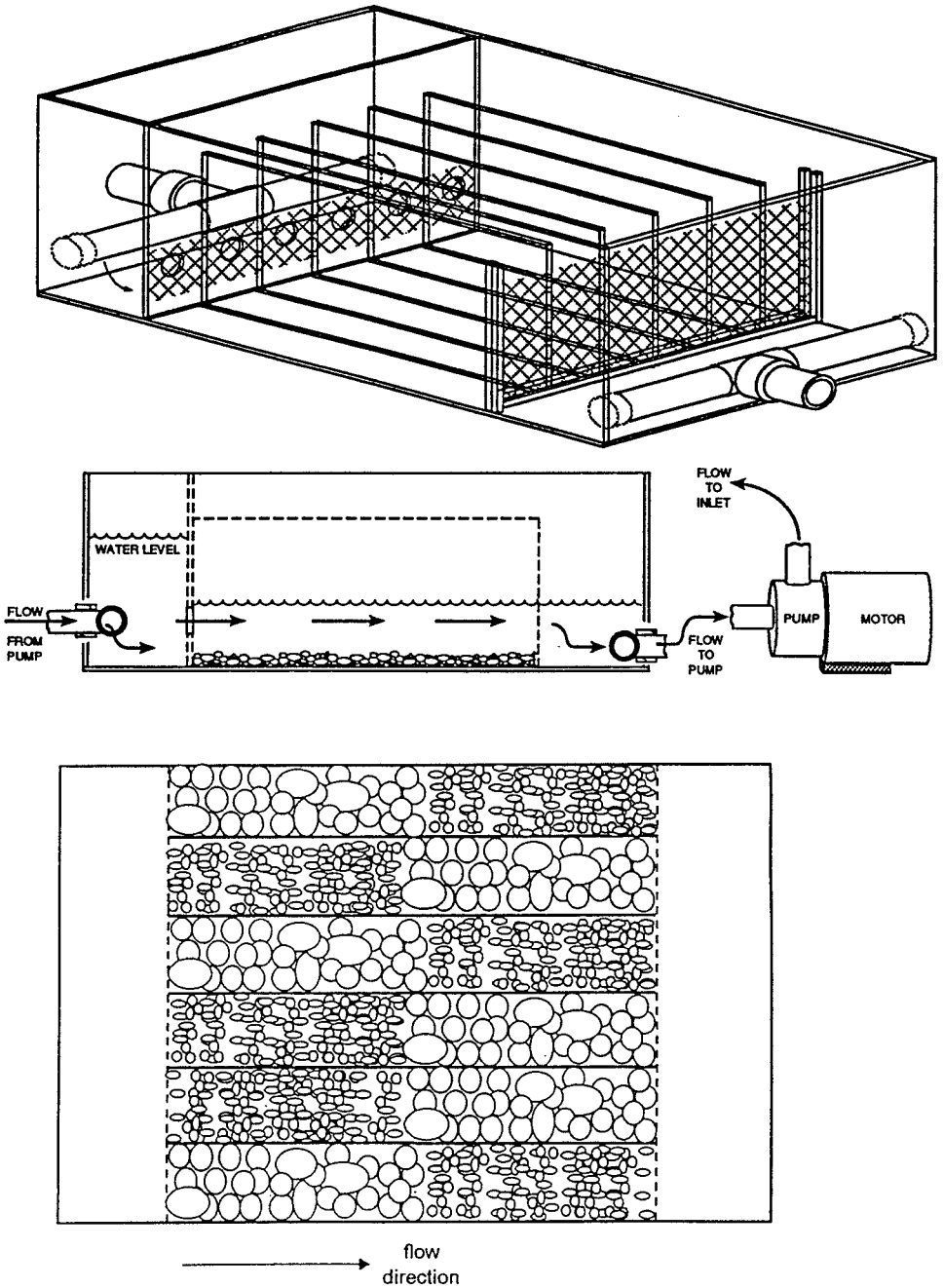


FIG. 1.—Experimental streams used to examine season, substrate position, and predator effects on prey substrate use. Dimensions are reported in Methods

selection of these two substrate sizes was a compromise between laboratory stream dimensions, prey microdistribution in the field and potential prey refuge. In a series of similar laboratory trials, Michael and Culver (1987) showed that hydropsychid caddisfly larvae gained predation refuge from the hellgrammite *Corydalis cornutus* (L) in gravel substrates like those used here.

New stream water was collected for all trials. Measurements of basic water chemistry (pH, conductivity, total alkalinity, dissolved oxygen, and temperature) were taken at the beginning, middle, and end of each trial. Water pH was determined using a pHTestr 2 (Oakton Corporation). Room and water temperatures were measured with an immersion thermometer. Conductivity was determined using a Corning Checkmate 90 conductivity meter. Dissolved oxygen and total alkalinity were determined titrimetrically by Winkler and methyl-orange methods, respectively.

