Positioning on substrates, positioning changes, and diel drift periodicities in mayflies

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Diel changes in the positioning of several mayflies (Ephemeroptera) on the top and bottom surfaces of artificial substrates were examined. Stream drift samples were taken in conjunction with substrate samples. No significant diel changes in positioning were observed while all taxa exhibited nocturnal increases in drift. All taxa had apparent surface preferences. *Baetis* species occurred largely on top surfaces while *Ephemerella* spp., *Paraleptophlebia mollis*, and Heptageniidae largely occupied bottom surfaces. Diel positioning changes did not appear to be an important mechanism producing diel drift periodicities. Drift propensity showed large variation between taxa and was positively correlated with the proportion of individuals on top surfaces. For most taxa, drift probability varied markedly between dates and was correlated with high growth rates.

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Les changements journaliers de position à la surface supérieure et à la surface inférieure de substrats artificiels ont été suivis chez plusieurs espèces d'Ephéméroptères. Des échantillons de dérive ont été recueillis en complément des échantillons de benthos. Il ne se produit pas de changements journaliers signifitifs de position, mais toutes les espèces se retrouvent en plus grands nombres dans la dérive la nuit. Tous les taxons ont des préférences de position. Les espèces de *Baetis* se retrouvent surtout à la surface supérieure des substrats, alors que les espèces d'*Ephemerella*, *Paraleptophlebia mollis* et les Heptageniidae préfèrent les surfaces inférieures des substrats. Les changements journaliers de position ne semblent pas avoir une grande influence sur la périodicité de la dérive journalière. La tendance à la dérive varie beaucoup en fonction de l'espèce et est en corrélation positive avec la proportion d'individus présents à la surface supérieure des substrats. Chez la plupart des taxons, la probabilité de la dérive varie beaucoup d'une date à une autre et est reliée à des taux de croissance élevés.

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Introduction

The occurrence of invertebrate drift in streams has received considerable attention in the past three decades. Yet relatively little is known about mechanisms of entry into the water column and mechanisms responsible for diel periodicities in drift. The well-documented diel periodicity of drift is generally hypothesized to result from diel changes in the positioning of invertebrates on stones and(or) diel changes in activity (Waters 1972). Either positioning changes or changes in activity rate alone could potentially account for diel drift periodicites. Laboratory studies of Elliott (1968) and Bailey (1981), however, indicate that positioning changes accompany activity rate changes. Consequently, sorting out the potential roles of positioning and activity in affecting diel drift periodicities requires careful experimentation and observation, or evidence that one factor does not vary appreciably on a diel basis.

Most field studies of insect positioning on stones have dealt with organisms that are fairly large and not capable of rapid movement such as case-building and net-spinning Trichoptera (Scott 1958; Moretti and Gianotti 1962; Thorne 1969; Wallace 1975; Kovalak 1976; Malas and Wallace 1977). For these taxa, stones can simply be lifted from a stream and the number of individuals on various stone surfaces assessed visually. This technique is not applicable to highly mobile and often small taxa such as many Ephemeroptera and Plecoptera. Consequently, information on mayfly and stonefly positioning on stones in the field has largely been qualitative and conjectural (Hynes 1941; Brinck 1949; Chapman and Demory 1963). Quantitative studies of mayfly positioning have been restricted to the laboratory where direct observations can be made (Elliott 1968; Bohle 1978; Wiley and Kohler 1980; Bailey 1981). Here I use a simple technique to examine mayfly diel positioning patterns *in situ*.

The purposes of this study were to describe the general positioning behavior and diel positioning changes of several mayfly taxa on artificial substrates and to examine relationships between positioning on substrates and stream drift.

Methods

Studies were conducted in the Pigeon River, Otsego County, Michigan. Detailed descriptions of the stream in the vicinity of the study site have been reported elsewhere (Kovalak 1976). The study site was the upper 15 m of an extensive (100 m) riffle. A long, moderately deep pool was immediately upstream of the study site. In the study area, the

stream was 10 m wide and was characterized by highly uniform depth (25–30 cm) and current velocity (40–50 cm/s). The substratum was largely cobble and pebble with the moss *Fissidens grandifrons* occurring on much of the stone substrata in the riffle.

Artificial substrates were used to examine mayfly positioning patterns. Each substrate consisted of two unglazed quarry tiles (15.25 × 15.25 × 1.25 cm) held together with modeling clay. Substrates were placed on the stream bottom and given 4 weeks for colonization. When implanted, natural substrata were moved so that the artificial substrates lay flat on the stream bottom. When sampled, a substrate was quickly removed from the stream, separated, and each half was placed into a plastic bag. Substrates sampled with a net held behind them indicated that loss of animals was negligible ($< 5\%$). Substrate surfaces were scraped clean with a hard toothbrush and the sample contents preserved with 4% formalin. Sample contents were concentrated with a 210-μm sieve and invertebrates were separated using a dissecting microscope under 10× magnification.

Eighteen substrates were placed in a 6 × 3 configuration approximately 10 m downstream from the head of the riffle. Substrates were separated by at least 25 cm on all sides. Three substrates were sampled at random at 4-h intervals for 24 h beginning at 1000. At night, substrates were located with the aid of a red light. Samples were collected on 1–2 August and 31 August – 1 September 1978 (hereafter referred to as August and September). Sunset on these dates occurred at 2050 and 2010, respectively. Both dates fell during a new moon.

