Day-night changes in stream benthos density in relation to current velocity

By William P. Kovalak, The University of Michigan, Ann Arbor

With 7 figures and 3 tables in the text

Abstract

Day-night changes in stream benthos density on bricks were studied in relation to current velocity between June and November, 1973 in the Pigeon River, Michigan, U.S.A. Current-related differences in the magnitude and direction of nocturnal density changes were variable among species and among dates but one general pattern emerged. Over the range of currents studied (40—100 cm/s) the pattern was typically bimodal with two peaks of density increase separated by either smaller density increases or density decreases. Small density increases or density decreases frequently occurred on either side of the peaks as well. There was a tendency for peaks of density increase to occur at faster current velocities at higher temperatures and as insects increased in size. A model based on the assumption that density changes depend on the balance between immigration and emigration via drift was developed which accounted for most of the current-related differences in the magnitude and direction of nocturnal density changes reported here.

Introduction

Recent studies (reviewed by Waters, 1972) have emphasized the magnitude of invertebrate drift and its implied importance to the population dynamics of stream benthos. Although most drift activity follows a diel periodicity with a nocturnal maximum (Waters, 1972), few attempts have been made to determine the impact of drift on stream benthos by assessing day-night changes in benthos density. Clifford (1972) compared benthos density in areal samples collected during the day and at night on six dates and reported nighttime densities were higher in 30 cases, lower in 31 cases and unchanged in 3 cases. Kovalak (1978 b) reported that on stones collected at noon and midnight in three Michigan rivers, nighttime densities were higher in 37 cases, lower in 35 cases and unchanged in 3 cases. There were considerable variations in the magnitude and direction of diel density changes among dates and among rivers which were attributed to variations in current velocity, water temperature and organism size not controlled in that study.

Changes in benthos density depend on the balance between rates of immigration and emigration (ULFSTRAND, 1968). The most important modes of migration are drift, upstream movement and vertical movement from and to surface and subsurface gravel (WILLIAMS & HYNES, 1976) which have been shown to be influenced by many factors including current velocity, water temperature and organism size (ANGELIER, 1962; BISHOP & HYNES, 1969 a, 1969 b; ELLIOTT, 1971; WATERS, 1972). Therefore, this study was carried out to assess diel changes in benthos density on stony substrates primarily in relation to current velocity and secondarily in relation to water temperature and organism size. Emphasis was placed on the fauna living on stony substrates as it has been hypothesized that organisms enter drift by being swept from the tops of stones where the erosive action of current is greatest (WATERS, 1965; ELLIOTT, 1967 McLAY, 1968).

Methods

This study was conducted at the Pigeon River, Otsego Co., Michigan in the vicinity of the Pigeon River Trout Research Station which has been described elsewhere (KOVALAK, 1976, 1978 b). The study site was a 27 m long riffle where current velocities ranged between 40 and 100 cm/s. Mean stream width was 13.2 m and mean depth at modal flow was 0.31 m (range 0.05—0.46 m). The stream bottom was composed primarily of cobble and pebble with some gravel and sand.

Sand-cast bricks were used as standardized substrates to eliminate the variability in the size and shape of naturally occurring stones. Forty bricks (20.6 × 9.8 × 5.9 cm) were placed in the riffle with their longitudinal axes parallel with the direction of flow and pushed 1 cm into the bottom. To facilitate sampling and analysis, current velocities on the riffle were grouped into six 10-cm/s intervals covering the 40—100 cm/s range. An attempt was made to place at least six bricks in each current interval, but this was not always possible because the fraction of riffle area represented by each current interval changed with variations in discharge. Bricks were exposed for colonization about four weeks before sampling.

Samples were collected on seven dates (see Table 1) between June and November, 1973. A minimum of two bricks was collected at noon and at midnight from each current velocity interval. Before collecting noon samples current velocity measurements were made on both sides of all bricks using a Gurley pygmy current meter (Model 625). Current measurements were made with the center of the meter's cups 2.5 cm above the bottom which corresponded to the midpoint of the exposed portion of the bricks. Bricks at locations where current velocity differed by more than 6 cm/s between the two sides were not used.

Bricks were collected by placing a small hand net (156 μm mesh) directly behind them and then carefully lifting the bricks free of the bottom and placing them in the net. Day samples were always collected first and in a manner that minimized disturbance to samples collected at night. Bricks collected at night were marked with thin steel rods inserted into the stream bottom about 15 cm downstream from the bricks and were located with a flashlight with a red lens. The red lens reduced light intensity and presumably gave wavelengths that mi-

nimized phototactic disturbance of organisms (ELLIOTT, 1968). To avoid possible phototactic disturbance by moonlight (ANDERSON, 1966) samples were collected during new moon or, in one case, on a completely overcast night.

To remove organisms, bricks were soaked for 10—15 min in tepid water. Organisms and debris were scraped from the brick surface with a hard tooth-brush, concentrated in a sieve (156 μm mesh) and preserved in 10 % formalin. Bricks were thoroughly cleaned with a wire brush and hot water to remove re-sidual debris (e.g., periphyton and marl) before reuse in the next experiment.

Insects were separated from debris under 10× magnification. For the most abundant taxa, headwidth across the eyes was measured to the nearest 0.05 mm using an ocular micrometer.

Results

Although current velocities on the riffle were divided into six intervals, samples were collected from only five current intervals on any date. Be-tween June and August 6 samples were collected from the 40 to 80 cm/s in-tervals but between August 27 and November samples were collected from the 50 to 90 cm/s intervals.

