

DIEL CHANGES IN STREAM BENTHOS DENSITY ON STONES AND ARTIFICIAL SUBSTRATES

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Abstract

Diel changes in stream benthos density were studied by comparing faunal densities on naturally occurring stones collected at noon and at midnight and on artificial substrates (bricks) collected at 2 hr intervals for 24 hr. Over all dates and all rivers, on stones, nighttime densities were higher in 37 cases, lower in 35 cases and unchanged in three cases. The magnitude of nocturnal density increases (expressed as a proportion of daytime density) ranged between 0.03 and 1.08 and the magnitude of nocturnal density decreases ranged between 0.01 and 0.81. Diel density changes on bricks generally were variable and not synchronized with changes in light intensity, but in most cases (60%) densities were greater at night.

A new, accurate and rapid method to estimate the area of stone surface is also described.

Introduction

High invertebrate drift rates reported for many rivers (reviewed by Waters, 1972) have raised questions regarding the impact of drift on stream benthos density (Waters, 1965; Ulfstrand, 1968). Although it is well known that most drift activity follows a diel periodicity with a nocturnal maximum (Waters, 1972), remarkably little is known about diel changes in benthos density. Clifford (1972) compared benthos density in samples collected on a riffle during the day and at night on six dates and showed nighttime densities were higher in 30 cases, lower in 31 cases and unchanged in three cases. None of these differences was statistically significant but this may have been a result of methods used.

This study was carried out to provide more information on diel changes in benthos density. Diel density changes were studied by comparing benthos densities on naturally occurring stones collected at noon and at midnight and on artificial substrates (bricks) collected at 2 hr intervals for 24 hr. Emphasis was placed on the fauna living on stones as it has been hypothesized that insects enter drift by being swept from the tops of stones where the erosive action of current is greatest (Waters, 1965; Elliott, 1967; McLay, 1968).

Quantitative analysis of fauna living on stones has been limited by difficulties in estimating the area of stone surfaces. Early workers (reviewed by Schwoerbel, 1970; Calow, 1972) attempted direct estimates of surface area using tape measures and compasses which were tedious, time consuming and of questionable accuracy. Later workers used various measures of stone size as indices of surface area. Although these methods were rapid, they were inaccurate because they only provided a relative measure of surface area and they assumed stone shape was constant. A new, direct method to estimate stone surface area which is rapid, accurate and independent of stone shape is described here.

Study Areas

Most of the research reported here was conducted at the Pigeon River, Otsego County, Michigan in the vicinity of the Pigeon River Trout Research Station. Collections of stones also were made on one date in both the west branch of the Sturgeon River near Wolverine, Cheboygan County, Michigan and the north branch of the Au Sable

River near Lovells, Crawford County, Michigan. Description of the Sturgeon R. and Au Sable R. are provided by Ball & Hooper (1963) and Shetter (1937), respectively.

The Pigeon River is a moderately cool, hardwater stream that originates in a series of cedar swamps and springs near Sparr, Otsego County, Michigan and flows northward about 96 km to Mullett Lake. The drainage basin, which is largely glacial till, covers about 470 km² of predominantly mixed hardwood and abandoned farm land. Water temperatures range between a winter minimum of 0°C and a summer maximum of 25°C. Frazil ice occurs periodically between December and March. Discharge is fairly stable (variability ratio 0.581 (Velz & Gannon, 1960) and ranges between 1.1 and 9.2 m³sec⁻¹.

The two study sites used here were selected for relative uniformity of water depth and current velocity. Site 1 had a mean width of 12.5 m, mean water depth ranged between 0.24 and 0.41 m and mean current velocity ranged between 0.61 and 0.75 m sec⁻¹ depending on discharge. Site 2 had a mean width of 15.3 m, mean water depth ranged between 0.18 and 0.27 m and mean current velocity ranged between 0.42 and 0.63 m sec⁻¹ depending on discharge. At both sites the stream bottom was predominantly cobble and pebble with some gravel and sand.

Methods

Surface Area of Stones

Surface area was estimated by counting the number of squares of known area placed on stones using an inked marking pad. The marking pad was made from a piece of synthetic sponge 1 cm sq and 3-4 mm thick glued (epoxy worked best) to a wood backing also 1 cm sq. This pad was glued to a dowel handle. Pads 1 cm² worked well for stones of 100-500 cm² surface area. For smaller stones, the area of the pad should be reduced. The ink used depended on the porosity of the stones. Common writing ink diluted 25% with water was used for porous stones (e.g., sandstones, marl covered stones). India ink, with a few drops of detergent added, was used for smooth, non-porous stones (e.g., granites). Detergent minimized 'crawling' on smooth surfaces.

The marking procedure was initiated by placing a line of marks along the longest axis of the stone. Subsequent marks were placed lateral to the initial band and extended around the stone or to edges of the area to be estimated. At the end of the procedure, unmarked spaces which were irregularly shaped and smaller than the area of the pad

remained. This area had to be estimated but with practice the error in these estimates was minimal.

Because the marks were placed adjacent to each other, it was usually impossible to recognize individual marks when finished. Therefore, marks were counted as they were applied to the stone.

The sponge pad wore with use, changing the shape and area of the mark. Changes in the area of the pad were determined by measuring the dimensions of marks placed on paper. A correction factor was then used to improve the accuracy of the estimates of surface area. To minimize these problems, markers should be discarded after use on about 20 stones.

