Predator–prey interactions in a variable environment: responses of a caddis larva and its blackfly prey to variations in stream flow

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Predator–prey studies in streams have traditionally focused on mayfly–stonefly interactions in relatively constant flow conditions. In reality, however, lotic prey encounter multiple types of predators, most of which are restricted to low-velocity microhabitats. By contrast, some invertebrate prey may occur in very high current velocities. For example, many blackfly species are able to feed at velocities of 100 cm s^{-1}, whereas even moderate currents reduce the hunting efficiency of their invertebrate predators. The caddisfly larvae of the genus *Rhyacophila*, however, may be an exception to the pattern of reducing predator efficiency with increasing velocity. Using a combination of laboratory and field experiments and behavioral field observations, we examined the interaction between predatory *Rhyacophila* caddis larvae and larval blackflies along a velocity gradient of 20–120 cm s^{-1}. In laboratory experiments, *Rhyacophila* preferred currents slower than 50 cm s^{-1} while blackflies exhibited a wide tolerance of currents and frequently occurred in currents exceeding 100 cm s^{-1}. In direct field observations, total activity and distance moved by *Rhyacophila* were similar at all current velocity regimes tested, but frequency of predation attempts on blackflies was lowest at the highest velocities (> 100 cm s^{-1}). In a field colonization study, blackflies avoided substrates with the slowest velocities (< 40 cm s^{-1}), as also did the caddis larvae. Only velocities approaching 100 cm s^{-1} provide blackflies with refuge from predation by *Rhyacophila*. Being able to maneuver across a wide range of velocities, *Rhyacophila* may have more pervasive effects on their prey than other lotic invertebrate predators.

Introduction

Flow is a "master variable" (Power *et al*. 1995) in the life of benthic organisms, influencing their populations and communities. Many lotic organisms are directly dependent upon stream flow, and flow also modifies the outcome of predator-prey interactions and interspecific competition

(Hart & Finelli 1999). Both observational and experimental studies have shown that invertebrate grazers, for example, are constrained by high current velocities, with subsequent effects on the spatial variability of algal assemblages (Poff & Ward 1995). However, very few studies have explicitly considered flow variability as a factor modifying predator–prey interactions in streams (but *see* Malmqvist & Sackmann 1996). Furthermore, predator–prey studies in streams have traditionally used predatory stoneflies as model organisms (e.g. Allan *et al.* 1987, Peckarsky & Penton 1989, Tikkanen *et al.* 1997). In nature, however, stream invertebrate prey face multiple predators (e.g. stoneflies, caddisflies, and dragonflies), all of which are effective at slightly different flow conditions (*see* Huhta *et al.* 1999). As a rule, however, the majority of invertebrate predators are greatly impaired by high and variable flows, while some prey types are unrestricted by even very high current velocities (Malmqvist & Sackmann 1996, Meissner *et al.* 2002).

Larval blackflies attain high springtime densities in boreal lake outlets and rivers, and they often serve as principal prey for several vertebrate and invertebrate predators (Malmqvist *et al.* 2004). Blackflies are highly vulnerable to invertebrate predation and are strongly preferred by many lotic predators (Allan *et al.* 1987, Tikkanen *et al.* 1997, Muotka *et al.* 2006). Blackfly ingestion rates typically increase with water velocity (Charpentier & Morin 1994, Finelli *et al.* 2002), although some species show maximum rates at moderate velocities (Malmqvist & Sackmann 1996). Nevertheless, many blackfly species are able to feed in velocities far exceeding 100 cm s^{-1}, and behavioral avoidance of low-velocity microhabitats through increased emigration has been reported (Fonseca & Hart 1996). In sharp contrast, even moderate current velocities restrain many predators of blackflies, such as flatworms (Hansen *et al.* 1991) and perlodid stoneflies (Malmqvist & Sackmann 1996), and high-flow environments may thus represent a refuge for blackflies from invertebrate predation (Hart & Merz 1998).

An exception to the pattern of reducing predator efficiency with increasing velocity might be the caddisfly larvae of the genus *Rhyacophila*.

Rhyacophila are often the principal macroinvertebrate predators of larval blackflies in boreal streams (Muotka 1993, Malmqvist 1994) and are able to aggregate in blackfly patches at near-bed velocities of 60–80 cm s^{-1} (Muotka & Penttinen 1994). Similarly, Malmqvist and Sackmann (1996) showed in a laboratory experiment that current velocity did not impair the foraging efficiency of *Rhyacophila* at velocities of 50 cm s^{-1}, but information on rhyacophilid predation success at higher velocities is lacking.

We examined the interaction between *Rhyacophila* caddis larvae and their blackfly prey along a wide current velocity gradient (ca. 20–120 cm s^{-1}), using a combination of direct field observations, a field colonization study, and laboratory experiments. We first studied the microhabitat selection of blackflies and *Rhyacophila* in relation to patch-scale habitat structure and current velocity in the laboratory. We then examined how the foraging behavior of *Rhyacophila* varies along a broad velocity gradient in the field. Finally, we conducted a short-term colonization study to examine whether simuliids and rhyacophilids show distinct velocity preferences in the field.

