

Size-dependent diel foraging periodicity of a mayfly grazer in streams with and without fish

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We tested the hypothesis that predation risk from diurnal fish influences the diel foraging periodicity of the mayfly grazer, *Baetis tricaudatus* Dodds, in a size-dependent manner by examining habitat use and foraging activity of mayflies in streams with and without these fish predators. In each stream diel habitat use was determined by counting the number of small (3 mm total length) and large (6 mm total length) *Baetis* larvae foraging on the upper surfaces of replicate, natural cobble during 4–8 sampling periods within a 24-h cycle over three seasons. Additionally, larvae were collected and preserved so that the diel periodicity in gut fullness could be determined. In fishless stream reaches small and large larvae exhibited seasonally consistent patterns of aperiodic, or weakly diurnal, periodicities in both gut fullness and the use of exposed, upper surfaces of stones. In contrast, the diel patterns of gut fullness and use of exposed substrate surfaces in stream reaches with abundant fish populations provided strong evidence that foraging by large *Baetis* was nocturnal and that small larvae were aperiodic foragers. Thus, when sympatric with diurnal fish predators, large *Baetis* appear to be constrained to feed at night when predation risk from day active fish is low. Conversely, small *Baetis* grazed from stones throughout the day and night and were unconstrained by these fish predators. This movement pattern of large larvae, from the underside of stones during the day to the sides and tops of stones at night in habitats where diurnal fish predators are present, is similar to the normal vertical migration observed for marine and freshwater zooplankton. The diel vertical migration of large *Baetis* larvae suggests that there is a tradeoff based inherently on an evaluation of predation risk and food reward. That this size-dependent impact of fish predators has not been quantified before could explain some of the contradictory patterns of *Baetis* diel periodicity evident within the literature and future studies need to consider this predator-mediated, size-dependent component of stream insect periodicities.

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Predation is hypothesized to be an important biotic force that impacts diel foraging periodicities of aquatic animals (Stein 1979, Dill 1987). In stream ecosystems, benthic fish and invertebrates are thought to exhibit strong nocturnal feeding patterns in the presence of visual predators (Culp 1989, Flecker 1992) because visual predators are least efficient at night when illumi-

nation is greatly reduced. For example, diel behavior patterns of stream insects, such as peak periods of drift (Allan 1978, 1984) and feeding and positioning on stone surfaces (Cowan and Peckarsky unpubl.), have been directly linked to the risk of predation from visual feeding fish.

If visual feeding fish are a dominant force causing

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stream insects to be constrained to nocturnal patterns of diel foraging and migration as indicated by Flecker (1992), then larger individuals or taxa, which are more vulnerable to these fish predators, are more likely to be nocturnal than smaller ones. In fact, this appears to be the case for downstream drift of aquatic invertebrates (Allan 1978, 1984, Newman and Waters 1984, Anderson et al. 1986). Although diel changes in epibenthic activity have been examined previously (Kovalak 1978, Allan et al. 1986, Casey 1987, Allan et al. 1991), the size-dependent effect of visual feeding fish on stream insect foraging periodicities has not been quantified or examined. This is despite the fact that researchers have suggested that weak nocturnal periodicities observed for some populations of the mayfly, *Baetis*, could be related to small larval size (Rader and Ward 1990). For insect grazers in streams that obtain food resources from stone surfaces exposed to predation from visual feeding fish, the body size of larvae and, thus, their vulnerability as prey, likely play a key role in determining diel foraging patterns.

Our principle objective was to test the hypothesis that diel foraging periodicity of the mayfly grazer, *Baetis tricaudatus* Dodds, was influenced by larvae size and the presence or absence of visually feeding fish. Essentially, this design represents a natural experiment (Diamond 1983), where activity of *Baetis* in streams containing fish was compared with that in fish-absent streams. We predicted that, in the presence of these fish, small larvae (<3 mm) would exhibit aperiodic foraging periodicities, while large larvae (>5 mm) would be restricted to nocturnal foraging activity because large larvae experience substantial predation from visual feeding fish (Culp and Scrimgeour unpubl.). In the absence of predators, both size classes were predicted to feed aperiodically throughout the 24-h diel period. We tested these hypotheses by observing the abundance of small and large *Baetis* larvae on stone surfaces through a diel cycle in the summer, autumn and spring in reaches of the Bow River, Alberta and in Big Hill Springs, Alberta, along reaches with and without fish. In addition, we examined the gut fullness of small and large larvae in these two streams and in Jumpingpound Creek, a tributary of the Bow, to determine whether diel patterns in use of stone surfaces was associated with food ingestion.