All species occurred over the entire range of current velocities sampled, but on most dates densities were higher in specific current intervals (Fig. 1).
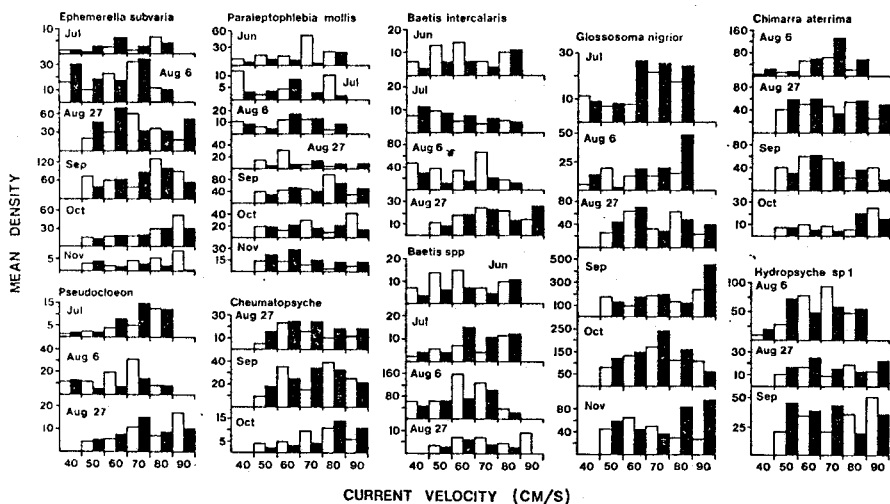

Fig. 1. Mean density (number/brick) of stream insects in relation to current velo-city during the day (open bars) and at night (black bars).

The preferred current interval varied among species, among dates and be-tween day and night. Although there was some tendency for insects to move into faster currents at higher temperatures, this pattern was not consistent. *Paraleptophlebia mollis, Baetis intercalaris* and *Ephemerella subvaria* moved progressively into faster current intervals as they grew.

One-way analysis of variance (ANOVA) was performed separately on the day and night samples to determine if differences in density among current intervals were significant (Table 1). To perform ANOVA, counts of in-

Table 1. F-statistics from ANOVA comparing benthos densities (number/brick) at five current velocities during the day (D) and at night (N). Significantly unequal variances among current velocities are denoted by U.

Taxon	June		July		6 August	
	D	N	D	N	D	N
Allocapnia						
Total Plecoptera	1.14	7.81*	3.58	U 7.18*	0.75	0.81
Baetis levitans						
B. intercalaris	0.28	2.08	5.08	0.48	U 1.04	1.35
Baetinae	0.70	0.28	0.47	1.45	U 1.56	0.70
Pseudocloeon	2.09	2.36	1.45	8.91**	0.85	2.76
Ephemerella subvaria					0.87	0.54
E. deficiens	0.91	1.11	0.48	0.57		
Paraleptophlebia mollis	0.46	0.44	2.50	0.96	1.05	0.95
Stenonema						
Total Ephemeroptera	0.38	0.56	0.73	0.36	U 1.29	U 0.71
Cheumatopsyche						
Hydropsyche sp. 1					1.74	U 0.27
sp. 4						
Hydropsychidae			U 9.43**	U 4.65*	U 1.51	U 0.62
Chimarra aterrima					3.54	1.66
Helicopsyche borealis	1.41	1.28			U 0.75	U 1.51
Protoptila					3.91	2.65
Glossosoma nigrior				1.83	1.23	12.27**
Total Trichoptera	1.16	0.67	3.23	U 3.40	1.97	U 0.48

dividual taxa (X) were transformed ot $\log_{10}$ (X + 1). Normality of the transformed data was not tested but equality of variances among current intervals was; significantly unequal variances are denoted in Table 1 by U.

ANOVA was performed on 161 cases over the seven dates, but in only 10 cases were density differences among current intervals significant (Table 1). Of the 10 significant density differences, 8 occurred during the period of highest water temperatures (July—August, 20—24 °C). In general, F values from ANOVA were greatest during the period of highest water temperatures suggesting density differences among current intervals were greatest at that time. Further, all cases where variances were significantly different among current intervals occurred during the period of highest water temperatures.

The direction and magnitude of day-night density changes over all current intervals are summarized in Table 2. Day and night densities are the

mean of all samples in a collection regardless of the current intervals from which they were collected. No attempt was made to weight means for unequal sample sizes among current intervals because on each date sample size within a current interval was the same day and night. Changes in density were expressed as a proportion of daytime density.

Table 1 (continued)

27 August		September		October		November	
D	N	D	N	D	N	D	N
				2.49	0.62	0.11	1.02
3.73	1.27	0.69	0.32	2.16	0.50	0.29	2.01
U 0.26	0.71						
U 0.52	U 2.67						
U 0.98	0.51					·	
2.65	0.66						
1.98	1.34	1.43	1.31	1.23	1.24		
						0.80	1.24
1.16	0.66	10.48**	0.23	3.24	0.24	4.78*	2.89
		1.04	0.47				
2.13	1.82	1.63	1.29	1.98	0.23	0.90	0.90
U 2.46	0.37	0.68	0.17				
2.03	1.46	1.16	0.73	0.82	2.97		
0.08	1.98	0.76	0.72				
0.35	0.81	0.32	1.94				
		0.89	0.31				
1.09	0.91	0.63	0.36	0.72	0.32	0.28	2.36
1.09	1.24	3.23	0.92	3.11	0.43		
0.97	8.60*	2.60	0.59	0.33	0.43	0.60	1.58
1.36	3.95	0.88	2.33	0.82	0.97	0.31	1.97

* $P \leq 0.05$; ** $P \leq 0.01$.

