

Diel vertical movements by lotic mayfly nymphs under variable predation risk

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Abstract. 1. The diel foraging periodicities of two grazing mayfly (Ephemeroptera) nymphs, *Heptagenia dalecarlica* and *Baetis rhodani*, under variable fish (European minnow) predation risk were examined in a series of laboratory experiments.

2. *Heptagenia dalecarlica* were almost exclusively nocturnal in their use of feeding areas on stone tops. There was a sharp increase in the proportion of nymphs out of refuge at nightfall, both in the control and fish-odour treatments. In a treatment with freely moving fish, *H. dalecarlica* decreased their activity during both the day and night. In feeding trials with three freely foraging minnows, nymphs were completely safe when they had access to refuges beneath stones, whereas almost half the nymphs were consumed when no refuges were available.

3. *Baetis rhodani* nymphs reduced their use of stone tops when exposed to four caged minnows or a freely moving fish, but this occurred both day and night. In feeding trials, *B. rhodani* were captured only while in the water column, and their mortality risk was independent of refuge availability.

4. It is suggested that because *H. dalecarlica* lack efficient post-encounter defences, they must rely on pre-encounter mechanisms to reduce the threat of fish predation. It appears that in order to dwell sympatrically with fish, *H. dalecarlica* have evolved a coexistence by hiding strategy. In contrast, *Baetis* are vulnerable to fish attacks only if they enter drift in daylight, and are thus able to remain on stone tops both during the day and at night.

Key words. *Baetis rhodani*, diel periodicity, fish predation risk, *Heptagenia dalecarlica*, mayfly nymphs, refuge use, streams.

Introduction

Prey animals are often confronted with a conflicting situation: the best foraging areas commonly support dense populations of predators, forcing prey to balance foraging and antipredator needs. Because risk from visually foraging predators varies on a diel basis, prey should enter the best feeding sites only under the cover of darkness. The most celebrated example of such predator-induced nocturnality is undoubtedly the diel vertical migration of zooplankton (Neill, 1990, 1992; Lampert, 1993; Pijanowska, 1993). Avoidance of visually feeding fish is now widely accepted as the unifying concept underlying the evolution of diel vertical migration (Lampert, 1993). Similar arguments have been put forward to explain the nocturnally-

biased drifting of stream invertebrates (e.g. Allan, 1978; Flecker, 1992). Both behaviours were long believed to be fixed antipredator responses to invariably high predation pressure (Gliwicz, 1986; Luecke, 1986; Sih, 1987; Flecker, 1992); however, evidence has now accumulated that these nocturnal prey behaviours are in fact induced by the presence of fish (Lampert, 1993; Pijanowska, 1993; Douglas *et al.*, 1994; Tikkanen *et al.*, 1994).

In streams, stone tops support the highest amounts of periphytic algae, but are also unsafe habitats owing to the threat posed by fish feeding on epibenthic prey (Kohler & McPeck, 1989; Culp *et al.*, 1991; McIntosh & Townsend, 1995). It is thus not surprising that lotic invertebrate grazers have been shown to express diel movements from refuges beneath stones during the day to exposed surfaces at night (Culp & Scrimgeour, 1993; Cowan & Peckarsky, 1994; McIntosh & Townsend, 1994; Tikkanen *et al.*, 1996). A majority of studies concerning predator avoidance behaviours

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of lotic prey has used mayflies, especially those of genus *Baetis* spp. *Baetis* possess a wide array of flexible anti-fish behaviours, including nocturnal drifting and use of stone tops (e.g. Kohler & McPeck, 1989; Tikkanen *et al.*, 1994). It has been shown previously that the mayfly *Heptagenia dalecarlica* Bgtss. is even more strictly nocturnal than *Baetis* in its feeding behaviour, abandoning refuges beneath stones only after the onset of darkness (Huhta *et al.*, 1995). These observations were made in laboratory stream tanks, where mayflies were isolated from fish cues. The nocturnal activity of *H. dalecarlica* could thus represent a case of fixed predator avoidance behaviour (see Sih, 1987). By contrast, only small nymphs of *Baetis rhodani* Pict. reacted to fish presence by reducing their daytime use of stone tops, whereas large nymphs did not show any positioning responses. It was suggested that the reason for such an unexpected lack of response could be the high capacity of large *Baetis* nymphs to parry fish attacks (Tikkanen *et al.*, 1994; see also Scrimgeour & Culp, 1994b), indicating that fish predation risk for *Baetis* is strongly size-dependent and does not necessarily increase monotonically with nymphal size.