*Season and prey effects on predator movements.*—Two types of trials were used to investigate effects of season on predator movement behaviors: 1) long term starved predator trials and 2) prey substrate-use trials. Long term starved predator trials were used to compare seasonal movement patterns in stream channels with no prey. Fishflies were collected in July ( $n = 24$ ) and November ( $n = 12$ ) and starved 48 h prior to addition to experimental streams. A single predator was placed at the midpoint of a channel in the morning hours and acclimated to channels for approximately 8 h. The coordinate location of each predator was determined at 2-h intervals over a 56-h period using the acetate grids under each channel. Cumulative distance moved was calculated on a SummaSketch digitizing pad by summing the coordinate distances moved per observation period. Summer and winter distances moved were compared using a Kolmogorov-Smirnov test to determine whether the cumulative distributions differed between seasons.

Season and prey effects on movement behavior of foraging predators were examined using prey substrate-use trials (described below). The effect of prey presence on predator movement behavior was assessed by calculating the distance moved per hour ( $\text{mm} \cdot \text{h}^{-1}$ ) during 40-h trials. Each predator's coordinate position was recorded at  $t + 0.5, 1.5, 15, 20, 24,$  and  $40$  h after introduction into experimental stream channels. The cumulative distance moved over the five time periods was divided by 40. The effect of season and prey taxa on predator movement distance was examined using a 2-way ANOVA on  $\log(n + 1)$ -transformed data.

*Prey substrate use with and without predators.*—I conducted single-species and mixed-species prey substrate-use trials in summer and winter; single-species trials were conducted in June (mayflies), August (caddisflies), and December (mayflies and caddisflies), whereas mixed-species trials were conducted in May and December. Each trial was initiated at 1600 h and lasted 40 h to provide two night feeding cycles for predators. Twenty prey and a single predator were used per channel in single-prey trials, whereas mixed-prey trials received 10 of each prey type plus a single predator. There were 6–12 replicate streams per trial (Table 1). All treatments in the same season were initiated within 24 h of the end of a previous trial. The number of replicates per trial differs because, on a few occasions, predators escaped into adjacent streams, compelling me to omit those data.

Trials were initiated by introducing half of the prey into the upstream end of a channel after the flow was restricted. Current was slowly restored and prey positions were monitored for 15 min to assure all prey remained within the substrate where they were placed. Any prey moving between substrates was replaced with a new prey to ensure equal initial prey densities in both substrate types. After all prey remained stationary for at least 15 min, the remaining prey were added to the downstream section of each channel. One large fishfly predator (head size  $\geq 3.5$  mm) was introduced at the midpoint of a channel. After 40 h, the

TABLE 1.—Number of replicate streams and prey used in 40 h prey substrate-use trials and comparison to field densities

Treatment	No. of rep. streams	No. of mayfly prey	No. of caddisfly Prey	Field density (no. m <sup>-2</sup> ·h <sup>-1</sup> )	Laboratory density (no. m <sup>-2</sup> ·h <sup>-1</sup> )
<b>Summer</b>					
Mayfly	12	20	0	116.3	1142.8
Mayfly + fishfly	11	20	0	125.1	1199.9
Caddisfly	11	0	20	1424.2	1142.8
Caddisfly + fishfly	12	0	20	1432.0	1199.9
Mayfly + caddisfly	10	10	10	1540.5	1142.8
Mayfly + caddisfly + fishfly	9	10	10	1548.3	1199.9
<b>Winter</b>					
Mayfly	6	20	0	673.6	1142.8
Mayfly + fishfly	6	20	0	680.5	1199.9
Caddisfly	6	0	20	250.1	1142.8
Caddisfly + fishfly	6	0	20	257.0	1199.9
Mayfly + caddisfly	9	10	10	923.7	1142.8
Mayfly + caddisfly + fishfly	9	10	10	930.6	1199.9

number of prey remaining in either gravel (small) or pebble (large) substrate was enumerated by visual counts after removing all substrate. I used a chi-square test to determine if prey showed a substrate preference in each season by comparing observed numbers of prey in pebble substrates of predator-free streams against the expectation that 50% would be in that substrate. I also examined whether the position of pebble substrates (*i.e.*, upstream or downstream position) and the presence of predators affected the number of prey remaining in pebble substrates using 2-way ANOVA's for each prey type and season.