The direction and magnitude of day-night density changes varied among taxa and among dates (Table 2). Over all dates nighttime densities were higher for 35 of the 62 cases analyzed. The mean increase in density at night (expressed as a proportion of day density) averaged over all taxa exhibiting higher nighttime densities was 0.46 (range 0.02—3.50). The mean decrease in density for taxa exhibiting lower nighttime densities was 0.25 (range 0.01—0.77).

The relationship between the magnitude and direction of day-night density changes (expressed as a proportion of daytime density) and current velocity was highly variable among taxa and among dates (Fig. 2) but one general pattern emerged. This pattern was typically bimodal with two peaks of density increase separated by either smaller density increases or density

decreases (e.g., *Paraleptophlebia mollis,* October and November). Small density increases or density decreases frequently occurred at the low and high ends of the current velocity spectrum as well. This very general pattern and slight modifications thereof were observed for *Ephemerella subvaria* (Aug.

Table 2. Mean density (number/brick) over all current velocities during the day (D) and at night (N) and day-night changes in density (△) expressed as a proportion of day density.

Taxon	June			July			6 August		
	D	N	△	D	N	△	D	N	△
Allocapnia									
Total Plecoptera	1.8	0.9	—.50	1.0	1.8	+.80	5.2	4.5	—.13
Baetis levitans									
B. intercalaris	12.6	5.1	—.60	5.8	6.8	+.17	38.1	16.4	—.57
Baetinae	11.5	5.5	—.52	5.5	8.5	+.55	96.8	63.6	—.34
Pseudocloeon				4.5	3.6	+.89	17.1	8.3	—.31
Ephemerella subvaria				2.2	5.3	+.64	19.8	21.5	+.09
E. deficiens	11.3	7.3	—.35	6.9	4.8	—.23			
Paraleptophlebia mollis	18.5	7.5	—.59	4.1		+.17	9.8	10.0	+.02
Stenonema									
Total Ephemeroptera	53.4	27.9	—.48	41.4	47.6	+.15	202.1	140.7	—.30
Cheumatopsyche									
Hydropsyche sp. 1							55.6	52.4	—.06
sp. 4									
Hydropsychidae				12.7	29.2	+1.3	203.7	212.5	+.04
Chimarra aterrima							35.9	62.6	+.94
Helicopsyche borealis	4.2	4.7	+.12				10.5	8.3	—.21
Protoptila									
Glossosoma nigrior	1.0	4.5	+3.5	14.4	19.6	+.36	15.9	21.8	+.37
Total Trichoptera	32.4	26.6	—.18	55.6	80.8	+.45	367.4	405.2	+.10

27), *P. mollis* (Aug. 6, Sept., Oct., Nov.), *Baetis intercalaris* (July, Aug. 27), *Baetis* spp. (early instar *B. intercalaris* and *B. levitans*) (July), *Chimarra aterrima* (Aug. 6, Aug. 27), and *Glossosoma nigrior* (July, Sept.). Larger deviations from this pattern may have resulted from the limited range of current velocities studied here. Had a broader range of currents been studied, the bimodal pattern may have been evident in more cases as indicated by the hypothesized relationships given in Figure 2.

Temporal changes in the current intervals where peaks of nocturnal density increase occurred appeared to be related to seasonal changes in water temperature and organism size. In general, as water temperature decreased, peaks of density increase occurred at progressively lower current speeds and as insects increased in size, peaks of density increase occurred at progressively faster current speeds. For *E. subvaria* the peak of density increase at

the faster end of the current spectrum occurred at progressively lower current speeds as water temperatures decreased between August and November (Fig. 2). There was no change in pattern between September and October, which was a period of rapid growth. For *P. mollis* peaks of density increase occurred at progressively faster current velocities between July and August 27 which was a period of relatively stable temperature and steady growth but with

Table 2 (continued)

\u200b	27 August		September			October			November		
D	N	Δ	D	N	Δ	D	N	Δ	D	N	Δ
						21.4	14.5	—.32	11.2	11.1	—.01
3.0	4.6	+.53	13.1	12.0	—.08	24.3	17.8	—.27	16.9	17.7	+.04
33.4	7.7	—.77									
25.3	21.4	—.15									
22.1	17.7	—.20									
8.1	9.6	+.19									
37.4	47.7	+.25	70.6	71.7	+.02	26.4	24.8	—.06	4.4	2.3	—.48
									7.4	11.4	+.54
15.5	12.0	—.23	45.1	48.5	+.08	20.0	19.7	—.02	11.6	19.3	+.66
			33.6	28.6	—.15						
168.5	145.0	—.14	168.8	143.9	—.15	65.8	68.4	+.04	40.2	47.1	+.19
14.7	21.5	+.46	24.5	26.9	+.10	7.4	6.9	—.07			
13.6	17.9	+.32	30.0	39.3	+.31	6.7	5.5	—.18			
16.3	18.0	+.10	48.5	57.5	+.19						
			55.7	66.4	+.19						
48.1	41.6	—.14	48.1	46.6	—.03	9.9	11.2	+.13			
7.1	6.0	—.15	25.0	23.9	—.04	15.4	14.6	—.05			
16.4	19.9	+.21	12.9	39.4	+2.1	7.7	9.1	+.18			
42.3	45.5	+.08	158.5	199.7	+.26	126.8	167.9	+.32	54.8	69.4	+.27
302.2	303.4	+.00	366.8	455.6	+.24	201.8	249.3	+.24	70.9	86.8	+.22

lower temperatures in October and November peaks of density increase occurred at lower current velocities.

