Anim. Behav., 1996, **51,** 1391–1399

Fishless-stream mayflies express behavioural flexibility in response to predatory fish

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(Received 12 April 1995; initial acceptance 26 June 1995;
final acceptance 27 October 1995; MS. number: 4904)

Abstract. The fish avoidance behaviour of nymphs of the grazing mayfly *Baetis rhodani* (Ephemeroptera) was examined. The nymphs originated from a fishless stream. To study their responses to the addition of predator cues, nymphs were exposed to (1) chemical cues from a caged fish, or (2) a freely moving diurnal fish (European minnow, *Phoxinus phoxinus*). The nymphs immediately increased their refuge use when exposed to a live fish, whereas chemical cues alone did not cause any avoidance responses. In a second experiment, the effects of (1) fish chemicals and (2) a fish model plus fish chemicals on the diel refuge use patterns of *Baetis* nymphs were examined. In the presence of a fish model, more nymphs were outside the refuges during the first few hours of darkness, when fish predators are not active, than at any other time of day. A similar but non-significant trend was observed when only chemical cues of fish were present, whereas refuge use in the control treatment was aperiodic. *Baetis* nymphs were thus able to assess the fish predation risk and to respond by quickly adjustable, flexible avoidance behaviour. Spatial and temporal variation in predation risk, and adult dispersal between fishless and fish-inhabited streams, may be the key factors promoting the maintenance of flexible fish avoidance behaviour in stream-dwelling mayfly nymphs.

Most prey animals are exposed to spatially and temporally variable predation pressure, which should select for flexible anti-predatory traits (Dodson 1989; Neill 1992; Pijanowska 1993). Fixed (canalized) responses should evolve only if the predation regime is relatively invariant and predictable. To adopt appropriate anti-predatory responses, prey must obtain information about the prevailing predation environment. If gathering such information renders prey vulnerable to predation, fixed responses should evolve even if predation pressure is highly variable (Sih 1987).

Many recent studies have shown that stream insects are much more flexible in their responses to both fish (Kohler & McPeek 1989; Douglas et al. 1994; McIntosh & Townsend 1994; Tikkanen et al. 1994) and invertebrate (Soluk & Collins 1988a) predators than previously thought. In a recent paper (Tikkanen et al. 1994), we examined size-dependent anti-predatory responses, especially diel periodicities in drift and refuge use, of the mayfly *Baetis rhodani* Pict. under a gradient of predation pressure. *Baetis* nymphs are highly mobile and frequently enter the water column to drift downstream (e.g. Kohler 1985). Drift of large *Baetis* nymphs was mainly nocturnal in all treatments involving fish cues. In contrast, no diel periodicity in drift was observed when the water was not conditioned with fish chemicals. Fish presence had no effect on the drift of small nymphs. Chemical cues alone did not change the refuge use of any of the *Baetis* size classes, but in the presence of a freely foraging fish, small nymphs increased their daytime use of refuges. Together, these results indicate that *Baetis* nymphs are able to assess the prevailing predation pressure and to adjust their behaviour accordingly.

The results of our previous study, which was conducted on *Baetis* living in fish streams, motivated a similar experiment on nymphs that

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0003–3472/96/061391+09 $18.00/0

had no experience of fish, to see whether they also express plastic behavioural responses to fish predators. Inter-population differences in prey behaviour are known to occur in many aquatic organisms, for example, cladocerans (Parejko & Dodson 1991; Pijanowska et al. 1993), treehole mosquitoes (Juliano & Reminger 1992) and fish (Giles & Huntingford 1984; Magurran 1990; Mathis et al. 1993). Such behavioural differences between populations are often fixed, with individuals from low-predation sites showing little or no response to predators. However, mayflies allopatric with fish may have retained the capacity for appropriate avoidance responses if prey populations in adjacent streams are inter-connected. In our earlier paper (Tikkanen et al. 1994) we suggested that fixed behavioural patterns are highly unlikely to evolve in a species with winged adults (such as lotic mayflies), especially in a region with no obvious barriers to aerial dispersal and, thus, gene flow.