Error in this technique was estimated using five variously shaped objects of known surface area (a rectangular box, pyramid, spheres of 7.6 and 10.2 cm diameter and a hemisphere). Two estimates of surface area were made on each object using the marking technique and compared with the known surface areas. Percent error (the difference between the known and estimated surface areas divided by the known area) was small, averaging about 2.2%. The largest error was 8.5% for a sphere, however, most errors were less than 2%.

Day-Night Changes in Density on Stones

Day-night changes in benthos density on naturally occurring stones were estimated by comparing benthos densities on stones collected at noon and midnight E.S.T. Samples of this type were collected on three dates (29 June, 27 July, and 8 September 1972) at Site 1 in the Pigeon R. and on one date (6 September 1972) in the Au Sable R. and (7 September 1972) in the Sturgeon R.

On each date 20 stones (10 in day collections and 10 in night collections) encompassing a wide range of size (50-500 cm² total surface area) were collected. Initially, the stones were located visually and marked by inserting thin steel rods into the streambed about 6 cm downstream of the stones. Then 10 stones, representative of the size range selected, were collected by placing a small handnet (156 μ mesh) behind the stone and then lifting it free of the bottom. Stones and debris in the net were placed in polyethylene bags for transport to the laboratory. Day collections were always made first and in a manner that minimized disturbance to stones to be collected at night. Stones collected at night were located using the aforementioned steel markers and a flashlight with a red lens. The red lens reduced light intensity and presumably gave wavelengths that minimized phototactic disturbance of the fauna (Elliott, 1968). To avoid

phototactic disturbance by moonlight, collections were made either during new moon or on nights with complete cloud cover.

To remove organisms, stones were soaked for 10-15 min in lukewarm ($\approx 30^{\circ}\text{C}$) water. Organisms and debris were then scraped from the stone surface with a hard toothbrush, concentrated in a sieve ($156\ \mu$) and preserved in 10% formalin. Insects were separated from debris under 10x magnification.

Estimates of areas of the top surface and bottom surface of the stones were made using the technique described earlier. Top area was that portion of the stone exposed above the stream bed and identified by its pale green color from periphyton. Bottom area was that portion of the stone buried in the streambed and identified by its creamy, beige color from marl.

Diel Changes in Benthos Density on Artificial Substrates

Sand-cast bricks were used as standardized substrates to eliminate variability in the size and shape of naturally occurring stones. Twenty-four bricks were positioned in the riffle with their longitudinal axes parallel to direction of flow and were pushed 1 cm into the stream bottom. The bricks were arranged in six transverse rows about 0.6 m apart, the four bricks in each row being aligned in columns about 0.5 m apart. Bricks were exposed for colonization approximately four weeks before sampling.

Samples were collected on four dates (13-14 June, 13-14 July, 29-30 August and 9-10 October 1972) at Site 2 in the Pigeon R. Two bricks were collected every 2 hr for 24 hr. The sampling order was determined by numbering each brick and drawing random numbers. The collection of bricks and treatment of bricks in the laboratory was the same as for stones described above. Following removal of organisms, bricks were thoroughly cleaned with a wirebrush and hot water to remove residual debris (e.g., periphyton and marl) before re-use in the next experiment. Collections were made either during new moon or on nights with complete cloud cover.

Results

Day-Night Density Changes on Stones

The relationship between counts of individual taxa and stone surface area was analyzed using least squares regression. To compute regressions, counts of individual taxa (X) were transformed to $\log_{10}(X + 1)$. Multiple linear regression equations and coefficients of determination

(R^2) were computed for the relationship between counts of individual taxa (dependent variable) and top area and bottom area of stones (independent variables). With few exceptions, the use of both top area and bottom area in the multiple linear regression yielded lower residual variances (i.e., higher R^2 values) than did top area, bottom area, or total area used individually in a simple linear regression model.

The significance probabilities of the multiple regressions varied between day and night, among dates and among rivers (Table 1). The R^2 values for night collections generally were lower than for day collections. Over all dates and all rivers, 49% of day regressions and only 35% of night regressions were significant at the 0.05 level. In the Sturgeon R., 61% of all regressions were significant whereas in the Pigeon R., 45% and in the Au Sable R. only 19% were significant.

The multiple regression equations suggested that a substantial portion of the fauna was present on tops of stones during the day and that there were diel changes in positioning on the stones (Table 2). With one exception (June, Pigeon R.) over all dates and all rivers during the day most taxa (75%) were either more strongly associated with the top of stones or equally associated with the top and the bottom of stones. In June, in the Pigeon R., most of the taxa (66%) were associated with the bottom of stones during the day. Over all dates in the Pigeon R., there generally was an increase in the association of fauna with the top of stones at night whereas in the Au Sable R. and the Sturgeon R., there generally was a decrease in the association of fauna with the top of stones at night.

Statistical analysis of day-night density changes by testing the equality of the regression equations was precluded by the small number of significant regressions. Therefore, day-night changes in density (Table 3) were determined by comparing day and night densities predicted using the multiple regression equations where it was assumed that top area of stones was $120\ \text{cm}^2$ and bottom area was $100\ \text{cm}^2$. These areas were comparable to the mean top area ($112.5\ \text{cm}^2$) and mean bottom area ($94.1\ \text{cm}^2$) of all stones collected during this study.

The direction and magnitude of day-night density changes varied among taxa, among dates and among rivers (Table 3). In the Pigeon R., densities generally were greater at night in June and July whereas in September densities generally were lower at night. The mean increase in density at night (expressed as a proportion of day density) averaged over all taxa exhibiting higher night densities was 0.46 in June, 0.48 in July, and 0.33 in Sep-

Table 1. Coefficients of determination (R^2) and significance of multiple linear regressions for the relationship between counts of individual taxa and the top and bottom surface area of stones during the day (D) and at night (N) in the Pigeon R., Au Sable R., and Sturgeon R.