There was no consistent pattern to relationships between mean individual headwidth and current velocity in either the day or night samples (Table 3). In some cases insects were larger in the fast currents; in others they were larger in the slower currents or at intermediate currents. In most cases the differences in mean size among current intervals were small. The significance of day-night size changes in each current interval was tested by comparing the day and night size frequency distributions using the Kolmogorov-Smirnov t (CONOVER, 1972). In only a few cases were day-night size changes significant and these appeared to be related to the larger numbers of insects collected on those dates. As sample size increases, the

K-S t becomes sensitive to smaller differences in size frequency distribution. Overall, there were no apparent relationships between patterns of day-night density changes and either current-related size differences or day-night size changes.
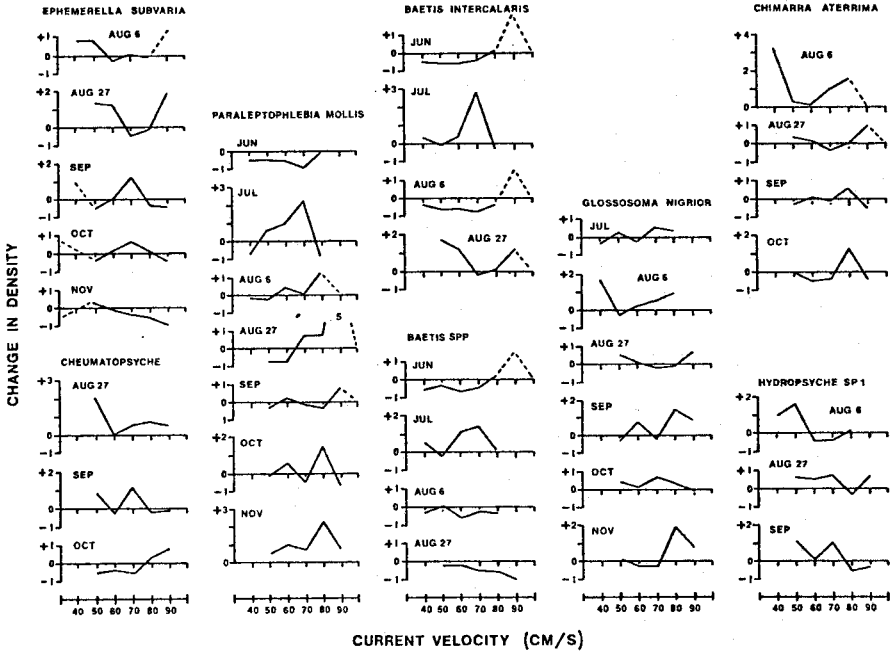

CHANGE IN DENSITY

CURRENT VELOCITY (CM/S)

Fig. 2. Relationships between day-night changes in benthos density (expressed as a proportion of day density) and current velocity. Dashed lines indicate hypothesized relationships.

Discussion

Current-related variations in density reported here mimicked patterns reported by earlier workers (e.g. SCOTT, 1958; AMBÜHL, 1959; CHUTTER, 1969; PETR, 1970; MINSHALL & MINSHALL, 1977). Higher densities at specific current velocities presumably reflect current preferences (HYNES, 1970) whereas occurrence over the entire current spectrum presumably results from genetic variability, intraspecific competition and the randomizing effects of drift.

Changes in benthos density depend on the relationship between rates of immigration and emigration (ULFSTRAND, 1968) both of which are primarily a function of drift rate (MÜLLER, 1954; WATERS, 1964, 1965; ULFSTRAND, 1968; WILLIAMS & HYNES, 1976). Several workers (e.g. ELLIOTT, 1967; ANDERSON & LEHMKUHL, 1968; PEARSON & FRANKLIN, 1968;

Table 3. Comparison of mean headwidth of insects (expressed in 0.05 mm units) during the day (D) and at nigth (N) in relation to current velocity.

Tascon	Current Interval (cm/s)	June		July		6 August		27 August		September		October		November	
		D	N	D	N	D	N	D	N	D	N	D	N	D	N
Ephemerella	40					5.6	7.2*								
subvaria	50					5.5	5.0	4.7	4.4	6.2	6.6**	7.7	7.1		
	60					6.4	6.9	4.9	4.8	6.6	6.6	8.7	7.5		
	70					6.1	5.2	4.6	4.3	7.9	6.9	7.5	8.2		
	80					7.9	6.7	5.0	4.0	6.9	6.6	8.4	7.9		
	90							5.6	4.3	6.3	6.9	7.7	8.1		
Baëtis intercalaris	40	12.3	12.5	13.8	15.9*	13.3	13.9								
	50	13.9	12.8	14.7	15.4	13.0	12.9	11.0	12.3						
	60	12.0	13.2	14.7	15.4	12.1	14.3**	11.2	13.0**						
	70	—	11.5	13.2	14.8	12.1	11.9	12.8	14.0**						
	80	12.5	13.6	13.6	14.1	12.9	13.4	12.6	14.2						
	90							11.3	14.3**						
Baetinae	40	6.3	6.5	7.2	5.9	6.5	5.4*								
	50	6.5	6.7	7.1	6.4	5.9	5.6								
	60	6.7	5.6	6.1	6.4	5.9	5.4**								
	70	6.6	6.2	6.4	6.5	6.2	5.6**								
	80	7.4	7.0	6.5	6.5	5.4	5.8								
	90														
Paraleptophlebia mollis	40	16.0	19.1	20.9	21.3	6.2	4.9								
	50	20.3	19.5	22.0	21.8	6.0	6.0			6.9	6.8	8.0	7.6	9.2	9.2
	60	19.9	17.5*	21.1	21.6	6.5	5.5*			7.0	7.0	7.3	8.6**	8.3	9.2*
	70	18.2	—	—	22.0	6.0	6.2			7.1	6.9	8.2	7.2	9.7	8.2
	80	19.2	16.7	21.5	—	5.3	5.6			7.2	7.0	8.7	8.5	9.1	9.3
	90														
Glossosoma nigrior	40			6.9	8.1	10.4	9.5								
	50			7.4	6.5	9.0	—	9.9	8.2	6.1	7.4**	8.4	7.8	9.0	9.3
	60			6.9	7.1	8.5	9.4	6.5	5.4**	5.9	5.9	7.4	7.8	9.1	9.3
	70			7.0	6.3	7.2	7.8	8.2	8.9	5.4	6.2**	7.2	7.2	10.2	9.7
	80			6.2	6.1	10.0	8.4	8.3	8.7	6.0	7.0**	8.0	7.6	10.3	9.4*
	90							8.8	6.3**	6.7	5.8**	8.3	8.1	10.2	9.2**
Chimarra aterrima	50							8.9	8.6	8.0	10.2	9.8	8.8		
	60							8.6	8.2	8.8	10.2	10.4	8.7		
	70							7.5	8.8	8.9	9.3	9.4	9.9		
	80							8.0	8.4	12.4	9.5	8.3	9.7		
	90							7.2	7.9	10.6	9.6	10.0	9.9		

