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Reduction of predation risk under the cover of darkness: Avoidance responses of mayfly larvae to a benthic fish

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Summary. Mayfly larvae of *Paraleptophlebia heteronea* (McDunnough) had two antipredator responses to a nocturnal fish predator (*Rhinichthys cataractae* (Valenciennes)): flight into the drift and retreat into interstitial crevices. Drift rates of *Paraleptophlebia* abruptly increased by 30 fold when fish were actively foraging in the laboratory streams but, even before fish were removed, drift began returning to control levels because larvae settled to the substrate and moved to areas of low risk beneath stones. This drifting response was used as an immediate escape behavior which likely decreases risk of capture from predators which forage actively at night. Surprisingly, drift most often occurred before contact between predator and prey, and we suggest that in darkness this mayfly may use hydrodynamic pressure waves for predator detection, rather than chemical cues, since fish forage in an upstream direction. Although drifting may represent a cost to mayfly larvae in terms of relocation to a new foraging area with unknown food resources, the immediate mortality risk probably outweighs the importance of staying within a profitable food patch because larvae can survive starvation for at least 2 d. In addition to drifting, mayflies retreated from upper, exposed substrate surfaces to concealed interstitial crevices immediately after a predator encounter, or subsequent to resettlement on the substrate after predator-induced drift. A latency period was associated with this response and mayflies remained in these concealed locations for at least 3 h after dace foraging ceased. Because this mayfly feeds at night and food levels are significantly lower in field refugia under stones, relative to exposed stone surfaces, predator avoidance activity may limit foraging time and, ultimately, reduce the food intake of this stream mayfly.

Key words: Predation risk – Behavioral response – Mayfly – Fish – Streams

Individuals can reduce predation risk through antipredator defenses which operate to increase the probability of prey surviving predator encounters (Edmunds 1974). Various types of these antipredator defenses have been described including flight, withdrawal into a retreat, startle responses, feigning death, attack deflection or aggression. For aquatic insects, the most commonly observed antipredator defenses are flight or withdrawal to a refuge (Peckarsky 1980; Wiley and Kohler 1981; Michael and Culver 1987; Sih 1987; Rahel and Stein 1988; Ydenberg and Dill 1986). For example, lotic mayflies sometimes exhibit a flight response by drifting into the water column after an encounter with a predator (Peckarsky 1980; Corkum and Clifford 1980; Peckarsky 1987; Malmqvist and Sjostrom 1988). Additionally, some lotic invertebrates may change their vertical distribution in the streambed, possibly seeking interstitial refugia in response to predators (Peckarsky 1980; Walton 1980; Peckarsky 1987).

Antipredator behavior of lotic macroinvertebrate prey has been studied only during short-term experiments. This precludes examination of a potentially important aspect of prey responses after encounter with predators; the time period that prey behavior remains affected once the predator has left the area. This latency (Rahel and Stein 1988) or recovery (Giles 1983) period may have an associated cost if, for example, prolonged hiding by prey limits their foraging opportunities (Sih 1980, 1982; Power 1984; Holbrook and Schmitt 1988). Although latency periods of up to 24 h have been reported for fish (Rahel and Stein 1988), these latency responses have not been examined in lotic macroinvertebrates, and could have potentially important implications for the survivorship and fitness of the prey.

Our study examines the antipredator responses and the associated latency periods of a lotic mayfly (*Paraleptophlebia heteronea* (McDunnough)) in response to foraging by a predacious benthic fish, the longnose dace (*Rhinichthys cataractae* (Valenciennes)). Initially, we estimated the daily per capita mortality rates incurred by late instar *Paraleptophlebia* as a result of dace predation

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in the field. Predation risk from dace occurs only at night as dace are strictly nocturnal in the study streams (Culp 1989). Dace have very short reactive distances to their prey (<1 cm) and use a mobile foraging search mode (Huey 1981), which consists of fish slowly moving upstream while prodding the substrate surfaces with their snout (Beers and Culp 1990). We hypothesized that mayflies on these substrate surfaces should be able to reduce predation risk from dace by using two categories of antipredator responses: flight by drifting into the water column and retreating into interstitial crevices. Thus, since dace represent an important predation risk to *Paraleptophlebia*, our specific laboratory objectives were to determine: (1) whether *Paraleptophlebia* exhibited antipredator escape responses to foraging dace; and (2) if lengthy latency periods are associated with any of the antipredator responses. We also determined the diel feeding periodicity of *Paraleptophlebia* and the amount of algal biomass on stone surfaces in the field in order to identify periods of temporal overlap with the predator and to evaluate whether prolonged periods of hiding after encounters could lead to substantial costs in terms of lost feeding opportunities.