Material and methods

Laboratory experiments

In a set of laboratory experiments, we examined the effects of variable flows on microhabitat choice of the predatory caddis larva *Rhyacophila nubila* and the larval blackfly *Cnephia pallipes*, a species contributing to mass occurrences of blackflies in regulated rivers in Finland (Meissner *et al.* 2002). We specifically examined current preferences of *Rhyacophila* and *Cnephia* and whether these preferences were affected by changes in flow. We further tested whether the predator and prey exhibit preference for mosses over other habitat types, and whether such preference was affected by flow level. Finally, we tested whether the microhabitat selection of blackfly larvae was modified by the presence of the caddis predator. Trials were conducted in early June 2002 using four experimental flumes at the West Finland Regional Environment

Centre, Kokkola. Flumes were 240 cm long and 14 cm wide with a total bottom surface area of 0.33 m², of which 0.269 m² were in experimental use (due to differing flow conditions, a short section at both ends of the arena was not used in the experiments). Flumes were constructed from plywood with bottoms of concrete cast. In all experiments, we offered the animals a choice between three substrate types: concrete, moss, and stone. Flumes were provided with six stones (7 × 8 cm) attached to the concrete cast. Patches of artificial "moss" (Finnturf® strip, 7 × 8 cm) were attached directly downstream of each stone. This spatial arrangement was used because mosses in boreal rivers are typically attached to the downstream end of stones (K. Meissner pers. obs). Patches were arranged alternately on the left- and right-hand side of a flume at 15-cm intervals. All substrate patches were attached to the concrete cast with non-toxic silicon.

Each flow treatment (low flow *vs*. high flow) was replicated four times. We conducted two trials per day, with trials for *Rhyacophila* and blackflies run on consecutive days. Treatments exposed to high flow (5.55 l s⁻¹; current velocities 1 cm above the bottom 30–180 cm s⁻¹) during the first run of a day were always subjected to low flow (1.25 l s⁻¹; 10–100 cm s⁻¹) during the second run of that day, and vice versa. The order of flow treatments was randomized for each flume (and each run).

A grid of 330 cells, each 2.33 × 3.5 cm, was painted onto the flume bottoms using non-toxic, water-permanent pens. We measured current velocities (average over 6 s) at the centre of each cell in each flume during both flow conditions using a Schiltknecht MiniAir®20 current meter fitted with a 10-mm diameter probe. We used river water (changed daily) from the adjacent Perhonjoki. Water was circulated from an upper storage tank (volume 1 m³) through adjustable valves into each flume and through the experimental arena, then entering a lower storage tank from where it was pumped back to the upper tank. Each arena was fitted with a drift net (mesh size 330 μm) at the downstream end of the arena

We collected animals from the Perhonjoki a day before they were used in the experiments and kept them overnight in storage tanks provided with stones and low current. Before start-ing a trial, we distributed either 100 blackfly larvae (mean head width ± 1 SD: 0.61 ± 0.02) or 20 fifth-instar *R. nubila* larvae (HW: 1.60 ± 0.04 mm) evenly across each flume. This density is well within the range of densities of *Rhyacophila* larvae in the field (Muotka & Penttinen 1994, Meissner *et al*. 2002). To keep the experimental system manageable, however, we used densities of blackflies lower than typically observed in the field in early summer. These low densities are nevertheless commonly found in boreal streams and rivers outside the springtime peak densities (Muotka 1993, Malmqvist 1994). Once the animals had settled in the experimental arena (usually within 15–20 min), a pump was turned on to provide a slow current. Animals were then given an additional five minutes to attach properly, after which the drift nets were checked for any emigrating animals (usually very few) which were returned to the flumes. Then the valves were fully opened in the flumes to receive the high-flow treatment. Each trial lasted 60 minutes, after which the positions of animals were mapped individually for each flume. Separate experiments were conducted for the predatory caddis larva and blackfly larvae. To test whether blackflies chose more sheltered positions on sides of stones (*vs*. stone tops) as flow increased, we recorded the number of larvae on different stone surfaces in both flow conditions. Velocity measurements indicated that stone sides provided lower-velocity microhabitats than stone tops, although velocities increased in both microhabitats with flow level (low flow: 72 ± 1.9 (mean across four flumes ± 1 SE) *vs*. 56 ± 1.7 cm s⁻¹; high flow: 96 ± 2.1 *vs*. 68 ± 1.7 cm s⁻¹ on stone tops *vs*. sides, respectively).