* P ≤ 0.05; ** P ≤ 0.01.

ULFSTRAND, 1968; BISHOP & HYNES, 1969 a; REISEN & PRINS, 1972) have reported a positive relationship between drift rate and flow rate (either current velocity or discharge) which suggests that nocturnal decreases in benthos density should have been greater at higher current velocities. Clearly this generally was not the case. Alternatively, I (unpublished) have developed a model which shows the relationship between drift rate and current velocity is a unimodal curve. Below, I use this drift model to develop a model of day-night density changes which accounted for much of the variability in the direction and magnitude of day-night density changes reported here.

The drift model was based on two assumptions. First, at constant temperatures, the probability of insects moving to tops of stones (exposure) at night was an inverse function of current velocity (Fig. 3). This assumption is supported by the observation that *Stenonema vicarium* (personal

observation) and *Paragnetina media* (D. R. OTTEY, personal communication) did not move to tops of stones at night when current was applied to bottoms of stones. At low current velocities a large proportion of *S. vicarium* were observed on tops of stones both during the day and at night. Several workers (e.g. ZAHAR, 1951; PHILLIPSON, 1956; SCOTT, 1958; AMBÜHL, 1959) have reported that many stream insects move to more sheltered microhabitats with increases in flow rate. Second, for those individuals on tops of stones, the probability of erosion was a positive function of current velocity (Fig. 3). The probability of drifting (the proportion of benthos removed
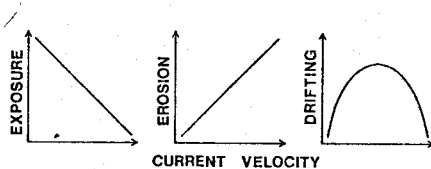
Fig. 3. Hypothesized relationships between the probabilities of exposure, erosion, and drifting and current velocity.

from an area of bottom per unit time) is the product of the probabilities of exposure and erosion and is a unimodal curve where the highest probability of drifting was at intermediate current velocities with lower probabilities of drifting at higher and lower current velocities (Fig. 3).

    To test the drift model, the data of ULFSTRAND (1968) were used. Probability of drifting was estimated by dividing 24-hr drift rates by benthos density. Because ULFSTRAND did not report current velocities, his estimates of discharge were used instead. The resulting relationship was a unimodal curve (Fig. 4) as predicted by the drift model which suggests that as a first approximation the drift model is valid. I am presently testing the drift model in the field and results of this study as well as further analysis of data in the literature will be presented in another paper.
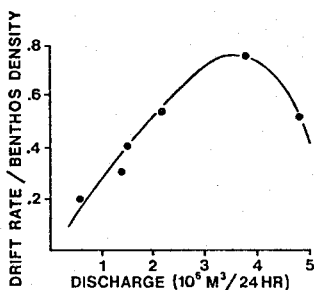

Fig. 4. Relationship between the probability of drifting and discharge; data from ULFSTRAND (1968).

The model of density changes developed below does not specifically address density changes on bricks or stones but those occurring over larger areas of stream bottom (i.e., m²). To develop the model of density changes, the drift model was modified to make it more realistic. It was assumed that rheophilic insects do not occur at current velocities less than 40 cm/s because deposition of unstable fine inorganic sediments (HYNES, 1970) significantly reduces habitable space. The assumed relationships between probability of exposure and erosion and current are given in Figure 5. The as-
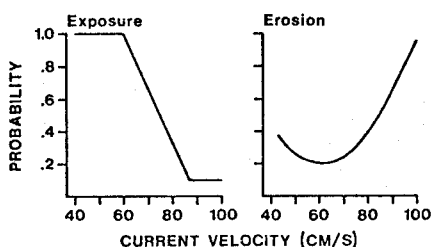
Fig. 5. Hypothesized relationships between the probabilities of exposure and erosion and current velocity used to predict day-night changes in density of *Paraleptophlebia mollis*.

sumed higher erosion rates at low current velocities were based on the observation that in slow currents, particularly at higher temperatures, insects often elevate themselves above the boundary layer thereby increasing the probability of erosion. Furthermore, in slow currents insects may swim from the surface of stones just as lotic baetids do when placed in still water (WATERS, 1969).

