

Diel foraging periodicity of lotic mayfly (Ephemeroptera) nymphs during the subarctic summer

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With 4 figures and 2 tables in the text

Abstract: We used a combination of gut content analysis and direct behavioural observations to examine the diel periodicity of lotic mayfly nymphs. In early July, close to the summer solstice, feeding of *Heptagenia sulphurea* was aperiodic. *Baetis rhodani* fed most actively during the day, yet drift of large nymphs peaked sharply during the short period of dusk around midnight. In August, *Heptagenia dalearlica* was strongly nocturnal, whereas only a slight tendency towards nocturnality was observed in baetid nymphs. All aspects of *Baetis* feeding behaviour indicated night-time activity in September. There were some differences between *Baetis* size-classes, small nymphs being less constrained to feed at night. Activity of heptageniid nymphs was low in September, but diel variation in gut fullness implied primarily nocturnal feeding. Diel variation in water temperature was not closely associated with mayfly periodicity, and we suggest that the tendency to night-time activity is best explained by fish predation risk. Although the presence of fish was not manipulated in this study, nymphs may have perceived chemical fish signals from the water used in the laboratory trials. Some behavioural patterns, e.g. strong nocturnality of *Heptagenia* nymphs in August, may be fixed predator avoidance responses of highly vulnerable prey. We emphasize the importance of considering predation risk and prey size in studies of lotic mayfly periodicity. In high northern areas, the role of these factors in affecting the foraging periodicity of aquatic insects may vary seasonally in concert with varying day-length.

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Introduction

Diel foraging periodicity of lotic invertebrates, especially mayflies, has attracted the attention of stream ecologists ever since the seminal works of HARKER (1953) and ELLIOTT (1968). Recently, interest has been mainly directed to the presumed relationship between feeding activity and invertebrate drift. ELLIOTT (1968) documented coincident peaks in the drift and epibenthic density of the mayfly *Baetis rhodani* PICT., with highest densities occurring during the night. He suggested that numbers in drift parallel numbers on stone tops simply because animals, while foraging on exposed surfaces, are more liable to accidental dislodgement by the flow. This "passive drift entry" hypothesis was later substantiated by other authors (e.g. WATERS 1972, PLOSKEY & BROWN 1980). However, many recent studies have failed to show any correspondence between epibenthic density and drift, thus rendering the passive entry hypothesis questionable (e.g. ALLAN et al. 1986, CASEY 1987, WILZBACH 1990). At present, there is no consensus regarding the relationship between diel periodicity in epibenthic density and drift of stream invertebrates.

Apart from its association with drift, diel foraging periodicity of lotic insects has evoked substantial interest as a potential predator avoidance mechanism. For example, in the presence of fish, mayfly nymphs have been observed to forage on periphyton-rich stone tops mainly during the night (KÖHLER & MCPHEEK 1989, CULP & SCRIMGEOUR 1993, COWAN & PECKARSKY 1994, TIKKANEN et al. 1994). On the other hand, many observational studies in the field and in the laboratory have demonstrated lack of diel periodicity (BOHLE 1978, KOVALAK 1978, KÖHLER 1983), or even a day-time peak (GRAESSER & LAKE 1984, STATZNER & MOGEL 1984, ALLAN et al. 1986, WILZBACH 1990) in numbers of stream insects on stone tops. SOLUK & COLLINS (1988) observed a nocturnal peak in the numbers of mayfly nymphs on tops and sides of stones, but only in the presence of interstitially foraging invertebrate predators. The presence of sculpin had no observable effects on the positioning of nymphs on various stone surfaces.

The purpose of our study was to examine the foraging periodicity of two lotic mayfly nymphs (*Baetis rhodani* and *Heptagenia* spp.) at different phases of the subarctic summer. Direct behavioural observations of stream invertebrates in the field are impractical for many reasons (CASEY 1987, RADER & WARD 1990, ALLAN et al. 1991). Thus, we observed nymphal feeding behaviour in a controlled laboratory environment, and the relevance of these results to field conditions was evaluated by examining diel periodicity in the gut fullness of live collected specimens. We also examined the relationship between positioning on stone tops and drift of *Baetis* nymphs in laboratory trials.