*Season and prey taxa effects on predation rates.*—Instantaneous mortality rates were calculated for each 40-h trial after Peckarsky (1996) using the equation:  $m = [\ln N_o - \ln N_f]/t$ , where  $m$  = prey mortality \* prey<sup>-1</sup> \* predator<sup>-1</sup> \* day<sup>-1</sup>;  $N_o$  = initial prey density; and  $N_f$  = final density of live prey. Season and prey taxa effects on instantaneous mortality rates were examined with a 2-way ANOVA.

## RESULTS

*Water chemistry.*—Water chemistry remained stable throughout all lab trials. Summer air and water temperatures were higher than winter temperatures, but the remaining parameters showed no major seasonal differences (Table 2).

*Laboratory vs. field organism densities.*—Caddisfly densities in single-prey, caddisfly substrate-use trials were roughly equivalent to summer field densities, but mayfly densities were approximately 9× field densities (Table 1). Similarly, predator densities were about 7× summer field densities, based on 15 Surber (0.1 m<sup>2</sup>) samples taken in August 1996. Prey also were significantly larger in summer trials compared to winter trials (mayflies: 1.52 vs. 1.16 mm head width,  $t = 3.25$ ,  $df = 262$ ,  $P = 0.0013$ ; caddisflies: 1.16 vs. 1.03,  $t = 6.34$ ,  $df = 534$ ,  $P \ll 0.001$ ). Constant prey density across seasons was used to make instantaneous mortality rate and prey density comparisons consistent. Experimental channel dimensions inflated predator densities.

*Season and prey effects on predator movements.*—Predators moved infrequently, moving more at night compared to daylight hours. When they moved they traveled short distances,

TABLE 2.—Water chemistry in experimental streams in different seasons. Data are means ( $\pm 1$  SE)

Parameter	June	August	December
Room temperature (C)	23.6 (2.3)	21.3 (1.67)	11.0 (0.58)
Water temperature (C)	17.5 (0.50)	17.5 (1.57)	5.9 (1.46)
pH	7.8 (0.12)	8.0 (0.09)	7.5 (0.19)
Conductivity ( $\mu\text{S} \cdot \text{cm}^{-1}$ )	191.3 (24.80)	218.3 (10.04)	203.6 (35.66)
Total alkalinity ( $\text{mg} \cdot \text{L}^{-1}$ )	24.8 (0.69)	41.3 (11.09)	24.6 (5.63)
Dissolved oxygen ( $\text{mg} \cdot \text{L}^{-1}$ )	9.3 (0.07)	9.8 (0.38)	10.2 (0.58)

averaging only 5 cm in the last 12 h of the 40-h, prey substrate-use trials. There was a significant season effect on predator movement distance in these trials ( $F_{1,46} = 9.51$ ,  $P = 0.003$ ; Table 3), with predators moving significantly more in winter than summer, contrary to expectations. Though not significant, predators tended to move more when prey were absent relative to when prey were present, especially in winter (Fig. 2). Movement patterns in the starved-predator trials corroborate the results from the prey substrate-use trials. The cumulative distance moved over 56 h was significantly greater in winter compared to summer (Kolmogorov-Smirnov  $D = 0.06$ ,  $P = 0.013$ ; Fig. 3).

*Prey substrate use and mortality rates.*—Prey showed no preference for substrate types in either season when alone in experimental channels (all chi square results  $P > 0.05$ ). Substrate use by prey was position- and predator-dependent, except for caddisflies in summer. In summer, the number of mayflies remaining in pebble substrates was determined by the presence of predators, but not substrate position (Table 4). Mayflies were most abundant when predators were absent, and they were least abundant when predators were present (Fig. 4A). In winter, both pebble position and predator presence affected the number of mayflies remaining after 40 h (Table 4). Mayflies were most abundant upstream when predators were absent and least abundant downstream when predators were present (Fig. 4B). Caddisflies were always most abundant when pebble substrates were in the downstream position, regardless of predator presence or season (Table 4). This position effect was significant in winter, but not in summer (Fig. 4C).

There was a significant interaction effect between prey taxa and season on instantaneous mortality rates (Table 5). In summer, predators consumed more mayflies than caddisflies and total consumption in mixed-prey trials was intermediate, suggesting an antagonism. In contrast, winter predation rates on both prey were lower than summer rates, but total consumption in mixed-prey trials exceeded summer consumption (Table 5). Additionally, winter mortality in mixed-prey trials was greater than the sum of mortality in single-taxa trials, suggesting a synergistic effect.