Methods

Field estimates of mortality risk, feeding periodicity and algal biomass

The daily per capita mortality risk of *Paraleptophlebia* to dace predators (q_p) was estimated from the equation, $q_p = (n_p \times P)/N$, where n_p is the daily mean number of prey eaten per fish, and P and N are, respectively, the densities (no./m^2) of dace and *Paraleptophlebia*. The study area was Jumpingpound Creek, a fourth order stream located in the foothill's of the Rocky Mountains approximately 30 km west of Calgary, Alberta (114°31′W, 51°9′N). Fish density (P) in the stream was estimated by setting blocking nets above and below the study reach (20 m × 15 m) on 20 June 1986 and then collecting four successive samples of dace by electrofishing within the netted area. Each sample consisted of electrofishing the entire area with a Smith-Root Model 15-A, backpack electroshocker and collecting the stunned fish in a 6 mm mesh minnow net. Dace densities were calculated following the Leslie catch-effort method described in (Bagenal 1978) which assumes the catch is proportional to the population number present. Our estimate indicates that the four successive samples cumulatively removed >75% of the population. Abundance of *Paraleptophlebia* within the area of fish collection was determined from eight replicate, 0.03 m^2 Hess samples (250 μm mesh) collected on 13 June 1986. The samples were preserved in 10% formalin for sorting and identification in the laboratory.

In this stream dace are exclusively nocturnal feeders and begin each feeding period with a largely empty gut (Culp 1989). Therefore, to estimate n_p, ten replicate fish (60 ± 1 mm total length) were collected at sunrise by electrofishing on 13 June 1986, and their gut contents removed by anal backflushing (Culp et al. 1988). Fish gut contents were preserved in 80% ethanol and examined under 12 × magnification in the laboratory to determine the number of *Paraleptophlebia* consumed per individual (n_p) during the previous nights feeding bout.

Diel feeding periodicity of *Paraleptophlebia* (4.5–7.0 mm body length) was established by collecting individuals at 1–4 h intervals over a 24 h period on 12–13 May 1989. During each sampling period, ten individuals were preserved in 10% formalin. Regurgitation of stomach contents did not occur. In the laboratory, mayfly stomachs were removed by dissection under 25 × magnification, the guts and their contents dried to constant mass at 60° C, and the mass determined to the nearest 0.01 mg with a Cahn 25 Automatic Electrobalance. For another 28 animals, we measured the dry mass of the stomach (SW) wall and the total body length from the anterior of the head to posterior of the abdomen (L). These data were used to generate the equation, $SW = L \times 0.0103 - 0.0314$, so that the gut mass estimates could be corrected for stomach wall dry mass. Body length and stomach wall mass were highly correlated ($r^2 = 0.88$, $F = 179.1$, $p < 0.001$). Mayfly gut fullness was calculated as (dry stomach mass – dry stomach wall mass)/dry body mass. Finally, fifteen samples of algae were scraped from the top, sides and bottom surfaces of stones with a stiff brush after each sample was delimited with a 1.0 cm^2 neoprene disk. Stone surface scrapings were dried to constant weight at 60° C and weighed to the nearest 0.01 mg on the electrobalance.