In the study reported here, the responses of mayfly grazers to predation risk from a visually hunting fish (European minnow, *Phoxinus phoxinus* L.; see Müller, 1973) were examined. First, laboratory predation trials were used to compare the vulnerability of *Heptagenia* and *Baetis* nymphs to freely foraging fish in the presence and absence of refuges. The diel periodicity in the use of stone tops by *H. dalecarlica* and *B. rhodani* under varying levels of fish predation risk were then compared. It was expected that *H. dalecarlica* would remain nocturnal regardless of fish manipulations, whereas *B. rhodani*, being less vulnerable to fish attacks, was expected to be largely aperiodic in its use of upper stone surfaces.

Materials and methods

Study species

Heptagenia dalecarlica is one of the most common grazing invertebrates in northern boreal streams. It feeds mainly on diatoms, but also includes fine particulate detritus in its diet (Jones, 1950; Huhta *et al.*, 1995). It occupies interstitial microhabitats underneath and between stream stones, and enters stone tops for short feeding bouts mainly during the night (Huhta *et al.*, 1995). Its life-cycle in northern Finland is univoltine, with fastest nymphal growth occurring from July to September. The flight period occurs synchronously in late June to early July (A. Huhta, unpublished).

Baetis rhodani is frequently the dominant invertebrate grazer in boreal streams. It occupies both upper and lower stone surfaces, feeding on attached algae and detritus (Huhta *et al.*, 1995). *Baetis rhodani* nymphs are efficient swimmers that frequently enter the water column and drift downstream in search of unexploited food patches (Kohler, 1985). *Baetis rhodani* also expresses diel vertical movements between stone surfaces, but these are less distinct than in *H. dalecarlica* (Huhta *et al.*, 1995). In the study area, *B. rhodani* has a one-year life-cycle, with overwintering nymphs. Fastest growth

occurs in early summer, and it has a long flight period extending from mid-June to late July (A. Huhta, unpublished).

Prey vulnerability

Vulnerability of prey in relation to refuge availability was examined by exposing 15 nymphs of each species to three actively foraging minnows in simple feeding trials. These trials were conducted in the same stream tanks that were used for behavioural observations (see below). Care was taken to use nymphs of the same size range as in the studies of nymphal behaviour. Minnows (mean \pm SE = 58 ± 2 mm total length, $n = 15$) were starved for 1 day before they were used in a trial. The hunger level of the mayflies was standardised by keeping them in holding tanks for 21 h without food. Nymphs were placed into the stream tanks at 15.00 hours, and minnows were added at 17.00 hours. Because preliminary observations showed minnows to be strictly day-active predators (see also Müller, 1973), the trials were conducted in daylight. The experiments were terminated at 21.00 hours, after which the tanks were searched thoroughly for any remaining nymphs. Aquaria were then cleaned thoroughly to prevent any carry-over of fish chemicals during the experiment. In this experiment, there were two treatments with contrasting levels of refuge availability. In one treatment, nymphs had free access to refuges beneath stones, while in the other, tiles on the arena were placed so that nymphs could not enter refuges. Six trials were run per day, and treatments were randomised among the days of the experiment and among the six stream tanks used each day. Behavioural observations (direct observations, 15 min per aquarium) were also made to examine whether nymphs were attacked/captured while in the water column (swim or drift) or on the substratum.

Vulnerability experiments were analysed with a two-way ANOVA, with prey species and refuge availability as the main factors. The number of replicates was six for all treatment combinations. The proportion of nymphs (arcsin square-root transformed) remaining after a trial was used as the response variable.