TABLE 3.—Results of 2-way ANOVA examining season and prey taxa effects on predator movement distance ( $\text{mm} \cdot \text{h}^{-1}$ ) during 40 h prey substrate-use trials. Data were  $\log(n + 1)$ -transformed. Results from the mixed taxa trials not included

Source of variation	df	MS	F	P
Season	1	0.643	9.51	<b>0.003</b>
Prey taxa	2	0.166	2.45	0.097
Season * prey taxa	2	0.085	1.25	0.295
Error	46	0.068		
Total	52			

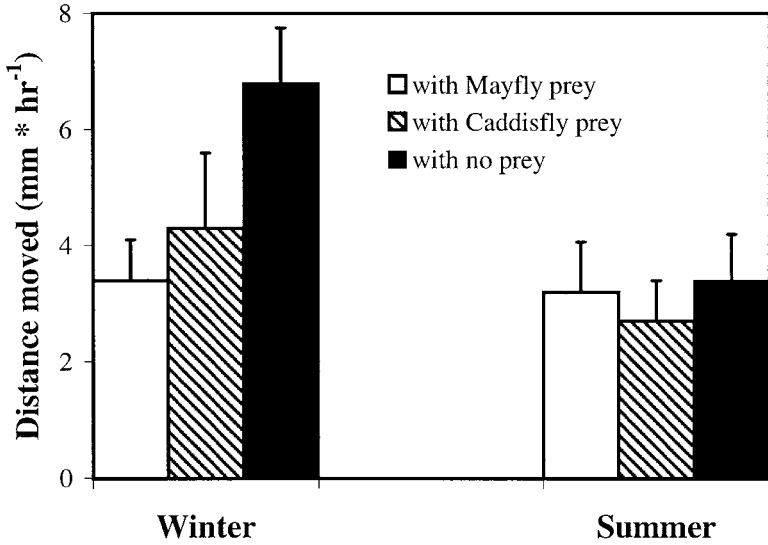


FIG. 2.—Seasonal differences in movement behavior of predatory fishflies in experimental channels during 40 h trials with and without prey present. Error bars = 1 SE

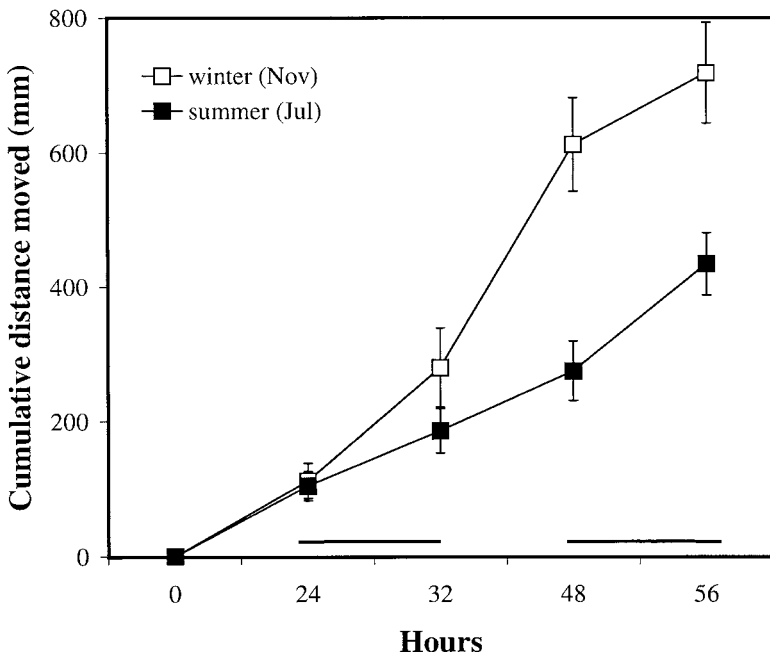


FIG. 3.—Seasonal differences in the cumulative distance moved (mm) of starved predators in the absence of prey in experimental channels. Error bars = 1 SE Black horizontal lines indicate nighttime

TABLE 4.—Results of 2-way ANOVA examining the effects of substrate position and predator presence on the number of prey remaining in gravel substrates after 40 h trials

Summer mayflies					Summer caddisflies				
	df	MS	F	P		df	MS	F	P
Position (A)	1	3.08	0.73	0.405	Position (A)	1	25.63	2.84	0.109
Predator presence (B)	1	82.88	19.51	<b>&lt;0.001</b>	Predator presence (B)	1	23.21	2.57	0.126
A * B	1	1.22	0.29	0.599	A * B	1	0.81	0.09	0.768
Error	19	4.25			Error	18	9.02		
Total	22				Total	21			
Winter mayflies					Winter caddisflies				
	df	MS	F	P		df	MS	F	P
Position (A)	1	33.33	25.00	<b>0.001</b>	Position (A)	1	33.33	13.33	<b>0.007</b>
Predator presence (B)	1	8.33	6.25	<b>0.037</b>	Predator presence (B)	1	12.00	4.80	0.059
A * B	1	0.33	0.25	0.631	A * B	1	1.33	6.53	0.486
Error	8	10.67			Error	8	2.5		
Total	11				Total	11			

