

Diel periodicity in density of Ephemeroptera nymphs on stream substrata and the relationship with drift and selected abiotic factors

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The diel periodicity in density of Ephemeroptera nymphs on an undisturbed stream bottom was documented by direct observation. The study was conducted in a second-order Rocky Mountain foothill stream in Alberta. Observations were made for 24-h periods, twice during a new moon and twice during a full moon; the times of the dark and light periods were noted. Nocturnal observations were made using a red light. The abundance of drifting nymphs, incident light, percent cloud cover in the sky, and water temperature were recorded to determine if they were related to the observed diel periodicity on top of the substratum. The taxonomic groups of Ephemeroptera nymphs examined were *Cinygmula*, Heptageniidae (*Cinygmula* and *Epeorus*), *Baetis*, *Baetis-Ameletus*, *Ameletus*, *Drunella coloradensis* Dodds, and total fauna (all groups including minor taxa). In response to the artificial light used for observations, total fauna, *Cinygmula*, and *Baetis* nymphs were not affected by the light, and the nymphs were not found to be negatively phototactic. Total fauna and Heptageniidae nymphs exhibited a diel periodicity between 24-h periods; the *Baetis-Ameletus* group also had a diel periodicity. *Cinygmula*, *Baetis*, and *D. coloradensis* nymphs did not exhibit a diel periodicity. Most taxonomic groups were at greater densities on the top of the substratum in the dark period than in the light period. For small and large size classes of nymphs examined, only the small Heptageniidae and *Baetis-Ameletus* nymphs showed a diel periodicity in density. Drift of the common groups of nymphs was aperiodic and not statistically correlated with the diel density of nymphs on the substratum. In general, incident light, percent cloud cover, and water temperature were not correlated with the diel density of the taxonomic groups on the top of the substratum.

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La périodicité journalière de la densité des larves d'Ephéméroptères a été déterminée par observation directe sur le fond intact d'un ruisseau d'ordre 2 des contreforts des Rocheuses en Alberta. Les observations se sont étalées sur 24 h à quatre reprises, deux fois en période de nouvelle lune et deux fois en période de pleine lune. Les périodes d'obscurité ont été notées et les observations nocturnes ont été faites à la lumière artificielle rouge. L'abondance des larves en dérive, la lumière incidente, le pourcentage de couverture de nuages et la température de l'eau ont été mesurés dans le but d'évaluer leur relation avec la périodicité de la densité des larves sur le substrat. Les groupes taxonomiques considérés étaient *Cinygmula*, les Heptageniidae (*Cinygmula* et *Epeorus*), *Baetis*, *Baetis-Ameletus*, *Ameletus*, *Drunella coloradensis* Dodds et la faune totale (y compris les taxons rares). La faune totale ainsi que les larves de *Cinygmula* et de *Baetis* n'étaient pas affectées par la lumière artificielle utilisée pendant les observations; ces larves ne montraient pas de phototactisme négatif. La faune totale, les larves d'Heptageniidae et du groupe *Baetis-Ameletus* avaient une périodicité journalière, alors que les larves de *Cinygmula*, *Baetis* et *D. coloradensis* n'en avaient pas. Dans la plupart des groupes, il y avait plus de larves sur les substrats pendant les périodes d'obscurité qu'à la lumière. Lorsque les tailles étaient considérées, seulement la densité des larves de petite taille d'Heptageniidae et de *Baetis-Ameletus* suivait une périodicité journalière. La dérive des groupes abondants était aperiodique et il n'y avait pas de corrélation statistique entre la dérive et la densité journalière des larves sur le substrat. En générale, la lumière incidente, la couverture de nuages et la température de l'eau n'étaient pas reliées à la densité journalière des larves des divers groupes taxonomiques sur les substrats.

[Traduit par la revue]

Introduction

Before the 1960's there were few studies on the diel periodicities of aquatic insects. Notable exceptions were studies by Moon (1940) and Harker (1953). In the 1960's, interest was stimulated by the discovery of diel periodicity in the drift of stream invertebrates. Since that time, diel periodicities of drift have been demonstrated for many taxa and in many parts of the world (see reviews by Waters 1972; Müller 1974). However, the mechanisms involved in this diel periodicity are still not well understood. Two types of periodicity on the substratum have been identified: diel positioning changes and diel activity levels (Wiley and Kohler 1984). Diel positioning changes of benthic invertebrates, as indicated by diel changes in density on the top of the substratum, are considered here.

There is much debate as to whether diel drift periodicity is accounted for by an assumed accidental displacement or by an active release of animals from the substratum (see Wiley and Kohler 1984; Allan et al. 1986). Whether drift is due to accidental or active departure from the substratum, it would be expected to be directly related to diel densities of the zoobenthos on the substratum. If drift and density are unrelated, accidental

displacement can be rejected as the predominant mechanism to explain the diel periodicity in drift. Several hypotheses have been proposed to explain diel density changes of the zoobenthos on the substratum. A premise of these hypotheses is that benthic animals are present on the top surfaces of the substratum mainly at night. Phototaxis, responses to predation, foraging periodicity, and respiratory needs of animals may account for this phenomenon (see reviews by Hynes 1970; Waters 1972; Wiley and Kohler 1984).