Material and methods

Study site and species

The study was carried out at Oulanka Biological Station, northeastern Finland, on 1–4 July, 10–13 August and 16–19 September 1993. Mayfly nymphs used in the experiments were collected from the outlet of a small lake, Lake Vällilampi (66° 14' N, 29° 10' E), which harbours both benthic (burbot *Lota lota*) and drift-feeding (ten-spined stickleback *Pungitius pungitius*, European minnow *Phoxinus phoxinus* and brown trout *Salmo trutta*) fishes.

In our study area *Baetis rhodani* has a one-year life cycle with overwintering nymphs. The flight period is long, lasting from mid-June until late July (HUHTA et al., unpubl.; see also ELLIOTT et al. 1988). *B. rhodani* has many, partly overlapping cohorts, which allowed us to use two different size-classes in the July and September experiments. *B. rhodani* is a typical grazer, which commonly occupies upper surfaces of stones, grazing on attached algae and detritus (e.g. BROWN 1961, BOHLE 1978).

Heptagenia sulphurea (MÜLLER) and *Heptagenia dalecarlica* Bgtss. both have a one-year life cycle with flight periods in June (*H. dalecarlica*) or late July-early August (*H. sulphurea*; HUHTA et al., unpubl.). These life cycle differences forced us to use different species at different times of the season. Thus, *H. sulphurea* was used in the beginning of July, whereas *H. dalecarlica* was more easily obtained later in the season. These two species are closely related, being morphologically distinguishable only on the basis of the reverse asymmetry of the nymphal mandibles (SAARISTO & SAVOLAINEN 1980). In fact, their status as independent species has been questioned, and only recently have SAVOLAINEN et al. (1991) proved, using enzyme electrophoresis, that they are reproductively isolated bona species. Heptageniid nymphs live mainly in sheltered locations beneath and between stones, and are only rarely seen on stone tops. Their diet commonly consists of both detritus and periphytic diatoms (e.g. JONES 1950).

General procedures

The experiments were run in an outdoor building where illumination was close to that of a shaded stream. Nymphal feeding behaviour was observed in glass aquaria (40 × 20 × 19 cm) modified from the model of SOLUK & COLLINS (1988). Water recirculated in an aquarium so that animals entering drift inevitably returned to the experimental arena (for a detailed description of the stream system, see TIKKANEN et al. 1994). Flat, light-coloured stones collected from a nearby stream were used as substrate in the aquaria. Stones at the outlet site where the nymphs were collected from were darker and could not be used in the trials. The stones were arranged in two rows parallel to the flow, and were raised from one edge by a shallow support to ensure that mayflies on all stone surfaces could be readily observed. The upper area of the stones, harbouring periphyton for the mayflies, was about the same in each trial (stone area per aquarium: $\bar{x} = 242 \text{ cm}^2$, SE = 24). Current velocity near the bottom was 15 cm/s, which is within the range of velocities at which *B. rhodani* and heptageniid nymphs occur in nature (A. HUHTA, pers. obs.).

To examine whether mayflies depleted their food during the trials, periphyton samples of predetermined area (20 cm²) were scraped with a stiff brush from randomly selected stones (two stones per aquarium) after each trial, and their chlorophyll-a content was measured spectrophotometrically. As a control, we also sampled periphyton from stones held in experimental conditions but without grazers. The controls were always run simultaneously to the trials. The amount of chlorophyll-a in the stream tanks was lowest in September and highest in July, and differences between experimental and control tanks were not significant on any of the three dates (Table 1). Thus, there was no sign of food depletion, which could have affected the feeding behaviour of grazers during the trials.

Mayfly nymphs (nymphs with black wing pads excluded) were collected from the outlet, and quickly sorted and size-matched in the laboratory to obtain ten small and ten large *B. rhodani* nymphs. In August, only small-sized nymphs of *B. rhodani* were available. In trials with *Heptagenia*, ten nymphs of a uniform size were used (for sizes of experimental animals, see Table 2). To maintain similar experimental densities for both species, ten small *Heptagenia* nymphs were added to each stream tank (as were also ten small *Baetis* nymphs in August), but since these smaller nymphs could not be observed accurately, no data on their foraging behaviour was collected. Nymphs were introduced to the experimental arenas two hours before the start of the trials. The animals were allowed to settle in standing water, whereafter the flow was slowly increased. Experimental density was 800 ind./m² for both species, which is within the natural densities in streams of the Oulanka area (90–6500 for *B. rhodani* and 20–1500 ind./m² for *H. dalecarlica*, respectively; HUHTA et al., unpubl.).