Taxon	Pigeon						Au Sable		Sturgeon	
	June		July		Sept.		Sept.		Sept.	
	D	N	D	N	D	N	D	N	D	N
<i>Allocapnia</i>									.33	.61*
<i>Isoperla transmarina</i>							.34	.67*	.93**	.72*
<i>Isoperla</i> sp.							.46	.01		
<i>Ephemerella subvaria</i>	.49	.77*	.58*	.37	.28	.54	.31	.11	.86**	.65*
<i>E. invaria</i>					.72*	.39	.79**	.14	.64*	.78**
<i>E. deficiens</i>	.62*	.64*								
<i>Baetis intercalaris</i>					.20	.24				
<i>B. levitans</i>							.18	.63**		
<i>B. vagans</i>							.53	.47	.47	.65*
<i>Pseudocloeon</i>									.36	.52
<i>Paraleptophlebia mollis</i>					.70*	.31	.44	.10	.38	.86**
<i>Stenonema</i>							.31	.17		
<i>Cheumatopsyche</i>					.75**	.46	.73**	.42		
<i>Hydropsyche</i> sp 1			.70*	.46	.26	.24	.48	.21	.68*	.78**
sp 2					.40	.39				
sp 3					.21	.33				
sp 4					.59*	.42	.60	.65*		
<i>Chimarra aterrima</i>	.31	.09	.21	.11	.78**	.14	.37	.10		
<i>Glossosoma nigrior</i>					.58*	.27	.87**	.70	.14	.09
<i>Protoptila</i>					.34	.22				
<i>Helicopsyche borealis</i>	.55	.11			.70*	.37				
<i>Micrasema rusticum</i>	.64*	.35	.85**	.46	.71*	.40			.69*	.06*
<i>Mayatrichia ayama</i>	.61*	.84**	.49	.21						
Elmidae (larvae)	.64*	.76**	.70*	.67*	.50	.60*			.82**	.54
Chironomidae	.65*	.91**	.77**	.59*	.73**	.49	.73	.40	.86**	.73*
<i>Simulium</i>	.53	.26	.42	.26	.18	.42	.47	.24	.56	.45
<i>Atherix variegata</i>	.72*	.86**	.52	.70*	.81**	.62*	.40	.67	.63*	.53
<i>Antocha saxicola</i>	.30	.62**	.50	.31	.78**	.63*	.50	.38		
<i>Hemerodromia</i>	.81**	.59*	.73**	.34	.76**	.47	.64*	.24		
Total less Chironomidae	.77**	.82**	.78**	.49	.73**	.43	.86**	.50	.85**	.77**

* $p < 0.05$

** $p < 0.01$

tember. The mean decrease in density for taxa exhibiting lower night densities was 0.26 in June, 0.18 in July, and 0.39 in September.

In September in the Au Sable R., densities generally were greater at night whereas in the Sturgeon R. densities generally were lower at night (Table 3). In the Au Sable R., the mean of nocturnal density increases was 0.44 and the mean of nocturnal density decreases was 0.23. In the Sturgeon R., the mean of nocturnal density increases was 0.36 and the mean of nocturnal density decreases was 0.34.

Diel Changes in Benthos Density on Artificial Substrates
Time series plots for the most abundant taxa in the four

periodicity experiments are given in Figures 1-4 (night is the period between sunset and sunrise).

On 13-14 June, most taxa exhibited large and apparently random variations in density between sampling times (Fig. 1). Only *Helicopsyche borealis* and Elmidae larvae exhibited changes in density which may have been synchronized with changes in light intensity. For these taxa densities were low during the day and during the middle of the night, whereas densities were relatively higher at sunset and at sunrise. Total density (exclusive of Chironomidae) remained relatively constant over the 24 hr period.

On 13-14 July, most taxa exhibited changes in density which were related to changes in light intensity (Fig. 2).

Table 2. Positioning of insects on stones during the day (D) and night (N) where T denotes a greater proportion on top, B a greater proportion on bottom and E an equal distribution on top and bottom.

Taxon	Pigeon						Au Sable Sturgeon			
	June		July		Sept.		Sept.		Sept.	
	D	N	D	N	D	N	D	N	D	N
<i>Allocapnia</i>									B	T
<i>Isoperla transmarina</i>									B	T
<i>Isoperla</i> sp.									T	T
<i>Ephemerella subvaria</i>	B	B	T	T	B	E	E	B	T	B
<i>E. invaria</i>					T	B	T	T	T	B
<i>E. deficiens</i>	E	T								
<i>Baetis intercalaris</i>					T	T				
<i>B. levitans</i>							T	E		
<i>B. vagans</i>							T	B	F	T
<i>Pseudocloeon</i>									B	T
<i>Paraleptophlebia mollis</i>					E	B	T	T	T	E
<i>Stenonema</i>							T	T		
<i>Cheumatopsyche</i>					B	B	T	B		
<i>Hydropsyche</i> sp. 1			T	T	T	T	E	B	T	E
sp. 2					T	T				
sp. 3					T	T				
sp. 4					T	E	T	B		
<i>Chimarra aterrima</i>					B	B	B	T		
<i>Glossosoma nigrior</i>	T	E	B	T	E	T	B	B	T	T
<i>Protophila</i>					T	T				
<i>Helicopsyche borealis</i>	B	T			B	B				
<i>Micrasema rusticum</i>	E	T	T	T	E	B			T	B
<i>Mayatrichia ayama</i>	B	E	T	T						
Elmidae (larvae)	B	T	B	B	B	T			T	E
Chironomidae	B	E	T	T	E	T	T	E	T	B
<i>Simulium</i>	E	E	E	T	E	T	T	T	B	T
<i>Atherix variegata</i>	B	T	B	T	B	B	T	B	T	E
<i>Antocha saxicola</i>	B	T	T	T	T	T	T	E		
<i>Hemerodromia</i>	B	B	T	T	B	E	T	T		
Total less Chironomidae	B	T	T	T	T	T	T	T	T	B