Many immature aquatic insects have been reported to be negatively phototactic. Therefore, the organisms would be present beneath the substratum particles during the daylight and migrate to the top surfaces of the substratum in the dark. Visually foraging predators, such as fish, are thought to cause the zoobenthos on top of the substratum to move to the bottom of the rocks during daylight hours. High densities of zoobenthos on the top of the substratum may also be related to feeding periodicity of the animals. Because many immature aquatic insects feed on attached algae and fine organic material on the upper surfaces of the substratum, nocturnal foraging behaviour might reduce risk of predation. High nocturnal densities of prey

on top of the substratum may be more evident in larger animals because these organisms will be most likely chosen by a visually feeding predator. A nocturnal decrease in dissolved oxygen in the substratum may cause a migration from the bottom surfaces of the substratum, or from deep in the substratum, to more exposed surfaces at night (Wiley and Kohler 1980).

My study was designed to determine, using direct observations, whether the stream zoobenthos in Dyson Creek, Alberta, exhibited a diel periodicity in density changes on the top of the substratum. Abiotic factors were measured and observations were made during two new moon phases and two full moon phases to determine if they were related to diel density changes. Also, drift was measured to determine if drift was related to the diel periodicity of the zoobenthos on the substratum.

Material and methods

Dyson Creek is a second-order stream in the eastern foothills of the Canadian Rocky Mountains (50°37' N, 114°39' W). A 10-m length of a slow-flowing riffle (elevation 1555 m) was chosen because the substratum size (mean = 4.7 cm, range = 2.1–8.2 cm), water velocity, and depth in this area were spatially uniform. Mean water velocity and depth in the riffle were 21 cm s⁻¹ and 12 cm, respectively. During this study, the diel range in water temperature was 4–18°C. The stream rocks were generally well covered with epilithon, and the particles were rarely disturbed by the current.

Direct observations were made with a rectangular observation box (50 × 25 × 30 cm) with Plexiglas walls (thickness = 1.2 cm) and a glass bottom (thickness = 0.5 cm). On the top rim of the box, four pipes (length = 4 cm) were attached to the corners of a wooden frame (6.8 × 1.8 cm). Four stainless steel legs (length = 65.5 cm, diameter = 1.3 cm) were secured into each pipe by wing nuts that could be used to adjust the leg length, allowing the level of the glass bottom to be positioned relative to the water depth. This was necessary to obtain a clear view of the bottom substratum with a maximum depth of water between the glass and the substratum. The mean distance between the glass bottom of the box and the top of the substratum was about 6 cm. The box was carefully positioned on the substratum to minimize disturbance to the substratum under the box. To determine whether the box was creating unnatural water currents, a suspension of fluorescent particles was released around and underneath the box; I observed no currents caused by the box. Occasionally an anti-fog wax was applied to the inside of the glass bottom between observations to prevent condensation. Direct observations were made by kneeling about 30 cm away from the box and leaning over it to obtain an unobstructed view of the substratum.

In the dark period (ca. 22:00–05:30; the 24-h time in my study was recorded at mountain daylight saving time), including dusk and dawn, observations were made with a hand-held red light by shining the light through the bottom of the box onto the substratum. The light source was an automobile headlight (face = 12 × 12.5 cm, with an H3 halogen bulb, 12 V, 55 W) with a handle attached to the back of the light; the power source was a heavy duty 12 V battery. A sheet of neoprene (area = 17 × 17.5 cm, thickness = 0.5 cm) with a porthole (diameter = 4 cm) cut in the centre was attached to the front of the light. Between the neoprene and the light, a photographic glass-mounted filter (Tiffen AA No. 29, diameter = 52 mm) could be secured. The filter transmitted deep red to infrared wavelengths (transmission range = 600–900 nm). The headlight was painted mat black except for an area at the front to allow the light to pass through the filter. The sides and back of the light were enclosed to prevent light escaping from the apparatus. In 1983, preliminary results at night were obtained by using a flashlight with hard red plastic (diameter = 6 cm, thickness = 1 mm) taped over the lens (diameter = 4.5 cm). The results demonstrated that the flashlight beam was weaker than that of the headlight; this reduced the area illuminated, which caused poor visibility and consequently required more observer movement. The flashlight was not as effective as the headlight apparatus described above. I determined whether the density

of animals observed on the substratum during daylight was different when observations were made using red light (with filter), white light (no filter), and no light. These observations were made between 07:50 and 13:00 on 2 days (June 19 and 20, 1984) at 30-min intervals at different and adjacent sites. Seven sequences of the three observation methods, which were randomly chosen, were used.

To determine diel densities of the zoobenthos on the substratum surface, direct observations were made over two new moon and two full moon phases on four series of dates in 1984: study NM1 on June 27–29, NM2 on July 25–28, FM1 on July 11–13 and FM2 on August 8–11. Observations for each study were made in four 6-h blocks to make up a 24-h day, with 12 h between any of the four 6-h blocks. In each 6-h block, observations were made at 30-min intervals, i.e., a total of 12 readings. Within any 6-h block, observations were taken 0.5–1.0 m from the stream edge at 12 sites, beginning at the furthest downstream site. Twelve sites were chosen to reduce the chances of recording the same organism twice. The longitudinal axis of the box was placed parallel with the stream edge, with about 10 cm between each of the 12 sites. The bottom of the box contained eight 10 × 10 cm quadrats. Potential disturbance to animals on the rocks by moving the box to a new site between 30-min intervals was reduced by leaving the box in place for about 20 min before starting observations. Before taking observations, I spent 2–3 min motionless, kneeling in position over the box. Only rarely did some of the nymphs react to my approach by moving to the sides or bottom surfaces of the rocks, but they usually returned to the upper surfaces of the rocks. All observations were recorded using a portable tape recorder to minimize movements that might disturb the benthic animals. Individual organisms in each 10 × 10 cm quadrat were counted during 1-min periods (this was sufficient to include all of the organisms in a quadrat); the quadrats furthest downstream were observed first. The organisms were identified and their body length (less the cerci) was estimated using a ruler (scale = 1 mm) in the bottom of the observation box.