Refuge use periodicity

The experiments were run at Oulanka Biological Station, north-eastern Finland, in August 1994 and September 1995. Experiments were conducted in stream tanks modified from the model of Soluk and Collins (1988; see also Tikkanen *et al.*, 1994, for a detailed description of the stream system). The tanks ($40 \times 20 \times 19$ cm) hold 13.3 l of water, and a recirculating flow is created with air pumped through a diffuser. Flow rate in the experimental arena on the bottom of the aquarium is $15\text{--}20\text{ cm s}^{-1}$, well within the range of velocities where heptageniid and baetid nymphs occur in nature. Mesh cloth on the bottom of the arena provided a foothold for the nymphs, and eight unglazed ceramic tiles ($49 \times 49 \times 5$ mm) were used as the experimental substratum. The tiles were arranged so that they could be observed readily from all directions. One corner

of each tile was raised slightly to provide the prey with a refuge from fish. The tiles were incubated in a nearby fishless stream for 3–4 weeks before they were used in the trials. During this period, a visible periphyton layer developed on the upper tile surfaces, and the amount of periphytic algae was, on average, five-fold higher on the tops than on the bottoms of the tiles (5.4 vs. 1.0 $\mu\text{g chl-a cm}^{-2}$, respectively; see Tikkanen *et al.*, 1994). To further ensure that only stone tops would support food for the mayflies during the trials, the undersides of the tiles were brushed clean of periphyton. Tiles in each aquarium were replaced at the end of each day of the experiment. Aerated water transferred from a nearby fishless stream was used in all trials.

Mayfly nymphs were collected 1 day before they were used in the trials, and held in circular Plexiglas® aquaria (490 cm² planar area) with recirculating flow (see Mackay, 1981). Nymphs were collected from a stream containing both drift-feeding (minnow, brown trout) and bottom-feeding (burbot) fish, with an overall density of ≈ 0.20 fish m⁻². The experiments were run in six stream tanks per day; each tank received 15 size-matched *H. dalecarlica* (mean body length without cerci \pm SE = 6.2 ± 0.5 mm, $n=25$) or *B. rhodani* (4.1 ± 0.4 mm, $n=25$) nymphs. This experimental density (≈ 190 individuals m⁻²) approximates natural densities in streams of the Oulanka area (20–1500 individuals m⁻² for *H. dalecarlica* and 90–6500 m⁻² for *B. rhodani*, respectively; A. Huhta, unpublished).

The experimental design incorporated eight treatment combinations in a 4 \times 2 factorial structure. The experimental factors were: fish presence (zero, one, or four caged fish or one freely moving fish) and time of day (day vs. night). Each treatment combination was replicated six times. The same set of nymphs was used in all observations during a trial, so time of day was a within-subject factor in repeated measures ANOVA. A gradient in predation risk was established by keeping zero, one, or four minnows in an opaque plastic tube with netting at both ends. The tube was placed parallel to the flow on the horizontal baffle of the aquarium, so that mayflies could not see the fish, but the water flowing through the tube carried fish chemicals. As a fourth level of predation risk, a freely moving fish was used. To establish this treatment, the fish were anaesthetised with sodium bicarbonate (500 mg l⁻¹), and their mouths were sewn shut loosely with a few stitches of cotton thread. This did not affect the behaviour of minnows: after recovery from anaesthesia, the search activity (proportion of time spent actively searching for or pursuing prey) of sewn fish did not differ from that of control individuals ($t_8=0.70$, $P>0.05$). To ensure that the fish would behave normally, they were allowed a 5-h recovery period before being used in the trials. In this treatment, an empty tube was added on the horizontal baffle of the aquarium to control for any possible hydrodynamic effects of the tube. In the study area, minnow and heptageniid and baetid nymphs live sympatrically in most stream pools, and both mayflies occur frequently in minnows' diet (P. Tikkanen, unpublished). After a day's trials, fish were kept in large holding tanks for 24 h, being fed with live mayflies. No fish died during this surveillance period, and because they all seemed to be feeding normally, they were

returned to the stream from which they were collected. Most of the mayflies (excluding those preserved for size measurements) were also returned to the stream of their origin.