Ephemerella subvaria and Elmidae larvae exhibited two density peaks during the daylight hours. *E. subvaria* exhibited peaks of density about 2½ hrs before sunset and 2½ hrs after sunrise, and Elmidae larvae exhibited peaks of density about ½ hr before sunset and ½ hr after sunrise. Both early instar Hydropsychidae and *Simulium* exhibited a single peak of density during the night at 11 p.m. and 1 a.m., respectively. Increases in the density of Chironomidae and *Simulium* during day appeared to be correlated with increases in water temperature. As in June, total fauna densities (exclusive of Chironomidae) remained relatively constant over the 24 hr period.

On 29-30 August, most of the taxa exhibited a peak of density at 11 p.m. suggesting this sample was biased in some way (Fig. 3). In fact, there was a strong similarity in the overall patterns of diel changes in density of *Hydropsyche*, *Micrasema*, *Antocha*, Elmidae larvae and total fauna (exclusive of Chironomidae). *Glossosoma* exhibited peaks of density about 2 hrs before sunset and 2 hrs after sunrise and *Helicopsyche* exhibited peaks of

density at 1 p.m. and 1 a.m.

On 9-10 October, most taxa exhibited large changes in density which were not synchronized with changes in light intensity (Fig. 4). Most of the taxa, however, exhibited a peak of density at 9 a.m. As in July, *E. subvaria* exhibited two peaks of density about 2½ hrs before sunset and 2½ hrs after sunrise. Elmidae larvae also exhibited two peaks of density at 11 p.m. and 9 a.m. Total fauna density (exclusive of Chironomidae) varied considerably but exhibited two nocturnal peaks at 11 p.m. and 5 a.m.

Discussion

Changes in benthos density depend on the relationship between rates of emigration and immigration (Ulfstrand, 1968). Nocturnal density increases on stones in the Pigeon R. and Au Sable R. show immigration rates generally were greater than emigration rates. These results are tentative because diel changes in density on bricks showed that the observed magnitude and direction of density changes depended on the time of day samples were collected. Furthermore, day and night densities predicted using the regression equations depended on the values for top area and bottom area used to make the predictions. Had it been assumed that bottom area of stones was greater than top area, which is not an unlikely situation, in most cases densities would have been lower at night. Density changes were a function of the ratio of top area to bottom area because of diel changes in the positioning of insects on stones.

There are three important modes of immigration and emigration: downstream drift, upstream movement, and vertical movement from surface and subsurface (hyporheic) gravel on the streambed (cf. Williams & Hynes, 1976). As part of this study, several attempts were made to determine the importance of each of these modes of movement in accounting for diel density changes. Results were inconclusive but suggested that although drift was of primary importance in accounting for nocturnal density increases of most species, upstream movement and vertical movement also were important. Patterns of diel density changes on bricks also suggested drift was not the only factor accounting for density changes. Nocturnal changes in density on bricks generally were not synchronized with peaks of drift activity observed in the Pigeon R. by Hildebrand (1973). Consequently, it appears diel density changes depended on a complex interaction between the three modes of move-

Table 3. Predicted number of individuals on stones (see text) during the day (D) and night (N) and nocturnal change in density (C) (expressed as a proportion of day number) in the Pigeon R., Au Sable R., and Sturgeon R.