Methods

Study animal

Baetis tricaudatus is a lotic grazer that forages on the algae, bacteria and associated particulate organic material present on stone surfaces. Generally, it is bi-voltine in southern Alberta, Canada. A fast growing summer generation completes emergence by early autumn while a slower-growing winter generation develops during the autumn and winter to emerge for reproduction in the

spring. These cohorts overlap in the autumn and spring when the size-frequency distribution of *Baetis* consists of large (>5.0 mm) and small (<3.0 mm) individuals which occupy similar microhabitats.

Sampling strategy and site selection

Field observations to determine if *Baetis* abundance on upper stone surfaces (i.e., top and sides) varied over a 24-h period initially were made only in the fishless (upstream) and fish-present (downstream) reaches of Big Hill Springs on 27 June, 1989. Although these results suggested that the presence of fish affected *Baetis* periodicity on upper stone surfaces, drifting individuals from the upper, fishless reach had the potential to reach the downstream section, thus confounding these diel trends. All further observations at Big Hill Springs were restricted to the fishless reach. A new fish-present site was established on the Bow River, but it was not possible to establish a fishless site on this river. This sampling strategy also allowed us to test the generality of the response in diel foraging periodicity of *Baetis* to fish in two rivers. We added a second fish-present site on Jumpingpound Creek to extend our examination of diel changes in food ingestion in the presence of diurnal feeding fish.

Thus, study sites were located on the Bow River, a fifth order river in Calgary, Alberta, Canada (51°03'N; 114°03'W) and two of its tributary streams, Jumpingpound Creek, Alberta (51°9'N; 114°31'W) a fourth-order trout-stream (Glozier 1989), and Big Hill Springs (50°15'N; 114°23'W), a first order spring-fed stream (Walde and Davies 1984). A small barrier waterfall divides Big Hill Springs into an upstream section that is naturally fishless and a downstream section with a large population of diurnal feeding brook stickleback (*Culaea inconstans* Kirtland) and brook char (*Salvelinus fontinalis* Mitchell) (Culp and Scrimgeour unpubl.). The Bow River and Jumpingpound Creek sites have abundant populations of visual foragers like rainbow trout (*Oncorhynchus mykiss* Richardson) and the nocturnally active longnose dace (*Rhinichthys cataractae* Valenciennes) (Culp 1989). Fish diversity is higher in the Bow and other common species include brown trout (*Salmo trutta* Linnaeus), mountain whitefish (*Prosopium williamsoni* Girard) and spoonhead sculpin (*Cottus ricei* Nelson) (Culp et al. 1992).

Diel habitat use of stone surfaces

Behavioral observations of *Baetis* abundance on natural stone substrate surfaces (i.e., top and sides) were carried out on three sampling dates in Big Hill Springs (27 June, 12 July and 19 September, 1989) and the Bow River (12 July and 31 August, 1989; 24 April, 1990). On each sampling date 8–16, 625-cm² sampling locations

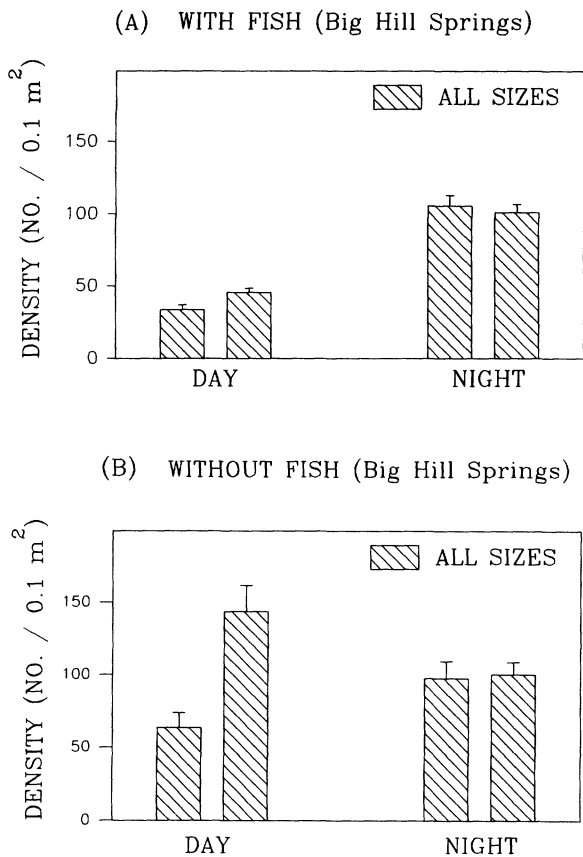


Fig. 1. Mean density (No./0.1 m² + 1 SE) of *Baetis tricaudatus* observed on upper stone surfaces (i.e., top and sides) in June 1989 for reaches of Big Hill Springs (A) with; and (B) without brook stickleback. Replicate observations (n = 16) were made during two time periods of the day and night at both sites.