Comparisons of prey responses in stream insect populations with historically contrasting levels of exposure to fish are rare. Malmqvist (1988), Flecker (1992) and Douglas et al. (1994) have shown that drift of mayfly nymphs is more nocturnal in streams with fish. Douglas et al. (1994) introduced rainbow trout, *Oncorhynchus mykiss*, to previously fishless streams, and observed an immediate reduction in the day drift density of *Baetis* mayflies. McIntosh & Townsend (1994) compared prey responses of a siphlonurid mayfly, *Nesameletus ornatus*, from streams with different fish predation regimes. They observed both flexible and fixed responses, depending on the predation history of the nymphs and on the predator cues to which they were exposed (brown trout, *Salmo trutta*, versus common river galaxias, *Galaxias vulgaris*, versus no fish).

In this paper, we document results from two laboratory experiments where *Baetis* nymphs with no previous experience of fish were exposed to different signals of fish presence. For the reasons outlined above, we predicted that in the presence of an actively foraging fish, nymphs would increase their daytime use of refuges. Chemical signals, on the other hand, may be inaccurate and not connected to imminent predation threat (Tikkanen et al. 1994; see also Bouskila & Blumstein 1992). Therefore, reliance on chemical cues alone could lead to unnecessary confinement to low risk and low food microhabitats beneath stones. Thus, no diel changes in refuge use were expected when only chemical cues of fish were present. We also tested whether a simple fish model would elicit prey responses, or whether more precise information about predator activity and the probability of encounters with and attacks by a fish are required for appropriate avoidance responses to occur.

METHODS

Baetis rhodani (Ephemeroptera) often dominates the guild of grazing stream invertebrates in northern Finland (A. Huhta, personal observation). In most streams it occurs sympatrically with fish, especially brown trout, alpine bullhead, *Cottus poecilopus* Haeckel, and European minnow, *Phoxinus phoxinus* L., which all feed on *B. rhodani* (P. Tikkanen, unpublished data). In our study area, *B. rhodani* is mainly univoltine. Fast growth occurs in the early summer, and two different size classes commonly co-occur in June, giving rise to a rather long flight period in June–July. Nymphs develop during the late summer, and in September–October they are of a fairly uniform size (A. Huhta, personal observation).

We collected nymphs of *B. rhodani* from the Juhtipuro stream (66°18′N, 29°33′E) in Oulanka National Park, northern Finland. In this stream, a series of waterfalls act as a barrier for fish migration. The absence of fish from the stream was confirmed by repeated, extensive (covering ca 200 m section of the stream) electrofishing surveys. Nymphs were collected before noon, sorted immediately and kept at 7°C for 2–3 h before the trials were started. Minnows collected with a dip-net from the Hangaspuro stream (66°20′N, 29°20′E) were acclimated to the experimental conditions for 2–3 days, during which time they were fed with live benthic insects. To standardize the hunger level of the minnows, they were starved for 24 h before being used in the trials. After the trials (usually the next day), the minnows were returned to the stream. Aerated water from the Juhtipuro stream was used in all trials. Water temperature in the aquaria was similar to natural stream temperatures, ranging from 3 to 8°C.

Trials were conducted in stream tanks modified from those described by Soluk & Collins (1988b) (Fig. 1). Recirculating flow was created with an air diffuser and maintained at 15 cm/s, which is

