

Multiple predator effects on microdistributions, survival, and drift of stream hydropsychid caddisflies

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Abstract. We studied microdistributions, survival, and drift of larval hydropsychid caddisflies in the physical and/or chemical presence of 2 types of benthic predators with different foraging modes. Sculpins (*Cottus bairdi*, *C. cognatus*) are ambush predators, whereas perlid stoneflies (*Acroneuria*, *Paragnetina*) are stalkers, and stoneflies are an intermediate predator consumed by sculpins. Hydropsychid larvae in a northern Michigan stream were significantly more abundant in crevices than on flat surfaces on real cobbles in riffles with both predators. Larval colonization on experimental substrates (bricks) in 7 riffles was greater in crevices (grooves) than on flat surfaces, and the greatest differences in larval densities between these microhabitats occurred where predator densities were highest. Mean size (head capsule width) of larvae in both microhabitats was negatively related to densities of sculpins, but not stoneflies. A multifactorial experiment done in artificial stream channels revealed that caddisflies selected crevices over flat surfaces even in predator-free conditions. Sculpin and stonefly effects on hydropsychid survival were additive, suggesting a lack of multiple predator effects. Crevices provided a refuge from predators; however, stoneflies were more effective than large sculpins (>65 mm total length) at consuming hydropsychids in crevices. Like caddisflies, stoneflies predominantly occupied crevices, but stonefly crevice use and activity were not affected by sculpins, and no stoneflies were consumed by sculpins. Caddisfly drift was ~3 to 4× greater in the physical presence of each predator than in predator-free channels. However, drift by caddisflies in the physical presence of both predators was lower than expected (i.e., nonadditive), suggesting it is less risky to remain in retreats (i.e., immovable cases) than to drift when both predators are present. Elevated chemical cues of either predator did not trigger drift responses by these sedentary prey. Crevice use and drift appear to be key mechanisms enabling larval hydropsychid caddisflies to coexist with a multispecies complex of predators.

Key words: caddisfly crevice use, stoneflies, sculpins, predator chemical and physical presence, intermediate predator, predator size, retreat construction.

Prey often encounter multiple predators in natural communities. Multiple predators can have risk-reducing (Rosenheim et al. 1993, Wisinger and McGrady 1993, Crowder et al. 1997) or risk-enhancing (Soluk and Collins 1988a, Soluk 1993) effects on prey, if they cause lower or higher predation rates than expected, respec-

tively. These different effects can be ascribed to different foraging modes and efficiencies of predators, and to interactions among predators (Crowder et al. 1997, Sih et al. 1998, Eklöv and Werner 2000). Thus, different predators pose different threats to prey, and to each other (i.e., intraguild predation). Further, prey responses to multiple predators are influenced by environmental cues that allow prey to assess the relative risk of predation from any one predator. Prey often use a variety of cues (e.g., chemical, visual, tactile) to detect the presence of predators (Dodson et al. 1994); yet these cues may vary in im-

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portance depending on a suite of interacting biotic and physical conditions, such as predator foraging mode (e.g., ambush vs stalking), predator density, and chemical cue concentration and type. Evaluating trophic, microdistributional, and behavioral responses between predators and between predators and prey, and the cues that trigger these responses, is critical to understanding multiple predator effects (MPEs) in aquatic systems (McIntosh and Peckarsky 1999, Turner et al. 1999, Eklöv and Werner, 2000).

Our study examines how 2 common benthic-feeding predators, sculpins and perlid stoneflies, affect microdistributions and survival of sedentary hydroptychid caddisflies. Larval hydroptychids are net-spinning filter feeders and are often an integral part of food webs in small streams to large rivers (Wiggins 1996). Many species construct retreat tubes of tiny stones or plant material on surfaces of stones in riffles (e.g., Fairchild and Holomuzki 2002). Retreats serve a dual purpose as refuge from predators (Fuller and Rand 1990) and substrate for attaching silken, food-capturing (sestonic diatoms, leaf detritus, and microcrustaceans) nets (Fuller and Mackay 1980). Larval hydroptychids are eaten by both sculpins (Flecker and Allan 1984) and stoneflies (Michael and Culver 1987). Further, perlid stoneflies affect hydroptychid drift rates in structurally simple environments (Holomuzki et al. 1999) and distributions among stone sizes (Michael and Culver 1987). Sculpin effects on hydroptychid behaviors are largely unknown. Differences in foraging behaviors and trophic status between these predators may elicit different responses by caddisflies. Sculpins forage nocturnally by ambushing prey (Greenberg 1991), using both visual (Newman and Waters 1984) and mechanical (e.g., substrate vibrations detected by lateral line organ, Janssen 1990) cues to locate prey, whereas stoneflies typically forage by stalking, using mostly tactile cues to detect prey (Peckarsky 1980). Moreover, sculpins eat stoneflies and can alter their habitat use and feeding rates (Soluk and Collins 1988b).