Observations of nymphal behaviour were made on five occasions: three times in daylight (at 15.00, 17.00, and 09.00 hours the following morning: day trials), and twice in darkness (at 21.00 and 23.00 hours: night trials). Nymphs were placed into the stream tanks ≈ 2 h before the first day observation began, and the tube and the live fish were placed 1 h before the first day observation. Water temperature in the stream system (range: 10–17.5 °C) reflected closely diel variation in ambient temperature. Lights were turned off 1 h before the first night-time observations, and were turned on again at 08.00 hours. This light cycle is very similar to the natural light regime in northern Finland in late autumn. Observations in the dark were facilitated by dim red light, to which baetids do not react, but heptageniids are sensitive to some degree (see Peckarsky & Cowan, 1995). If this affects diel periodicity of the mayflies, however, it should reduce their occurrence on stone tops more at night than during the day, making nymphs appear less nocturnal than they would be in complete darkness. Moreover, nymphs on stone tops fed continuously, indicating that they were undisturbed by the red light (see also Culp & Scrimgeour, 1993). To reduce any disturbance to nymphs further, all observations were made from behind a dark board in which small observation windows were cut.

The observation protocol was similar to that in earlier work on mayfly behaviour (see Tikkanen *et al.*, 1994; Huhta *et al.*, 1995), with some minor modifications. In each stream tank, the number of nymphs on sides and tops of stones (i.e. exposed to fish) was recorded during a 10-s period. These counts were repeated every 30 s, 15 times for each tank during an observation period. The mean proportion of nymphs on exposed stone surfaces during an observation period (i.e. mean of 15 successive counts) was used as the response variable in the statistical analysis. The same set of observations was repeated, in a randomised order, in all six aquaria. After the last observation period at 09.00 hours, the nymphs were collected and measured, and the aquaria were emptied and cleaned thoroughly. To prevent any carryover effects of fish chemicals, the fish-present treatments were run in separate aquaria from the no-fish treatments. Otherwise, treatments were randomised among the stream tanks. To control for any position effects, the positions of the aquaria were changed systematically among the days of the experiment.

The null hypothesis that the proportion of *H. dalecarlica* or *B. rhodani* nymphs out of refuge did not differ between (1) fish presence levels and (2) time of day was tested with a two-factor repeated measures ANOVA. Data from all day trials were pooled and data from night trials were pooled. Separate analyses were conducted for each species, because, unlike the vulnerability trials, behavioural experiments were run separately for *H. dalecarlica* and *B. rhodani*; thus, species identity was not an explicit factor in the ANOVA. To correct for inequality of variances, surface use data were arcsin square-root transformed.

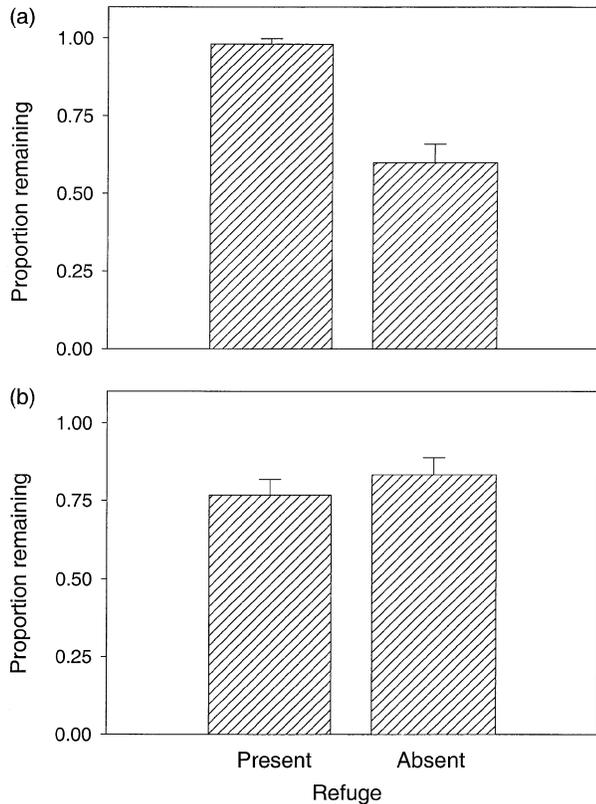


Fig. 1. Number of (a) *Heptagenia* and (b) *Baetis* nymphs (mean \pm SE) remaining after a 4-h exposure to three freely foraging European minnows, in the presence and absence of beneath-stone refuges. Initial number of nymphs was 15 per trial. Each treatment combination was replicated six times. Difference between the refuge availability treatments is significant for *H. dalecarlica* (*t*-test, $t_{10}=4.88$, $P<0.01$) but not for *B. rhodani* ($t_{10}=0.73$, $P>0.05$).