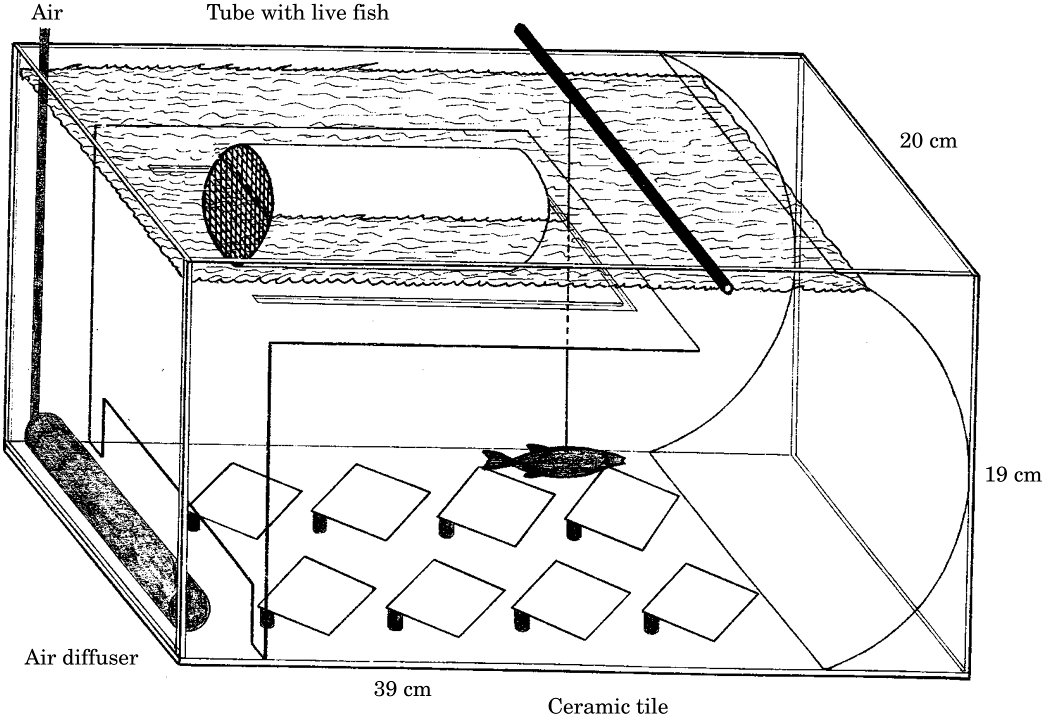

Figure 1. Stream tank used in the experiments. Recirculating flow was created with the air diffuser. Water flowed through the tube containing a live minnow. A fish model was manoeuvred with a rod pushed through a U-shaped cut on the horizontal baffle.

within the range of velocities where *B. rhodani* occurs in nature (P. Tikkanen, personal observation). A dense mesh cloth on the bottom of the arena provided a foothold for the nymphs. In the arena, eight tiles (4.9 × 4.9 × 0.5 cm) were arranged in two rows parallel to the flow. The tiles were raised from one corner by a shallow support so that we could easily see the nymphs on all tile surfaces. Tiles had been incubated in a fishless stream for 3–4 weeks, during which time a visible periphyton layer developed on the upper surfaces. The undersides of the tiles were brushed clean of periphyton to ensure that only the tile tops would provide food for *Baetis* during the trials. The average amount of periphyton on the upper tile surfaces was 5.4 ± 0.3 μg chlorophyll-a/cm^2 ($\bar{X} \pm$ SE). Thirty-five per cent of the bottom arena was tile surface containing food for *Baetis*. The lower tile surfaces and the arena beneath the tiles provided refuges from fish. To avoid periphyton depletion, tiles were replaced on each day of the experiment. In a previous experiment with an identical set-up *Baetis* nymphs did not deplete periphyton within 18 h (Tikkanen et al. 1994). The aquaria were cleaned every morning, and fresh water was added and circulated for some hours before a new trial was started. At 1300 hours, 20 nymphs ($\bar{X} \pm$ SD body length without cerci 5.00 ± 0.10 mm; $\bar{X} \pm$ SD head width 0.79 ± 0.07 mm, $N=84$) were gently poured into each aquarium and allowed to settle on the bottom arena in standing water, after which the flow was slowly increased to experimental conditions. The nymphs were allowed to acclimatize for 2 h before the trials were started. The experiment was run in a building where daylight entered the room from open doors, and illumination was close to that of a shaded stream (light regime 13:11 h light:dark). During night trials, observations were facilitated by a dim red light. Heise (1992) has shown that mayfly nymphs may react to red light; however, he studied nymphs of the family Heptagenidae, which, in our experience, are more sensitive to red light than *Baetis* nymphs. In the experiments reported here, nymphs exposed to a red light source continued to feed apparently undisturbed (that is, we saw no abrupt changes in the feeding behaviour of nymphs; see also Culp & Scrimgeour 1993).

We provided chemical signals of fish by placing a live minnow (about 6 cm total length) in an opaque plastic tube with mesh cloth at both ends. The tube was placed parallel to the flow on the horizontal baffle of the aquarium. The minnow could not be seen by the *Baetis* nymphs, but flow through the tube carried the chemical exudates of the fish. To control for the potential hydrodynamic effects of a tube, we added an empty tube to all control treatments. Because of contamination risk, two of the six aquaria were reserved for control treatments, whereas the treatments involving fish cues were each day randomly allocated to the remaining four aquaria. Position effects were controlled for by systematically changing the positions of the aquaria every day.