Laboratory experiments

In the first experiment, we determined the effect of foraging dace on (i) the drift rate of *Paraleptophlebia* larvae and (ii) the proportion of larvae occupying exposed positions on the substrate. Circular plexiglas streams (6 L, planar area = 470 cm^2), similar in design to those described in Glozier and Culp (1989), were used to examine the response of the mayfly *Paraleptophlebia* to foraging dace. To simulate the physical structure of the field streambed, each stream had two large (24 cm^2) and 16 small (3.8 cm^2) substrates made of clear plexiglas (Fig. 1). In addition, a single layer of glass beads (4 mm in diameter) filled the interstitial spaces between and beneath the substrates. Filtered, oxygen-saturated tap water was continuously circulated to the stream from a Frigid Units water management system, and a mid-summer photoperiod (14 h light:10 h dark) and temperature regime (range of 8–15° C) was maintained (Glozier and Culp 1989). This water was aged for 1 wk prior to the experiments and had a chemical composition similar to that of Jumpingpound Creek (unpubl. data). Current velocity was measured ($n = 15$) with a Novonics micro-current meter with mean velocities (± SE) within the streams maintained at 13.6 ± 0.4 cm/s in the water column and 7.7 ± 0.5 cm/s 1 cm above the substrates.

Dace (64 ± 1 mm total length) from Jumpingpound Creek were acclimated to the experimental conditions (described below) for at least 4 d. This period provides sufficient time for the capture rate of prey by dace to reach an asymptote, thereby eliminating the effects of the initial learning curve (Glozier 1989). After this period dace were starved for 24 h since, at these experimental temperatures, this duration is adequate to clear the guts (Culp et al. 1988). Dace were then fed 25 mg of commercial trout food 2–3 h prior to the experiment to ensure gut fullness levels near field conditions 1–2 h after sunset (Culp 1989). One hour after the simulated sunset, one randomly chosen dace was introduced into each of the five replicate fish treatment streams and allowed to forage for 15 min. Dace were immediately removed after this foraging bout without disturbing the mayflies by gently prodding the fish into a net suspended in the water column. Gut contents of the

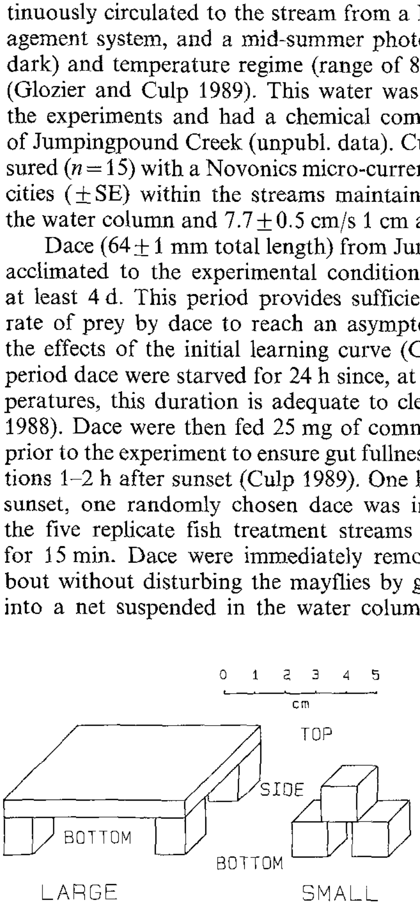

Fig. 1. Configurations of the small and large artificial substrates used in the experimental streams noting the upper (i.e., top and side) substrate surfaces. A single layer of glass beads (4 mm diameter) filled the interstitial spaces between and beneath the substrates

fish were collected by anal backflushing. This experimental design simulated foraging by dace in a prey patch and resulted in less than 10% prey depletion per replicate. Prey densities in the streams were calculated over the total planar area (470 cm^2) and were approximately 1500 mayflies/m^2. This value is slightly higher than ambient field levels during the period of June to August, 1986.