Table 1. The mean amount (µg/cm², 1 SE in parentheses, n = 16) of chlorophyll-a on stones in stream tanks with (= experimental) and without (= control) grazers. All differences between experimental and control trials are non-significant (t-test, p > 0.19).

	July	August	September
Experimental tanks	0.25 (0.07)	0.19 (0.03)	0.17 (0.02)
Control tanks	0.33 (0.06)	0.22 (0.12)	0.09 (0.02)

Table 2. Mean sizes (dry weight (DW) in µg; head width (HW) in mm, 1 SD in parentheses) of the animals used in experiments.

		<i>Heptagenia</i>	large <i>Baetis</i>	small <i>Baetis</i>
July	DW	799 (85)	500 (54)	50 (0.9)
	HW	1.54 (0.19)	0.82 (0.07)	0.40 (0.01)
August	DW	990 (104)	370 (31)	–
	HW	1.91 (0.14)	0.73 (0.07)	–
September	DW	1320 (165)	390 (39)	80 (10.4)
	HW	2.18 (0.27)	0.75 (0.06)	0.45 (0.07)

Behavioural observations and data analysis

Observations in the dark were done with dim red light (room light), which did not seem to affect the behaviour of nymphs (see also ALLAN et al. 1986). As a precaution, the observations were always preceded by a 3–4 min waiting period to allow potentially disturbed individuals to resume their earlier behaviour; this, however, happened in only a few cases with the heptageniid and never with the *Baetis* nymphs. Feeding activity of the nymphs was observed at three hour intervals for 24 hours. In the beginning of a ca. 15 minute observation period we recorded the number of nymphs on exposed surfaces. Next, number of nymphs feeding (on all surfaces) was recorded during 10 s, at 30-s intervals for 15 successive observations (see ALLAN et al. 1986). A nymph was recorded feeding when its head and mouthparts were in direct contact with the stone surface. All drift entries during an observation period were also noted. The same set of observations were repeated (in a randomized order) in four different aquaria. At the end of ca. 1 h of observations, we measured water temperature and the level of illumination in the aquaria.

The null hypothesis of no diel changes in the proportion of nymphs feeding and proportion on exposed surfaces was tested with a repeated measures ANOVA (PROC GLM, SAS Institute 1988). Proportions were arcsine square-root transformed to stabilize variances. Spearman rank correlations were used to test for the associations between diel periodicity in surface use and drift rate of *Baetis* size-classes. Relationships between different attributes of feeding activity (% feeding, % on exposed surfaces, gut fullness) and water temperature were also analysed with Spearman rank correlations.

Gut fullness periodicity and gut evacuation rate

In parallel to laboratory observations, we collected nymphs of *B. rhodani* and *Heptagenia* sp. at three hour intervals from the outlet of Lake Vällilampi. Care was taken to ensure that field-collected specimens were within the same size-range as the experimental animals. Gut contents were measured by dissection and separate assessment of algal cells and detritus following the methods of COFFMAN et al. (1971), as modified by ALLAN et al. (1991). Guts from one to five individuals were dissected, expressed into distilled water and sonified to break down clumps. Five replicates were prepared for each time interval and species/size-class. All algal cells in 20 random fields were counted at 400× magnification to estimate the total number of algal cells per gut, and the dry mass of algae was calculated using the estimate of COFFMAN et al. (1971) for a single cell (8.34×10^{-3} µg). The amount of detritus per gut was estimated by determining the percent of area occupied by detritus particles in each of the 20 fields. The conversion term for detritus (30.3 µg/mm²; COFFMAN et al. 1971) then gives an estimate of dry mass of detritus per mayfly gut. Repeated measures ANOVA was again used to test for diel variation in the gut fullness of live-collected nymphs.