Experiment 1: Short-term Exposure

In this experiment, we studied the immediate fish avoidance responses of *Baetis* nymphs from a fishless stream. We also examined whether nymphs are able to recognize fish as potential predators on the basis of chemical cues or whether tactile and/or visual signals are needed as well. The experiment was conducted on 23–29 September 1992. We used a 3 × 2 factorial design where the factors were fish presence (fish chemicals versus freely swimming fish versus control with no fish cues) and time of day (day versus night). The same set of nymphs was observed during the day (1500–1700 hours) and at night (2200–0000 hours). Each treatment combination was replicated seven times. We used change in the number of nymphs on exposed surfaces of the tiles during a 20-min observation period as the response variable. This interval was chosen to minimize numbers of prey consumed in trials with freely foraging fish. However, nymphs were eaten in four trials, with an average of 0.9 (± 0.53 SE, $N=14$) nymphs per trial.

At the beginning of an observation period, we recorded the number of nymphs on exposed surfaces. Then, a live fish, a tube containing a fish (chemical cues) or an empty tube (control) were added, and the number of drift entries (departures from the substrate to the water column) by the nymphs during a 20-min period were counted. We recorded the number of nymphs on exposed surfaces again at the end of an observation period, after which the fish was removed from the aquarium. The sequence in which the six aquaria were observed was randomized, and the same set of observations was made for each aquarium. In trials where nymphs were eaten, the proportion of nymphs on exposed surfaces at the end of a trial was counted as numbers exposed/numbers remaining. The activity of freely foraging minnows was evaluated on an ordinal scale (0, completely passive; 5, highly active, frequent encounters with and attacks on mayflies). Trials where minnows obtained a score less than three were omitted from the analyses. The European minnow is presumed to be a predominantly diurnal feeder (Müller 1973), yet in these experiments it was active throughout the day and night (see also Tikkanen et al. 1994).

The null hypotheses of no difference in drift rates ($\log(x+1)$-transformed) and refuge use between treatment combinations were both tested with repeated measures ANOVA. No transformation of refuge-use data was needed, as shown by Shapiro–Wilk test (for normality) and Levene's test (for homogeneity of variances).

Experiment 2: Long-term Exposure

In this experiment, nymphs were exposed to predator cues for a longer period (up to 17 h). In addition, to avoid the potential confounding effects of variable fish activity, we used a fish model to standardize the predation risk. A rubber fish model was taken from a fishing lure (Mepps Aglia, size 3). The model was of similar size and general appearance to the live minnow in experiment 1. A U-shaped cut was made to the horizontal baffle of the aquarium, and a steel rod with the predator model was pushed through the cut. The position of the model in the water column was fixed at 2 cm above the tiles (see Fig. 1). The observer manoeuvred the model with the steel rod, simulating the movement of a live fish. During each presentation (at 1600 hours and 2200 hours), the model was moved 10 times along the U-shaped path, corresponding to an average swimming rate of approximately 0.5 cm/s. In this experiment, the 'fish' and/or the tube were not removed from the aquarium between the observation periods. When the model was not