We also ran trials with both predator (*Rhyacophila*) and prey (blackfly larvae) present (*n* = 4; number of individuals = 20 and 100, respectively), but because of the onset of pupation, numbers of *Rhyacophila* drifting out of the flumes started to increase, and their densities at the end of a trial varied among the replicates (2–7 per flume). We therefore report only microhabitat selection by blackflies in these treatments, but emphasize that these results are not fully comparable to those from the single-species trials. Nevertheless, any responses by blackflies to *Rhyacophila* in these experiments

are conservative estimates of true responses, because of the low density and decreased foraging activity of the caddis predator. Notwithstanding the relatively high number of predators, no direct interference between them was observed during the trials.

Current preferences, irrespective of substrate type, of the two taxa were calculated using Chesson's index (*see* Chesson 1983). The index value ranges from 0 to 1, random selection being indicated by $\alpha = 1k^{-1}$, where k is the number of current categories. Five evenly spaced current regimes in 25 cm s^{-1} increments were used for *Rhyacophila*. Since blackflies occurred also at velocities exceeding 125 cm s^{-1}, six categories were used for blackflies. The deviation of the mean preference value for each current regime from random expectation was tested using a paired *t*-test with sequentially adjusted α-levels (Tikkanen *et al.* 1997).

We used χ^2 goodness-of-fit tests to analyze microhabitat selection of *Rhyacophila* and blackflies among the three substrate types (concrete *vs*. mosses *vs*. stones). To evaluate whether the choice of a particular substrate type deviated significantly from random selection, we examined standardized residuals. These are distributed approximately standard normal; thus, a residual of 1.96 can be interpreted as being significant at $\alpha = 0.05$ (*see* Schofield 2003). To test for differences in preference between the substrate types we ran *a-priori* contrasts on data combined across flow treatments. Contrasts compared: (i) concrete substrate *vs*. moss + stone, and (ii) stone *vs*. moss. These analyses were conducted separately for the prey (blackflies) and the predator (*Rhyacophila*) as well as for prey in the presence of the predator

Behavioral field observations

Behavioral field observations were conducted in the outlet of Välilampi, northern Finland (66°14´N, 29°10´E). This is a shallow (5–30 cm during summer-low flows), clear-water (< 20 Pt mg l^{-1}) and narrow (3–4 m) stream. It maintains substantial blackfly populations and almost lacks aquatic vegetation, making it ideal for direct observations of *Rhyacophila* foraging

behavior. The average density of larval blackflies, mainly *C. pallipes* (ca. 90% of all blackfly larvae present at the outlet in early summer), at this site can exceed 500 000 ind. m^{-2}. Density of *Rhyacophila* is also very high, with a mean of 120 larvae m^{-2} in mid June. This stream also supports abundant populations of other invertebrates that *Rhyacophila* are reported to feed on (e.g., *Baetis* and *Heptagenia* mayflies, *Hydropsyche* caddis larvae, *Protonemura* stoneflies).

Our goal in this part of the study was to examine whether the velocity preferences observed in the laboratory would translate into similar field preferences and, more specifically, whether *Rhyacophila* were able to occur and forage actively in high-velocity microhabitats in the field. We therefore observed fifth-instar *Rhyacophila* foraging behavior in four current velocity regimes: (i) slow (< 40 cm s^{-1}), (ii) medium (45–69 cm s^{-1}), (iii) high (70–100 cm s^{-1}) and (iv) very high (> 100 cm s^{-1}). We first located relatively homogeneous stream areas (ca. 0.1 m^2) representing the four flow categories, then selected randomly patches in each category and searched for actively foraging *Rhyacophila* larvae in that patch; if none was found, we selected a new patch, until a sufficient number of larvae in each flow category was found ($n = 12$, except 3 in the highest current category). When an actively foraging predator was located, we monitored its behavior through a tiny viewing box (8 cm long, bottom diameter 5 cm) for five minutes. Occasionally, when a larva vanished out of sight, it was abandoned and new observations were started with another larva in the same or adjacent patch. No effect of the viewing box on larval behavior could be detected, i.e. larvae did not seem to respond to the viewing box, if this was moved very slowly and from downstream direction.

During an observation period, we recorded the number of attacks, capture success, distance moved, and total activity time (time spent moving or handling prey) for each predator. We also noted the number of attacks that resulted in drift entry by blackfly larvae. Two rulers attached perpendicularly to the bottom of the viewing box facilitated the measurement of distances moved. Since *Rhyacophila* larvae are sluggishly moving predators, a foraging individual rarely moved

more than 5 cm during an observation period, and were therefore readily observed without having to move the viewing box from its original position. The position of the head of a larva in the beginning and end of an observation period marked the endpoints of a larva's trail. All observations were done by one person (AJ). Current velocities along two to five equidistant points of the trail chosen by *Rhyacophila* were measured and averaged at the end of each observation period. Due to the short distances covered by the larvae during 5 minutes of observations, no larva shifted to another flow category during the observation period. Because the ambient light level in our study area varied little at this time of the season, we made all observations between 14:00 and 18:00 during two consecutive days in mid-June 1997. Differences in behavioral variables among the velocity regimes were analyzed using one way ANOVA. Analyses were run on either log- or arcsine-square root transformed data to meet the assumption of homogeneity of variances.