We integrate observations from field surveys with experimental data to document the potential risk-enhancing or risk-reducing effects of sculpins and predatory stoneflies on rock surface distributions (crevice use), drift, and survival of hydroptychid caddisflies. Some benthic organisms use crevices on rock surfaces as a refuge from predation (e.g., marine invertebrates,

Catsby and McKillup 1998) or herbivory (e.g., diatoms, Dudley and D'Antonio 1991), indicating these microspaces may be particularly important in maintaining populations of small prey. We define crevices as "recessed areas on rock surfaces, such as pits and . . . cracks" (Bergey 1999) large enough for 4th- and 5th-instar hydroptychid larvae to enclose their retreat tubes. Thus, crevices can be triangular or polygonal in shape, are ≥ 3 mm deep and ≥ 4 mm long, and have a cross-sectional angle of $\leq 90^\circ$. We first quantified crevice use by larvae on real stones in riffles containing both predators. We also conducted an in situ colonization experiment using artificial substrates to relate hydroptychid microdistributions to predator abundance to eliminate historical consequences of larval dispersal on crevice use. Last, we ran a multifactorial experiment in artificial stream channels with controlled flow and substrate conditions to test how larval crevice use, drift, and survivorship were affected by both the chemical and physical presence of sculpins and/or stoneflies. Our aim was to assess single and combined predator effects, and to identify the environmental cues that elicit these effects.

Methods

Study system

The study was conducted in the East and Main branches of the Maple River in Emmet County, northern Michigan, USA. The East Branch is a warm-water, 3rd-order stream that drains Douglas Lake. The East Branch joins the West Branch at Lake Kathleen (lat 45.25°N, long 84.45°W) to form the Main Branch, a 4th-order stream that flows southerly for ~9 km into Burt Lake. Both branches are permanent and flow through mixed coniferous and birch-aspen forests. Streambeds consist mostly of sand (>75%), interspersed with patches of gravel (<16 mm diameter), pebbles (16–64 mm), and cobbles (64–256 mm) that armor underlying sand in shallow, fast-flowing areas. Boulders (>256 mm) are rare, with most being anthropogenically placed near road culverts and steep banks to abate erosion.

Hydropsyche betteni Ross and *Ceratopsyche sparana* Ross are the dominant hydroptychids in the system. Densities of *H. betteni* are highest immediately below lake outlets and beaver dams,

and are positively related to water temperature and amount of algal seston (Fairchild and Holomuzki 2002). In contrast, *C. sparna* densities are highest in distal reaches to lentic habitats and are positively related to total seston. The overwintering generation of both species matures to pupae in mid June, and hatches of new early instars are present by late June to early July. Hydropsychid larvae disperse (i.e., drift) mostly at night (e.g., Holomuzki et al. 1999), and are most abundant on stony substrates (cobbles and boulders) and affixed logs (Fairchild and Holomuzki 2002).

The dominant benthic vertebrate predators in both stream branches are the mottled (*Cottus bairdi* Girard) and slimy (*C. cognatus* Richardson) sculpin. Hydropsychid larvae and baetid mayflies are key food items of both species (Fairchild 2001). The dominant invertebrate predators include the perlid stoneflies *Acroneuria abnormis* Newman, *Agnatina capitata* Pictet, and *Paragnetina media* Walker, and the hellgramite *Nigronia serricornus* Say (Holomuzki 1996). *Paragnetina* generally emerge in late July; however, *A. abnormis* and *A. capitata* are present through August. Hydropsychid larvae comprise ~5% of the diet of perlid stoneflies in both stream branches, and stoneflies are infrequently eaten by sculpins (Fairchild 2001).

Crevice use on cobbles

Use of stone crevices by hydropsychid larvae was quantified in riffles with both predators in 1999 and 2000. Sampling in 1999 was conducted in a 15-m-long, cobble-dominated riffle on the East Branch (mean current speed: 46 cm/s; mean depth: 21 cm) on 8 August, whereas sampling in 2000 was done along a 25-m-long riffle on the Main Branch (46 cm/s; 18 cm deep) on 21 June. Number of crevices and larvae were counted on randomly selected cobbles (64–148 mm, b-axis) in both years (1999: $n = 18$; 2000: $n = 20$), but larval counts in 2000 were separated on the basis of stone surface microhabitat (crevices and flat surfaces). To convert larval counts into density, stone surface area was determined using the aluminum foil technique (Reice 1980). Regression analysis (SAS, version 8, SAS Institute Inc., Cary, North Carolina) was used to assess the relationship between crevice number on stones and hydropsychid density ($\log [x + 1]$ transformed). For stones collected

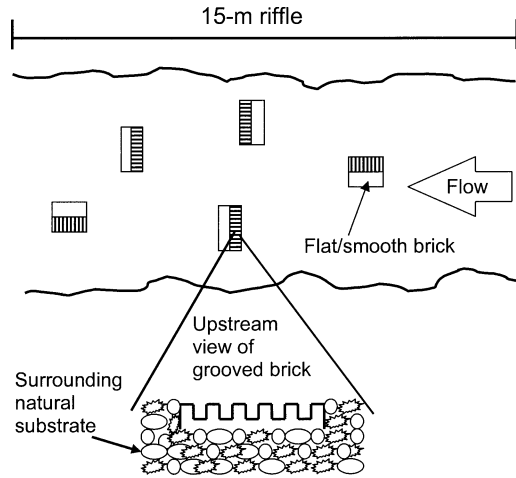


FIG. 1. Diagram of the in situ colonization experiment using 5 brick pairs (1 grooved, 1 flat/smooth) per riffle.

in 2000, the proportion of surface area occupied by crevices was estimated by wrapping the stone in a clear plastic sheet with equidistantly spaced (1 cm) dots, and counting the number of dots touching crevices. The relative area occupied by crevices was calculated by multiplying the number of dots on crevices by total stone area. χ^2 goodness of fit tests using pooled frequencies were done to determine whether microhabitat distributions of larvae were proportional to areas covered by crevices and flat areas on stones.