Taxon	Pigeon R.									Au Sable R.			Sturgeon R.		
	June			July			September			D	N	C	D	N	C
	D	N	C	D	N	C	D	N	C						
<i>Allocaenia</i>													2.7	0.5	-0.81
<i>Isoptera transmarina</i>										5.6	8.6	+0.54	2.1	2.1	0.00
<i>Isoptera</i> sp.										4.3	2.6	-0.40			
<i>Ephemerella subvaria</i>	31.6	49.1	+0.55	9.4	9.7	+0.03	12.2	15.8	+0.30	19.7	21.7	+0.10	10.4	9.1	-0.13
<i>E. invaria</i>							44.3	13.5	-0.70	81.7	59.4	-0.27	3.8	2.9	-0.24
<i>E. deficiens</i>	16.8	27.7	+0.65												
<i>Baetis intercalaris</i>							3.7	2.4	-0.35						
<i>B. levitans</i>										12.1	10.0	-0.17			
<i>B. vagans</i>										14.7	21.6	+0.47	9.5	8.4	-0.12
<i>Pseudocloeon</i>													5.2	4.9	-0.58
<i>Paraleptophlebia mollis</i>							15.5	5.7	-0.63	4.6	5.6	+0.22	1.1	1.7	+0.55
<i>Stenomama</i>										5.0	5.7	+0.14			
<i>Cheumatopsyche</i>							58.6	28.2	-0.52	63.1	98.2	+0.56			
<i>Hydropsyche</i> sp. 1				21.5	34.1	+0.59	29.2	29.2	0.00	3.5	5.0	+0.43	3.3	2.3	-0.30
sp. 2							6.0	9.2	+0.53						
sp. 3							39.6	32.5	-0.18						
sp. 4							17.5	13.5	-0.23	4.7	8.7	+0.85			
<i>Chimarra aterrima</i>							13.3	4.2	-0.68	20.5	16.4	-0.20			
<i>Glossosoma nigrior</i>	3.6	3.2	-0.11	3.4	3.6	+0.06	5.5	8.4	+0.53	5.6	5.2	-0.07	64.1	37.8	-0.41
<i>Protopila</i>							111.4	114.8	+0.03						
<i>Helicopsyche borealis</i>	4.9	3.5	-0.29				6.9	4.7	-0.32						
<i>Micrasema rusticum</i>	22.0	22.7	+0.03	4.8	5.0	+0.04	23.6	17.5	-0.26				5.8	6.8	+0.17
<i>Mayatrichia ayama</i>	40.3	50.0	+0.24	12.5	7.2	-0.42									
Elmidae (larvae)	16.7	27.4	+0.64	21.4	20.2	-0.06	29.2	33.1	+0.13				5.3	4.7	-0.11
Chironomidae	606.7	843.3	+0.39	351.6	712.9	+1.03	1137.6	966.1	-0.15	246.6	268.5	+0.09	33.9	29.9	-0.12
<i>Simulium</i>	67.5	55.6	-0.39	10.0	20.8	+1.08	12.5	21.3	+0.70	5.9	3.7	-0.37	18.2	7.9	-0.56
<i>Atherix variegata</i>	7.3	13.8	+0.89	7.4	10.1	+0.36	6.7	8.2	+0.22	2.5	5.1	+1.04	3.7	3.7	0.00
<i>Antocha saxicola</i>	5.5	8.3	+0.51	4.7	4.4	-0.06	8.4	9.9	+0.18	13.6	9.3	-0.32			
<i>Hemerodromia</i>	16.5	20.5	+0.24	6.6	10.8	+0.64	28.7	22.0	-0.23	6.7	6.6	-0.01			
Total less Chironomidae	402.7	446.7	+0.11	186.2	205.2	+0.10	674.5	476.4	-0.29	575.4	626.6	+0.09	194.5	123.0	-0.37

ment. Temporal, spatial and specific variations in rates of drift, upstream movement and vertical movement regulated by factors (e.g., water temperature, current velocity and organism size) not controlled in this study probably accounted for much of the variability in magnitude and direction of diel density changes reported here.

The occurrence of large numbers of insects on tops of stones during the day was unexpected because earlier workers (e.g., Chapman and Demory, 1963; Elliott, 1967; 1968) reported that stream insects generally were photonegative and spent daylight hours under stones or in interstitial spaces. Macan (1963) and Hynes (1970), however, observed insects moving from the top to the bottom of stones when disturbed by their presence. Subsequently, I observed large numbers of insects (e.g., *Epeorus vitrea*, *Baetis intercalaris*, *B. levitans*, *B. cingulatus*, and *Pseudocloeon* spp.) on tops of stones during the day when water temperatures were high (> 17°C). At higher temperatures oxygen supply at the bottom of stones or in interstitial spaces of gravel may be inadequate to meet the oxygen demands of the insects (cf. Madsen, 1968). Consequently the insects may move to tops of

stones where oxygen supply is greater because of greater current which increases the rate of water renewal at respiratory surfaces.

Nocturnal movements to tops of stones also may be related to respiratory considerations although earlier workers (e.g., Elliott, 1967; 1968; Ulfstrand, 1968; Bishop, 1973) suggested that insects move to tops of stones at night to feed on algae. Greater aggregation on tops of stones at night may be related to nocturnal increases in respiration rate controlled by physiological rhythms (Zoladek & Kapoor, 1971; Kapoor, 1972; Ulanoski & McDiffett, 1972). Kovalak (1976) reported that at higher water temperatures (> 19°C) and lower current velocities (< 70 cm sec⁻¹) *Glossosoma nigrior*, an herbivore, aggregated on the upstream face of bricks where oxygen richness was greatest because of turbulence rather than on faces where algal abundance was greatest. Aggregation of *G. nigrior* on the upstream face was greater at night.

Nocturnal increases in density on stones may be for feeding on algae which are most abundant there. This seems unlikely as it implies most stream insects are obligate herbivores, a point not substantiated by recent