Colonization study

The field colonization study was carried out in mid-June in the same stream. In this study, we examined whether larval blackflies and *Rhyacophila* exhibit differential colonization patterns for artificial substrata placed in different current velocity regimes. As colonization substrata, we used artificial "leaves" made of pieces of rope (15 cm long, diameter 1 cm). The ropes mimicked the trailing vegetation frequently used for attachment by blackfly larvae and allowed a proper foothold for *Rhyacophila*. We selected stream areas with homogenous currents, each representing one of 4 current velocity regimes: 20–40 cm s^{-1}, 40–60 cm s^{-1}, 60–80 cm s^{-1}, and 80–100 cm s^{-1}. In each plot, perpendicular to the flow, we fastened between two bricks a 30-cm metal rod to which four pieces of a rope were attached with a single thin thread. The distance (5–6 cm) between the rope pieces in each sampling unit was such that they did not touch each other or the stream bottom while trailing downstream. We placed four such units in each flow category, thus providing four replicates for each category. Upon sampling, one rope from

each unit was selected randomly at intervals of 1, 3, 5, and 12 days. The thread holding the rope was cut and the rope with attached animals was quickly placed in a container with 70% alcohol. The animals were later identified and counted in the laboratory. Current velocity (average over 6 s) at the time of sampling was measured for each replicate with the Schiltknecht current meter. Water depth at the study site varied within ± 1 cm during the 12 days of the experiment. Repeated measures ANOVA was used to analyze the colonization data. Densities of blackfly and fifth-instar *Rhyacophila* larvae on each sampling date formed the within subject factor (Time) and current regime (four levels) the between subject factor (Current).

Results

Laboratory preference trials

Kriging maps (Fig. 1) summarize the flow conditions in the experimental flumes. At the low flow treatment, current velocities ranged from < 10 cm s^{-1} (behind stones and among artificial moss tufts) to 110 cm s^{-1}. At the high flow treatment, the same low-velocity microhabitats still provided refugia (15–20 cm s^{-1}) while currents in the main channel exceeded 150 cm s^{-1}.

In single-species trials with no added prey, the predatory caddis *Rhyacophila* preferred currents < 50 cm s^{-1} at the low flow treatment, ($t = 3.61$, df = 3, $P = 0.036$) (Fig. 2A). No *Rhyacophila* were found in the highest velocities (> 75 cm s^{-1}) during the low flow treatment. The slowest current regime (< 25 cm s^{-1}) was still preferred under the high flow treatment, but only weakly so ($t = 1.75$, $P = 0.179$). Currents between 25 and 75 cm s^{-1} were chosen in proportion to their availability, whereas currents exceeding 75 cm s^{-1} were avoided by *Rhyacophila* ($t = -15.00$, $P < 0.001$) (Fig. 2A).

In the absence of predators, blackfly larvae exhibited a wide tolerance of current velocities, although there was a slight tendency ($t = -2.18$, $P = 0.117$) to avoid currents slower than 25 cm s^{-1} in both flow treatments (Fig. 2B). Blackflies frequently occurred in currents faster than 100 cm s^{-1} during both low and high flows.
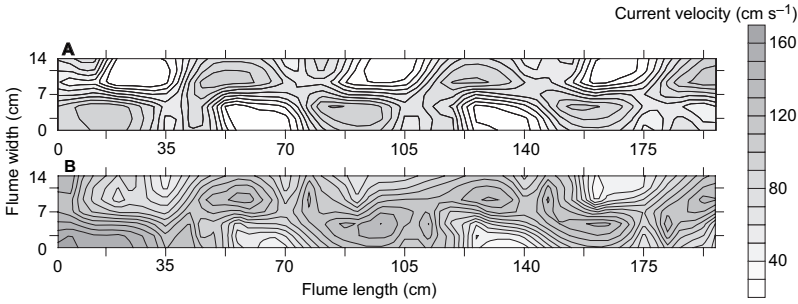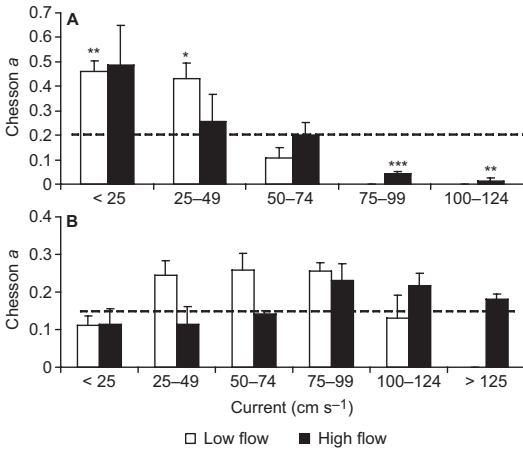
Fig. 2. Preference (Chesson index values, mean ± 1 SE) by (**A**) *Rhyacophila* and (**B**) blackfly larvae for different current velocity regimes in low *vs.* high-flow conditions (*n* = 4 for each flow level). Asterisks denote significant deviation from random selection (indicated by the dotted line).