When gut fullness is used as an indicator of feeding periodicity, it is imperative that gut evacuation rate closely coincides with the sampling interval used. COWAN & PECKARSKY (1994) have recently shown that the gut clearance time is two to four hours in *Baetis bicaudatus* DODDS. No similar information is available for *Heptagenia* sp. Thus, we measured the gut evacuation time of *H. dalecarlica* on 14–16 August

1993. We collected 50 nymphs from the outlet of Lake Vällilampi, and to standardize their hunger level, we kept them in stream tanks for 24 h without food. After this, stones with a well-developed periphyton layer were added to stream tanks, and the animals were allowed to feed ad libitum. In two hours most of the nymphs had their foreguts full of food, and were then transferred to another aquarium, where no food was available. Five nymphs were collected immediately and their gut contents were analysed as described above. Groups of five animals were then similarly processed in time intervals of 1 h, 2 h, 3 h, 5 h, 8 h, 11 h, 14 h, 18 h and 24 h. Water temperature during the experiment varied from 14 to 17 °C.

Results

Diel periodicity of *Heptagenia* nymphs

Nymphs of both *Heptagenia* species spent most of their time underneath the stones, entering the upper surfaces only for short feeding bouts. Nymphs on the lower stone surfaces were often observed feeding, yet diatoms were the most important food item for both heptageniids in the field. Percent of diet consisting of detritus was 27 in July, 15 in August and 22 in September. Algal biomasses on different stone surfaces were not monitored during this study, but in a previous experiment we have shown the standing crop of periphyton to be five-fold higher on stone tops ($5.4 \mu\text{g chl-a/cm}^2$) compared to stone bottoms ($1.0 \mu\text{g/cm}^2$) (TIKKANEN et al. 1994; see also CULP et al. 1991, where the difference between stone surfaces was even more pronounced).

In July, when illumination was high throughout the day, feeding behaviour of *H. sulphurea* was entirely arrhythmic (Fig. 1). In contrast, nymphs of *H. dalecarlica* were strongly nocturnal in August. While generally less than 10 percent of *Heptagenia* nymphs occurred on exposed stone surfaces, almost 30 percent were feeding on stone tops during the few hours of darkness in August (Fig. 1).

In September, when the dark period of the day lasted for ca. 6 hours, heptageniid nymphs were active mainly during the night. This was, however, evident only in the gut contents of field-collected specimens, whereas feeding behaviour in the laboratory indicated lack of diel periodicity (Fig. 1). Water temperature in the stream tanks closely tracked variation in the ambient temperature, falling down to 2.5 °C during the night (see Fig. 1). At the same time, temperature conditions in the lake outlet remained more benign, being around 6 to 7 °C at the time of the highest nymphal feeding activity (daily maximum: 7.4 °C, minimum: 3.6 °C). Thus, thermal conditions in the outlet may have been more favourable than in the laboratory, enhancing higher overall activity of *Heptagenia* nymphs. In the low temperatures of the laboratory stream tanks, nymphs exhibited a very low level of activity throughout the day.