Paraleptophlebia larvae were collected from the field site and held less than 7 d at 10° C with ad libitum amounts of leaf litter detritus available for food. Seventy mayflies (mean body length ($\pm$SE)$=5.2 \pm 0.1$ mm) were randomly assigned and introduced into each stream 24 h before observation of behavior. Mayfly behavior in five, replicate control (dace absent) and fish treatment streams was recorded 1 h prior to the simulated sunset, during the 15 min period when dace were foraging in the fish treatment streams (i.e., 1 h after simulated sunset), and 0.5, 1.5, 3, 6, 9, 22 and 24 h after fish removal. Nighttime observations were recorded under low intensity red light, which did not appear to affect mayfly or dace behavior (pers. obs.). We counted the number of mayflies drifting during a one minute period in the control and fish treatment streams before fish were added, during the period of dace foraging and, subsequently, at each of the seven observational periods. Then, the number of mayflies occupying upper (i.e., tops and sides, Fig. 1) and lower substrate surfaces, and those remaining within the glass beads was recorded. The glass beads and clear plexiglass greatly facilitated visual observation and a calibration study showed that an observer's total counts were within 1% of the number of mayflies known to be in the stream. Since dace captured mayflies only from the upper substrate surfaces (pers. obs.), these surfaces were defined as exposed to dace predators. Interstitial spaces between the glass beads and the undersides of the plexiglass substrates were not accessible to dace (i.e., refugia). Therefore, in the control streams the proportion of mayflies occupying exposed positions during each period was calculated by dividing the number of individuals on the upper surfaces by the total number of individuals in the stream. However, in treatment streams we calculated the proportion of mayflies exposed after correction for drifting mayflies ($<2\%$) and for those consumed by dace ($<7\%$).

In a second experiment, we determined whether mayfly drifting behavior was initiated before or after physical contact with the fish. To do this, mayflies were again collected and acclimated and two experimental streams containing 70 mayflies/stream were setup as before. The next day a randomly chosen dace which had been acclimated as described above was introduced to each stream 1 h after sunset and allowed to forage for a 15 min period. The interactions between dace and *Paraleptophlebia* were videotaped in darkness with a Panasonic WV-BD 400 infrared sensitive camera (wavelength >710 nm) mounted above the stream and connected to a Panasonic 6010 time-lapse recorder. Our analysis concentrated on mayflies which entered the drift when a foraging dace was <1.5 cm from the mayfly. We used this cutoff because it is near the upper limit ($x \pm 2$ SE) for the reaction distance of dace to mayflies in darkness (Beers and Culp 1990). We further restricted our analysis to those drift events which could unequivocally be assigned to one of the following categories of drift initiation: (1) *non-contact*, without physical contact with the fish; (2) *attack-contact*, during or immediately after an attack by a foraging fish; and (3) *swim-contact*, after contact with the body or fins (usually pectoral or caudal) of a swimming fish and not associated with an attack. For non-contact drift events, we also recorded the distance ($<$ 1 cm) between the fish and mayfly at the instant of drift entry by the mayfly (i.e., prey reactive distance). Because of the overhead camera position, vertical distances could not be reliably estimated. Thus, we restricted these measurements to cases where both the attacking fish and its mayfly prey occupied the same horizontal plane.

We tested the hypothesis that short-term foraging by dace in a prey patch did not change the proportion of *Paraleptophlebia* larvae occupying exposed positions (after arcsine, square-root transformation) by applying a model I, two-factor ANOVA with repeated measures in time after homogeneity of variance was confirmed by Bartlett's test. The two factors were time since dace foraging and fish treatment level (i.e., control or fish treatment streams). Similarly, to determine if dace foraging affected drift rates of *Paraleptophlebia* we used a two-factor test but, because of the inequality of variances associated with the drift rates (i.e., several zero values with no variance), we applied the nonparametric Friedman's two-factor test (Zar 1984). For both analyses, the sample 2 h prior to fish addition was not included because the treatments were identical at this time. However, to confirm that the initial behavior patterns of mayflies were the same in the control and fish treatments, the behavioral patterns of the mayflies 2 h prior to fish addition (i.e., 1 h prior to sunset) were compared with either a two-sample t-test (proportion of mayflies exposed) or a Mann-Whitney U test (drift rates). For the observations of *Paraleptophlebia* feeding periodicity in the field, we used a model I, single-factor ANOVA to test the hypothesis that gut fullness (after arcsine, square-root transformation to stabilize the variance) showed no significant diel change. Finally, we tested the hypothesis that there was no difference in algal biomass levels on the top, sides and bottom of stones with a single-factor ANOVA (after log transformation to stabilize the variance). All hypothesis testing was performed at a probability level of $p<0.05$.