In situ colonization on artificial substrates

A colonization experiment using clay bricks was done to test whether larval abundance on crevices and flat surfaces was related to predator density. Bricks ($19 \times 9 \times 5.4$ cm) were placed at 3 separate riffles on the East Branch and 4 on the Main Branch on 17 June 2000. Riffles were 15 to 25-m-long stretches of mostly gravel and cobbles, selected on the basis of accessibility, the presence of larval hydropsychids, and similarity in current velocities (26–50 cm/s). Five brick pairs were randomly placed in each riffle so that tops of the bricks were flush with the streambed. Paired bricks were placed side by side, but one brick was placed with the flat surface exposed, whereas the other was placed with the grooved surface exposed (Fig. 1). Grooved bricks provided crevices of one size

(7 mm deep, 14 mm wide, 54 mm long; 5 per brick). Orientation of the grooves to stream flow (parallel or perpendicular) was determined by coin toss.

On 7 July 2000, retreats of hydropsychid larvae were counted in grooves and on flat surfaces of all 35 brick pairs using a viewbox (i.e., glass-bottomed bucket, 20 cm diameter). Previous work showed that 95 to 98% of retreats contained a larva (Fairchild and Holomuzki 2002), and uninhabited retreats were rarely intact (MPF, personal observation). Density in each microhabitat was calculated as the number of larvae per area of each microhabitat per brick (crevices: 76.5 cm²; flat: 102.6 cm²). Subsets of randomly selected larvae (≤ 10 individuals) from grooved and flat microhabitats on each brick were preserved in 70% ethanol to relate size of larvae in microhabitats at each riffle to predator density. Head capsule width, our size metric, was measured to the nearest 0.01 mm using an ocular micrometer. Stonefly and sculpin densities were estimated at each riffle ≤ 1 wk after caddisfly collections. Stonefly density was estimated by averaging larval counts in 5 to 6 Surber samples (30 cm \times 30 cm) from randomly selected locations in each riffle. Sculpin numbers were estimated by electroshocking (Smith-Root[®] model 1029) using a 3-pass depletion procedure (Reynolds 1983), after setting block nets (10-m-long seines) at upstream and downstream ends of each riffle. Linear regressions that incorporated catchability (i.e., degree of diminishing catch per unit effort) were used to estimate the total number of sculpins in each riffle (Krebs 1999).

Differences in hydropsychid densities (log [$x + 1$] transformed) were compared among microhabitat types (groove, flat) and groove orientations (parallel or perpendicular to flow direction) using a 2-way ANOVA (SAS, version 8). Densities in grooves and flat areas were correlated (Pearson's r) with densities of sculpins and stoneflies at riffles. Average head capsule widths of hydropsychids in both microhabitats were also correlated with predator densities at each riffle to assess size-specific effects of predators on caddisfly microdistributions.

Single versus multiple predator effects

Experimental set-up.—Multiple predator effects on hydropsychid microdistributions, drift, and

survival were assessed in a 2 \times 2 factorial design experiment with 4 treatments: 1) no predators, 2) sculpin only, 3) stoneflies only, and 4) both sculpin and stoneflies. Predator combinations were manipulated in artificial channels from 15 to 18 August 2000 at the University of Michigan Biological Station Stream Research Facility located 3 km east of Pellston, Michigan. The facility lies adjacent to the East Branch of the Maple River, from which water was drawn into channels using 3 Monarch[®] pumps. Pumps diverted water to 8 headtanks (each 65-L capacity). Netting (200 μ m) over inflow pipes into headtanks prevented the introduction of other macrobenthic animals into channels. Each headtank supplied water to 4 channels (2.5 m \times 0.2 m \times 0.15 m) constructed of wood and finished with marine varnish. Water flowed through channels for 1 wk prior to the experiment to dissipate varnish odors. Both head tanks and valves at the heads of channels allowed regulation of discharge (0.88 L/s) in the 32 flow-through channels. Water in each channel flowed first through a substrate-free plunge pool (0.5 m long) then through a 1.5-m-long substrate-containing section. A brick (19 \times 9 \times 5.5 cm) with holes (10 holes, each 1.5 cm dia.) at the downstream end of the plunge pool served as a collimator to help reduce turbulence of inflow before reaching substrate-containing sections. Substrates were 8 clay tiles (8 \times 8 cm) fastened to the bottom of each channel with nontoxic silicone sealant. A mosaic of crevices and flat areas was created by randomly placing and gluing 7 smaller clay tiles (2 \times 3 \times 1.3 cm) to the tops of every other large tile using silicone sealant. This arrangement provided hydropsychids with 2 surfaces upon which to construct retreats: crevices and flat surfaces. Knee-high nylon stockings (~ 200 μ m mesh) fastened to PVC outlet tubes (20 cm long, 10 cm diameter) with hose clamps captured drifting hydropsychids and stoneflies. Hardware cloth (6 mm mesh) placed across downstream outlets allowed caddisflies and stoneflies, but not sculpins, to leave channels. Channels were shaded to $\sim 10\%$ incident light (~ 200 μ m quanta m⁻² h⁻¹) with shade cloth to simulate light conditions in the East Branch. Diel temperatures (16–19.5°C), current velocity (~ 26 cm/s), and water depth (~ 7 cm) were similar among channels.