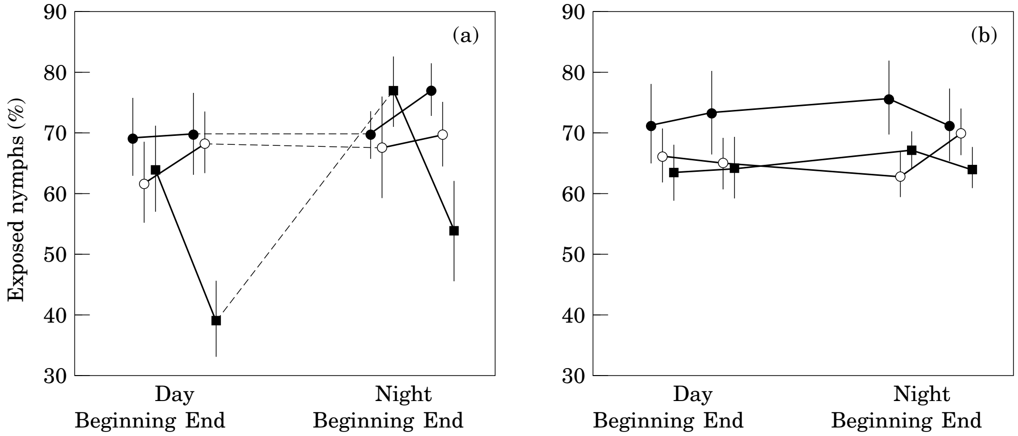

Figure 2. Percentage of *Baetis* nymphs ($\bar{X} \pm$ SE) on exposed surfaces at the beginning and end of a 20-min observation period, during the day and at night. (a) Experiment 1: ●: control; ○: fish chemicals present; ■: free-swimming fish present. Fish was not present in the aquarium between the day and night trials (broken line). (b) Experiment 2: ●: control; ○: fish chemicals present; ■: fish model plus fish chemicals present. Fish treatments were established after the first day's observation ('beginning'), and were present throughout the experiment.

Table I. Repeated measures ANOVA for the effects of time of day (day versus night) and fish presence (control versus fish chemicals versus free minnow) on the change in the number of nymphs on exposed surfaces during a 20-min observation period

Source of variation	*df*	SS	*F*	*P*
Within-subjects				
Time	1	0.84	0.16	0.698
Time ∗ Fish	2	8.13	0.75	0.485
Error	18	97.12		
Between-subjects				
Fish	2	286.86	25.43	<0.001
Error	18	101.52		

manoeuvred, it was left 'resting' in a fixed position at the back of an aquarium.

Experiment 2 was conducted between 26 September and 1 October 1993. The fish presence treatments were: (1) control, (2) fish chemicals (provided as in experiment 1) and (3) fish chemicals plus a fish model. Nymphs were introduced to stream tanks at 1300 hours, and fish treatments were established just after the first daytime observation at 1600 hours. Night observations were conducted at 2200 hours. The observation procedure was identical to that of experiment 1. We also counted the number of nymphs on exposed surfaces at 1800, 2000 and 0900 hours the following morning. In this experiment, we were interested in the dynamics of refuge use of *Baetis* nymphs, and, therefore, we made planned, a priori comparisons (within-treatment difference contrasts) between the mean proportion of nymphs on exposed surfaces in consecutive observation periods. Not all of these contrasts are truly orthogonal, and the experiment-wise error rate was maintained at the level it would have been for four mutually orthogonal contrasts (number of means − 1), each at the $\alpha=0.05$ comparison-wise rate ($4 \times 0.05=0.20$), and the comparison-wise rate was then modified for the 12 contrasts ($0.20/12=0.017$; for more details of the method, see Dunson & Travis 1991). All proportions were angularly transformed (arcsine of the square root) before analysis to satisfy the homogeneity-of-variances assumption.

RESULTS

Baetis responded to the addition of a freely foraging fish by immediately increasing their refuge use, both during the day and at night. Nymphs that hid during the day re-emerged before night. Nymphs in the control and chemical signal treatments had no distinct diel patterns in refuge use (Fig. 2a; Table I).

The main effect of fish presence on drift rates in experiment 1 was significant ($F_{2,17}=6.80$,

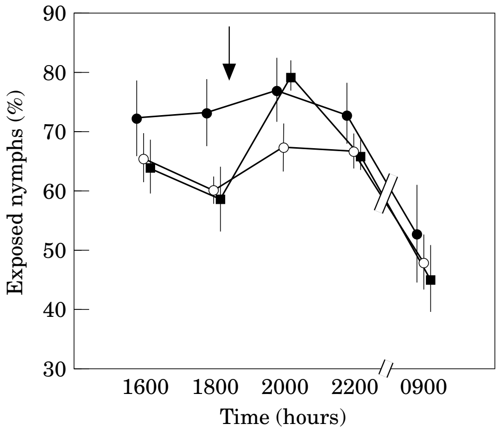

Figure 3. Percentage of *Baetis* nymphs ($\bar{X}$ ± SE) on exposed surfaces in experiment 2. ●: Control; ○: fish chemicals present; ■: fish model plus fish chemicals present. Arrow indicates the onset of darkness. For times 1600 and 2200 hours, the mean of counts before and after an observation period have been used.