Results

Field observations

Density estimates yielded mean values (± 1 SE) of 987 ± 157 individuals/m^2 for *Paraleptophlebia* and 2.3 ± 0.1 individuals/m^2 for dace, while the mean consumption rate (± 1 SE) of *Paraleptophlebia* by dace was 3.2 ± 0.9 individuals/d. These values were used to calculate a daily per capita mortality risk of *Paraleptophlebia* to dace predators (q_p) of 0.008. Assuming that the daily mortality risk is constant and that mortality is expressed as a negative exponential decay in the population size of *Paraleptophlebia*, then the 30 d mortality risk to this predator is 0.21. Note that the 30 d period represents approximately 10% of the generation time for this univoltine mayfly.

Gut fullness of *Paraleptophlebia* corrected for stomach wall mass varied significantly over the diel study period ($F=3.3$, $p<0.005$). The gut fullness results indicate consumption was strongly nocturnal and further suggest that feeding activity began near sunset and ended near sunrise (Fig. 2). The most rapid increase in gut full-

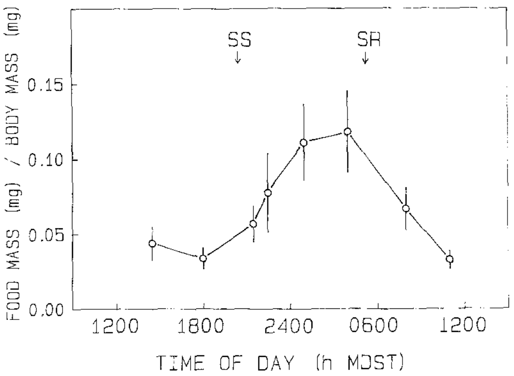

Fig. 2. Diel periodicity in mean gut fullness (food mass/mayfly mass$\pm$1 SE; $n=10$) of *Paraleptophlebia heteronea* larvae at Jumpingpound Creek on 12–13 May 1989. *SS*, sunset; *SR*, sunrise

ness occurred during the first 4 h after sunset which coincides with the peak period of feeding by dace (Culp 1989). Additionally, mean algal biomass varied significantly among stone surfaces (F = 27.4, $p < 0.001$). Tukey's test indicated biomass on the top surfaces (68.0 mg/cm^2) was higher than the sides (9.5 mg/cm^2), while biomass on the bottom surfaces (3.8 mg/cm^2) was lower than the sides.

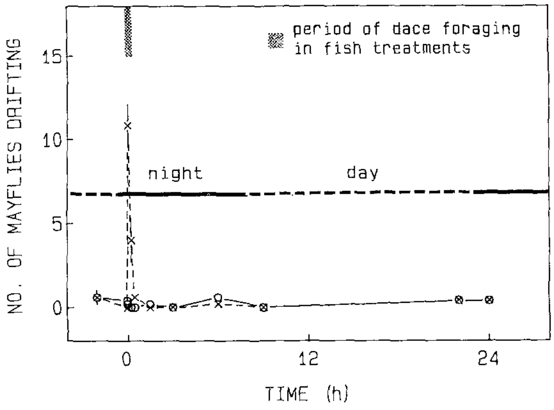

Fig. 3. The mean number of *Paraleptophlebia heteronea* larvae drifting (±SE; $n = 5$) in control (*open circle*) and treatment (x) streams during the night (*solid line*) and day (*dashed line*) over the 24 h experimental period

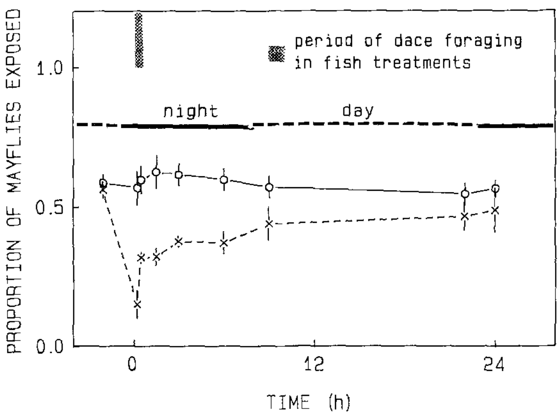

Fig. 4. The mean proportion of *Paraleptophlebia heteronea* larvae on the upper substrate surfaces (±SE; $n = 5$) in control (*open circle*) and treatment (x) streams during night (*solid line*) and day (*dashed line*) over the 24 h experimental period