Predator physical and chemical cues.—To evaluate environmental cues used by larvae to assess

predator presence, the experiment was done in 2 phases: a 48-h-long phase in which larvae were exposed only to predator chemical cues, immediately followed by a 24-h-long phase in which larvae were physically exposed to predators. However, because the Stream Research Facility draws water from a stream with predator-borne chemicals, our chemical phase compared ambient to elevated levels of predator chemical cues. Late-instar *A. abnormis* (13–21 mm long) and *P. media* (14–23 mm long) and mottled and slimy sculpins (58–78 mm total length [TL]) were collected from the East Branch on 14 August. Stoneflies and sculpins were held separately in aerated aquaria (17–18°C) overnight. On 15 August, sculpins and/or stoneflies (75% *Acro-neuria*, 25% *Paragnetina*) were caged and placed in plunge pools. Cages were 20-cm-long, PVC pipe with ends covered by nylon screening (2 mm mesh) to contain animals but allow predator chemicals to diffuse into channels. Only one sculpin was stocked per cage (7.6 cm diameter), but cages with stoneflies (5.1 cm diameter) contained 4 larvae to attempt to equalize predator biomass per channel. After cage placement, 50 caddisflies (4th and 5th instars [head capsule width: 0.9–1.2 mm]; ~90% *H. betteni*) collected from the Main Branch were sorted into groups of 10 in plastic containers and added to substrate sections of each channel. Discharge was briefly reduced by ~95% to allow larvae to attach to tiles. Any larva that washed into drift nets at the time of stocking was retrieved and replaced in the tile area of each channel. Experimental densities of hydropsychids (130 individuals/m²) and stoneflies (10 individuals/m²) were within natural limits (Holomuzki et al. 1999); however, sculpin densities (2.5 fish/m²) were higher than those in the Maple River (0.3–1.0 fish/m²).

Forty-eight hours after larval additions (~1300 h), caddisfly retreats in different microhabitats were counted with a viewbox. Animals in drift nets also were counted to evaluate hydropsychid drift responses to elevated predator chemical cues. Immediately after the chemical cue phase, predators were removed from cages and allowed to move freely in channels. For combined predator treatments, stoneflies were released from cages 15 min before sculpins. Predator activity was observed 8 h after predator release between 2200 and 2400 h to relate hydropsychid drift to predator movements and

to assess whether stonefly activity was affected by sculpin presence. Predator positions were observed by scan sampling using a red-filtered headlamp and recorded every 20 min (~35 s per channel) for 2 h from a grid system over channels. Grid schematics consisted of a visual quartering of each large clay tile in channels. Activity was scored differently for the 2 predators because individual stoneflies were not marked, and hence could not be distinguished. Stonefly activity per scan was scored from 0 to 4, depending on how many stoneflies were in different positions in each of the 6 scans. Stonefly activity in each channel was expressed as the total number of position changes/h. For each sculpin, activity was scored as the sum of the distances moved between quadrats over all scans, and expressed as cm moved/h.

Twenty-four hours after predator release, hydropsychids were again counted in each microhabitat and in drift nets. However, in this phase, caddisfly survival in each channel was also quantified. Recovered dead larvae (i.e., partially eaten), plus those missing from the original 50, were used to compute hydropsychid survivorship. Stoneflies and sculpins were preserved in 70% ethanol and 10% formalin, respectively, dissected, and gut contents analyzed to help quantify survivorship.

Statistical analyses.—Separate 2-way ANOVAs (SAS, version 8) were used to test single versus MPEs on caddisfly crevice use, drift, and survivorship. Demonstrating MPEs requires evaluation of the interaction term in a 2-way ANOVA (i.e., stonefly × sculpin interaction) (Billick and Case 1994, Sih et al. 1998). However, because crevice use, drift, and survivorship were interdependent, MANOVAs were first run for each phase of the experiment. For the 1st phase, the effects of predator chemical cues on crevice use (log [$x + 1$] transformed densities) and drift (arcsine-transformed proportions) were assessed. Crevice use was only analyzed during the chemical phase of the experiment because decisions whether to build retreats or drift are made shortly after larval placement in channels (Holomuzki et al. 1999). For the 2nd phase, the effects of the physical presence of predators on caddisfly survivorship (arcsine-transformed proportions) and drift (i.e., retreat abandonment) were assessed. Survivorship was not assessed in the 1st phase because it was only quantified at the end of the experiment. In addition,