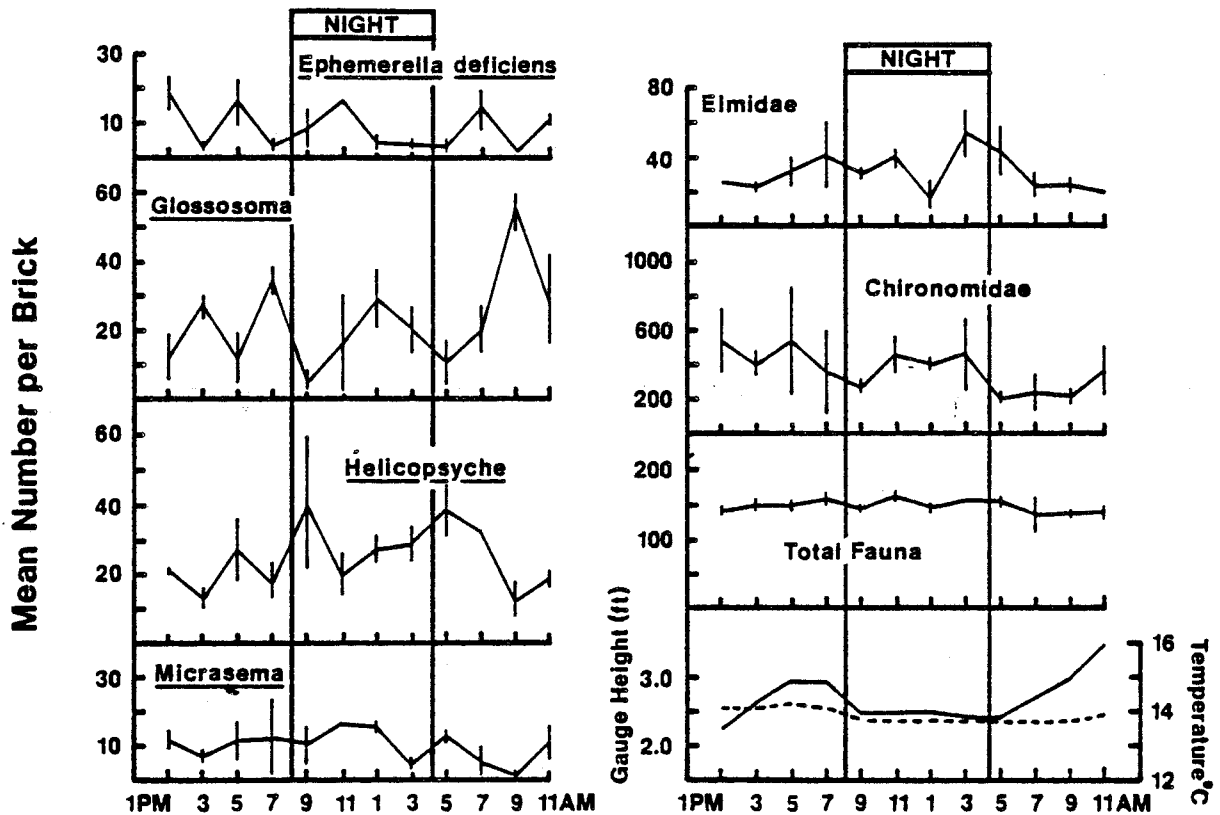


Fig. 1. Diel changes in benthos density on bricks (vertical lines indicate range of values), water temperature (solid line) and gauge height (relative discharge) (broken line), June 1972.

studies of gut contents (e.g., Chapman & Demory, 1963; Cummins, 1973). Alternatively, nocturnal increases in density may have resulted from movements of nymphs and larvae from areas of low oxygen supply to areas of higher oxygen supply. During the day, oxygen under stones or in interstitial spaces of gravel may be adequate to meet oxygen requirements of the insects, but at night, because of higher oxygen consumption rates, insects moved to the upper surfaces of stones. This would explain why the magnitude and direction of diel density changes, predicted using the regression equations, depended on the ratio of top area to bottom area. This also explains some of the variability in diel density changes on stones among dates and among rivers. In the Pigeon R. the greater nocturnal increases in density on stones in June and July may be related to higher water temperatures during those months. At higher temperatures the oxygen consumption rates of the ectothermic insects would have been greater resulting in greater rates of movement onto stones. Similarly, in September, nocturnal increases in

density were greater in the Au Sable R. and Pigeon R. which had higher temperatures than the Sturgeon R. Clifford (1972) also showed that nocturnal density increases on a riffle occurred during the warmest part of the year.

The highly variable patterns of density change on bricks provide little insight into the reasons for nocturnal movements onto stony substrates. If these movements are related to respiratory considerations than much of the variability in these data as well as in the stone data may be related to temporal and spatial variations in the distribution of insects between stones and interstitial microhabitats and to variations in the size and metabolic rates of the various species. Additional variability was introduced by changes in the balance between rates of immigration and emigration regulated by factors not controlled in this study. Clearly, elucidation of the reason(s) for nocturnal changes in density depends on experimentation under more controlled conditions.