Laboratory experiments

Drift rates in fish and control treatments were initially similar (U = 12.5, $p > 0.20$), but drift immediately increased in the fish treatments after dace were introduced (Fig. 3). Significantly different values were recorded for the effects of the factors of treatment (H = 3.9, $p < 0.05$), time (H = 22.5, $p < 0.01$) and the interaction between treatment and time (H = 30.5, $p < 0.001$) on *Paraleptophlebia* drift rate. This interaction between treatment and time is not surprising since mayfly drift rate in the control streams showed no temporal change, while drift rate in the fish treatment streams exhibited a short, but dramatic, peak during the period of dace foraging. Although the drift rate in treatment streams began to decline even before dace were removed from these streams, multiple contrast tests indicated that drift rates during this 15 min foraging period in treatment streams were significantly different from drift rates recorded in all other fish treatment and control streams during the 24 h study period (q range = 4.62 to 15.69, $p < 0.05$). The rapid return of drift rates to control levels after dace removal suggests that no latency period was associated with this drifting escape response.

Video observations showed that, of the drift events which conformed to our criterion for inclusion in the analysis (i.e., fish < 1 cm from the mayfly), most drift entry was initiated without physical contact with the fish (non-contact = 67%; $n = 21$). The remaining events were nearly equally divided between attack-contact (19%) and swim-contact (14%). Qualitative observations also showed that non-contact drifting always was preceded by the mayfly orienting its head and antennae towards the fish. The mean reactive distance (±1 SE) of *Paraleptophlebia* to the dace in cases of non-contact drifting was 8.6 ± 0.7 mm ($n = 8$). Regardless of how drift was initiated, the distances larvae drifted was < 15 cm and drifting was generally followed by the mayfly moving into a refuge upon resettlement to the substrate.

Approximately 60% of mayflies occupied exposed positions on the substrate in the control streams throughout the 24 h period (Fig. 4), and the distributions in the fish and control treatment streams were initially the same (t = 0.50, $p > 0.50$). However, after 15 min of foraging by dace, less than 20% of the mayflies occupied exposed positions in the fish treatment streams. Since drifting and consumed mayflies were accounted for in these calculations and, together, comprised < 9% of the initial larval density, this 40% reduction in the percentage of exposed mayflies is attributable to a shift in mayfly spatial distribution. In contrast to the drift response, a latency period was associated with the hiding response and a two-factor ANOVA indicated that treatment (F = 32.3, $p < 0.001$), time (F = 3.9, $p < 0.002$) and the interaction term between treatment and time (F = 4.7, $p < 0.001$) all significantly affected larval distribution. The significant treatment and time interaction resulted from mayflies occupying a similar proportion of exposed positions throughout the 24 h period in the control streams, while mayflies in the first treatment streams changed their exposure level through the night as the latency effect of dace foraging was reduced. Multiple contrast testing indicated this latency period lasted for at least 3 h as the proportion of larvae on exposed surfaces in the control and treatment streams were significantly different for this duration (q range = 4.86 to 12.30, $p < 0.005$). This is likely a conservative estimate of the latency period since the proportion of mayflies on exposed surfaces in the treatment streams remained depressed compared to the control streams for up to 9 h after dace removal (i.e., until the simulated dawn; Fig. 4).

Discussion

The longnose dace represents a potentially important mortality risk to the univoltine mayfly, *Paraleptophlebia heteronea*, even when this risk is projected for only a 30 d period. In fact, dace forage on this mayfly throughout the ice-free period (April–November) with dace per capita consumption of *Paraleptophlebia* varying seasonally and ranging between 0.5–3.7 larvae per day (Culp unpubl. data). Besides the measured mortality risk, this mayfly must also experience a high probability of encountering dace. Although it is difficult to measure encounter rates between mayflies and dace in the field, dace encounter rates with mayflies in laboratory streams are 1.4–3.3 times the rate of capture (Glozier 1989; Beers and Culp 1990). Because mayflies are small compared to other lotic invertebrates like stoneflies, Soluk and Collins (1988) hypothesized that (i) mayflies have low encounter rates with bottom-feeding fish and (ii) benthic fish likely have not been an important selective force in the development of mayfly antipredator behavior. In contrast to this hypothesis based on predator-prey interactions between mayflies and a sit-and-wait benthic fish predator, our field data suggests the longnose dace, which uses a mobile foraging mode, can be an important source of predation risk to mayflies. Furthermore, mayflies may be expected to reduce predation risk from this type of active benthic predator by responding to encounters with antipredator defenses.