Results

Vulnerability of *H. dalecarlica* and *B. rhodani* nymphs to minnow predation: the role of refuge accessibility

The two-way interaction term (species \times refuge) in the ANOVA was highly significant ($F_{1,20}=16.90$, $P<0.001$), indicating that the importance of refugia to prey mortality risk was different for the two species. Availability of refuges was clearly important for *H. dalecarlica*: practically no heptageniids were eaten by fish when nymphs had unconstrained access to refuges. Conversely, when access to refuges was denied, the risk of being preyed upon was substantially higher; almost half the nymphs were consumed in trials where prey were exposed to fish continuously (Fig. 1a). Nymphs were captured only while on the substratum; no *H. dalecarlica* entered drift during behavioural observations. Instead, nymphs mainly stayed motionless on the sides of the stones, which probably provided a partial refuge from fish. Nymphs that entered stone tops were attacked and consumed by minnows almost immediately. In *B. rhodani*, the presence of refuges did

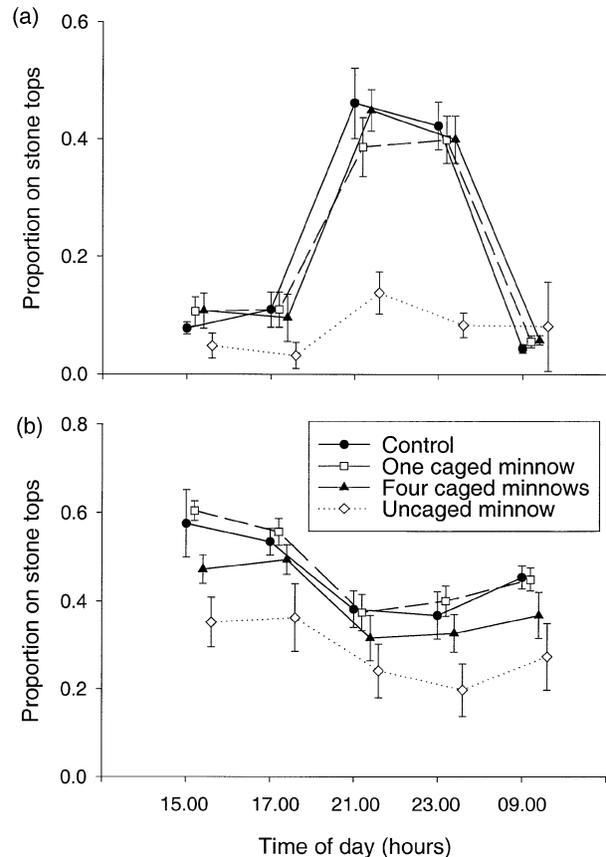


Fig. 2. Proportion (mean \pm SE) of (a) *Heptagenia* and (b) *Baetis* nymphs on stone tops during the day (15.00, 17.00, and 09.00 hours) and at night (21.00 and 23.00 hours) in different fish presence treatments.

not affect prey mortality risk (Fig. 1b), however entering the water column was extremely risky for *B. rhodani*: all seven nymphs that entered drift during observations were captured by minnows. In contrast, fish showed no reaction to nymphs remaining on stone tops.

Diel periodicity in the use of exposed stone surfaces by mayfly nymphs

The use of stone-top microhabitats by *H. dalecarlica* was conspicuously nocturnal. There was a sharp increase in the number of nymphs on stone tops at nightfall, and at sunrise nymphs withdrew to their hiding places beneath the stones (Fig. 2a). Nymphs exhibited a similar pattern of night-time activity in all but the free-minnow treatments. In the proximity of a freely roaming fish, *H. dalecarlica* reduced their overall activity and were less nocturnal than in all other treatments; hence the significant time \times fish interaction term in the repeated measures ANOVA (Table 1). Thus, *H. dalecarlica* altered their refuge use periodicity only when subjected to an

Table 1. Repeated measures ANOVA for the effects of time of day (day vs. night) and fish presence (zero, one, or four caged minnows or one freely foraging minnow) on the proportion of mayfly nymphs on stone tops (arcsin square-root transformed).