#### DISCUSSION

Mayflies and caddisflies showed no seasonal substrate preference, either when tested alone or in mixed assemblages and did not migrate to predator-free substrate patches in the presence of a sit-and-wait predator. Possibly, prey did not perceive a predation risk from these stationary predators as they have been shown to do when faced with mobile, searching predators like stoneflies (*e.g.*, Peckarsky and Cowan, 1995). Some *N. serricornis* larvae were observed remaining in the same stream location for up to 24 h (C. Pennuto, pers. obs.) before moving to a new location, thus reducing potential encounters with prey. Hayashi and Nakene (1989) also reported that a related corydalid, *Protohermes grandis*, remained motionless in stream substrates in an ambush predation mode. In fact, some predators in their study did not change substrate positions for up to 17 d. Cooper *et al.* (1985) showed that encounter rates were more important than attack rate, capture success, and ingestion rate in determining prey selectivity for a variety of predators with differing foraging tactics. Thus, the low-mobility, low drift propensity prey used in these trials had a low encounter rate with this ambush predator, reducing their perception of predation risk.

Even if encounter rates between *N. serricornis* and prey were high, the lack of an avoidance response might simply be a behavioral constraint, at least for the ephemereid mayflies. Most research on invertebrate predator-prey interactions in streams showing positive prey responses have focused on mobile predators and prey, especially stoneflies and baetid mayflies (*e.g.*, Fuller and DeSteffan, 1988; Scrimgeour and Culp, 1994; Peckarsky and Cowan, 1995). Because encounter rates are critical in determining predation rates (Cooper *et al.*, 1985; Peckarsky and Cowan, 1995), inactive prey would have fewer encounters with inactive predators, and thus, lower predation rates. Alternatively, the evolution of defensive mechanisms like scorpion postures in mayflies (*e.g.*, Peckarsky, 1987) may, in part, influence the decision to move when encountering a predator. The high summer predation rates on mayflies suggest that the defense postures effective in deterring stonefly predators are less effective against fishflies. Perhaps the large size of fishfly predators relative to stoneflies limits the effectiveness of this mayfly defense or fishfly predation has not been a significant selective force in the evolution of predator-avoidance in these mayfly prey. Regardless of the