The high-flow treatment caused an overall shift in preference toward higher velocities (Fig. 2B).

Distributions of both predator and prey clearly differed from those expected by chance in both flow treatments ($\chi^2 > 63.6$, $P < 0.0001$). Standardized residuals from goodness-of-fit tests indicated strong rejection of concrete substrate and a correspondingly strong preference for moss by both species at both flow levels (all $P < 0.001$). Stones were preferred by blackflies in both flow conditions ($P < 0.001$), whereas *Rhyacophila* showed a significant preference for stones only in the low-flow treatments ($P < 0.007$) (Fig. 3A and B).

Blackflies showed a weak tendency to abandon stone tops during high flows (32% ± 12% of larvae on stone tops during high flows *vs.* 50% ± 12% during low flows; means ± 1 SE, n = 4 flumes), and there was a corresponding increase in the proportion of larvae on sides of stones (50% ± 12% *vs.* 65% ± 9% during low *vs.* high flows, respectively). The interaction term (Position × Flow) was, however, non-significant (two-way ANOVA on arcsine transformed proportions: $F_{1,15} = 3.152$, $P = 0.101$), indicating that blackflies were not to a noticeable degree using stone sides as refugia during high-flow events.

A priori contrasts indicated no preference between stone and moss patches in blackflies (*see* Fig. 3A), whereas *Rhyacophila* showed consistent preference for mosses compared to stones (Fig. 3B) ($P = 0.0017$, Table 1). In the presence of *Rhyacophila*, however, blackflies preferred mosses over stones (Table 1 and Fig. 3C). Although blackflies and *Rhyacophila* often shared the same grid cell, they nevertheless occupied distinctly different microhabitats. Blackflies occurred on tips of moss branches, whereas *Rhyacophila* always occupied more sheltered areas at the base of moss tufts. Current velocities in these microhabitats differed significantly, with blackflies experiencing higher currents than *Rhyacophila* during both low and high flows (blackflies: 57 ± 2 cm s^{-1} *vs.* 99 ± 4 cm s^{-1}; *Rhyacophila*: 21 ± 4 cm s^{-1} *vs.* 49 ± 3 cm s^{-1} in high *vs.* low flows, respectively; means ± 1 SE, n = 4) (two-way ANOVA main effect of species: $F_{1,15}$ = 108.6, $P < 0.0001$; Species × Flow, $P > 0.05$).

Behavioral observations

Total activity time and distance moved by a *Rhyacophila* larva during the observations were similar across all flow regimes, though there was a tendency for longer movements in currents of 70–94 cm s^{-1} (Fig. 4A and B). By contrast, total number of predation attempts (Fig. 4C,

one-way ANOVA: $F_{3,46} = 6.57$, $P = 0.0001$) and capture success (Fig 4D; $F_{3,46} = 2.89$, $P = 0.045$) differed significantly between the flow regimes, attack frequency being lowest at highest current velocities (> 94 cm s⁻¹), while capture success was highest (ca. 23%) at intermediate velocities. Interestingly, *Rhyacophila* foraged exclusively on blackflies: during the 250 min of observations, no attacks on other prey were observed. A major proportion (45% across all flow regimes) of attacks by *Rhyacophila* resulted in drift entry by a blackfly, and the rate of predator-induced drift paralleled the attack rate of the predator, being lowest at the highest current velocities. However, the proportion of attacks that resulted in drift entry by a blackfly did not differ significantly among the flow regimes (one-way ANOVA: $F_{2,44} = 1.82$, $P = 0.170$).

Colonization study

Blackfly larvae colonized the artificial substrates within one day, with little density changes thereafter, until the last day of the experiment when almost all blackflies had either pupated or emerged (Fig. 5A) (significant main effect of time, Table 2). *Rhyacophila* were slower to colonize, but after three days their densities varied little in most current regimes (Fig. 5B). Blackflies seemed to avoid substrates with the slowest velocities (< 40 cm s⁻¹), as also did the caddis larvae. The main effect of flow, however, was non-significant for blackflies, and only bordered significance for *Rhyacophila* (Table 2). Flow × Time interaction was non-significant for both species (Fig. 5B).
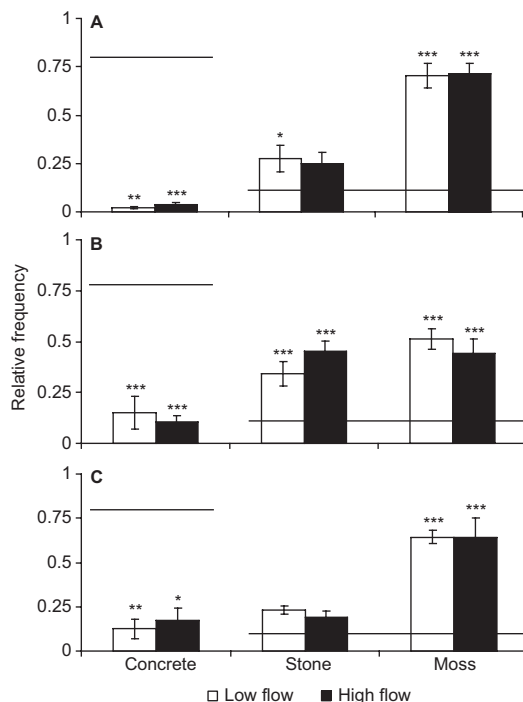