Paraleptophlebia larvae exhibited two general responses to this fish predator: movement into the drift and retreat into interstitial crevices. Predator-induced drift of this nocturnally active mayfly resulted in a short-term (<15 min), 30 fold increase in drift rates in laboratory streams compared to the controls without fish. Release of larvae into the drift likely acts as a mechanism which decreases the risk of mayflies to capture by bottom-feeding fish like dace, since dace reactive distances are reduced at night (<1 cm) and dace seldom attack drifting mayflies (Beers and Culp 1990). Similarly, active entry into the drift by mayflies may reduce predation risk from other nocturnal benthic predators whose foraging field is restricted by a small reactive distance to prey; this includes some sculpins (Hoekstra and Janssen 1985) and tactile stoneflies (Vaught and Stewart 1974; Malmqvist and Sjostrom 1980; Sjostrom 1985). Although drifting could represent a potential cost to the mayfly in terms of relocation to a new area of the streambed with unknown food resources (Otto and Sjostrom 1986), larvae can survive starvation for at least 2 d (unpubl. data), and the immediate mortality risk from encountering a nocturnal predator probably outweighs the importance of staying within a profitable food patch.

The increased release of mayflies appears to be primarily the result of an antipredator flight response by the mayfly initiated by an encounter with the predator. Behavioral observations show that only a small portion of drift events (14%) are attributable to non-attack related physical disturbances resulting from contact between larvae and the fin (i.e., pectoral or caudal) or body (i.e., trunk or caudal) regions of the fish. Conversely, most drift events (86%) occurred either from direct contact by an attacking dace or by non-contact detection of an approaching forager by the mayfly prey. It is surprising that non-contact flight was the most frequent source of drift (67%) and the stimuli producing this response could conceivably be visual, chemical or hydrodynamic (Williams and Moore 1985; Peckarsky and Penton 1989). However, the nocturnal timing of this predator-prey interaction and the upstream foraging direction of both the dace and mayfly decrease the likelihood that mayflies were detecting dace by visual or chemical stimuli. Alternatively, the short reactive distances (<1 cm) of *Paraleptophlebia* to the approach of the downstream predator suggests the mayflies are likely responding largely to the hydrodynamic pressure waves formed in front of the fish, as proposed for the mayfly, *Baetis bicaudatus*, reacting to approaching stonefly predators (Peckarsky and Penton 1989).

Regardless of the actual detection mechanism, mayflies exposed to fish predators used drift as an immediate escape response behavior. This response produced a brief pulse in drift rates, but video analysis indicated that drifting individuals quickly settled to the substrate and moved to areas of low risk beneath stones. Thus, drift began decreasing within minutes of the onset of dace foraging and may have returned to control levels even if fish had not been removed from streams. The recent literature examining the effects of fish on lotic invertebrates indicates that drift can be stimulated (Kohler and McPeek 1989) or depressed (Williams and Moore 1982, 1985; Andersson et al. 1986; Holomuzki and Short 1988) by fish presence. In fact, dace may have both positive and negative effects on invertebrate drift behavior, with the direction of the effect apparently depending upon the time elapsed since predator encounter. Together, the contrasting result of the various studies serve to highlight that behavioral response options of lotic invertebrate prey to fish predators are complex and include drift escape, movement to refuge microhabitats and reduction in activity (Kohler and McPeek 1989). Furthermore, because the cited studies used different species of predatory fish and invertebrate prey, it seems likely that the contrasting behavioral responses of lotic invertebrates are partially a result of the interaction among predator foraging mode (sit-and-wait vs. mobile foraging), invertebrate prey mobility and perceptive abilities of the predator and prey.