To account for nocturnal density increases attributable to accrual from the drift, settling rate was predicted from

$$N_x = N_0 e^{-Rx}$$

where N_0 is the initial number of insects in the drift, N_x is the number still in the drift after traveling distance x and R is a constant for settling rate (McLAY, 1970; ELLIOTT, 1971). R is equal to 1/D where D is mean drift distance at a given current velocity. Although ELLIOTT (1971) reported mean drift distance was an exponential function of current velocity, reanalysis of his data indicated a linear relationships was more appropriate and was used here. The mean drift distances (in meters) used here were taken from ELLIOTT's (1971) data for *Ephemerella ignita* where $D = 0.288 \, V$ and V is current velocity in cm/s.

The magnitude of nocturnal density increases (expressed as a proportion of day-time density) depends not only on the number of insects in

the drift (N_o) but also on daytime densities. To predict N_o, the following relationship was used:

$$N_0 = (1/c) \sum_{i=1}^{c} N_i/R_i$$

where N_i is the number eroded from current interval i and is equal to the product of erosion rate and the initial population density, R_i is the current specific settling rate and c is the total number of current intervals investigated. By dividing by c each unit of stream bottom was treated was though it were composed of equal proportions of each current interval for which predictions were being made.

Density changes were predicted for *P. mollis* (Fig. 6) using initial (daytime) densities patterned after those observed on bricks (Fig. 1). Except for August 6, the predicted (Fig. 6) and observed (Fig. 2) patterns were similar.
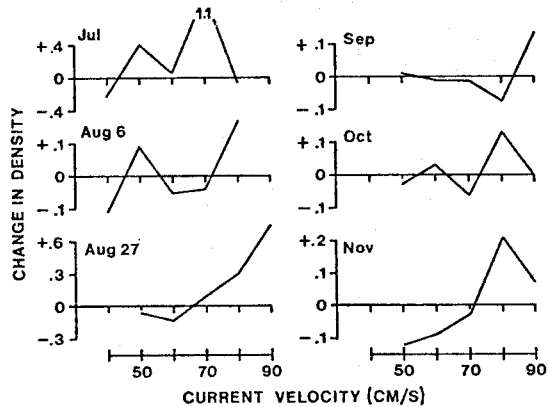
Fig. 6. Predicted relationships between day-night changes in density of *Paraleptophlebia mollis* (expressed as a proportion of daytime density) and current velocity.

The magnitudes of predicted density changes, however, were notably smaller than observed density changes which may be related to the fact that predictions were made for large areas of stream bottom rahter than for bricks or stones. Because little is known about nocturnal movements of insects onto stones, attempting to improve the accuracy of the model by correcting for this behavior is beyond the scope of this paper.

Agreement between the predicted and observed patterns was remarkable considering the potential sources of error. In manipulating the model it was clear that proportional changes in density were strongly dependent on initial densities. The potential for error in density estimates reported here was great because of small sample sizes (2 or 3 replicates). It also was apparent

that density changes depend on drift rates (N_o). Drift rates used here were equilibrium values based on the drift distance models of McLAY (1970) and ELLIOTT (1971). The advantage of this method was that variations in drift distance among taxa did not affect the predictions. In nature, however, any deviations from equilibrium values, particularly spatial variations on a riffle, would significantly affect the magnitude and direction of observed density changes.

The model used for *P. mollis* also accounted for some of the density changes observed for other taxa (e.g., *Baetis*). For most other taxa, however, the probabilities of exposure and erosion had to be varied, even between dates within species, to fit the observed patterns. Because there are no available experimental data for the probabilities of exposure and erosion and because the general relationships between exposure and erosion and current remain the same it seems counterproductive to generate a set of relationships to account for all of the patterns observed here. Clearly, the need for experimental determination of exposure and erosion rates under controlled conditions is indicated.

The probabilities of exposure and erosion can be expected to change primarily in relation to water temperature and organism size if the role of current in controlling nocturnal movements of insects to tops of stones is related to the importance of current in renewing oxygen supply to respiratory surfaces of insects. KOVALAK (1976) reported *Glossosoma nigrior* used positioning on bricks to help satisfy respiratory requierments. At high temperatures and low current velocities *G. nigrior* aggregated on the front (upstream) faces of bricks where turbulence increased the rate of oxygen supply. Aggregation on front faces was greater at night presumably because of higher oxygen consumption rates controlled by endogenous rhythms (see ZOLADEK & KAPOOR, 1971; KAPOOR, 1972; ULANOSKI & McDIFFETT, 1972). KOVALAK (1978 b) suggested that other taxa may move to tops of stones at night to satisfy nocturnal increases in oxygen consumption rate rather than for feeding as suggested by earlier workers (ELLIOTT, 1967, 1968; ULFSTRAND, 1968; BISHOP, 1973). Consequently, probability of exposure should increase with increases in water temperature because oxygen consumption rates are a positive function of temperature and oxygen content of water is an inverse function of temperature. Further, large individuals which have a lower surface area to volume ratio are more liable to respiratory stress. Therefore, at a given temperature and current, larger individuals should exhibit higher probabilities of exposure than smaller individuals.

The probability of erosion also should increase with water temperature because the thickness of the boundary layer decreases (AMBÜHL, 1959).

The probable effect of organism size on erosion is less clear. In some cases small individual appear more liable to drift because they are not as strong and cannot withstand the erosive action of current whereas in other cases large individuals are more liable to drift presumably because they project above the boundary layer (reviewed by WATERS, 1972).