P=0.007), mainly because drift entries were more frequent in the presence of a free-swimming fish ($\bar{X}$ ± SE no. drifts/20 min=5.71 ± 1.21) than in the presence of a chemical signal (2.00 ± 0.74) and in the control (1.86 ± 0.88) treatment. Neither the main effect of time ($F_{1,17}$=2.14, P=0.162) nor the interaction term (time $*$ fish; $F_{2,17}$=0.51, P=0.612) was significant, indicating lack of diel drift periodicity.

Unlike the live minnow, the fish model (plus chemical cues) did not elicit any immediate anti-predatory responses by the prey (Fig. 2b). However, long-term exposure to fish cues did cause significant alterations in refuge use patterns especially in the fish model treatment (Fig. 3). A priori difference contrasts showed that, in the presence of both visual/hydrodynamic and chemical cues of fish, significantly more nymphs were exposed at the onset of darkness (2000 hours) than at 1800 or 2200 hours (Table II). In all treatments, nymphs tended to abandon the exposed surfaces by the next morning (0900 hours; Fig. 3, Table II). For drift rates in experiment 2, both main effects (fish presence, $F_{2,21}$=0.24, P=0.787; time, $F_{1,21}$=1.97, P=0.175) were non-significant, as was the interaction term ($F_{2,21}$= 0.58, P=0.569).

DISCUSSION

Diel vertical movements and nocturnally constrained drifting of lotic macro-invertebrates have previously been regarded as fixed responses for avoiding visually feeding, diurnal fish (Elliott 1968; Allan 1978; Sih 1987; Flecker 1992). However, recent studies have shown that at least some aquatic insects possess a capacity for highly flexible and quickly adjustable anti-predatory responses (e.g. Soluk & Collins 1988a; Kohler & McPeek 1989; Douglas et al. 1994; Scrimgeour &

Table II. Repeated measures ANOVA for different fish presence treatments, showing the effect of time of day on the proportion (angularly transformed) of *Baetis* nymphs on exposed surfaces, and a priori difference contrasts for the fish presence treatments

	Pillai's trace	*F*	*df*	*P*
Treatment				
Control	0.752	3.03	4, 4	0.154
Fish chemicals	0.835	6.31	4, 5	0.034
Fish model	0.969	23.68	4, 3	0.013

Contrasts	Control		Fish chemicals		Fish model	
	F	*P*	*F*	*P*	*F*	*P*
1600 versus 1800 hours	0.01	0.912	2.21	0.175	1.05	0.344
1800 versus 2000 hours	0.20	0.666	8.26	0.021	12.49	**0.012**
2000 versus 2200 hours	4.96	0.061	0.05	0.835	11.41	**0.015**
2200 versus 0900 hours	5.00	0.060	14.36	**0.005**	9.48	0.022

Contrasts significant at the adjusted α-level are in bold. Details for maintaining the experiment-wise error rate at α=0.05 are given in the text.

Culp 1994; Tikkanen et al. 1994). For example, the drifting of large *Baetis* mayflies in response to chemical cues from fish peaked at night (Tikkanen et al. 1994). Moreover, the daytime use of stone tops decreased, but only after exposure to a freely foraging fish.

The present study provides further evidence for the plasticity of prey responses in mayfly nymphs. Nymphs with no previous experience of fish increased their refuge use when exposed to an actively foraging fish, whereas chemical cues alone did not elicit immediate prey responses. Although the nymphs entered the refuges shortly after being confronted with a live minnow, they re-emerged on to the tops of the tiles as soon as the predator was removed. Mayflies from a fishless stream thus appeared more risk-reckless (sensu Fraser & Huntingford 1986) than their fish stream counterparts, which remain in refuges even when the risk of predation is not acute (Tikkanen et al. 1994; see also Culp et al. 1991). Sih (1992) suggested that such a time-lag should always occur if the prey, while hiding in refuges, cannot receive reliable information about predator presence. However, although nymphs that abandon refuges immediately after the predator has left seem to be taking excessive risk, this behavioural trait might be beneficial in their natural habitats: if predation is usually not a serious threat (as in streams with no or very few fish), waiting for safe conditions would incur unnecessary costs (see also Huntingford & Wright 1992).