The other antipredator response of mayfly larvae to dace predators was a retreat from the upper substrate surfaces into interstitial crevices. Review of the video tapes indicated that this retreat response occurred either immediately upon predator encounter or after non-contact, swim-contact and attack-contact induced drift. Since dace are nocturnal foragers (Culp 1989), hiding beneath stones by mayflies reduces the probability of further encounters with dace during the night. Unlike the drift response of *Paraleptophlebia*, the retreating response included a latency period of at least 3 h, with some mayflies remaining in interstitial refugia until the simulated dawn. This delay in returning to upper surfaces during the nocturnal foraging period of dace suggests that mayflies perceive an increased risk of predation after they have experienced an initial predator encounter. As noted for a similar latency effect of predator intimidation in fish (Rahel and Stein 1988), this lengthy hiding period could be due to the prey's inability to detect when it is safe to resume activity on upper stone surfaces.

The delay in foraging resumption may be the result of a behavioral tradeoff between the costs of lost foraging opportunities relative to the benefits of lowering mortality risk (Lima et al. 1985; Ydenberg and Dill 1986; Morgan 1988; Sih et al. 1988). If this is the case, then our results represent the experimental situation where concealment reduces future encounters between this mayfly and dace without costs of lost feeding opportunities. Clearly, experiments in which food reward and predation risk are simultaneously varied are needed to develop a full understanding of the degree to which food availability can balance predation risk (Nonacs and Dill 1990).

Our field data nevertheless suggests that an extended latency period after predator encounters could potentially lead to lost feeding opportunities. Assessment of these costs requires knowledge of the normal feeding periodicity of the mayfly prey and dace predator as well as the food availability in the refuge relative to the upper stone surfaces. In Jumpingpound Creek epilithic algal biomass is significantly lower on the undersides of stones relative to the sides and tops of stones. Furthermore, gut content data indicate this mayfly is nocturnal and its highest feeding rate occurs during the first 4 h after sunset; a feeding pattern which coincides with that of its predator, the longnose dace (Culp 1989). Thus, for mayflies like *Paraleptophlebia*, which already have a limited diel foraging period, the further constraints placed on foraging time by predator avoidance activity clearly could lead to reduced food intake as observed for other aquatic prey (Stein and Magnusen 1976; Dill and Fraser 1984; Holbrook and Schmitt 1988).

Unlike the findings for soft-bottom slow streams (Gilliam et al. 1989), the direct impact of fish on the species composition and abundance of invertebrates in stony bottom streams has been difficult to detect in field experiments (Allan 1982; Flecker and Allan 1984; Culp 1986). This is despite field evidence which supports the hypothesis that size-selective predation by diurnally active fish has been an important evolutionary force in shaping the often observed diel drift pattern of nocturnal maxima for large, lotic invertebrates (Allan 1978, 1984; Newman and Wates 1984). In contrast to these field data, a growing body of evidence from the present, and other, laboratory studies demonstrates stream invertebrates exhibit distinct, but varied behavioral responses to fish predators including reduction in prey activity, escape responses by prey and movement to refugia (Williams and Moore 1982, 1985; Andersson et al. 1986; Holomuzki and Short 1988; Kohler and McPeek 1989). For example, we found that mayfly larvae use drift as an immediate avoidance response to an actively foraging nocturnal fish. Although drifting during the day may lead to increased predation risk from drift foragers (Kohler and McPeek 1989), drift at night is a rapid and effective method for avoiding fish (e.g., dace) which use a mobile search mode, because prey can easily escape from the predator's small reactive field. Similarly, drift under the cover of darkness may be an effective escape mechanism from mobile invertebrate predators (Peckarsky 1980, 1987; Malmqvist and Sjostrom 1988). A caveat of this generalization is that, even at night, drift may increase the encounter rate of invertebrates with sit-and-wait predators, since these ambush predators more frequently encounter and capture evasive prey (Cooper et al. 1985). This could explain why Kohler and McPeek (1989) found that mayfly larvae do not increase their rate of movement in the presence of the sculpin ambush predator, *Cottus bairdi*. Finally, our experiments provide the first evidence that predation risk can provoke mayflies to exhibit a hiding response with a lengthy latency period. This delay in the resumption of foraging could produce longer term consequences for mayfly larvae, including a reduction in feeding and growth rates. Thus, in stony substrate streams where invertebrates have an abundant refuge space from fish, these indirect effects of fish predation ultimately could have important impacts on stream invertebrate community structure.

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