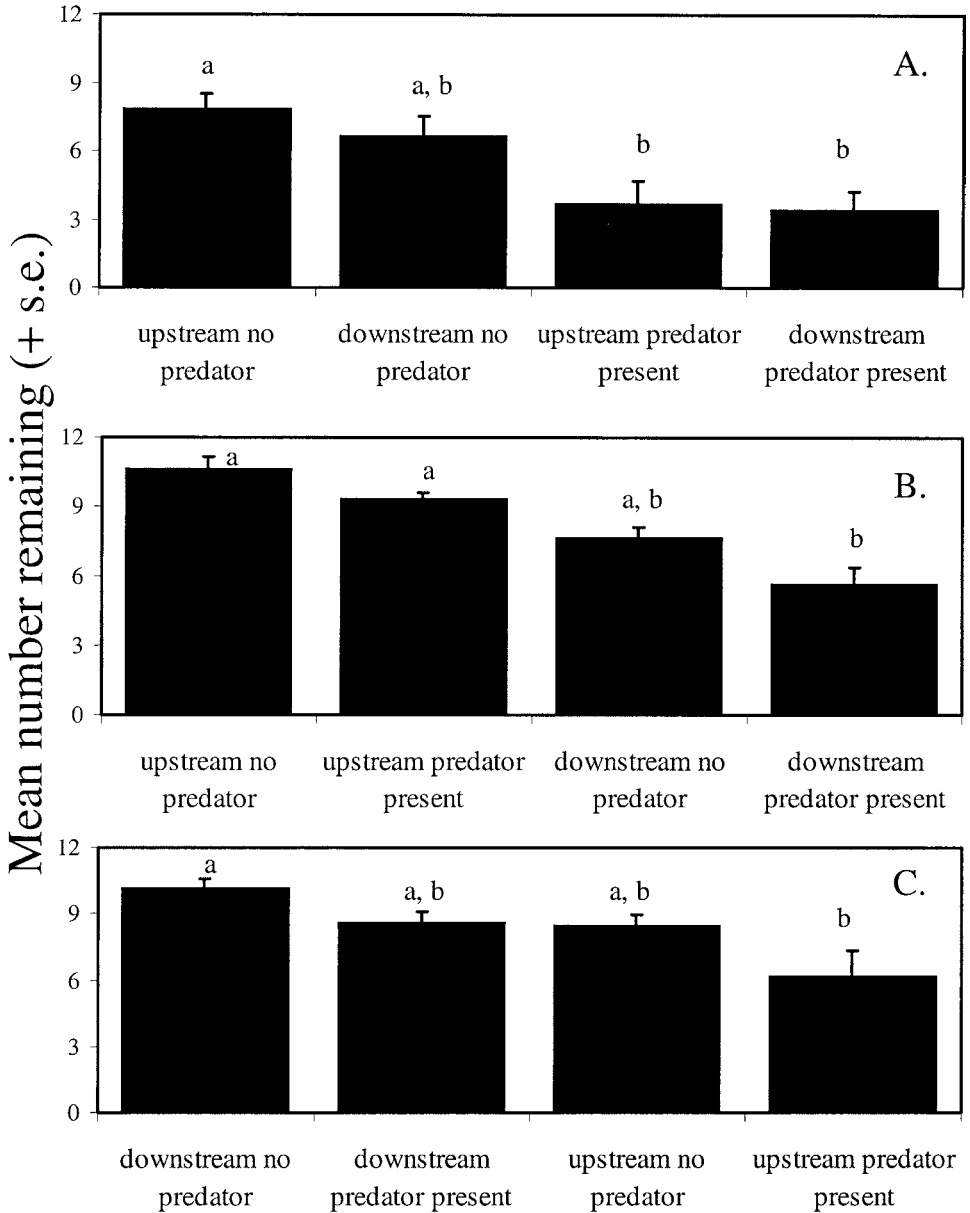


FIG. 4.—The effects of substrate position and presence of predators on the mean number of prey remaining in gravel substrates after 40 h. Error bars = 1 SE. Bars with the same letter are not significantly different from each other (Bonferroni multiple comparisons  $P > 0.05$ ). A = mayflies in summer; B = mayflies in winter; C = caddisflies in winter.

TABLE 5.—Results of 2-way ANOVA examining season and prey taxa effects on instantaneous mortality rates in 40 h prey substrate-use trials

Source of variation	df	MS	F	P
Season	1	0.0061	1.84	0.181
Prey taxa	2	0.0043	1.30	0.282
Season * prey taxa	2	0.0147	4.45	<b>0.017</b>
Error	47	0.0033		
Total	53			

Means (SE)	Summer	Winter
Mayfly	0.11(0.024)	0.02(0.011)
Caddisfly	0.05(0.013)	0.07(0.021)
Mixed	0.05(0.016)	0.13(0.021)

evolutionary mechanism, prey did not dramatically alter substrate use in the presence of predators in these laboratory trials in either season.

Predators consumed both prey types in both seasons, but consumed more mayflies in the summer and more caddisflies in the winter. Fuller and Hynes (1987) showed a similar diet shift for fishflies in the Speed River, Ontario and our field data corroborate this result. Summer predation on mayflies was less in mixed prey trials than in single prey trials, suggesting that the presence of caddisfly prey reduced predator impacts on mayflies. Because predators did not exhibit a prey preference in summer and because prey densities were held constant for all trials, the reduced predation on mayflies was attributed to a modified interaction resulting from caddisfly presence (*see* Wootton, 1994). The availability of alternative prey may significantly influence predation decisions by predators if the prey differ in profitability but are equal in terms of vulnerability, or because consumption of one prey type precludes consumption of the other at the same time (Wootton, 1994). While I did not assess prey caloric value, morphologically the caddisflies appear to have a higher percent of digestible tissue than the mayflies (*i.e.*, a proportionally larger unscleritized abdomen) potentially increasing their profitability. In contrast to the summer observations, winter mortality rates in mixed prey trials were greater than the sum of rates from single taxa trials, suggesting that the presence of alternative prey had a synergistic effect. Possibly, prey vulnerability to predators was increased in winter because of interspecific interactions between prey, though I have no behavioral observations on prey to illuminate this possibility. Alternatively, because predators moved more in winter (as indicated in both the long term starved predator trials and the prey substrate-use trials), their prey encounter rates may have been higher, increasing mortality rates. Other studies on seasonal changes in predation effects have shown mixed results. Whereas Lancaster *et al.* (1988) showed a strong seasonal effect on predator-driven patch selection in caddisflies, Moutka (1993) found mixed seasonal responses because of resource aggregation. In the present study, resource levels for prey were constant across seasons, eliminating aggregation as a mechanism explaining predator responses. These predators showed seasonal differences in cumulative movement distances with prey absent and in distance moved per h with prey present. If greater movement distances resulted in higher encounter rates with prey, this could explain the higher winter season mortality rates.