At 2-h intervals during the test of the effect of the red light and the four 24-h studies, the following abiotic factors were recorded: incident light (Gossen Lumasix meter, about 10 cm above the water surface), an estimate of the percent cloud cover, and water temperature. Water velocity and depth were measured at irregular intervals. In 1985, two drift samples were taken at 3-h intervals over a 24-h period on August 5–6 (almost during a full moon phase) in an area 300 m upstream of the study area. The drift nets had a large opening (frame = 1.0 × 0.5 m, net length = 2 m, mesh = 0.211 mm) and they were placed about 10 cm above the stream bed.

Data analysis

For the analyses of the taxonomic groups, the total number of animals observed at any 30-min interval (i.e., in eight 10 × 10 cm quadrats) was treated as one sample because the quadrats were not independent samples. During the FM1, NM2, and FM2 studies, I had difficulty identifying some of the taxa because of large influxes of small nymphs. For these studies, *Cinygmula* and *Epeorus* nymphs were considered in the Heptageniidae taxon. For the FM2 study, the morphologically similar *Baetis* and *Ameletus* nymphs were treated as a single group; most of these nymphs were *Baetis*. Other taxonomic groups of nymphs were *Baetis* (probably *Baetis bicaudatus* Dodds and *Baetis tricaudatus* Dodds) (NM1, FM1, and NM2 studies), *Drunella coloradensis* Dodds (NM1, FM1, NM2, and FM2 studies), *Cinygmula* (NM1 study), *Ameletus* (FM1 and NM2 studies), and total fauna (NM1, FM1, NM2, and FM2 studies). The total fauna group included Heptageniidae (about 44% of the total observed in the 24-h studies), the *Baetis*–*Ameletus* group (26%), *Baetis* (18%), *D. coloradensis* (6%), *Cinygmula* (4%), *Ameletus* (2%), and minor taxa (Trichoptera and Plecoptera, <0.7%) (Table 1).

Friedman's test was used to test the null hypothesis that there was no difference in density of organisms observed using red light, white light, and no light. In the analysis, treatments were the observation method and blocks were individual days. To determine if there was a periodicity in the diel density of the Ephemeroptera nymphs on the substratum, I used the Kolmogorov–Smirnov goodness of fit test. The

TABLE 1. The total number of organisms and the number of organisms per 30-min interval observed in the dark and light periods for taxonomic groups of Ephemeroptera nymphs and 24-h studies; the ratio of the number of organisms per 30-min interval in the dark period to the number in the light period, and the mean and standard deviation (SD) of these ratios for each taxonomic group and 24-h study are also given

Taxonomic group	24-h study	No. of organisms observed	No. in dark/30 min	No. in light/30 min	Dark : light		
					Ratio	Mean	SD
Total fauna	NM1	750	16.13	15.39	1.05	1.12	0.10
	FM1	1271	28.13	25.66	1.10		
	NM2	1697	36.88	34.52	1.07		
	FM2	2769	66.28	52.53	1.26		
<i>Cinygmula</i>	NM1	257	3.67	6.12	0.60	—	—
	FM1	732	14.63	15.56	0.94	1.04	0.09
	NM2	1225	25.77	25.48	1.01		
FM2	919	20.94	18.07	1.16			
<i>Baetis</i>	NM1	452	12.00	8.24	1.46	1.21	0.34
	FM1	463	11.63	8.66	1.34		
	NM2	217	4.00	4.81	0.83		
<i>Ameletus</i>	FM1	34	0.81	0.66	1.23	0.97	0.36
	NM2	65	1.06	1.52	0.70		
<i>Baetis-Ameletus</i>	FM2	1700	40.44	32.40	1.25	—	—
<i>Drunella coloradensis</i>	NM1	7	0.27	0.09	3.00	2.08 ^a	0.44 ^a
	FM1	34	0.94	0.59	1.59		
	NM2	190	6.24	2.71	2.30		
	FM2	150	4.89	2.07	2.36		

NOTE: Minor taxa (<0.7% of the total number of organisms observed) are included in total fauna. NM1 and NM2, new moon studies; FM1 and FM2, full moon studies.

^aNM1 was not included in this calculation.

observed diel density data for each 24-h study and each taxonomic group of nymphs were tested against the null hypothesis that density was random (using the Poisson distribution as a model) over a 24-h day. *Ameletus* nymphs could not be included in the analysis because they were present in low densities (Table 1). For the taxonomic groups showing a nonrandom distribution over a 24-h day, I used Kendall's coefficient of concordance rank test (Siegel 1956; Conover 1980), to determine if temporal trends in the substratum diel densities of the new moon and full moon studies were associated. Kendall's coefficient of concordance varies from 0 (no concordance) to 1 (complete concordance). The χ^2 test was used to determine whether Kendall's coefficient value (W) was significantly different from 0 (Siegel 1956). If the χ^2 result was statistically significant, it would suggest that the ranks of 48 densities (for each 24-h study) between individual 24-h studies were related.