were established in cobble substrate (16–64 cm²) and the numbers of large and small *Baetis* on upper stone surfaces were recorded twice during both the day and night. Exceptions to these methods occurred in April in the Bow River when only large *Baetis* were present and in June 1989 on the first Big Hill Springs sampling period when the size classes were not separated into small and large individuals. All observations during the day and night were made by viewing the substrate surface through a transparent Plexiglas box (50 × 50 × 10 cm) to eliminate distortion caused by light refraction at the water surface. By approaching the observation area from downstream and by avoiding casting shadows on the sample area, mayfly behavior was not detectably altered by the observation process. Observations between dusk and dawn were facilitated by using low intensity red light to illuminate the substrate (Allan et al. 1986). Although Allan et al. (1991) indicated that red light may affect mayfly behavior, this was not evident in our study. We found that animals grazing on rock surfaces were easily visible with this light source.

More importantly, individual larvae apparently were undisturbed by the light since they grazed continuously throughout the period of observation.

The hypothesis that the density of small and large *Baetis* on stone surfaces did not change significantly between day and night was tested with a model I, two-factor ANOVA with repeated measures in time for each sampling date. For these dates, the two factors were time of day (i.e., day, night) and mayfly size (i.e., small, large). Because size was not a factor in the analysis for April 1990 in the Bow River and June 1989 in Big Hill Springs, a model I, single factor ANOVA was used in these instances to test the hypothesis that *Baetis* abundance was not significantly affected by time of day. For all analyses, inequality in variance was rectified with log₁₀(x + 1) transformation after analysis of the residuals. In April 1990 this transformation could not correct the inequality of variance caused by time periods with null counts, and a non-parametric Kruskal-Wallis, single-factor ANOVA was used for hypothesis testing. Where appropriate, Student-Newman-Keuls a posteriori tests were applied.

We determined the relative abundance of *Baetis* larvae on the upper stone surfaces on 9 May, 1991 in the Bow River and on 10 July, 1991 in Big Hill Springs. At both sites, the number of small and large larvae on the upper surfaces of 18 replicate stones (450 ± 50 cm²) were recorded at night. The following day benthic collections were made so an estimate of total *Baetis* density on each stone could be determined. Collections were made by surrounding a stone with a U-net (Scrimgeour et al. in press), then gently lifting the stone into the net and removing all individuals on the stone and within the upper 5 mm of loose sand beneath it. All mayflies were sorted and counted under 6× magnification in the laboratory.

Diel feeding periodicity

Diel feeding periodicity of *Baetis* was established on 27 June, 1989 in Big Hill Springs, 2 June, 1989 in the Bow River and 12 May, 1989 in Jumpingpound Creek. Ten individual larvae were collected from replicate riffles at 3–6 h intervals over the 24-h sampling period on each sampling date. Larvae were preserved in 10% formalin for two days which is ample time for the stomach wall and stomach contents to be fixed into a firm, discrete mass. Preservation of larvae in formalin did not result in regurgitation of their stomach contents.

In the laboratory, mayfly stomachs and their contents were removed by dissection under 25× magnification. Larvae were pinned onto wax dissecting dishes before making a dorsal incision from the anterior of the head to the base of the tail cerci. This practice provided access to the entire stomach tube, which could subsequently be removed by peeling back all exoskeleton and internal tissues. The mass of the stomach tube, including the

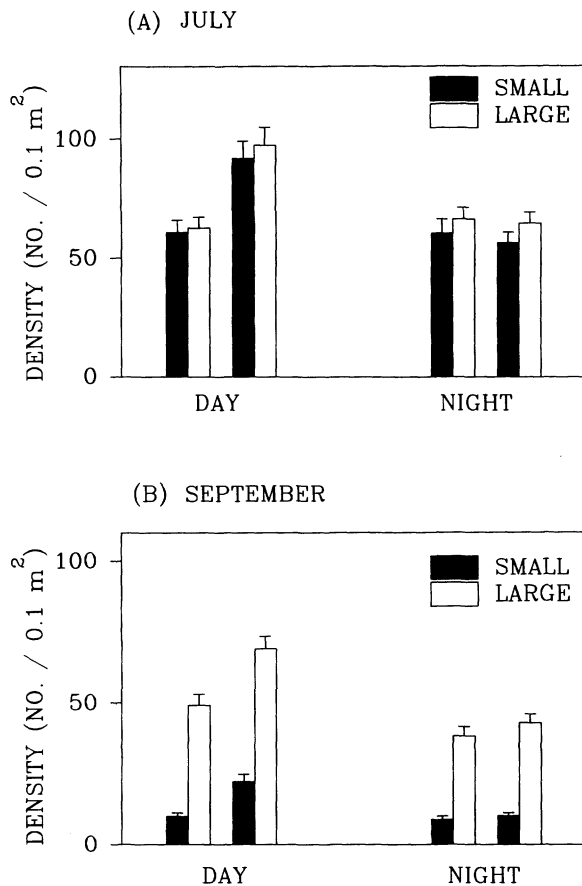


Fig. 2. Mean density (No./0.1 m² + 1 SE) of small (black) and large (white) size-classes of *Baetis tricaudatus* observed on upper stone surface (i.e., top and sides) in the reach of Big Hill Springs without fish during (A) July 1989 (n = 16); and (B) September 1989 (n = 8). Replicate observations were made during two time periods of the day and night in both months.