Peckarsky *et al.* (1997) call for further multiple-scale assessments of the role individual behavior plays in determining how inter- and intraspecific interactions manifest themselves at population and community levels. Basic information on seasonal changes in insect

behavior is lacking. In this study, predators continued to consume prey even when stream temperatures reflected winter field conditions, contrary to expectations and reminding us that enumerating the prey resource base in a single season will not adequately describe habitat suitability for predators. In addition, winter prey mortality rates in mixed species trials exceeded summer rates and were higher than the sum of rates in single species trials, suggesting a synergistic effect of prey presence on mortality. In contrast, summer mortality rates in mixed prey trials were reduced relative to single taxa trials, suggesting an antagonism where the presence of alternative prey reduced predation on both. In the field, where seasonal changes in abiotic conditions are expected in north temperate streams, species interactions should change as well. Collectively, these observations show that environmental context (*i.e.*, temperature, substrate position, and predator presence) modifies biotic interactions between stream dwelling insects and that cold season interactions, including predation, can be significant.

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#### LITERATURE CITED

- ABRAHAMS, M. AND L. M. DILL. 1989. A determination of the energetic equivalence of the risk of predation. *Ecology*, **70**:999–1007.
- CHARNOV, E. L. 1976. Optimal foraging: the marginal value theorem. *Theoret. Pop. Biol.*, **9**:129–136.
- COOPER, S. D., D. W. SMITH AND J. R. BENCE. 1985. Prey selection by freshwater predators with different foraging strategies. *Can. J. Fish. Aquat. Sci.*, **42**:1720–1732.
- CULP, J. M. AND G. J. SCRIMGEOUR. 1993. Size-dependent diel foraging periodicity of a mayfly grazer in streams with and without fish. *Oikos*, **68**:242–250.
- DILL, L. M. AND A. H. G. FRASER. 1997. The worm returns: hiding behavior of a tube dwelling marine polychaete, *Serpula vermicularis*. *Behav. Ecol.*, **8**:186–193.
- EVANS, E. D. AND H. H. NEUNZIG. 1996. Megaloptera and aquatic neuropteran, p. 298–308. *In*: R. W. Merritt and K. W. Cummins (eds.). An introduction to the aquatic insects of North America, 3<sup>rd</sup> ed. Kendall/Hunt Publishing, Dubuque, IA. 862 p.
- FELTMATE, B. W., R. L. BAKER, AND P. J. POINTING. 1986. Distribution of the stonefly nymph *Paragnetina media* (Plecoptera: Perlidae): influence of prey, predators, current speed, and substrate composition. *Can. J. Fish. Aquat. Sci.*, **43**:1582–1587.
- FRASER, D. F. AND F. A. HUNTINGFORD. 1986. Feeding and avoiding predation hazard: the behavioral response of prey. *Ethology*, **73**:56–68.
- FULLER, R. L. AND P. A. DESTEFFAN. 1988. A laboratory study of the vulnerability of prey to predation by three aquatic insects. *Can. J. Zool.*, **66**:875–878.
- AND H. B. N. HYNES. 1987. Feeding ecology of three predacious aquatic insects and two fish in a riffle of the Speed River, Ontario. *Hydrobiologia*, **150**:243–255.
- HAYASHI, F. AND M. NAKENE. 1989. Radio tracking and activity monitoring of the dobsonfly larva, *Protohermes grandis* (Megaloptera: Corydalidae). *Oecologia*, **78**:468–472.
- HEITHAUS, M. R. AND L. M. DILL. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology*, **83**:480–491.
- HILDREW, A. G. AND C. R. TOWNSEND. 1976. The distribution of two predators and their prey in an iron rich stream. *J. Anim. Ecol.*, **45**:41–57.
- HOLOMUZKI, J. R. AND S. H. MESSIER. 1993. Habitat selection by the stream mayfly *Paraleptophlebia guttata*. *J. N. Amer. Benthol. Soc.*, **12**:126–135.
- HURYN, A. D. AND J. B. WALLACE. 2000. Life history and production of aquatic insects. *Ann. Rev. Entomol.*, **45**:83–110.