Fig. 3. Relative frequencies (mean ± 1 SE, *n* = 4 replicates for each treatment) of (**A**) *Rhyacophila*, (**B**) blackflies, and (**C**) blackflies in the presence of *Rhyacophila* in the three microhabitats available in the flumes. Standardized residuals from goodness-of-fit tests were used to evaluate whether the habitat choice for a particular substrate type deviated significantly (as denoted by asterisks) from random selection. Solid lines indicate expected frequencies for each habitat type.

Discussion

Blackfly larvae showed a wide tolerance of current velocities in the laboratory, with little preference for any velocity range. Such relatively flat

Table 1. Results of log linear models (data combined across flow levels) for differences in preference between the substrate types by *Rhyacophila* and by blackfly larvae during the laboratory trials.

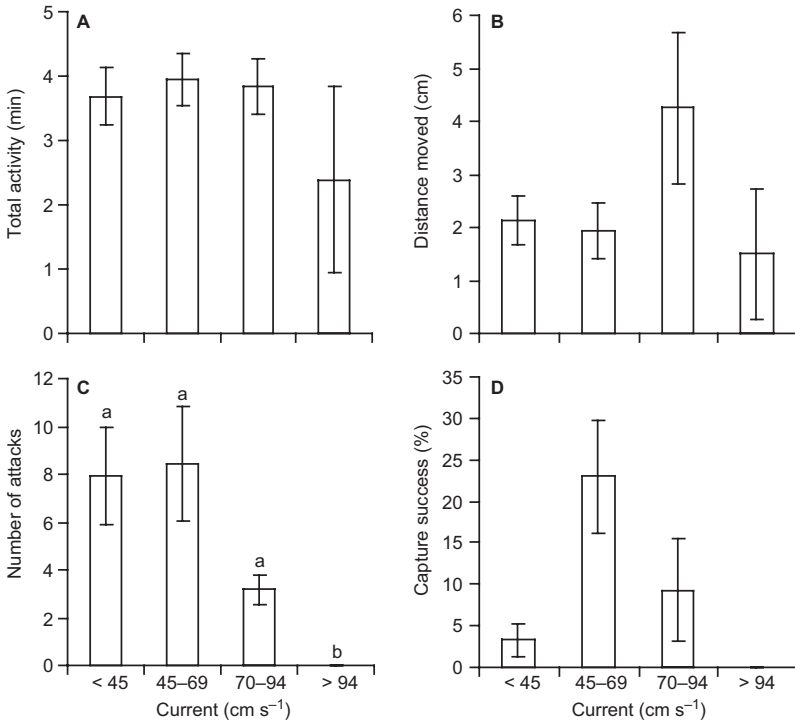| Taxon	Comparisons	Generalized log-odds ratio	SE	Wald	*p*
Rhyacophila	Concrete *vs.* stone + moss	2.53	0.55	21.23	< 0.0001
	Stone *vs.* moss	0.79	0.25	9.86	0.0017
Blackfly	Concrete *vs.* stone + moss	6.31	0.24	718.12	< 0.001
	Stone *vs.* moss	0.10	0.19	0.29	0.60
Blackfly with *Rhyacophila*	Concrete *vs.* stone + moss	6.69	0.29	524.30	< 0.001
	Stone *vs.* moss	0.68	0.24	7.89	0.005