For each taxonomic group and 24-h study, the mean number of animals per 30-min interval was calculated for both the dark and light period. This was done to determine if the substratum densities of individual taxonomic groups were proportionally greater in the dark than in the light period. In general, the dark period began and ended about 1.5 h before sunset and after sunrise, respectively. Ratios of the proportional numbers of animals present in the dark period divided by the numbers present in the light period for each 24-h study were calculated. (This method was also used to calculate proportional abundances of animals in the drift in the dark and light periods.)

For each taxonomic group, except total fauna and *D. coloradensis*, the animals were separated into two size classes based on body length to determine if small and large nymphs showed the same trend in diel density on the substratum as when the nymphs of each taxon were treated as a single size class. The size classes chosen were 1–4 mm (small) and 5–12 mm (large); these sizes made up 57% and 43%, respectively, of total fauna. The diel density data of these size classes were tested against the Poisson distribution using the Kolmogorov-Smirnov goodness of fit test. This test was also used to determine if the drift of *Cinygmula*, *Epeorus*, and *Baetis* nymphs exhibited a diel periodicity. The Spearman rank-correlation test was used to determine if drift and diel density were associated.

To determine if incident light, percent cloud cover, and water temperature were associated with the diel densities for each taxonomic group of nymphs (except *Ameletus*) on the substratum and for each 24-h study, I used the Spearman rank-correlation test.

Results

Nymphal behaviour

When I made the observations, there were characteristic reactions by certain nymphs to my movements, presumably as a result of nymphs perceiving my silhouette against the sky. For example, *Cinygmula* nymphs were easily disturbed when I moved suddenly. The nymphs would move quickly from the top to underneath the substratum. But if I moved slowly or only slightly, the nymphs usually did not react to my presence. *Epeorus* nymphs were less easily disturbed by movements than *Cinygmula* nymphs, and *Baetis*, *Ameletus*, and *D. coloradensis* nymphs generally did not seem to react to my movements. Similar reactions of heptageniid and *Baetis* nymphs have been reported by other workers (Madsen 1968; Allan et al. 1986).

Phototaxis

The densities of total fauna, *Cinygmula*, and *Baetis* nymphs observed in daylight with red light, white light, and without a light source were not significantly different among observation treatments (Friedman's test, $p = 0.73, 0.11, \text{ and } 0.51$, respectively). *Cinygmula* and *Baetis* were the dominant taxa of the 457 organisms observed in this test (35.7% and 62.8%, respectively). The mean incident light (daylight) and red light readings were similar (24'903 and 26 886 lx, respectively), and the white light reading (59 086 lx) was about twice those of the red and ambient light. When this test of the effect of light on the zoobenthos was made, all abiotic factors were similar between dates except for percent cloud cover.

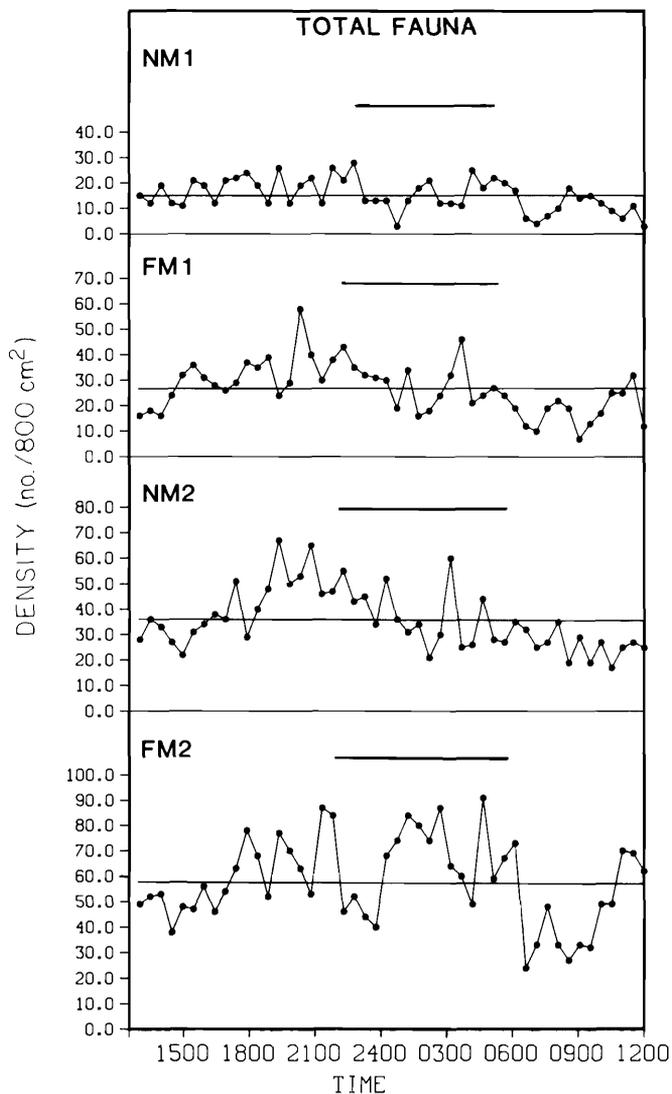


FIG. 1. Densities of total fauna nymphs (number per 800 cm² of substratum) at 30-min intervals during the four 24-h studies. NM1 and NM2, new moon studies; FM1 and FM2, full moon studies. Horizontal bars represent the dark period. The mean density for each 24-h study is shown by the horizontal line.