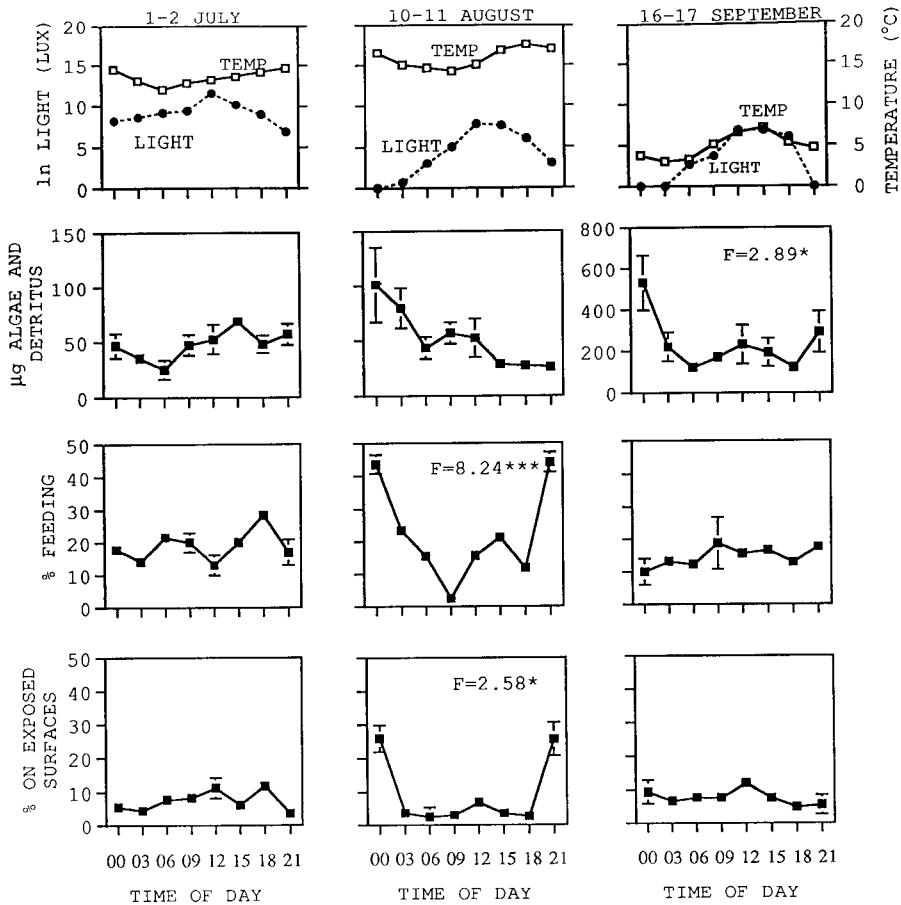


Fig. 1. Diel variations in ambient light and water temperature, and in the foraging activity of *Heptagenia* nymphs (*H. sulphurea* in July, *H. dalecarlica* in August and September). Each symbol represents mean \pm 1 SE of 4 (% feeding and % on exposed surfaces) or 5 (gut fullness) samples. Differences between sampling times were tested with a repeated measures ANOVA; only significant overall differences are given here. * $P < 0.05$; *** $P < 0.001$.

Diel periodicity in the feeding behaviour or gut contents did not correlate significantly with water temperature. The correlation between percent of nymphs feeding and water temperature was marginally significant only in September ($r_s = 0.60$, $P = 0.07$; all other correlations less than 0.40, $P > 0.10$).

The gut evacuation experiment was conducted during the warmest part of the season, yet gut clearance of *H. dalecarlica* nymphs was extremely slow. Complete evacuation did not occur even in 24 hours, and in three hours – the interval used in our gut fullness study – gut contents had decreased only by 30

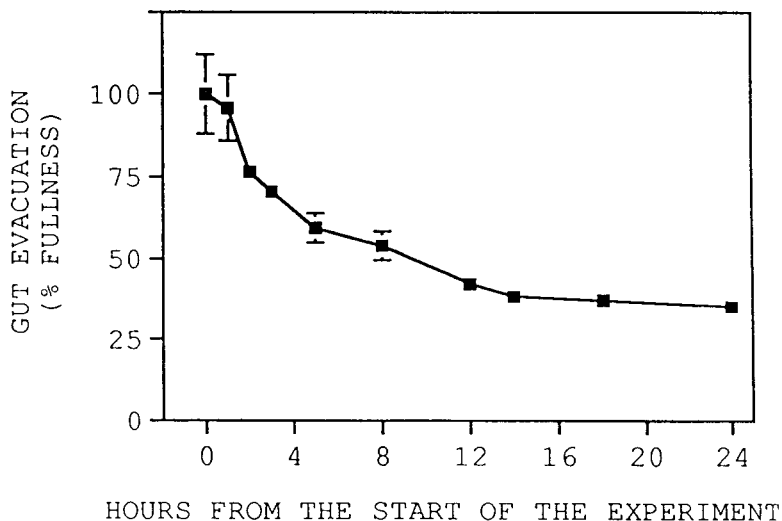


Fig. 2. Reduction in percent gut fullness over 24 hours in *Heptagenia dalearlica*. (Means \pm 1 SE).

percent (Fig. 2). Accordingly, gut contents may not always represent recent feeding in heptageniid nymphs, and the results on gut fullness periodicity must thus be interpreted with some caution.