- JOHNSON, P. D. AND K. M. BROWN. 1997. The role of current and light in explaining the habitat distribution of the lotic snail *Elimia semicarinata* (Say). *J. N. Amer. Benthol. Soc.*, **16**:545–561.
- KREBS, J. R. AND N. B. DAVIES. (eds.). 1991. Behavioural ecology: an evolutionary approach. Blackwell Scientific Publications, Oxford. 482 p.
- KOHLER, S. L. AND M. A. MCPEEK. 1989. Predation risk and the foraging behavior of competing insects. *Ecology*, **70**:1811–1825.
- LANCASTER, J. AND A. G. HILDREW. 1993. Flow refugia and the microdistribution of lotic macroinvertebrates. *J. N. Amer. Benthol. Soc.*, **12**:385–393.
- , A. G. HILDREW AND C. R. TOWNSEND. 1988. Competition for space by predators in streams: field experiments on a net-spinning caddisfly. *Freshwat. Biol.*, **20**:185–193.
- MATCZAK, T. Z. AND R. J. MACKAY. 1990. Territoriality in filter-feeding caddisfly larvae: laboratory experiments. *J. N. Amer. Benthol. Soc.*, **9**:26–34.
- MCÁULIFFE, J. R. 1984. Competition for space, disturbance, and the structure of a benthic stream community. *Ecology*, **65**:894–908.
- MICHAEL, D. I. AND D. A. CULVER. 1987. Influence of plecopteran and megalopteran predators on *Hydropsyche* (Trichoptera: Hydropsychidae) microdistribution and behavior. *J. N. Amer. Benthol. Soc.*, **6**:46–55.
- MINSHALL, G. W. 1984. Aquatic insect-substratum relationships, p. 358–429. *In*: V. H. Resh and D. M. Rosenberg (eds.). The ecology of aquatic insects. Praeger Publishers, Inc., New York. 625 p.
- MOORE, M. K. AND V. R. TOWNSEND, JR. 1998. The interaction of temperature, dissolved oxygen, and predation pressure in an aquatic predator-prey system. *Oikos*, **81**:329–336.
- MOUTKA, T. 1993. Microhabitat use by predaceous stream insects in relation to seasonal changes in prey availability. *Ann. Zool. Fenn.*, **30**:287–297.
- PANIS, L. I., B. GODDEERIS, AND R. VERHEYEN. 1996. On the relationship between vertical microdistribution and adaptations to oxygen stress in littoral Chironomidae (Diptera). *Hydrobiologia*, **318**:61–67.
- PECKARSKY, B. L. 1979. Biological interactions as determinants of distributions of benthic invertebrates of stony streams. *Limnol. Oceanogr.*, **24**:59–68.
- . 1984. Predator-prey interactions among aquatic insects, p. 196–254. *In*: V. H. Resh and D. M. Rosenberg (eds.). The ecology of aquatic insects. Praeger Publishers, Inc., New York. 625 p.
- . 1987. Mayfly cerci as defense against stonefly predation: deflection and detection. *Oikos*, **48**:161–170.
- . 1996. Predator-prey interactions, p. 431–452. *In*: F. R. Hauer and G. A. Lamberti (eds.). Methods in stream ecology. Academic Press, San Diego, CA. 674 p.
- , S. D. COOPER AND A. R. McINTOSH. 1997. Extrapolating from individual behavior to populations and communities in streams. *J. N. Amer. Benthol. Soc.*, **16**:375–390.
- AND C. A. COWAN. 1995. Microhabitat and activity periodicity of predatory stoneflies and their mayfly prey in a western Colorado stream. *Oikos*, **74**:513–521.
- PENNUTO, C. M. 2000. Effects of larval density and movement behavior on emergence success of a midge commensal. *Aquatic Ecol.*, **34**:177–184.
- AND F. J. DeNOVELLES, JR. 1993. Behavioral responses of *Drunella coloradensis* (Ephemeroptera) to short-term pH reductions. *Can. J. Fish. Aquat. Sci.*, **50**:2692–2697.
- ROBERTSON, A. L., J. LANCASTER AND A. G. HILDREW. 1995. Stream hydraulics and the distribution of microcrustacea: a role for refugia? *Freshwat. Biol.*, **33**:469–484.
- SCRIMGEOUR, G. J. AND J. M. CULP. 1994. Foraging and evading predators: the effect of predator species on a behavioral trade-off by a lotic mayfly. *Oikos*, **69**:71–79.
- , ——— AND K. J. CASH. 1994a. Anti-predator responses of mayfly larvae to conspecific and predator stimuli. *J. N. Amer. Benthol. Soc.*, **13**:299–309.
- , ——— AND F. J. WRONA. 1994b. Feeding while avoiding predators: evidence for a size-specific trade-off by a lotic mayfly. *J. N. Amer. Benthol. Soc.*, **13**:368–378.

- SWEENEY, B. W. 1984. Factors influencing life-history patterns of aquatic insects, p. 56–100. *In*: V. H. Resh and D. M. Rosenberg (eds.). *The ecology of aquatic insects*. Praeger Publishers, Inc., New York. 625 p.
- TURNER, A. M. 1997. Contrasting short-term and long-term effects of predation risk on consumer habitat use and resources. *Behav. Ecol.*, **8**:120–125.
- VAUGHN, C. C. 1986. The role of periphyton abundance and quality in the microdistribution of a stream grazer, *Helicopsyche borealis* (Trichoptera: Helicopsychidae). *Freshwat. Biol.*, **16**:485–493.
- WOOTON, J. T. 1994. The nature and consequences of indirect effects in ecological communities. *Ann. Rev. Ecol. Syst.*, **25**:443–466.

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