As noted earlier, patterns of density change were strongly dependent on initial (daytime) densities. To determine if observed daytime densities were controlled primarily by drift, the following exercise was carried out. Starting with a distribution where density was 1000 individuals m^{-2} at all current velocities, changes in daytime densities were followed through ten diel cycles (Fig. 7). In only a few cases did the resulting daytime distribution mimic those observed druing this study.
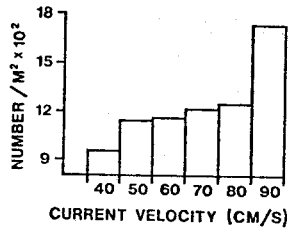
Fig. 7. Predicted relationship between the daytime density of stream benthos and current velocity assuming drift is the primary determinant of distribution and abundance.

Differences between the predicted and observed distributions suggest that other factors also are important in controlling daytime distiributions on bricks. Particularly important here are vertical movements to and from surface and subsurface (hyporheic) gravel and upstream movements. It is generally thought that insects which move onto stones during the night return to surface and subsurface gravel at dawn (WATERS, 1972). The portion of fauna moving to interstices of gravel probably depend on water temperature, current velocity (ANGELIER, 1962) and particle size. The importance of upstream movement in controlling daytime distribution also may be great. In another study, I (unpublished) observed that during the day insects were aggregated near the upstream end of a riffle in the fastest current. At night, distribution over the riffle became very uniform, but the following morning the insects were once again aggregated near the front of the riffle. Presumably one of the important mechanisms accounting for this diel change in distribution was upstream movement.

Temporal changes in distribution relative to current were characterized by movement of insects into faster currents with increases in mean indivi-

dual size and to a lesser extent with increases in temperature. Concurrent with movements into faster currents with temperature increases, there was an increase in the statistical magnitude of density differences among currents and an increase in the inequality of variances among currents. The overall pattern suggests insects may have been clumping in faster currents to help satisfy oxygen requirements.

Although insects moved into faster currents as they grew there was no consistent pattern to the relationship between mean individual size and current velocity. The lack of consistent patterns may be attributable to the randomizing effect of drift or to microdistributional patterns overlooked in this study. From the drift model it is apparent that large proportions of the fauna may be turned over per night. It is doubtful whether drift, which is here largely viewed to be a passive function of exposure and erosion, can act at a sensitive mechanism of microhabitat selection although recently WALTON et al. (1977) suggested that it could. Larger and more consistent differences in size relative to current reported by ALLEN (1951) and KOVALAK (1978 a) may be related to the fact that they sampled current regimes that were not contiguous. Spatially separated habitats would be less likely to be affected by the randomizing effects of drift.

Alternatively, variability in the size data may have resulted from differential selection of the various brick faces by individuals of different size. Although differential selection of faces of stones and bricks has been well documented (e.g., SCOTT, 1958; MORETTI & GIANOTTI, 1962; KOVALAK, 1976), no attempts have been made to determine if selection of faces is size-dependent. If positioning on stony substrates is used to help satisfy oxygen requirements (KOVALAK, 1976) and if surface area to volume ratios of insects decrease with increasing size, one would expect larger individuals to select faces with higher oxygen richness. Size-dependent differences in face selection coupled with the inequality of the area of each face may account for statistical variability in relationships between mean individual size on all brick faces treated as a unit and current velocity.

Zusammenfassung

Tag-Nacht-Änderungen in der auf Ziegelsteinen in Abhängigkeit von der Strömungsgeschwindigkeit im Laufe der Monate Juni bis November 1973 aufgetretenen Besiedlungsdichte von Flußbenthos des Pigeon River, Michigan State, wurden untersucht. Es zeigte sich, daß die strömungsbedingten Unterschiede in der Menge und Richtung der nachts auftretenden Besiedlungsdichte von Art zu Art verschieden waren und sich auch von dem Zeitpunkt der Probeentnahme abhängig erwiesen; aber es ließ sich ein allgemein gültiges Muster für diese Beziehungen ableiten. Im Gesamtbereich der beobachteten Strömungsgeschwindigkeiten (40—100 cm/s) war das Muster typisch bimodal mit zwei Maxima der Besiedlungszunahme, von einander getrennt durch schwächere Dichtezunahmen oder Besiedlungs-

abnahmen. Diese schwachen Zunahmen bzw. Abnahmen traten häufig an beiden
Seiten der Maxima auf. Eine Tendenz der schnellen Besiedlungszunahme wurde
bei größeren Strömungsgeschwindigkeiten und bei höheren Temperaturen beobach-
tet, desgleichen auch dann, wenn die Insekten an Größe zunahmen. Es wurde ein
Modell der Besiedlung entwickelt und zwar unter der Voraussetzung, daß die
Besiedlungsänderungen vom Gleichgewicht zwischen Immigration und Emigration
auf dem Wege der Drift abhängig sind. Tatsächlich war die Drift für die meisten
der hier beobachteten strömungsbedingten Unterschiede in Menge und Richtung
der nächtlichen Besiedlungsänderungen verantwortlich.