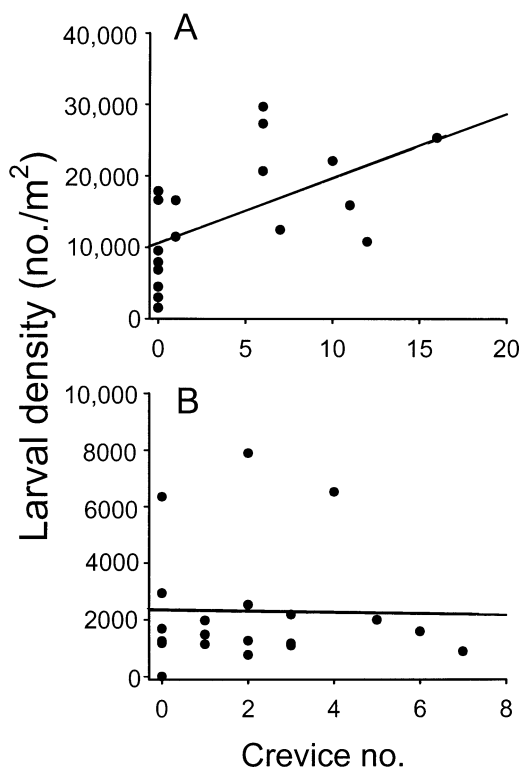


FIG. 2. Hydropsychid density as a function of crevice number on cobbles in the East Branch in August in 1999 (A) and in the Main Branch in June 2000 (B). The line in 1999 was derived from the regression: $y = 10,635 + 903x$.

block (i.e., headtank) was included as a covariate in both models to account for a slight decrease in discharge in the 3 headtanks farthest from the pumps. Two-way ANOVAs were run following significant MANOVAs to assess MPEs.

Correlation analyses were used to evaluate whether hydropsychid drift was related to sculpin and stonefly activity. Size-dependent effects of sculpins and stoneflies on caddisfly survival were tested by regressing the number of larvae consumed against TL of the individual predator. To determine sculpin effects on stoneflies, stonefly activity was compared with and without sculpins using 1-way ANOVA. Whether stonefly microhabitat use (i.e., nos. in crevices and flat areas) differed in the presence and absence of sculpins was determined using a χ^2 goodness of fit test.

At the end of the experiment, 2 channels had 3 more hydropsychid larvae than the initial 50

placed in each stream. Observations from these channels were deleted from all analyses.

Results

Crevice use on cobbles

Hydropsychid densities were a function of crevice number on cobbles in the East Branch in June 1999 ($r^2 = 0.27$, $n = 18$, $p = 0.015$), but not in the Main Branch in August 2000 ($r^2 = 0.01$, $n = 20$, $p = 0.93$) (Fig. 2A, B). Larvae occurred on 15 of 20 stones in 2000 when surface areas of microhabitats on each cobble were quantified. Crevices were occupied in disproportionately higher frequencies than their occurrence on stones (0 to 20% of surface area) ($\chi^2 = 187.8$, $df = 1$, $p < 0.001$), but flat surfaces were occupied in proportion to their area on stones ($\chi^2 = 0.8$, $df = 1$, $p > 0.90$).

In situ colonization on artificial substrates

Hydropsychid colonization was significantly greater in crevices (grooves) than on flat surfaces of bricks (ANOVA: $F_{1,68} = 20.13$, $p = 0.0001$) (Fig. 3A). A total of 171 larvae constructed retreats in crevices on bricks in all riffles, whereas 162 occupied flat surfaces, despite flat areas comprising 69.6% of all available habitat. Hydropsychid densities in crevices were not influenced by orientation to streamflow (microhabitat \times orientation interaction term: $F_{1,68} = 1.95$, $p = 0.17$).

Larval densities in crevices were not related to densities of either predator (sculpins: $r = -0.014$, $F_{1,5} = 0.001$, $p = 0.977$; stoneflies: $r = 0.431$, $F_{1,5} = 1.14$, $p = 0.335$). Densities on flat areas also showed no relationship with predator density (both $p \geq 0.224$). However, the greatest difference in caddisfly densities between crevices and flat surfaces occurred in riffles 1, 2, and 3 on the East Branch (Fig. 3A), where stonefly and sculpin densities were highest (Table 1). Moreover, most caddisflies in these 3 riffles were 2nd instars, whereas those at the other sites were a mix of 2nd through 5th instars. Mean size (head capsule width) of larvae in microhabitats (Fig. 3B) was negatively related to densities of sculpins (crevice: $r = -0.729$, $F_{1,5} = 5.67$, $p = 0.063$; flat: $r = -0.782$, $F_{1,5} = 7.85$, $p = 0.038$), but not of stoneflies (both $p \geq 0.192$).