Fig. 4. (**A**) Time spent active, (**B**) distance moved, (**C**) number of attacks, and (**D**) capture success (means ± 1 SE; $n = 12$ observations per current regime, except 3 for the highest regime) by *Rhyacophila* larvae at 4 different flow regimes during direct field observations. Regimes sharing the same letter do not differ significantly (Tukey's test: $p < 0.05$).
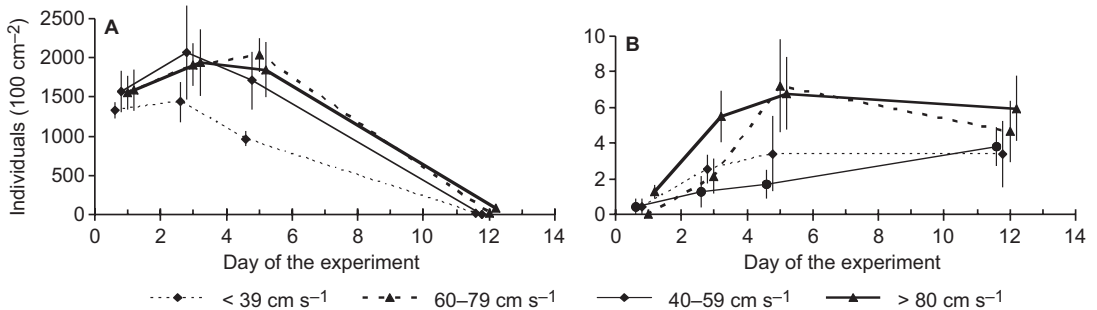

Fig. 5. Colonization by (**A**) blackfly and (**B**) *Rhyacophila* larvae of the artificial vegetation at different current velocity regimes in the field. Shown are the mean numbers of larvae per 100 cm^2 (± 1 SE, n = four replicates per current regime and sampling date).

preference curves are not atypical of blackflies (e.g., Morin *et al*. 1986), and may reflect either real tolerance of a wide range of velocities, or the inadequacy of propeller-type flow meters to describe near-bed velocities (Hart *et al*. 1996). High drag associated with high currents restricts blackfly larvae (Lacoursière & Craig 1993), and species' distributions are related to labral fan size and morphology (Zhang & Malmqvist 1996). Furthermore, larvae show phenotypic plasticity in fan morphology in response to flow variation (Zhang & Malmqvist 1997). Therefore, short-

term experiments are more likely to reflect tolerance of than actual preference for high currents by blackfly larvae.

Importantly, however, there was a shift in the velocity preference of blackflies in relation to flow level: more larvae tended to occur in high to very high velocities during high compared to low flows. Under rapidly changing flows, a larva may have to move around in search of a suitable microhabitat. If such habitats are located nearby, e.g., on a different surface of the same stone, then larvae could reach those habi-

tats via short-distance, stepwise movement, or "looping" (Fonseca & Hart 2001). However, we found no strong evidence of such targeted movements during scouring flows. Instead, blackflies appeared not only able to withstand very high currents, but even to actively choose high-velocity microhabitats whenever such were available. This observation is well in line with the finding that *C. pallipes* is the most prominent member of the blackfly community in short-term regulated rivers where current velocities during flow releases can be very high (Meissner *et al.* 2002).

In the laboratory, the predatory caddis *Rhyacophila* preferred velocities < 45 cm s^{-1}, whereas in the field they hunted blackflies at velocities of 70–80 cm s^{-1}. They occurred in even higher velocities, but at a cost of lower foraging efficiency. We suspect that this discrepancy results at least partly from the spatial distribution of current velocities in our simplified laboratory setting where most microhabitats were hydraulically rough, forcing *Rhyacophila* to remain in low-velocity microhabitats within moss tufts. Also, in the field *Rhyacophila* only entered high-velocity microhabitats when actively hunting, while between foraging bouts they resided beneath stones, in substratum interstices, or other flow refugia (T. Muotka pers. obs.). Furthermore, as shown by Wotton *et al.* (1993), there is always considerable among-predator and day-to-day variability in the feeding behavior of individual predators, which may affect the interpretation of preference patterns in the field *vs.* the laboratory.

Moss was the preferred microhabitat of the predator in both flow treatments. Such preference for mosses by *Rhyacophila* has also been recorded in the field (Malmqvist & Sjöström 1984, Muotka 1993). Mosses are a key habitat structure for many stream invertebrates (Suren & Winterbourn 1992) where *Rhyacophila* can maintain high encounter rates with their macroinvertebrate prey. However, larval blackflies are often the preferred food by *Rhyacophila* (Muotka *et al.* 2006), mainly because blackflies are by far the prey most vulnerable to attacks by *Rhyacophila* (Muotka *et al.* 2006). Also, *C. pallipes* is likely to be highly nutritious for the predator because, being autogenous, these females develop large fat reserves (Wotton 1982, Crosskey 1990). Blackfly larvae therefore constitute

a rewarding but, because of their rapid development, transient prey type for lotic predators in boreal streams. Most other lotic insect predators, e.g., flatworms (Hansen *et al.* 1991, Hart & Mertz 1998) and perlodid stoneflies (Malmqvist & Sackmann 1996) are strictly excluded from stone tops and other high-velocity microhabitats occupied by blackflies. They may therefore loose affordable feeding opportunities on a preferred prey type (Tikkanen *et al.* 1997, Elliott 2000), which may confer a competitive advantage to *Rhyacophila*. On the other hand, dense aggregations of blackfly larvae may modify microcurrents and therefore indirectly facilitate the occurrence of some predators, e.g. the muscid fly *Limnophora*, in the high-velocity microhabitats they could not otherwise occupy (*see* Merritt & Wotton 1988).