mass of ingested material, was dried to constant mass at 60°C, and their dry mass determined to the nearest 0.01 mg with a Cahn 25 Automatic Electrobalance. This dry mass represents the mass of both the stomach wall and stomach contents and is, therefore, an overestimate of the mass of ingested food. To overcome this problem, the dry mass of each stomach content was determined by subtracting the mass of an average stomach wall. The mass of the stomach wall was estimated by gut-clearing 20 small and 25 large larvae and establishing the relationship between dry mass of the stomach wall (SW) and the total larval body length (BL). These data were used to generate linear regressions of body length versus dry mass of the stomach wall of small (SW = -0.016 + 0.0105 BL; N = 20, r² = 0.88, p < 0.001) and large larvae (SW = -0.0769 + 0.0264 BL; N = 26, r² = 0.83, p < 0.001). Thus, gut fullness was calculated as: (dry stomach mass - dry stomach wall mass)/dry body mass. The hypothesis that mayfly gut fullness (after arcsine, square-root transformation to stabilize the variance) of

small and large *Baetis* larvae showed no significant diel change was tested with a model I, two-factor ANOVA (i.e., factors of time and larvae size).

Results

Diel habitat use of stone surfaces in streams with and without fish

Brook stickleback were abundant in the downstream reach of Big Hill Springs and, in June 1989, *Baetis* foraging activity in this reach increased at night (F = 62.9, p < 0.001; Fig. 1). In fact, night-time abundances of *Baetis* on stone surfaces were double those during the daytime (q range = 10.9 - 16.0, p < 0.001). In contrast, *Baetis* foraging activity in the fishless reach of Big Hill Springs was aperiodic and abundances on stone surfaces always exceeded 60 larvae m⁻² in June 1989 (Fig. 1). However, larval densities on stones in the fishless reach did vary significantly over the 24-h diel period (F = 29.9, p < 0.001) because daytime densities were both significantly higher (afternoon samples, q range = 4.6 - 5.8, p < 0.001) and lower (midday samples, q range = 7.4 - 8.6, p < 0.001) than night-time abundance values (Fig. 1).

Further sampling in the fishless reach of Big Hill Springs during July and September 1989 indicated a similar aperiodic trend in habitat use for both small and large *Baetis* larvae (Fig. 2). As a result of life cycle patterns for this species, the July population featured equal abundances of large and small larvae, while the September population was dominated by large larvae. However, these differences in density did not appear to affect diel patterns of habitat use. Thus, in both months patterns of habitat use by small and large larvae were similar throughout a diel period except for an increase in larval densities on upper surfaces in mid-afternoon

Table 1. Two-factor repeated measures ANOVA showing the effect of larvae size and time of day on the mean density of *Baetis tricaudatus* observed on upper stone surfaces in stream reaches. *: significant, ns: not significant.

Site and date	Source of variation	F	p
Without fish Big Hill Springs (July 1989)	Size	0.7	0.419 ns
	Time	77.4	<0.001*
	Size × Time	0.9	0.430 ns
Without fish Big Hill Springs (September 1989)	Size	151.7	<0.001*
	Time	33.3	<0.001*
	Size × Time	2.6	0.062 ns
With fish Bow River (July 1989)	Size	17.5	<0.001*
	Time	4.6	<0.005*
	Size × Time	4.7	<0.004*
Without fish Bow River (August 1989)	Size	45.0	<0.001*
	Time	22.4	<0.001*
	Size × Time	47.8	<0.001*