Diel periodicity in density

Taking account of all taxonomic groups in Dyson Creek, the nymphs had peaks in density in the light and dark periods (Figs. 1, 2, 3, and 4). However, during each 24-h study, total fauna (except for one 24-h study), Heptageniidae, and *Baetis-Ameletus* groups of nymphs exhibited a periodicity in density over a 24-h day (Table 2). *Cinygmula*, *Baetis*, and *D. coloradensis* nymphs did not exhibit a diel periodicity in density on the substratum. During the NM1 study, the mean water velocity and depth values were about twice those of the other 24-h studies (Table 3). The substratum particles were occasionally disturbed by the current during the NM1 study. For the taxonomic groups observed during the NM1 study (total fauna, *Cinygmula*, and *Baetis*) the diel densities were random over a 24-h day (Table 2).

For the taxonomic groups with a diel periodicity, densities of total fauna and Heptageniidae between the three 24-h studies examined for each group (see data analysis for details) were similar ($W = 0.56$ and 0.61 , respectively) and the rankings were

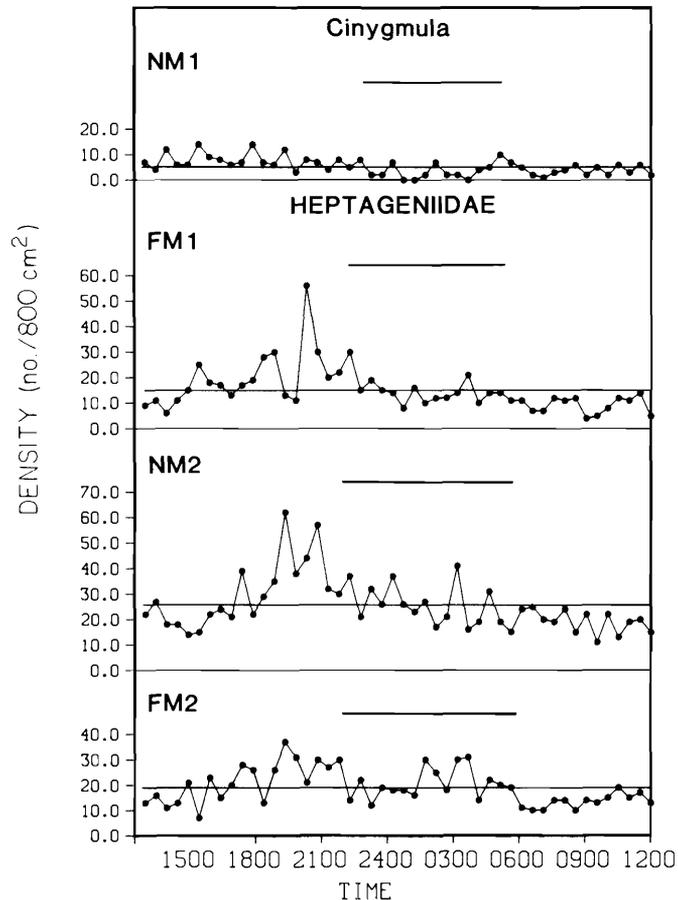


FIG. 2. Densities of *Cinygmula* (NM1) and Heptageniidae (FM1, NM2, and FM2) nymphs during the 24-h studies. The mean density for each 24-h study is shown by the horizontal line. See Fig. 1 for details of 24-h studies.

significantly related between these studies (χ^2 test, $p < 0.01$ and $p < 0.001$, respectively) (see Figs. 1 and 2).

For most taxonomic groups, including the three taxonomic groups exhibiting a diel periodicity, there was a tendency for the greatest proportional mean density of nymphs on the substratum to be in the dark period (Table 1). For total fauna nymphs, the higher mean density in the dark compared with that of the light period is due mainly to high densities of *D. coloradensis* and to a lesser extent the *Baetis-Ameletus* and *Baetis* nymphal groups (Table 1 and Figs. 1, 3, and 4).

Size-class differences

Only the small-size class of Heptageniidae and *Baetis-Ameletus* nymphs had a diel periodicity (similar to when the size classes were considered together for these groups of nymphs) (Table 2). *Drunella coloradensis* nymphs were mostly in the large-size class and the Kolmogorov-Smirnov test was not used.

Drift

The drift of *Cinygmula* and *Epeorus* nymphs, as well as *Baetis* nymphs (which were common in the drift samples), was aperiodic (Kolmogorov-Smirnov test, $p = 0.71$, 0.88 , and 0.61 , respectively) (Fig. 5). The abundances of *Cinygmula* and *Baetis* nymphs in the drift and on the substratum (for the 24-h studies examined) were not significantly correlated ($p > 0.05$; *Cinygmula*, $r_s = -0.625$; *Baetis*, $r_s = -0.19, 0.30, 0.16$). The relationship between *Epeorus* nymphs in the drift and on the

TABLE 2. Probability levels from the Kolmogorov–Smirnov goodness of fit test against the null hypothesis that density of nymphs was random (i.e., aperiodic) over a 24-h day, for the diel density of each taxonomic group on the substratum; results are given for three size classes (small, large, and small and large combined)