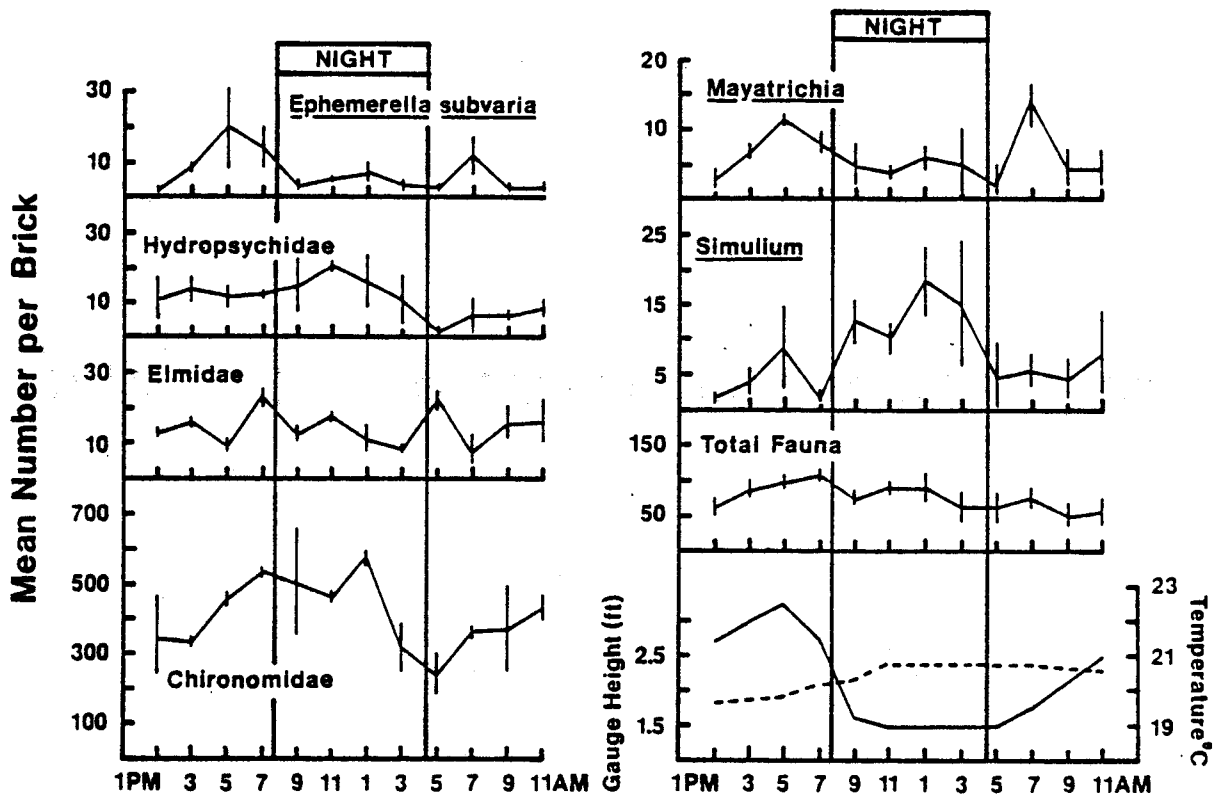


Fig. 2. Diel changes in benthos density on bricks (vertical lines indicate range of values), water temperature (solid line) and gauge height (relative discharge) (broken line), July 1972.

Summary

Diel changes in stream benthos density were studied by comparing faunal densities on naturally occurring stones collected at noon and at midnight in the Pigeon R., Au Sable R. and Sturgeon R., Michigan and on artificial substrates (bricks) collected at 2 hr intervals for 24 hr in the Pigeon R. The direction of density changes on stones varied among taxa, among dates and among rivers. In the Pigeon R. and Au Sable R. densities generally were greater at night whereas in the Sturgeon R. densities generally were lower at night. Over all dates and all rivers, the magnitude of nocturnal density increases (expressed as a proportion of daytime density) ranged between 0.03 and 1.08 and the magnitude of nocturnal density decreases ranged between 0.01 and 0.81. Diel density changes on bricks generally were variable and not synchronized with changes in light intensity, but in most cases (60%) densities were greater at night.

In all rivers a substantial portion of the fauna was present on tops of stones during the day. In the Pigeon R.

the proportion on top increased at night whereas in the Au Sable R. and Sturgeon R., the proportion on top decreased at night.

Although nocturnal movements onto stones and bricks may have been related to feeding activity, it was hypothesized that nocturnal increases in density as well as nocturnal aggregation on tops of stones resulted from movements of insects from areas of lower oxygen supply to one of higher oxygen supply. Because of nocturnal increases in respiration rate, insects under stones or in interstitial spaces where oxygen supply is low moved to tops of stones where oxygen supply was greater because of greater exposure to current which increased the rate of water renewal at respiratory surfaces of the insects.

A new, accurate and rapid method to estimate the area of stone surfaces also was described. Error in this method was about 2%.