Source of variation	d.f.	MS	F	P
<i>Heptagenia</i>				
Within subjects				
Time	1	0.854	597.08	<0.001
Time × Fish	3	0.074	49.97	<0.001
Error	20	0.001		
Between subjects				
Fish	3	0.121	56.27	<0.001
Error	20	0.002		
<i>Baetis</i>				
Within subjects				
Time	1	0.005	0.23	0.662
Time × Fish	3	0.032	1.22	0.327
Error	20	0.026		
Between subjects				
Fish	3	0.307	5.31	0.007
Error	20	0.058		

imminent predation threat, in which case they almost ceased moving.

By contrast, *B. rhodani* nymphs showed no nocturnality in their use of stone tops; if anything, they were slightly diurnal, especially in fishless controls and in treatments with one caged minnow (Fig. 2b). Overall, *B. rhodani* were clearly capable of assessing the prevailing predation risk: the higher the risk, the more reluctant the nymphs were to abandon refuges, both during the day and at night (Fig. 2b; see also the significant main effect of risk in rMANOVA, Table 1).

Discussion

It should always be in the interests of prey to interrupt a predation sequence at the earliest possible stage (Endler, 1991). Early defences should therefore be more frequent than behaviours used after a predator contact, leading to a predominance of avoidance versus antipredator mechanisms of prey defence (Brodie *et al.*, 1991; Endler, 1991). Being active at night is a common predator-avoidance mechanism, whereby prey reduce the likelihood of predator encounters (e.g. Sih, 1987). Among lotic insects, some mayfly nymphs have been shown to express nocturnal foraging movements from concealed hiding places to exposed stone tops (e.g. Culp & Scrimgeour, 1993; Cowan & Peckarsky, 1994; McIntosh & Townsend, 1994; Tikkanen *et al.*, 1996). Such behaviours are usually triggered by the presence of fish, and are thus examples of plastic prey responses to variable predation threat. In the present study, *H. dalecarlica* nymphs strongly avoided entering exposed stone surfaces in daylight, although they would clearly increase their food intake by spending more time on upper stone surfaces with periphytic food. Entering stone tops during the day, however, would constitute an excessively

high mortality risk for *H. dalecarlica*, thus selecting for fixed diel periodicity.

Until the late 1980s, it was widely believed that anti-predatory behaviours of aquatic insects were relatively hard-wired, showing little plasticity to alterations in local predation risk (e.g. Allan *et al.*, 1986; Sih, 1987; Flecker, 1992). Many recent studies have challenged this view: it is now becoming evident that at least some aquatic invertebrates are able to assess changes in predation regime, displaying facultative behavioural alterations in the presence of predators (see, for example, Kohler & McPeck, 1989; Douglas *et al.*, 1994; Tikkanen *et al.*, 1994; references therein). Such a reduction in mortality risk incurs costs, however; in aquatic insects, avoiding predator encounters often entails a loss of feeding opportunities, which ultimately leads to lowered individual fitness (Feltmate & Williams, 1991; Scrimgeour & Culp, 1994a). On the other hand, fixed behavioural traits also involve costs. If the predation regime is variable, albeit generally low, fixed behaviours should result in high fitness variance, thus decreasing the expected mean fitness (Sih, 1987). It is known from previous studies that heptageniid nymphs feed preferentially on diatoms (more so than do baetids; Huhta *et al.*, 1995), and that their growth rates are higher on a diet of natural stream periphyton than on leaf detritus (Webb & Merritt, 1987). Furthermore, there is evidence that fish predation risk is not constantly high but varies spatially and temporally even at the scale of a single stream reach (e.g. Muotka *et al.*, 1998). Thus, flexible prey responses induced by the presence of fish should presumably have been selected for in heptageniid mayflies. Why, then, do they not express such plasticity in their antipredator behaviour?