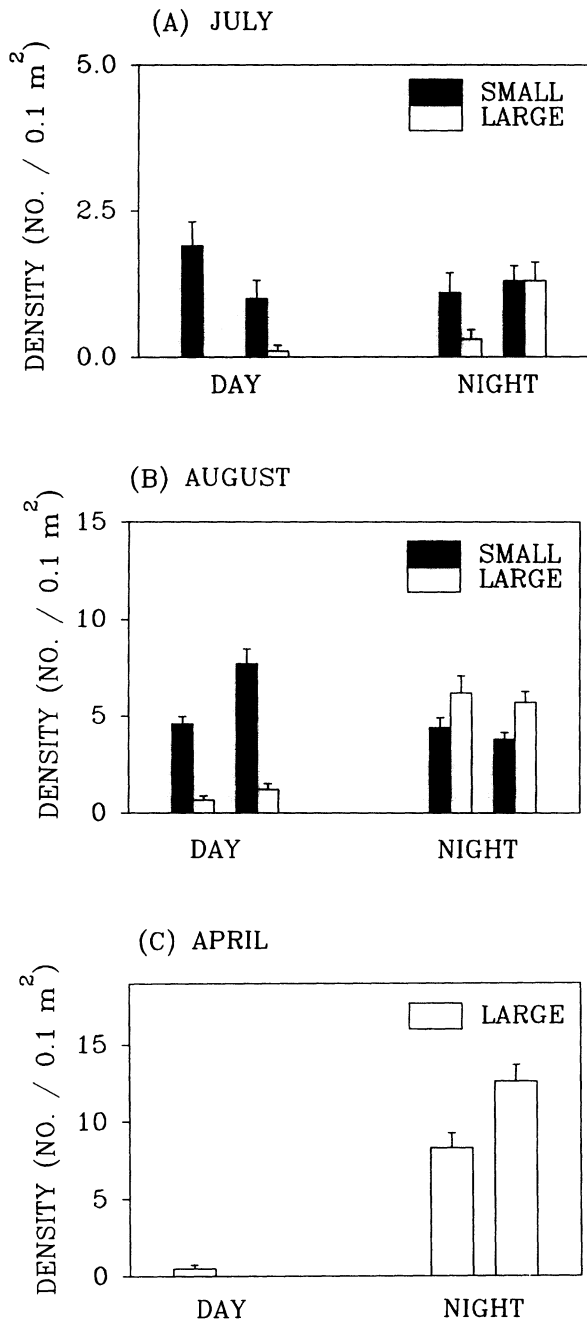


Fig. 3. Mean density (No./0.1 m² + 1 SE) of small (black) and large (white) size-classes of *Baetis tricaudatus* observed on upper stone surfaces (i.e., top and sides) in the Bow River reach with fish during (A) July 1989; and (B) August 1989; and (C) April 1990. Replicate observations (n = 16) were made during two time periods of the day and night in all months.

(Table 1; July q range = 16.8 – 18.3, $p < 0.001$; September q range = 9.8 – 13.0, $p < 0.001$). Larval densities at night ranged between 50–75 individuals 0.1 m⁻² in July and 10–45 individuals 0.1 m⁻² in September. Estimates made in May 1991 suggest that night-time counts represent 43% of the total *Baetis* population. Despite the significantly higher abundances of large larvae compared to small larvae ($F = 151.7$, $p < 0.001$), diel periodicities of the two size classes were similar in September as indicated by the non-significant time and size interaction term (Table 1). Neither larval size or the interaction of size and time significantly affected *Baetis* diel habitat use in July (Table 1).

In the Bow River fish were abundant throughout the study reach. We hypothesized that predation effects should produce different patterns in use of stone surfaces by small and large *Baetis*. Indeed, the significant interaction terms for July and August indicate that small and large *Baetis* displayed different diel patterns of habitat use (Table 1, Fig. 3). For example, the use of upper surfaces by small larvae was aperiodic in July (q range = 0.27 – 3.3, $p > 0.05$) and slightly diurnal in August (q range = 4.1 – 5.7, $p < 0.05$), a pattern similar to *Baetis* larvae in the fishless reaches of Big Hill Springs. In comparison, large *Baetis* in the Bow River were nocturnal and changed their use of upper surfaces from a minimum during the day to peak use at night (July q range = 4.2 – 5.6, $p < 0.05$; August q range = 2.5 – 15.1). This nocturnal periodicity was also observed in the Big Hill Springs reach with fish. The May 1991 measurements suggest that night-time counts on stone surfaces represented 30% of the total number of *Baetis*

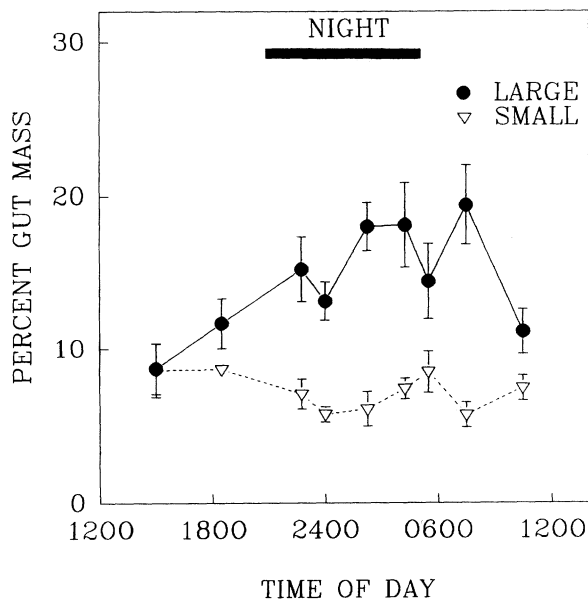


Fig. 4. Diel periodicity in mean gut fullness (food mass/insect body mass + 1 SE) of small (open triangle) and large (closed circle) size-classes of *Baetis tricaudatus* during June 1989 in the reach of Big Hill Springs without brook stickleback.