Diel periodicity of *Baetis rhodani* nymphs

Feeding behaviour of *Baetis* nymphs differed markedly from that of the heptageniids. Proportion of nymphs on exposed surfaces was consistently rather high (Fig. 3), and individuals spent long intervals feeding on stone tops. Nymphs on the lower stone surfaces were rarely actively feeding, and accordingly, the diet of field-collected nymphs was dominated by diatoms. Percent of detritus in the diet varied from 9 (in September) to 40 (July) in small, and from 2 (September) to 27 (July) in large nymphs.

In the beginning of July, large *B. rhodani* nymphs exhibited a bimodal activity pattern. Feeding was highest around noon, at which time almost 50 % of large nymphs occurred on exposed surfaces. Another, smaller activity peak was observed late in the evening (Fig. 3). Gut fullness of field-collected specimens also showed two periods of intensive feeding, although the hours of day with highest gut load did not match exactly those of the greatest activity in the laboratory (Fig. 4). However, a time delay of a few hours from the start of an active feeding period is to be expected for an increase in gut fullness to become discernible. The feeding behaviour of small *B. rhodani* nymphs was aperiodic in July (Figs. 3 and 4). Drift of large nymphs was clearly nocturnal,

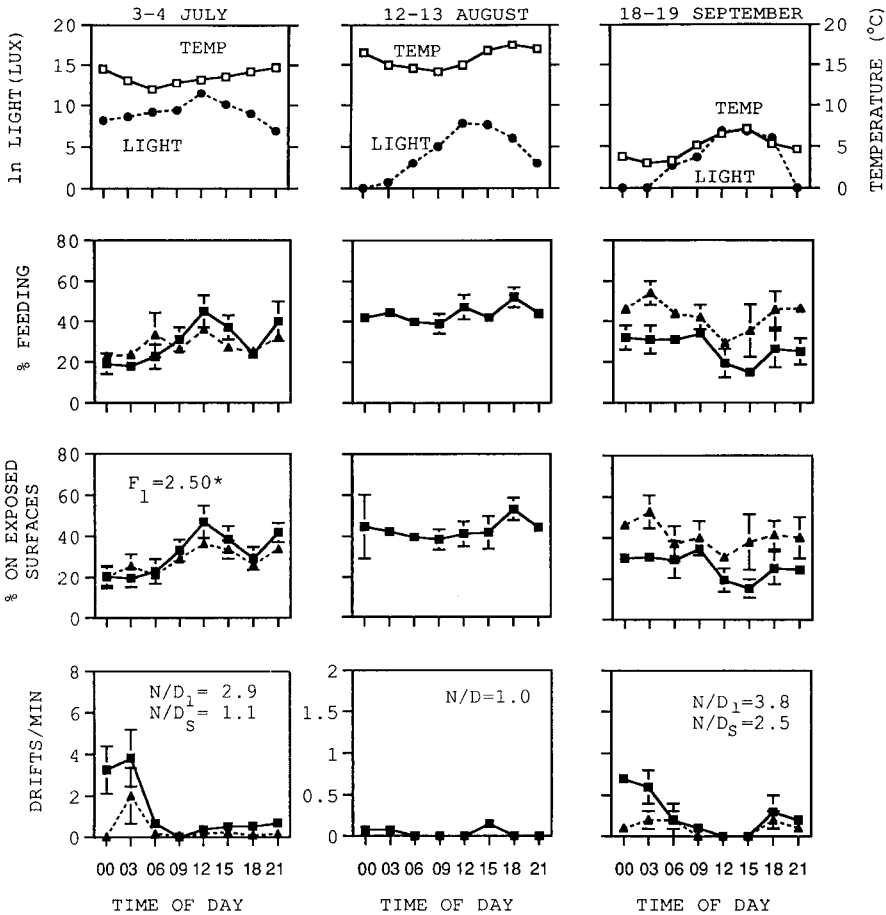


Fig. 3. Diel variation in the foraging activity of *Baetis rhodani* nymphs. Solid line: large nymphs, broken line: small nymphs. N/D indicates the night : day ratio of *Baetis* drift (l = large, s = small nymphs). Other details as in Fig. 1.

with only a few drift events occurring outside the short period of dusk around midnight. Drift rate and percent on upper surfaces were negatively, but non-significantly correlated for both size-classes ($r_s = -0.40$ and -0.36 for large and small nymphs, respectively; $P > 0.10$).