In contrast to a live minnow, the fish model (plus chemical cues) did not elicit any immediate avoidance responses in *Baetis* nymphs. This suggests that the nymphs did not perceive visual and chemical cues from a non-foraging fish as an indication of imminent danger. Because *Baetis* nymphs are relatively efficient at evading attacks by fish, they do not necessarily face a high mortality risk while they are on the tops of stones in the presence of fish (Scrimgeour & Culp 1994; Tikkanen et al. 1994). Nevertheless, under continued exposure to a fish model and fish chemicals, the use of exposed tile surfaces peaked sharply during the first hours of darkness. Apparently, even when the probability of being captured is rather low, the physical proximity of fish makes the nymphs perceive a general sense of danger, which limits their use of stone tops to a short period after sunset.

Chemical cues alone were not perceived by the nymphs as an increased predation threat. While in refuges, the prey still receives chemical signals of predator presence. This may result in an erroneous estimate of the actual risk level, and thus unnecessarily reduce the time allocated to other activities such as foraging (see also Petranka et al. 1987; Semlitsch & Reyer 1992). To assess the prevailing predation risk, *Baetis* nymphs apparently need more precise information about the probability of being encountered and attacked by fish. This information can be achieved only via tactile and/or hydrodynamic cues from an actively foraging fish (see also Stauffer & Semlitsch 1992).

In the experiments reported here, mayflies from fishless streams did not show nocturnally biased drifting when fish cues were present. The size of the nymphs used in these experiments (mean head width=0.79 mm) closely coincides with the threshold value of positive size-selection by salmonids on *Baetis* nymphs (Allan 1978). Therefore, drifting in daytime is perhaps not very risky for nymphs of this size, and only a weak tendency to drift nocturnally might be expected. Interestingly, in a previous experiment where the size-dependent prey responses of fish-experienced *Baetis* nymphs were examined (Tikkanen et al. 1994), only large nymphs (mean head width=1.46 mm) drifted nocturnally, whereas small nymphs (mean head width=0.79 mm) were aperiodic.

Three other recent studies have examined the prey responses of mayfly nymphs from fishless streams. Two of these have provided evidence in accordance with our results of flexible avoidance responses in mayflies from fishless streams. Cowan & Peckarsky (1994) observed a reduction in the daytime use of upper stone surfaces by fish-inexperienced *Baetis* nymphs when exposed to trout cues. Douglas et al. (1994) documented an immediate reduction in the daytime drift of *B. coelestis* following introduction of trout to three previously fishless streams. McIntosh & Townsend (1994) presented results that may appear quite contradictory at first sight. In their experiments, mayflies from streams without trout did not change their positioning or drift periodicities when confronted with trout. The reason for this apparent inconsistency may be historical: brown trout was introduced to New Zealand only about 100 years ago, and although mayflies from fishless streams could conceivably disperse between streams, they seem to lack sufficient evolutionary experience of trout to show flexible behavioural adjustments when confronted with it. When exposed to a native predatory fish, the common river galaxias, however, mayflies did exhibit plastic prey responses in this experiment also (McIntosh & Townsend 1994).

In this study we found evidence in support of our previous prediction (Tikkanen et al. 1994) that mayfly nymphs from fishless streams are able to adjust their behaviour according to the prevailing level of predation risk. We believe that highly variable predation pressure and aerial dispersal between streams are the key factors in maintaining this behavioural trait in populations allopatric with fish. McPeek (1990) has shown that damselfly larvae from fishless lakes cannot live sympatrically with fish because they lack appropriate behavioural mechanisms for surviving fish attacks. In such a situation, natural selection should favour low dispersal propensity, and indeed, dispersal of adult damselflies between fishless and fish-containing lakes was shown to be negligible (McPeek 1989). In contrast to many permanently fishless lakes, most fishless streams occasionally become invaded by fish, which are thus almost never predictably absent from streams (see also Allan 1983; Soluk & Collins 1988b). Furthermore, fish predation pressure varies spatially and temporally within streams, even within stream reaches (e.g. Grossman et al. 1982; Freeman & Grossman 1993). Such a wide variation in local predation risk, together with dispersal of winged adults may have promoted the maintenance of flexible fish avoidance traits in stream-inhabiting mayfly nymphs.

ACKNOWLEDGMENTS

Björn Malmqvist, Hannu Ylönen and two anonymous referees provided comments that greatly improved the manuscript, as did also some suggestions by S.-M. Horttanainen. Antti Juntunen aided in maintaining the aquaria. We thank Oulanka Biological Station for the working facilities and logistical support. Financial support was provided by the University of Oulu and the Finnish Cultural Foundation (to P.T.).

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