Sih (1992) proposed that lack of prey response to predator removal should be expected if the prey have exceedingly low probability of escape after a predator encounter. Feeding trials in this study showed that heptageniid nymphs survive fish attacks well if they have unconstrained access to spatial refuges. *Heptagenia dalecarlica* nymphs are highly inefficient swimmers, and if forced into the water column, they are captured easily by drift-feeding fish. Yet they rarely form the bulk of the diet of any stream fish (P. Tikkanen, unpublished), indicating a nearly complete reliance on pre-encounter fish avoidance behaviours. *Baetis rhodani* nymphs, by contrast, are much more effective in evading attacks by fish feeding on epibenthic prey (Scrimgeour & Culp, 1994b; Tikkanen *et al.*, 1994). Nevertheless, they do face a high risk of fish predation if they enter the water column in daylight. It is thus not surprising that *B. rhodani* are strongly nocturnal in their drift behaviour, especially in the presence of fish. It appears, however, that epibenthic feeding does not constitute such a high risk for *B. rhodani*, which would explain the lack of nocturnality in their use of stone tops in these experiments. Stream insects live in an environment where they must balance relative risks from different kinds of predators using different foraging modes (Soluk & Collins, 1988). *Baetis rhodani* are frequently consumed by interstitial invertebrate predators, and are claimed to be the favoured prey of many stream-dwelling predatory stoneflies (Peckarsky *et al.*, 1994). In marked contrast, heptageniid nymphs have highly efficient antipreda-

tory behaviours against invertebrate predators (Peckarsky *et al.*, 1994; Tikkanen *et al.*, 1997). Thus, while in the interstitial zone, heptageniids face a relatively low predation risk, but, owing to their high vulnerability to epibenthic fish, they can enter feeding areas on stone tops safely only during darkness. It thus appears that to dwell sympatrically with fish, heptageniid nymphs have evolved a coexistence by hiding strategy (see Sih, 1987). This behavioural response is modified only when the nymphs experience an imminent predation risk in the presence of an actively foraging fish; then they nearly cease feeding on stone tops, remaining in refugia even in darkness. Thus, their behaviour in relation to predation risk is not completely fixed, but involves a flexible component.

Fixed prey responses are notoriously difficult to demonstrate. Lack of response, e.g. no change in the diel periodicity of prey after fish removal, provides only weak support for the existence of a fixed trait (see also Sih, 1992). Douglas *et al.* (1994) reasoned that to present a good case for a fixed avoidance response, predator manipulations should be coupled with comparative studies documenting prey behaviour in environments with and without the presumed predator. Unfortunately, this could not be done with *H. dalecarlica*, because *Heptagenia* are absent from the few fishless brooklets found in the study area, for reasons probably connected with the resource base of these narrow, heavily shaded streams. Nevertheless, it is contended that the lack of behavioural response to predator removal, coupled with the extremely high predation risk when daytime retreat to refuges is prohibited, constitutes reasonable evidence for inflexible avoidance responses in this mayfly prey.

The antipredatory responses of *B. rhodani* have been reported to vary in relation to the predation history of the streams from which the nymphs come. Thus, nymphs from a fish stream should remain nocturnal even in the absence of fish, whereas nymphs in fishless streams are aperiodic, and only turn nocturnal when exposed to fish (Cowan & Peckarsky, 1994; McIntosh & Townsend, 1994). Large *B. rhodani* nymphs are considered nocturnal foragers, to the extent of 'not feeding during the day' (Culp & Scrimgeour, 1993). In the present study, however, baetid nymphs showed little response to fish presence. Furthermore, a relatively strong stimulus (odour of four minnows or a freely moving fish) was needed to induce any reduction in their use of stone tops. At present, there is no explanation for the discrepancy between results from different studies. It may be, however, that due to their relatively small body size (body length \approx 4 mm), nymphs in these experiments were in a size refuge from predation by fish feeding on epibenthic prey. The two *Baetis* species dominant in northern boreal streams, *B. rhodani* and *B. subalpinus*, overwinter as small larvae and grow rapidly in early summer, to emerge in late July (A. Huhta, unpublished). Large nymphs are thus present for only a short period of time around the solstice when there is continuous daylight in these high northern areas. Thus, the selection regime favouring the evolution of diel vertical movements in *Baetis* may not have occurred in these subarctic streams.

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Accepted 27 April 1999