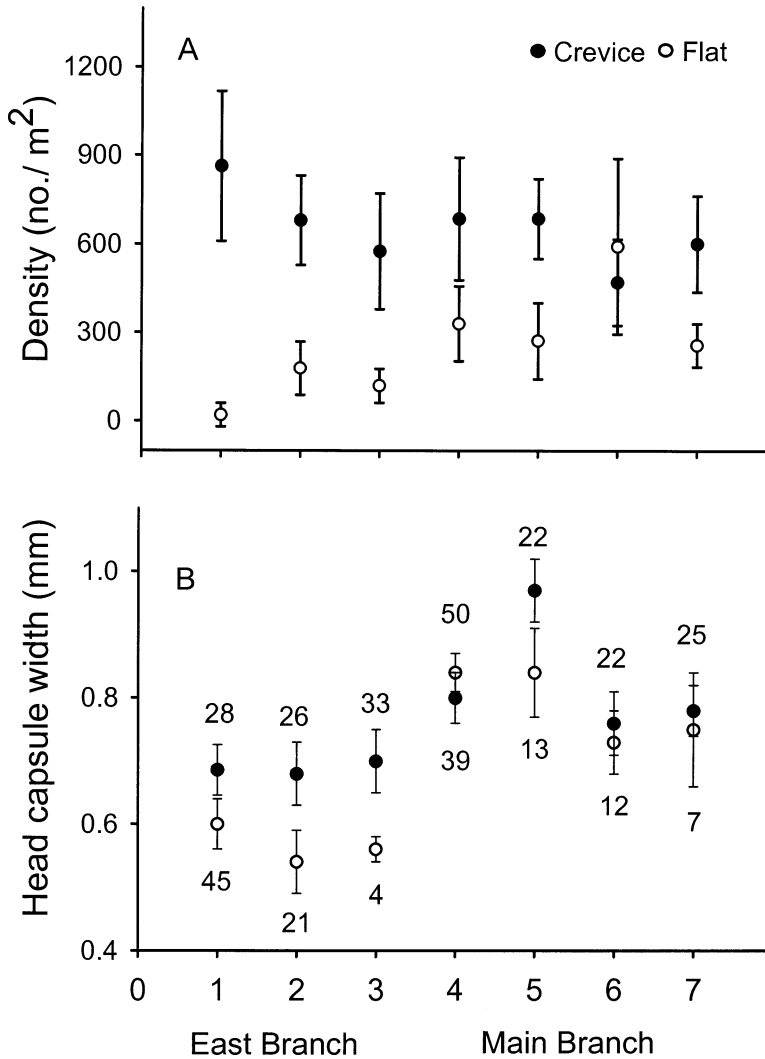


FIG. 3. Mean (± 1 SE) density (A) and head capsule widths (B) of hydropsychid larvae in crevices and on flat surfaces on artificial substrates (bricks) in the in situ colonization experiment on the East (riffles 1–3) and Main (riffles 4–7) branches. Numbers above and below symbols in panel B are numbers of head capsules measured in crevices and flat surfaces, respectively.

Single versus multiple predator effects

Larvae built more retreats in crevices (522) than on flat surfaces (7) ($\chi^2 = 1376.8$, $df = 1$, $p < 0.0001$), despite flat surfaces comprising 70% of available substrates. However, neither crevice use nor drift was affected by predator treatment during the chemical phase of the experiment (MANOVA: Wilks' $\lambda = 0.899$, $F_{6,48} = 0.440$, $p = 0.849$). Overall, hydropsychid drift was significantly higher in the chemical phase ($\bar{x} \pm 1$ SE: $12.9\% \pm 1.5$) than in the physical phase (3.5%

± 0.6) ($F_{1,59} = 33.25$, $p < 0.001$) (Fig. 4A, B), largely because drift or retreat construction decisions were made in the 1st phase of the experiment. However, caddisfly drift and survivorship were affected by the physical presence of predators (Wilks' $\lambda = 0.562$, $F_{6,48} = 2.669$, $p = 0.026$), but not block (i.e. headtank) (Wilks' $\lambda = 0.965$, $F_{2,24} = 0.440$, $p = 0.649$). Caddisfly drift was ~ 3 to $4\times$ greater in the physical presence of each predator than in predator-free channels (Fig. 4B). Drift was significantly affected by stonefly presence, but only marginally affected

TABLE 1. Mean (± 1 SE) predator densities in the 7 study riffles in the East and Main branches of the Maple River, Michigan. SEs are not presented for sculpin densities because estimates were made at the riffle scale.