Size class	24-h study	Probability			
		Total fauna	<i>Cinygmula</i> , Heptageniidae	<i>Baetis</i> , <i>Baetis–Ameletus</i>	<i>Drunella</i> <i>coloradensis</i>
Small + large (1–12 mm)	NM1	0.135	0.108	0.336	—
	FM1	0.011	0.019	0.997	0.823
	NM2	0.006	0.008	0.659	0.513
	FM2	0.007	0.038	0.011	0.199
Small (1–4 mm)	NM1	—	0.997	0.116	—
	FM1	—	0.080	0.704	—
	NM2	—	0.005	1.000	—
	FM2	—	0.062	0.002	—
Large (5–12 mm)	NM1	—	0.540	0.823	—
	FM1	—	0.064	0.850	—
	NM2	—	0.253	0.412	—
	FM2	—	0.609	0.349	—

NOTE: See Table 1 for details of 24-h studies. *Cinygmula* nymphs alone were present for one 24-h study (NM1). Heptageniidae for three studies (FM1, NM2, and FM2), *Baetis* for three studies (NM1, FM1, and NM2), and *Baetis–Ameletus* for one study (FM2).

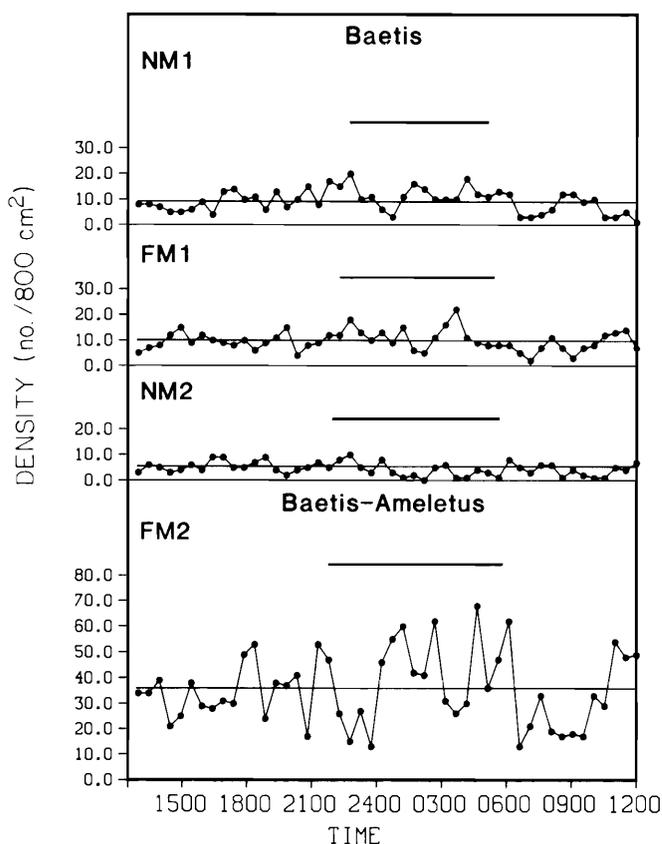


FIG. 3. Densities of *Baetis* (NM1, FM1, and NM2) and *Baetis–Ameletus* (FM2) nymphs during the 24-h studies. The mean density for each 24-h study is shown by the horizontal line. See Fig. 1 for details of 24-h studies.

substratum could not be determined because the nymphs on the substratum were included in the Heptageniidae taxonomic group.

When I made the direct observations of the density of nymphs on the substratum, I also noted incidents of drift. Drift was

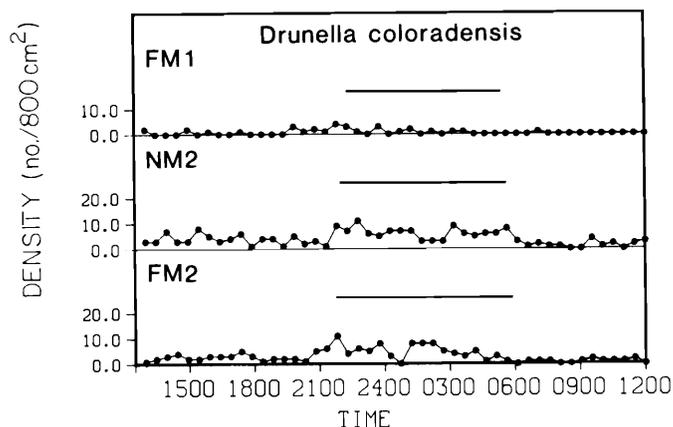


FIG. 4. Densities of *Drunella coloradensis* (FM1, NM2, and FM2) nymphs during the 24-h studies. The mean densities for the NM2 and FM2 studies are four and three organisms, respectively. See Fig. 1 for details of 24-h studies.

recorded as nymphs landing on the substratum from the water column or leaving the substratum to enter the water column, or both of these occurring during a single observation. I observed that only 0.8% of animals drifted, which was a low proportion of the zoobenthos found in the drift.

Abiotic factors

In general, for all taxonomic groups, incident light, percent cloud cover, and water temperature were not statistically correlated ($p > 0.05$) with the diel density of the group. For the 14 correlations tested for each abiotic factor and density, only 1 was statistically significant ($p < 0.05$) for incident light ($r_s = -0.4784$), 3 for percent cloud cover ($r_s = -0.4903$, -0.4903 , and 0.4749), and 3 for water temperature ($r_s = 0.4877$, 0.5694 , and 0.4686).