In August, feeding activity of baetid nymphs showed no diel periodicity in the laboratory (Fig. 3). In contrast, gut contents evidenced a distinct nocturnal peak in the food intake of field-collected nymphs (Fig. 4). Drift rate was very low in August (Fig. 3), and thus no conclusions about drift periodicity and its relationship to epibenthic activity could be made.

In September, most aspects of the feeding behaviour of large nymphs showed evidence of nocturnal activity (Fig. 3). Feeding intensity was lowest

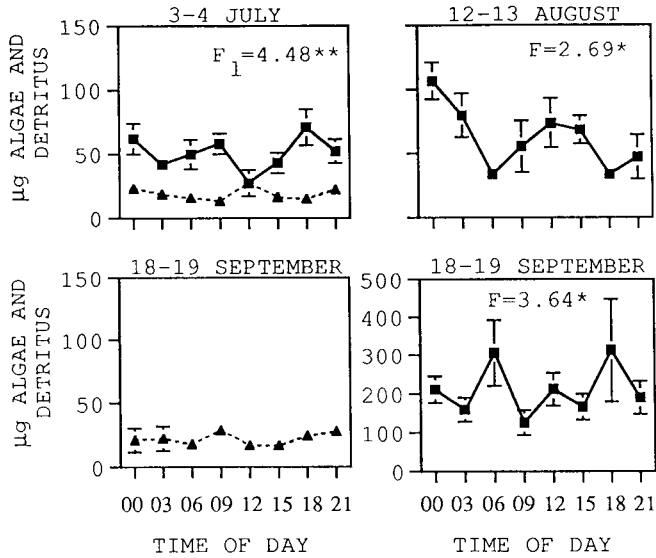


Fig. 4. Diel variation in the gut fullness of *Baetis rhodani* nymphs. ** $P < 0.01$. Other details as in Figs. 1 and 3.

during the day (at noon and at 1500 hours), although this trend was not statistically significant. Gut contents of large nymphs showed distinct peaks at dusk and dawn, whereas feeding of small nymphs was aperiodic (Fig. 4). Drifting was almost exclusively nocturnal, especially in large nymphs. Although drift rate and percent of nymphs on exposed surfaces both peaked at night and were lowest during the day, the match was far from perfect, and Spearman rank correlation did not detect a significant association between the two variables ($r_s = 0.36$, $P = 0.22$).

Correlation between diel variation in temperature and laboratory feeding activity was significant in September, when nymphs of both size-classes were most active during the coldest part of the day ($r_s = -0.67$; $r_s = -0.72$, for large and small nymphs, respectively; $P < 0.05$). Gut fullness was positively, but non-significantly correlated with water temperature for both size-classes on all sampling occasions. Highest correlation was observed for small nymphs in July ($r_s = 0.44$, $P = 0.16$).

Discussion

Most previous studies examining the diel periodicity of aquatic invertebrates have been conducted in the field, where accurate assessment of epibenthic densities is difficult for logistic reasons. Detailed behavioural observations of

small-sized animals like mayfly nymphs are certainly easier to make in simplified laboratory conditions (see also GLOZIER & CULP 1989). In the laboratory, however, animals may be isolated from important environmental cues, which may affect the timing and extent of their behaviour in the field. Water temperature and illumination are probably the key abiotic factors, and it is important to notice that our laboratory system closely paralleled natural variation in temperature and illumination. Furthermore, except for the extremely low activity of heptageniids in September, water temperature was not closely associated with the nymphal feeding behaviour (see also COWAN & PECKARSKY 1994).