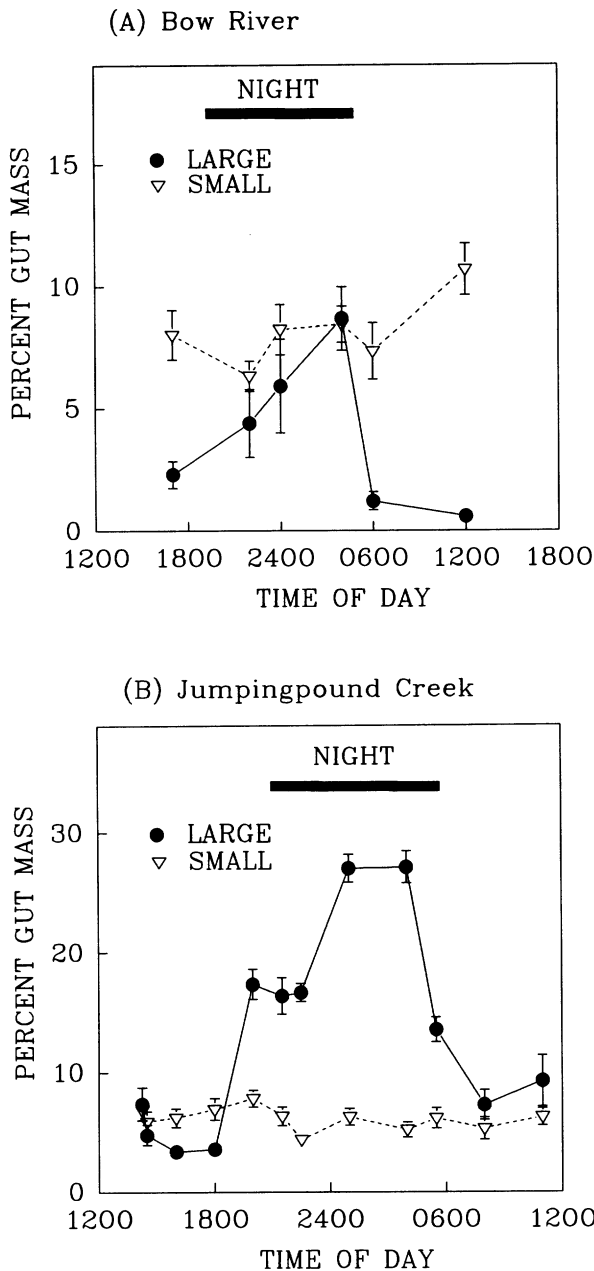


Fig. 5. Diel periodicity in mean gut fullness (food mass/insect body mass + 1 SE) of small (open triangle) and large (closed circle) size-classes of *Baetis tricaudatus* in river reaches with fish: (A) the Bow River (June 1989); and (B) Jumpingpound Creek (May 1989).

on the upper and lower stone surfaces. Thus, in the presence of a fish community composed of diurnal and nocturnal foraging fish, small *Baetis* larvae in the Bow River were aperiodic in their use of upper surfaces while large larvae were strongly nocturnal. In April 1990 when only large larvae were present in the Bow, observations again confirmed the significant nocturnal use of

upper stone surfaces by large *Baetis* (Fig. 3; $H_c = 54.0$, $p < 0.05$; q range = 4.1 – 6.1, $p < 0.05$).

Diel feeding periodicity in streams with and without fish

Gut fullness of *Baetis* larvae in the fishless reach of Big Hill Springs did not vary significantly over a diel period ($F = 1.6$, $p > 0.05$). However, gut fullness was significantly affected by the interaction between time of day and larval size ($F = 3.9$, $p < 0.001$) because of size-specific differences in diel foraging pattern. Gut fullness of small larvae was relatively constant throughout the day, while gut fullness of large individuals showed diel peaks at night and early morning (Fig. 4). Furthermore, gut fullness of large individuals was significantly higher than small larvae ($F = 83.5$, $p < 0.001$). Despite these differences, neither large or small *Baetis* had distinct nocturnal or diurnal feeding patterns and, thus, both size classes can be categorized as aperiodic foragers.