Discussion

Phototaxis

Red light is commonly used to observe the zoobenthos in the dark. When the effect of red light and dim white light has been

TABLE 3. Mean values (standard deviation in parentheses) of abiotic factors measured at 2-h intervals (except water velocity and depth, which were measured irregularly at the 12 study sites) during the four 24-h studies

24-h study	Incident light (lx)	% cloud cover	Water temp. (°C)	Water velocity (cm s ⁻¹)	Water depth (cm)
NM1	7 171 (9 766)	81 (16)	7.7 (2.5)	33.3 (2.9)	7.8 (0.8)
FM1	10 792 (14 375)	53 (37)	13.0 (2.9)	14.7 (4.5)	3.3 (0.5)
NM2	11 138 (11 892)	56 (29)	9.5 (2.5)	17.0 (5.7)	4.2 (0.4)
FM2	4 926 (6 690)	81 (19)	12.8 (3.3)	8.6 (4.1)	3.5 (0.6)

NOTE: See Table 1 for details of 24-h studies.

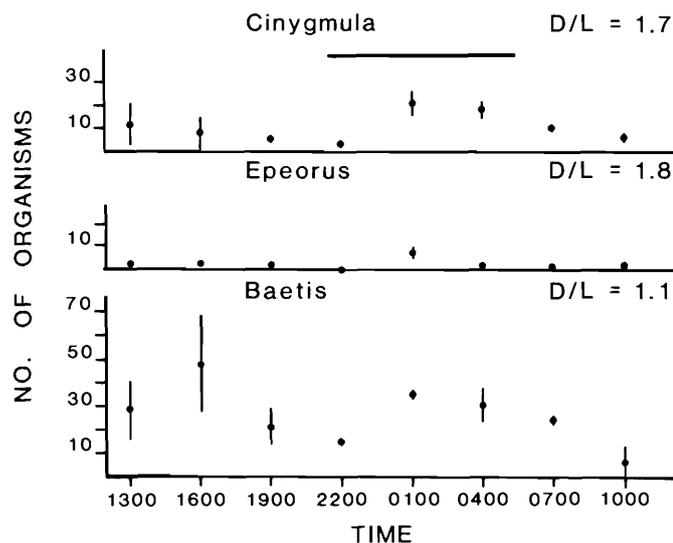


FIG. 5. Mean and range of abundances of two concurrent drift samples for *Cinygmula*, *Epeorus*, and *Baetis* nymphs taken at 3-h intervals over a 24-h period. D/L, number of nymphs in each 3-h sample in the dark period divided by the number in the light period. The horizontal bar represents the dark period.

tested on observed zoobenthos densities, no effect has been found in laboratory streams (Elliott 1968, 1970; Bailey 1981).

My results suggest that the use of red and white light did not affect the density of Ephemeroptera nymphs on the substratum, and that the nymphs were not negatively phototactic. Shining the light beam directly on the nymphs apparently did not cause a negative phototactic response. Bohle (1978) found similar numbers of *Baetis rhodani* nymphs in shaded and illuminated areas in a laboratory stream. My observations are generally contrary to other workers' results for the reaction to light by *Baetis* and heptageniid nymphs (Wodsedalek 1911; Lyman 1945; Scherer 1965; Elliott 1968).

Diel periodicity in density

Total fauna and Heptageniidae nymphs, which had a diel periodicity in density, showed a similar trend in density during the new moon and full moon phases together. However, in my study area of Dyson Creek, direct illumination from a full moon did not fall on the stream bed (where the observations were made) during darkness because of surrounding gorge walls. This was not known before the study, and the effect of moonlight on zoobenthos densities cannot be evaluated in the Dyson Creek study. Obstructions to moonlight may only have an effect on aquatic insects that can perceive only direct illumination (rather than dispersed light) from the moon.

My results indicate a diel periodicity in density for total fauna, Heptageniidae, and *Baetis*-*Ameletus* nymphs. Also,

there was a tendency for these taxonomic groups and *D. coloradensis* and *Baetis* nymphs to be found at proportionally greater densities on the top of the substratum in the dark than in the light period. Studies on the diel densities of immature aquatic insects in the field and the laboratory have shown increases in number at night (Moon 1940; Elliott 1968; Campbell 1980; Bailey 1981; Mogel et al. 1985) and in the daylight (Graesser and Lake 1984; Statzner and Mogel 1984, 1985; Allan et al. 1986), while other studies indicate no difference between day and night (Clifford 1972; Kovalak 1978, 1979; Wiley and Kohler 1981; Kohler 1983). Some of the disparities in these published results, other than those due to differences in taxa, are possibly accounted for by differences in methods.

For example, sampling the zoobenthos with a sampler causes disturbance to the substratum, and the animals collected from the upper layer of the substratum are not necessarily the organisms that were on the top of the substratum before the sample was taken (see also discussion in Allan et al. 1986). A field study using direct observations will cause the least disturbance to a natural system, and the results will likely best describe the actual situation; only the latter type of studies are considered in my discussion here.

Most field studies that employed direct observations on lotic insects have demonstrated density increases in the daylight (Statzner and Mogel 1984, 1985; Allan et al. 1986). Statzner and Mogel's (1984, 1985) studies were done in Germany, and Allan et al.'s (1986) study was done in the United States; in all three studies, the immatures of *Baetis*, *Cinygmula*, and *Micrasema* (Brachycentridae: Trichoptera) exhibited high daylight densities and low nocturnal densities on the substratum. The sharp change in diel densities in these studies appeared to be indirectly related to the amount of incident light. In contrast to these studies, the Dyson Creek study in one of the first to use direct observations to show peaks in density in both the dark and light periods, and a tendency for nocturnal increases in the proportional density of most taxonomic groups of Ephemeroptera nymphs on the substratum.