Fish predation risk is also known to affect the timing of activity in many stream invertebrates (e.g. CULP et al. 1991, COWAN & PECKARSKY 1994, TIKKANEN et al. 1994). This study was not originally designed to examine the effects of fish on the diel periodicity of mayfly nymphs, and fish cues were thus not manipulated. Nevertheless, since water to the stream tanks was transferred from a fish stream (River Oulankajoki), chemical fish signals may have been present, even though direct encounters with fish were precluded. Indeed, some of our results suggest that chemical cues of fish were perceived as predation threat by mayfly nymphs. For example, drift of large *Baetis* in July and especially in September was strongly nocturnal. While this could well be a fixed prey response to invariably high predation risk, our previous experiments have shown that nocturnal drift of large *Baetis* is a flexible avoidance response triggered by chemical cues of fish presence (TIKKANEN et al. 1994; see also DOUGLAS et al. 1994). In contrast, positioning of *Baetis* on stone surfaces does not seem to be affected by chemical signals alone (TIKKANEN et al. 1994; but see KOHLER & MCPEEK 1989, COWAN & PECKARSKY 1994). This is well in the line with the evidence shown here: neither large nor small *B. rhodani* nymphs exhibited distinct diel migrations from undersides of stones during the day to stone tops at night. On the other hand, gut contents suggested a nocturnal peak in the foraging activity of large nymphs in the field, a pattern previously reported for mayfly nymphs by MEIER & BARTHOLOMAE (1980), CULP et al. (1991), CULP & SCRIMGEOUR (1993) and COWAN & PECKARSKY (1994). A possible explanation for this apparent contradiction is that in the laboratory stream tanks direct encounters between mayfly prey and fish predators were prohibited. In TIKKANEN et al.'s (1994) experiment it was shown that nymphs do indeed avoid the upper stone surfaces in the presence of a freely foraging fish (or a fish model, TIKKANEN et al., unpubl.), especially during the day.

The pattern of diel periodicity exhibited by *H. dalecarlica* in August deserves extra scrutiny. Gut contents of field-collected nymphs were indicative of nocturnally biased feeding, and the same pattern was observed in the laboratory. For most of the time, heptageniids remained hidden beneath the stones,

making only short foraging trips onto the stone tops. A similar diel periodicity pattern was observed by PECKARSKY & COWAN (1995) for other heptageniid genera. *Heptagenia* nymphs seem to lead a "slow life-style" (sensu SIH 1987), which renders them safe from fish predation. Such strict nocturnality may either reflect an ability to detect fish via chemical signals, or else it may be a fixed predator avoidance response. If chances of escape after an encounter with a predator are low, a low-risk antipredatory trait may become fixed, even if predation pressure is highly variable (SIH 1987). By virtue of their well-developed escape mechanisms, baetid nymphs can accept some risk from epibenthically feeding fish (TIKKANEN et al. 1994). In contrast, *Heptagenia* nymphs may be morphologically constrained from acquiring such escape mechanisms, which forces them to rely on primary defences, that is, to completely avoid encounters with fish. To this end, a comparative study of predator avoidance mechanisms and their relative costs in *Baetis* and *Heptagenia* nymphs under variable predation pressure should prove rewarding.

Our study did little to support the passive drift entry hypothesis. In fact, the relationship between numbers in drift and on stone tops was negative in July, and even in September when these two aspects of *Baetis* feeding behaviour were more closely synchronized, peaks in drift and density on stone tops were not coincident. The fact that drift of large nymphs was clearly nocturnal while other aspects of *Baetis* feeding behaviour were arrhythmic or slightly diurnal in July, speaks strongly in favour of volitional drift entry. However, as noted by WILZBACH (1990), correlation – or lack of it – between drift rate and density on substrate surfaces may be a poor indicator of drift mechanisms, because drift entry may occur from other, more concealed locations than stone tops.

Research on aquatic insect periodicity has been bewildered by a general pursuit to reveal predictable patterns in diel feeding activity, and in its relation to drift. Diel periodicity of lotic mayflies and of other stream insects may, however, be a multi-faceted phenomenon with different expressions in different environmental settings. Apart from the potential effects of some abiotic factors, predation risk from both fish and predatory invertebrates may have varied between different studies, as may also the size distribution of prey. Furthermore, high flexibility of rhythmic behaviours are to be expected in the seasonally varying environment of high northern areas, where aquatic organisms are largely arrhythmic around the summer solstice (MÜLLER 1973, MALMQVIST 1986). This allows the animals to exploit all feeding opportunities, but simultaneously exposes them to an imminent predation threat throughout the day. Obviously, around the summer solstice, the risk of predation can not be reduced by nocturnal activity, and it may be that aquatic insects in subarctic areas use completely different sets of antipredatory tactics at different times of the year. Thus, we fully endorse COWAN & PECKARSKY (1994) in their appeal that variation in diel periodicity of lotic mayflies be regarded more as an op-

portunity for creative generation of hypothesis in future studies than as a source of continuing distraction.

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