In the Bow River (BR) and Jumpingpound Creek (JPC), streams with abundant fish populations, *Baetis* larvae exhibited similar diel foraging periodicities (Fig. 5). In these streams the foraging patterns of large and small larvae were distinctly different from one another as indicated by the significant interaction between time of day and larval size (BR $F = 7.7$, $p < 0.001$; JPC $F = 23.3$, $p < 0.001$). For example, the diel pattern of gut fullness for small larvae was aperiodic in both streams, a trend also noted in the fishless reach of Big Hill Springs. In contrast, consumption of algal and associated organic material by large *Baetis* was strongly nocturnal with feeding beginning near sunset and ending near sunrise (Fig. 5). Additionally, the level of gut fullness varied significantly between large and small larvae (BR $F = 78.3$, $p < 0.001$; JPC $F = 154.2$, $p < 0.001$). Thus, in the presence of fish, small and large *Baetis* larvae displayed aperiodic and nocturnal foraging patterns, respectively. These findings corroborate the foraging trends established by extensive behavioral observations on the use of stone surfaces.

Discussion

Predators can have strong effects on the spatial and temporal distributions of their prey (Stein 1979, Dill 1987, Sih 1987). In stream ecosystems, fish predators induce changes in microhabitat use (Kohler and McPeck 1989, Culp et al. 1991) and diel activity (Kohler and McPeck 1989). Clearly, the key result of our study is that predation risk from fish impacts the diel foraging periodicity of *Baetis* larvae in a size-dependent manner. In fishless stream reaches, small and large larvae exhibited consistent patterns of aperiodic periodicities in gut fullness and the use of exposed, upper surfaces of stones

in July and September 1989. A similar pattern was evident in June 1989, although we did not differentiate between larval size classes. Thus, throughout a 24-h period approximately 40% of the population could be found foraging on upper surfaces in a fishless stream reach. In contrast, the diel patterns of gut fullness and use of exposed substrate surfaces in stream reaches with abundant fish populations provided strong evidence that foraging by large *Baetis* was nocturnal and that small larvae were aperiodic foragers. Under this risk of predation by fish, large *Baetis* remained in refugia underneath stones during the day. Gut fullness data also indicated this was not an active period of feeding. After sunset large *Baetis* moved to exposed surfaces to feed and 30% of the population occupied the upper surfaces during the night. Small larvae did not appear to respond to this risk regime as analysis of gut fullness and use of exposed surfaces by larvae revealed aperiodic diel foraging patterns similar to those in fishless stream reaches. Foraging patterns of *Baetis* in reaches of the Bow River with fish were consistent among the sampling seasons of summer, autumn and early spring.

Differences in diel activity patterns of small and large *Baetis* in stream reaches with abundant fish populations could be related to changes in abiotic factors such as dissolved oxygen concentration (Wiley and Kohler 1980) and water temperature (Allan et al. 1986). However, our results do not support this hypothesis. In reaches with and without fish, small and large larvae fed on the same stones and differences in oxygen concentration and temperature among the tops, sides and bottoms of stones presumably were negligible. The most straightforward hypothesis to explain the size-specific foraging patterns in the presence of fish is that levels of mortality risk from day-active fish predators, like salmonids and sticklebacks, is directly related to larvae size of *Baetis*. Indeed, large *Baetis* appear to be constrained to feed at night when predation risk from day-active, visual fish is low. Conversely, foraging by small larvae appears to be unconstrained by these fish predators since small *Baetis* graze from stones throughout the day and night. This hypothesis is paralleled with Allan's (1978, 1984) size-specific explanation for ontogenetic changes in the drift behavior of stream insects. In addition, our data provide support for the hypothesis that diel periodicity behavior of *Baetis*, and likely other stream invertebrates, may be phenotypically variable.

Our diel observations for large *Baetis* indicate a net movement of this component of the population from the underside of stones during the day to the sides and tops of stones at night in habitats where diurnal fish predators are present. This diel pattern of movement is similar to the normal vertical migration observed for marine and freshwater zooplankton (Lampert 1989). Despite our study being limited to one species, *B. tricaudatus*, we have observed a similar trend for large individuals of other mayfly species in the Bow River system, including *Paraleptophlebia heteronea* McDunnough and *Epheme-*

rella aurivillii Bengtsson. Although other studies have linked increased night-time use of exposed substrates by *Baetis tricaudatus* (Kohler and McPeck 1989), *Baetis bicaudatus* Dodds (Cowan and Peckarsky unpubl.) and *Baetis* spp. (Rader and Ward 1990) with the presence of diurnal fish predators, our study is the first to demonstrate the size-dependent nature of these shifts in diel periodicity. We suggest that this may be a general diel behavior pattern exhibited by insect grazers in habitats where they must obtain food resources from stone surfaces that expose them to risk from diurnal fish predators. Indeed, the convergent diel activity patterns for several insect species in a variety of stream and geographic regions suggests that these diel activity changes have some adaptive value.