The results of diel periodicity studies using direct observations are difficult to explain because the diel periodicities do not show a consistent trend. For example, in Allan et al.'s (1986) study there were predominantly diurnal density peaks, which is unlike my results. Both of these studies were done in Rocky Mountain streams with similar zoobenthos fauna and daily water temperature range, and potentially similar visually feeding predators (there are no fish presently in the study area of Dyson Creek, although the area was stocked with trout on several occasions in the 1940's). But in a more recent study in the same mountain stream used by Allan et al. (1986), J. D. Allan and A. S. Flecker (personal communication) have found evidence of aperiodic and nocturnal increases in activity (equivalent to

density in their study) of nymphs. In a Michigan stream, Wiley and Kohler (1981) used cinematography over two consecutive 24-h periods and found no apparent diel periodicity of *Baetis vagans* nymphs.

The different diel periodicities and aperiodicities of these studies could simply be due to different populations of aquatic insect taxa. For example, the existence of geographic races with respect to photoperiodic reaction are known for a large number of insect species (Saunders 1982).

Predators in Dyson Creek include tactile foragers such as perlotid (Plecoptera) stoneflies, some of which exhibit a diel periodicity (Walde and Davies 1985). These stonefly predators, which are fast-moving foragers, may affect the distribution of their prey. Invertebrate predators such as perlotid stoneflies and *Rhyacophila* larvae, both of which are present in Dyson Creek, have been shown to have strong influences on the distribution and abundance of their prey, which include mayfly nymphs, on the substratum (Corkum and Clifford 1980; Peckarsky and Dodson 1980; Wiley and Kohler 1981). Unfortunately, these invertebrate predators were rarely observed on the Dyson Creek substratum and it is not known if they exhibited a diel periodicity.

Size-class differences

During preliminary observations in Dyson Creek, I often observed that small nymphs did not react to my movements as readily as did large nymphs. This was especially evident for the heptageniid nymphs. Larger nymphs are probably seen and preferred by benthic-feeding fish because of their greater size, movement, and nutritional value. Of the two size classes of insect nymphs in my study, I predicted that larger nymphs would show peak densities at night to reduce predation from visually feeding predators and that smaller nymphs would show an aperiodic density or density increases in the dark or light period. This hypothesis is similar to one proposed by Allan (1978) as a predator-avoidance adaptation for the nocturnal drift of stream invertebrates. However, at the level of size classification in my study there is little evidence from the densities of small and large Ephemeroptera nymphs to support this hypothesis.

Drift

In general, diel activity per se on the substratum and in the drift are not considered to be related (Corkum 1978; Allan et al. 1986). In Dyson Creek, the drift and diel density of *Cinygmula* and *Baetis* nymphs on the substratum were aperiodic and not statistically correlated. This suggests that accidental displacement of the zoobenthos from the substratum was not an important mechanism causing the diel periodicity of drift. The substratum and the drift densities of the nymphs were not recorded at the same time or at the same location in Dyson Creek. But in studies where the substratum and drift densities have been measured at about the same time, no clear relationship was found in either laboratory (Elliott 1968; Bohle 1978) or field studies (Bailey 1981; Kohler 1983; Graesser and Lake 1984; Statzner and Mogel 1984, 1985).

Kohler (1983) stated that migrations to and from exposed surfaces appeared not to dislodge organisms into the drift. In Dyson Creek, if drift is a result of an active release and not an accidental displacement, it is difficult to determine how this may be directly measured, as the directly observed incidence of drift was low. More importantly, I was unable to determine if the directly observed drift was caused by behavioural (active) release or accidental displacement from the substratum.

Abiotic factors

Incident light, water temperature, and percent cloud cover alone were not directly related to observed diel periodicities in Dyson Creek. Incident light has been shown to be important in the control of drift (see reviews by Waters 1972; Müller 1974; Statzner et al. 1984), and light was expected to be important in the control of zoobenthos diel densities in Dyson Creek. In the laboratory, photoperiod has been shown to affect zoobenthos diel densities when temperature is relatively constant (e.g., Elliott 1968; Bailey 1981).

Water temperature, which exhibits a daily cycle in the ice-free season, was rarely statistically correlated with the substratum diel density of the taxonomic groups in Dyson Creek. However, Allan et al. (1986) found the substratum diel densities of *Cinygmula* and *Baetis* nymphs to be positively correlated with water temperature. Also, in other studies where directed observations were made, substratum diel density and water temperature appeared to be directly related (Statzner and Mogel 1984, 1985). But negative or no correlations have more recently been found (J. D. Allan and A. S. Flecker, personal communication).

Concluding remarks

In this and other field studies using direct observations, diel periodicities and no periodicities in density were found for immature aquatic insects. Neither drift, incident light, water temperature, nor cloud cover were related to diel periodicity in density of Ephemeroptera nymphs in Dyson Creek. It seems likely that factors not considered in my study (such as invertebrate predation) could be involved in causing, either singly or together, the diel periodicity in density of at least certain groups of zoobenthos on the substratum in Dyson Creek.

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