The quality of flow-mediated prey refuges for larval blackflies is highly variable, apparently depending on the type of invertebrate predator prominent in a stream. While even moderate velocities (ca. 50 cm s^{-1}) exclude flatworms and predatory stoneflies, only velocities approaching 100 cm s^{-1} provide refuge against *Rhyacophila*. Because many blackfly species are well able to dwell in such high velocities, selecting high velocity microhabitats to avoid predation may bear little, if any, fitness consequences to larvae with suitable fan morphology (Malmqvist *et al.* 1999). In such microhabitats, the risk for an individual larva to fall prey is probably negligible, especially when they occur in extremely high

Table 2. Repeated measures ANOVA on densities of larval blackflies and *Rhyacophila* larvae colonizing the experimental substrates (artificial "leaves") in various flow regimes.

Source of variation	df	F	p
Current			
Blackflies	3	2.14	0.135
Rhyacophila	3	3.17	0.053
Time			
Blackflies	2.1*	58.83	< 0.001
Rhyacophila	3	9.01	< 0.001
Current × Time			
Blackflies	6.15*	0.92	0.492
Rhyacophila	9	0.97	0.480

* Greenhouse-Geisser corrected degrees of freedom.

densities typical of boreal lake outlets, large-river rapids, and regulated rivers.

In natural conditions, however, larval black-flies live in an environment where they are confronted by many types of predators simultaneously. Similarly, although *Rhyacophila* is a voracious predator on larval blackflies, it is simultaneously a preferred prey for many stream fishes (e.g. Meissner & Muotka 2006). In this paper we have studied one predator–prey interaction in isolation, while in reality it is embedded in a complex web of interactions of variable strength and importance. Multiple predation risk places the prey in a conflicting situation where they must balance relative risks from different types of predators, and avoidance of one predator may increase exposure to another (Soluk & Collins 1988, Huhta *et al.* 1999). Thus, larval blackflies may avoid invertebrate predators by occupying high-velocity microhabitats, but by doing so, they become exposed to benthic-feeding fish. Predator avoidance may sometimes form of a hierarchy where one predator presents a substantially higher predation risk (McIntosh & Peckarsky 1999). Being small relative to most other stream macroinvertebrates, blackflies are not always preferred prey for stream fish (e.g. Kreivi *et al.* 1998) whereas they are strongly preferred by invertebrate predators. It is therefore possible that the microhabitat selection of larval blackflies is more responsive to invertebrate than fish predators, although this has remained largely unstudied.

The strong rejection of the concrete substratum by both predator and prey likely resulted from surface roughness and high microturbulence associated with this substratum type. The tendency of blackflies to abandon stones in preference of moss-covered habitats in the presence of *Rhyacophila* may seem counterintuitive, because mosses were also strongly preferred by the caddis predator. Overlap in habitat use was, however, more apparent than real, and relates to the scale of observation: while the positioning of the predator and prey overlapped on a 2-dimensional map, blackflies always occurred on tips of the moss stems, where current velocities were significantly higher than within the moss tufts, where *Rhyacophila* typically resided. We lack direct behavioral data to pinpoint the mechanism behind this shift, but suspect that it is linked to the foraging activity of *Rhyacophila*. Blackflies typically respond to an approaching predator by entering drift. They then attach silken threads (Wotton 1986) to enable return to the original position. In our laboratory setting, a displaced larva trying to maintain contact with the substratum is likely to hit objects protruding into the water column, such as the artificial moss tufts. Another explanation for such partitioning of space is simply differential microhabitat requirements: blackfly larvae need fast currents to feed effectively, whereas *Rhyacophila*, by remaining within the mosses, avoids being swept away.

Consumer stress models predict that predators will have their strongest impact on prey communities in stressful environments (Menge & Sutherland 1987). As a corollary to this hypothesis, it has been suggested that the importance of predation is greatest where environmental conditions are most favorable to the predator. In stream ecosystems, environmental harshness is usually associated with flow-related disturbances, and it has indeed been observed that many invertebrate predators have their strongest impact on prey populations in hydraulic regimes favorable for the predator (e.g., Peckarsky *et al.* 1990, Lancaster 1996). By contrast, Thompson *et al.* (2002) showed that the impact of a predatory stonefly on its mayfly prey increased during floods, owing mainly to predator-induced prey emigration. Evidence for the harsh-benign model of community organization in streams is therefore ambiguous, but it does provide a theoretical framework for assessing the impact of different types of predatory invertebrates on larval blackflies and, perhaps, on lotic prey in general. Being able to maneuver in a wide range of velocities, including very high ones, *Rhyacophila* could be predicted to have stronger and more pervasive effects on their prey than other lotic invertebrate predators.

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