The adaptive value of behaviors like the migration of insect grazers from the undersides of stones to exposed surfaces is dependent upon the combined costs and benefits of behavioral alternatives (Dill 1987, Sih 1987). To maximize energy intake, stream-dwelling insects must forage on the upper surfaces of stones where their algal food resource is most abundant (Culp et al. 1991, Scrimgeour 1992). For grazing mayflies, the cost of restricting foraging to the period of darkness reduces total foraging time, which may have longterm effects on growth. Such costs of lost feeding opportunities for stream mayflies in the presence of fish have been hypothesized by Kohler and McPeck (1989) and Culp et al. (1991). Because fecundity of insect grazers like mayflies is directly related to mayfly body size (Clifford 1970), a reduction in growth rate has the potential to reduce individual fitness. In fact, this relationship has been established for two aquatic insects, the damselfly *Ischnura verticalis* Say and the chironomid *Chironomus tentans* Fab, whose antipredator responses to lentic fish produce costs in terms of reduced feeding rate and individual growth (Dixon and Baker 1988, Macchiusi and Baker 1992).

Recent advances in dynamic optimization models of vertical migration by juvenile sockeye salmon indicate that diel migrations are best understood as adaptations to the different food intake rates and the predation risk associated with sub-components of the habitat (Clark and Levy 1988). Similarly, the diel vertical migration of large *Baetis* larvae from high quantity food patches on stone surfaces at night, to the undersides of stones with low food quantity (Culp et al. 1991) during the day, suggests that there is a tradeoff based inherently on an evaluation of predation risk and food reward. While the observations and experiments of others have indicated that diel periodicity in aquatic invertebrate prey species is singularly influenced by predation risk (Rader and Ward 1990, Flecker 1992), we emphasize that such diel migrations may be better understood as the result of the dual effects of food reward and predation risk. Thus, in stream habitats with diurnal predators, the benefit of this strategy is a direct reduction in predation risk by insect grazers in a benthic environment that forces close

proximity between stream insects and their fish predators. This hypothesis explicitly identifies that the use of upper stone surfaces by insect grazers is influenced by both predation risk and food reward and is supported by experimental evidence demonstrating that insect grazers, like *Baetis*, make adaptive tradeoffs of predation risk and food reward (Kohler and McPeck 1989, Scrimgeour 1992). Our hypothesis assumes that risk from visual predators is directly related to light intensity since diurnal fish, like salmonids, generally locate their prey visually and cease, or greatly limit, foraging at low illumination (Mundie 1971, Henderson and Northcote 1985). Although the nocturnal foraging strategy can not eliminate the predation risk associated with night-active benthic fish, nocturnal benthic fish must present less risk to insect grazers, due to the predator's small reactive field (Beers and Culp 1990) and the well-developed antipredator abilities to nocturnal predators (Culp et al. 1991, Scrimgeour 1992).

Our results demonstrate the importance of a size-dependent component in the overall response of *Baetis tricaudatus* populations to the presence of diurnal fish predators. That this size-dependent impact of fish predators on mayfly foraging periodicity has not been quantified before could explain some of the contradictory patterns of *Baetis* diel periodicity evident within the literature (Elliott 1968, Kovalak 1978, Kohler 1983, Allan et al. 1986, Glozier and Culp 1989, Wilzbach 1990). Clearly, future studies need to consider this predator-mediated, size-dependent component of stream insect periodicities. This would include consideration of microhabitat features that reduce or eliminate exposure to predation risk from visual fish predators, such as the refuges on stone surfaces provided by filamentous algae (Rader and Ward 1990). We also argue that diel vertical movements observed for stream insects must be viewed as tradeoffs of predation risk and feeding rate by individuals, as noted in other ecosystems (Holmes 1984, Clark and Levy 1988). Viewed in this way, one can predict that insect grazers in streams will be constrained to nocturnal migrations to feed from upper stone surfaces when under a regime of predation risk from epibenthic, diurnal fish predators. These grazers may expand their diel foraging window even in the presence of visual fish predators if feeding rates are sufficiently low (e.g., oligotrophic streams). Furthermore, stream-dwelling insect grazers that are not at risk from predation because of morphological defenses, etc., should remain on stone surfaces in order to increase their daily feeding rate. Although our natural experiment provides an initial understanding of the size-dependent impact of diurnal fish predators on the diel foraging behavior of *Baetis tricaudatus*, we emphasize that our hypotheses detailing tradeoffs of predation risk and feeding rate by stream insects will be best examined in laboratory, mesocosm and field experiments.

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