Study sites	Sculpin density (no./m ²)	Stonefly density (no./m ²)
East Branch		
1	0.56	28.9 (4.4)
2	0.50	26.7 (9.0)
3	0.85	15.6 (6.7)
Main Branch		
4	0.41	6.7 (2.7)
5	0.23	18.5 (6.2)
6	0.36	20.0 (10.8)
7	0.28	4.4 (2.7)

by sculpin presence (Table 2). The higher-order interaction (significant sculpin \times stonefly term) suggests that the physical presence of sculpins and stoneflies on caddisfly drift was lower than expected (i.e., nonadditive) (Table 2, Fig. 4B). Hydropsychid drift was not related to sculpin (limits: 5–165 cm/h) or stonefly (limits: 0–8 movements/h) activity (both $r \leq 0.224$, both $p > 0.15$). Moreover, differences in stonefly activity were not detected between the combined predator and stonefly alone treatments (ANOVA: $F_{1,13} = 0.60$, $p = 0.56$), suggesting sculpins had no effect on stonefly activity. Like caddisflies, stoneflies predominantly used crevices (77% of all microhabitat observations) in both the presence ($\chi^2 = 19.2$, $df = 1$, $p < 0.001$) and absence ($\chi^2 = 22.3$, $df = 1$, $p < 0.001$) of sculpins. Sculpins did not eat any stoneflies in the combined predator treatment.

Hydropsychid survival was significantly negatively affected by stoneflies, but not sculpins (Table 2, Fig. 5). Number of hydropsychid larvae consumed by stoneflies was not influenced by sculpin movement or size (both $r^2 \leq 0.10$, $p \geq 0.40$). Consumption of caddisflies was not a function of stonefly size ($r^2 = 0.10$, $n = 60$, $p = 0.455$); however, small sculpins consumed more hydropsychids than large ones ($r^2 = 0.26$, $n = 15$, $p = 0.026$).

Discussion

Crevice use by hydropsychid larvae

Stone surface microtopography greatly influenced microdistributions of larval hydropsychid

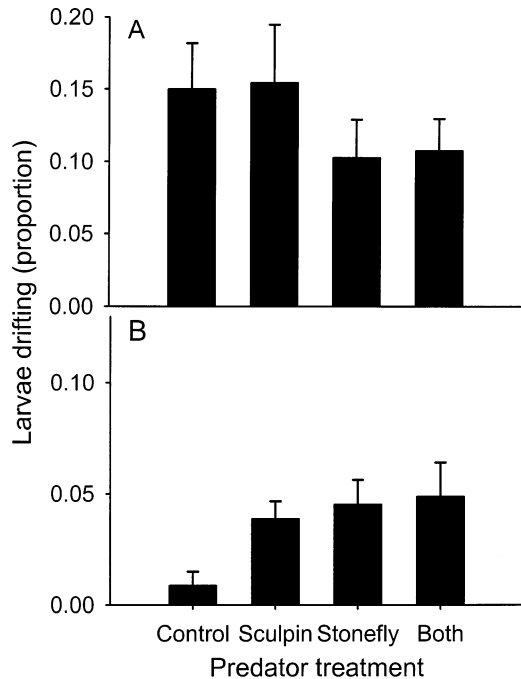


FIG. 4. Mean (± 1 SE) proportion of hydropsychids drifting in predator treatments during the chemical (A) and physical presence (B) phases of the multifactorial experiment. Number of channels used for analyses were: no predators ($n = 8$), sculpin alone ($n = 7$), stoneflies alone ($n = 7$), and both predators ($n = 8$).

caddisflies. Caddisfly density was greater in crevices than on flat areas, suggesting crevices provide survival advantages over other surfaces. Downes and Jordan (1993) similarly found that substrate surface topography (pit number) positively influenced hydropsychid density. Our work indicated that larval hydropsychids do not actively seek crevices to avoid benthic-feeding predators. However, crevices apparently do function as a refuge from some predators. In the colonization experiment, differences between densities in crevices and on flat surfaces were greatest in the 3 riffles where predator densities were highest. Moreover, in the multiple predator experiment, large sculpins (>65 mm TL) were relatively ineffective at consuming caddisfly larvae inhabiting crevices, presumably because crevice access was restricted by fish size. It is well recognized that increased structural complexity can diminish lethal predator effects on prey (e.g., Flecker and Allan 1984, Michael and

TABLE 2. Results of 2-way ANOVAs testing for single and combined predator effects on caddisfly drift and survival in the physical phase of the multifactorial experiment.

Source of variation	SS	df	F	p
Drift				
Sculpin	0.035	1	3.803	0.062
Stonefly	0.039	1	4.208	0.050
Sculpin \times stonefly	0.058	1	6.233	0.019
Error	0.242	26		
Survival				
Sculpin	0.021	1	0.457	0.505
Stonefly	0.191	1	4.145	0.052
Sculpin \times stonefly	0.001	1	0.0233	0.881
Error	1.195	26		

Culver 1987, Power 1992). Our results suggest that this relationship holds even at small spatial scales (i.e., single stones). Crevice use by hydropsychids may be a particularly effective means of deterring predators, given that other prey (e.g., tadpoles, mayfly and damselfly larvae) in similar multiple predator studies have suffered far greater mortality (>30%) when also provided structural refugia (Soluk and Collins 1988a, b, Wissinger and McGrady 1993).

Crevices on stone surfaces also may provide caddisflies refuge from hydraulic stress (e.g., shears, turbulence) in fast waters (Way et al. 1995), favorable hydrodynamic conditions (microvelocities) that enhance filtering efficiencies (Osborne and Herricks 1987), and stable attachment locations for retreats and catchnets (Dudley et al. 1986). These benefits also may explain why larvae overwhelmingly used crevices over flat areas even in the absence of predators in the multiple predator experiment.