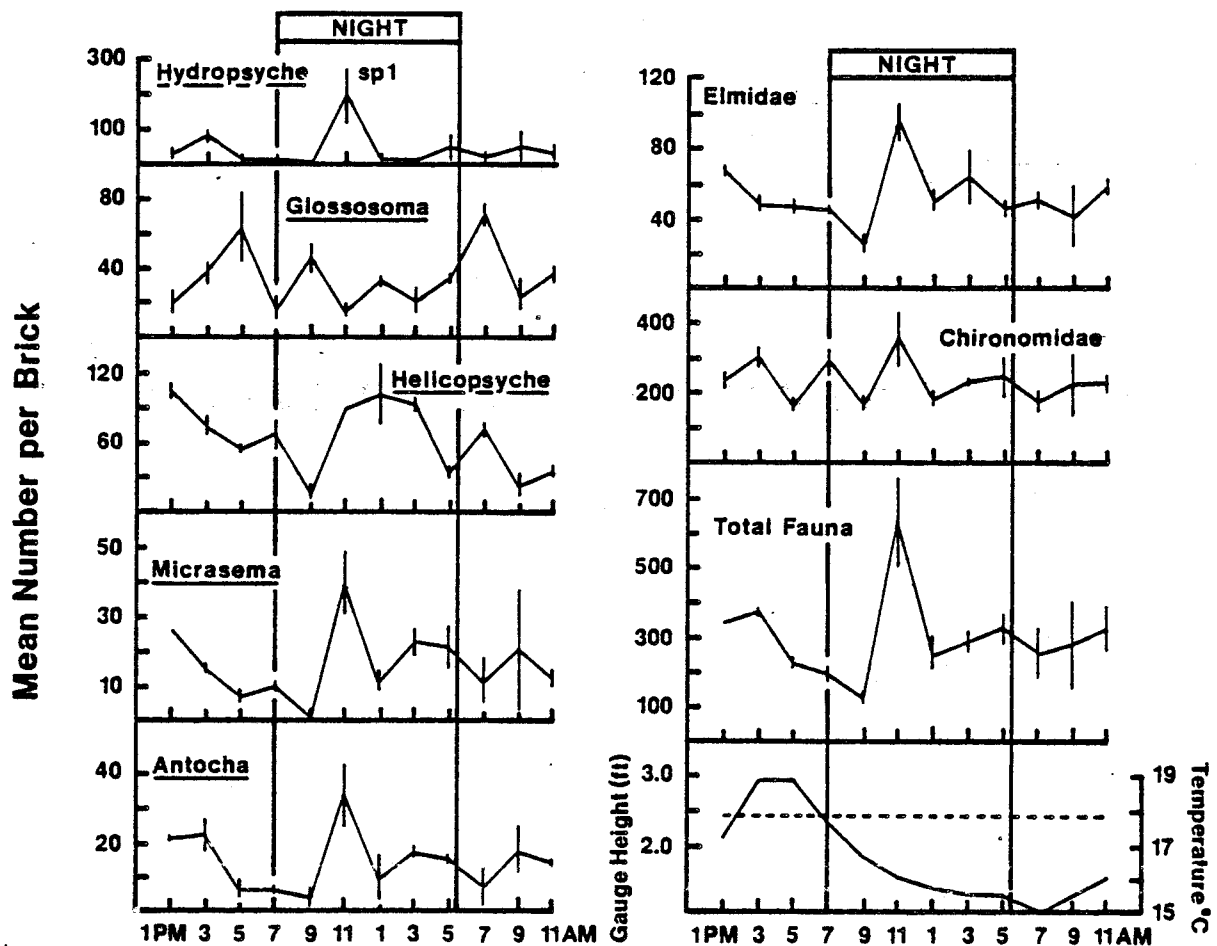


Fig. 3. Diel changes in benthos density on bricks (vertical lines indicate range of values), water temperature (solid line) and gauge height (relative discharge) (broken line), August 1972.

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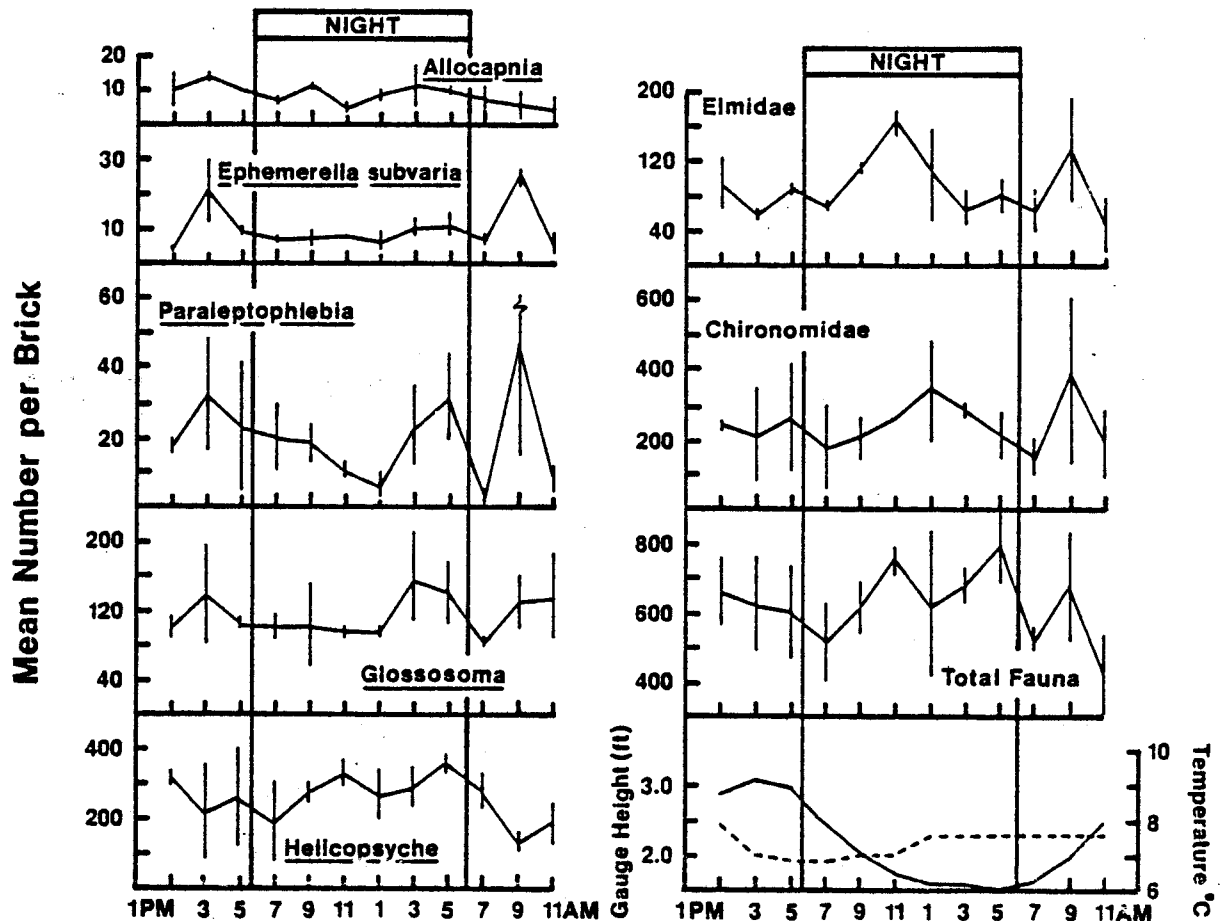


Fig. 4. Diel changes in benthos density on bricks (vertical lines indicate range of values), water temperature (solid line) and gauge height (relative discharge) (broken line), October 1972.

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