Acknowledgments

Literature Cited

ALLEN, K. R. (1951): The Horokiwi stream. A study of a trout population. —
    Fish. Bull. N. Z. 10: 231 p.
AMBÜHL, H. (1959): Die Bedeutung der Strömung als ökologischer Faktor. —
    Schweiz. Z. Hydrol. 21: 133—264.
ANDERSON, N. H. (1966): Depressant effect of moonlight on activity of aquatic
    insects. — Nature, Lond. 209: 319—320.
ANDERSON, N. H. & LEHMKUHL, D. M. (1968): Catastrophic drift of insects in
    a woodland stream. — Ecology 49: 198—206.
ANGELIER, E. (1962): Remarques sur la répartition de la faune dans le milieu in-
    terstitiel hyporhéique. — Zool. Anz. 168: 351—356.
BISHOP, J. E. (1973): Limnology of a small Malayan river Sungai Gombak. —
    Monogr. Biol. 22: 1—485.
BISHOP, J. E. & HYNES, H. B. N. (1969 a): Downstream drift of the invertebrate
    fauna in a stream ecosystem. — Arch. Hydrobiol. 66: 56—90.
—   — (1969 b): Upstream movements of the benthic invertebrates in the Speed
    River, Ontario. — J. Fish. Res. Bd. Can. 26: 279—298.
CHUTTER, F. M. (1969): The distribution of some stream invertebrates in rela-
    tion to current speed. — Internat. Rev. ges. Hydrobiol. 54: 413—422.
CLIFFORD, H. F. (1972): Comparison of samples of stream bottom fauna collected
    during the day and at night. — Limnol. Oceanogr. 17: 474—481.
CONOVER, W. J. (1972): Practical non-parametric statistics. — J. Wiley and Sons,
    Inc., New York. 462 pp.
ELLIOTT, J. M. (1967): Invertebrate drift in a Dartmoor stream. — Arch.
    Hydrobiol. 63: 202—237.
—   (1968): The daily activity patterns of mayfly nymphs (Ephemeroptera).
    — J. Zool. 155: 201—221.
—   (1971): The distances travelled by drifting invertebrates in a Lake District
    stream. — Oecologia 6: 191—220.

HYNES, H. B. N. (1970): The Ecology of Running Waters. — Univ. Toronto Press. 555 pp.

KAPOOR, N. N. (1972): Oxygen consumption of *Paragnetina media* (WALKER). Light-dark effect on respiratory rates. — Experientia 28: 1311—1312.

KOVALAK, W. P. (1976): Seasonal and diel changes in the positioning of *Glossosoma nigrior* BANKS (Trichoptera: Glossosomatidae) on artificial substrates. — Can. J. Zool. 54: 1585—1594.

— (1978 a): Relationships between size of stream insects and current velocity. — Can. J. Zool. 56: 178—186.

— (1978 b): Diel changes in stream benthos density on stones and artificial substrates. — Hydrobiologia 58: 7—16.

McLAY, C. (1968): A study of drift in the Kakanui River, New Zealand. — Aust. J. Mar. Freshwater Res. 19: 139—149.

— (1970): A theory concerning the distance travelled by animals entering the drift of a stream. — J. Fish. Res. Bd. Can. 27: 359—370.

MINSHALL, G. W. & MINSHALL, J. N. (1977): Microdistribution of benthic invertebrates in a Rocky Mountain (U.S.A.) stream. — Hydrobiologia 55: 231—249.

MORETTI, G. P. & GIANOTTI, F. S. (1962): Der Einfluß der Strömung auf die Verteilung der Trichopteren *Agapetus* gr. *fuscipes* CURT. und *Silo* gr. *nigricornis* PICT. — Schweiz. Z. Hydrol. 24: 467—484.

MÜLLER, K. (1954): Investigations on the organic drift in North Swedish streams. — Rep. Inst. Freshwater Res. Drottningholm. 35: 133—148.

PEARSON, W. D. & FRANKLIN, D. R. (1968): Some factors affecting the drift rates of *Baetis* and Simuliidae in a large river. — Ecology 49: 75—81.

PETR, T. (1970): The bottom fauna of the rapids of the Black Volta River in Ghana. — Hydrobiologia 35: 399—418.

PHILLIPSON, J. (1956): A study of factors determining the distribution of the blackfly *Simulium ornatum* MG. — Bull. Entomol. Res. 47: 227—238.

REISEN, W. K. & PRINS, R. (1972): Some ecological relationships of the invertebrate drift in Praters Creek, Pickens County, South Carolina. — Ecology 53: 866—884.

SCOTT, D. (1958): Ecological studies on the Trichoptera of the River Dean, Cheshire. — Arch. Hydrobiol. 54: 340—392.

ULANOSKI, J. T. & McDIFFETT, W. F. (1972): Diurnal variations in respiration of mayfly nymphs (Ephemeroptera). — Physiol. Zool. 45: 97—105.

ULFSTRAND, S. (1968): Benthic animal communities in Lapland streams. — Oikos Suppl. 10: 120 pp.

WALTON, O. E., Jr., REICE, S. R. & ANDREWS, R. W. (1977): The effects of density, sediment particle size and velocity on drift of *Acroneuria abnormis* (Plecoptera). — Oikos 28: 291—298.

WATERS, T. F. (1964): Recolonization of denuded stream bottom areas by drift. — Trans. Amer. Fish. Soc. 93: 311—315.

— (1965): Interpretation of invertebrate drift in streams. — Ecology 46: 327—334.

— (1969): Invertebrate drift-ecology and significance to stream fishes. — Symp. on salmon and trout in streams. H. R. MacMILLAN lectures in fisheries. T. G. NORTHCOTE (Ed.), Univ. British Columbia, Vancouver, B. C.: 121—134.

— (1972): The drift of stream insects. — Annu. Rev. Entomol. 17: 253—272.

WILLIAMS, D. D. & HYNES, H. B. N. (1976): The recolonization mechanisms of stream benthos. — Oikos **27**: 265—272.

ZAHAR, A. R. (1951): The ecology and distribution of blackflies (Simuliidae) in southeast Scotland. — J. Anim. Ecol. **20**: 33—62.

ZOLADEK, M. & KAPOOR, N. N. (1971): The periodicity of oxygen consumption in two species of stoneflies (Plecoptera). — Amer. Zool. **11**: 671.

The address of the author:

Dr. W. P. KOVALAK, College of Arts, Sciences and Letters, University of Michigan-Dearborn, Dearborn, Michigan 48129, U.S.A.