Predator effects on hydropsychid larvae

Hydropsychid survival was additive in the multiple predator experiment (i.e., non-significant sculpin \times stonefly interaction), suggesting that sculpins and stoneflies had neither risk-enhancing nor risk-reducing effects. However, these same predators can have MPEs on prey, depending on prey type and behavior. When allowed to prey upon *Ephemera* mayfly larvae, sculpins and stoneflies together captured more prey than expected (Soluk and Collins 1988a, b). Thus, the overall effect was risk-enhancing.

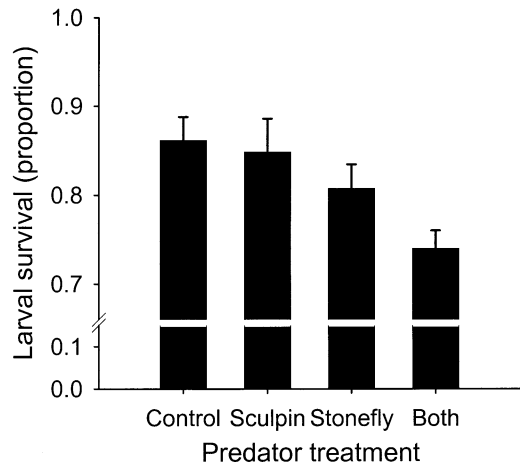


FIG. 5. Mean (+1 SE) proportion of larvae surviving in predator treatments in the physical presence phase of the multifactorial experiment. Number of channels used for analyses were: no predators ($n = 8$), stoneflies alone ($n = 7$), sculpin alone ($n = 7$), and both predators ($n = 8$).

However, when both preyed upon *Baetis* mayflies, fewer prey were taken than expected. Thus, the overall effect for *Baetis* was risk-reducing. The results of Soluk and Collins (1988a, b) stem from different escape tactics used by prey (i.e., *Ephemera*: crawl; *Baetis*: drift) and from altered stonefly behavior in the presence of sculpins (e.g., avoiding open areas, hiding). In contrast, we did not detect any sculpin effects on stonefly movement or microhabitat use, and no stoneflies were eaten by sculpins. The latter result is consistent with dietary information that suggests sculpins seldom eat stoneflies in either branch of the Maple River (Fairchild 2001). These collective results likely explain the lack of MPEs on caddisfly survival. Like *Baetis*, the primary escape tactic used by hydropsychids in our experiment was drift. However, their propensity to drift after retreat construction was relatively low, as evidenced in the physical phase of the multifactorial experiment. The threat of predation may have to be particularly high for larvae to abandon retreats that are energetically costly to construct.

Caddisfly drift significantly increased in the physical presence of stoneflies, but only marginally in the physical presence of sculpins ($p = 0.062$). Drift is a common predator escape mechanism used by many stream macroinvertebrates (e.g., Forrester 1994, Peckarsky 1996), including

hydropsychids (Michael and Culver 1987). Predator size and foraging mode may be particularly important in triggering drift responses by hydropsychids. Stoneflies were small enough to stalk and attack larvae in crevices in experimental streams, which resulted in retreat abandonment. Our findings also indicate small sculpins were more effective at consuming caddisflies than large ones, probably because smaller sculpins with comparatively smaller heads can more easily extract caddisflies from crevices. However, hydropsychid drift was lower than expected (i.e., nonadditive) when both predators were physically present. This MPE suggests that it is less risky for a larva to remain in a retreat than to drift when both sculpins and stoneflies are present. Abandoning a retreat, even in a crevice, and drifting to escape a stalking stonefly may increase the likelihood of consumption by ambushing sculpins or downstream drift-feeding predators (e.g., trout) (Dahl and Greenberg 1996). However, this risk may be relatively small for hydropsychids in our study system given that these caddisflies drift only short distances (<2 m) (Holomuzki and Van Loan 2002).

Elevated chemical cues (i.e., kairomones) of stoneflies and sculpins did not affect caddisfly drift. This response contrasts with numerous other studies reporting that chemical cues of predators elicited increased drift by benthic prey (e.g., anurans, salamanders, mayflies, amphipods; see review by Dodson et al. 1994). However, focal prey organisms in these kinds of studies have generally been highly mobile and able to quickly crawl or swim away from approaching predators. Hydropsychids are sedentary, and the undulatory movements and time needed to leave a retreat to drift may make a larva particularly vulnerable to a nearby, fast-attacking predator. Moreover, predator-borne chemical cues alone may not provide enough information on predation risk to cause larvae to abandon retreats that are energetically costly to construct. Hydropsychids likely heavily rely on mechanical stimuli (small hydrostatic pressure waves or substrate vibrations) that provide more reliable close-range information on predator approach and direction (i.e., upstream, downstream, adjacent) (Dodson et al. 1994). Regardless of prey mobility, our understanding of aquatic insect sensory modalities is limited. Further investigations focusing on how predators interact in natural habitats and on how prey de-

tect and respond to multiple predators will yield additional insight on the importance of MPEs on benthic predator-prey relationships.

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