Drift samples were taken immediately downstream of the substrate configuration for 30 min prior to sampling the artificial substrates. Two drift nets (230-μm mesh with 30 × 30 cm mouth opening and 2-m bag) were placed side by side. Nets sampled the entire water column. Water volume sampled was estimated by measuring the depth and mean current velocity on each side of a net. Drift samples were preserved with 10% formalin. Laboratory processing procedures were identical to those used for artificial substrates.

Current velocities at the back, sides, and front of the substrate configuration were measured 24 h before sampling began. Measurements were made with a Gurley pygmy current meter with the center of the meter's cups 2.5 cm above the bottom. Water temperature and dissolved oxygen (Winkler method) were measured at each sampling interval.

Results

Physical conditions

Stream physical characteristics were very similar on the two sampling dates. Water temperature was slightly higher in August (range, 15.5–20°C) than September (range, 14–19°C). Dissolved oxygen concentration fluctuated around 9 mg/L ($> 86\%$ saturation) during both studies. Because of similar discharges (August, 1.26 m^3/s; September, 1.4 m^3/s), current velocity around the artificial substrate configuration ranged between 40 and 50 cm/s on both dates.

Taxa considered

Fifteen mayfly species were taken in drift and substrate samples. From these, seven taxa were selected for detailed analysis because of their abundance in the samples and their general abundance in north temperate streams. The taxa comprised four species and three species groups. Species considered were *Baetis flavistriga* McDunnough, *B. intercalaris* McDunnough, *B. tricaudatus* Dodds, and *Paraleptophlebia mollis* (Eaton). Early instar *Baetis* which could not reliably be identified to species are considered as *Baetis* spp. Early instar *Ephemerella subvaria* McDunnough and *E. invaria* (Walker) were indistinguishable and are grouped as *Ephemerella* spp. A final grouping consisted of several heptageniids that were not sufficiently abundant individually to merit consideration. The taxa grouped as Heptageniidae included *Stenonema (Maccaffertium) vicarium* (Walker), *S. (M.) mediopunctatum* (McDunnough), *S. (M.) modestum* (Banks), *Stenacron interpunctatum* (Say), and early instar *Stenonema*.

Positioning on substrates

Ideally, positioning on substrates and positioning changes would be analyzed through consideration of densities on substrate surfaces. For example, for the one-dimensional (top–bottom) case considered here, a change in position on substrates by a population should be evidenced by an increase in density on one surface and a decrease in density on the opposite surface. This requires continuous observation of substrate surfaces on individual substrates for which total substrate density does not change over time. Because of characteristically high immigration and emigration rates in streams (e.g., Townsend and Hildrew 1976; Wiley and Kohler 1981) and the inability to visually observe bottom surfaces, such an approach is not possible in the field. An alternative approach taken here is to examine the proportion of individuals on the top surface (P_t) of artificial substrates for changes over time (see also Kovalak 1976). For each sampling time P_t was calculated for data pooled from the three substrates sampled. I tested for changes in P_t over time using the χ^2 test for differences in probabilities (Conover 1971).

When P_t was compared over the six sampling times, no significant differences ($p > 0.25$) were detected for any taxon on either date. On both dates, P_t tended to be greater immediately after sunset (2200) than immediately before sunset (1800). This occurred in 10 of the 13 possible cases. However, the increase was significant only for *Baetis intercalaris* in August ($p < 0.05$) and marginally significant for *Ephemerella* spp. in September ($p < 0.1$). No other positioning change trends between sampling times were apparent on either date.

Since significant diel positioning patterns were not detected, day (1000, 1400, 1800) and night (2200, 0200, 0600) samples were pooled, respectively, to

TABLE 1. Proportion ± standard deviation of individuals on the top surface of artificial substrates during the day (1000, 1400, 1800) and night (2200, 0200, 0600). Sample sizes are given in parentheses. See text for discussion of significant differences between proportions

| | Proportion on top surface | | | |
| | August | | September | |
Taxon	Day	Night	Day	Night
Baetis flavistriga	0.73±0.09 (26)	0.89±0.07 (19)	0.93±0.05 (29)	0.90±0.05 (31)
Baetis intercalaris	0.59±0.05 (83)	0.72±0.05 (82)	0.70±0.06 (60)	0.91±0.04 (48)
Baetis tricaudatus	—	—	0.95±0.05 (20)	0.95±0.05 (21)
Baetis spp.	0.65±0.04 (141)	0.72±0.05 (81)	0.87±0.03 (176)	0.88±0.03 (99)
Ephemerella spp.	0.12±0.02 (195)	0.17±0.02 (300)	0.16±0.02 (308)	0.18±0.02 (257)
Paraleptophlebia mollis	0.03±0.03 (31)	0.05±0.03 (41)	0.03±0.02 (78)	0.04±0.02 (70)
Heptageniidae	0.05±0.05 (20)	0.01±0.01 (70)	0.01±0.01 (78)	0.02±0.02 (31)

examine general positioning behavior and gross day–night positioning changes (Table 1). Sample sizes are the total number of individuals on substrates from a given time period. *Baetis tricaudatus* was not sufficiently abundant in August samples to merit consideration. Night P_t values were generally greater than day values (10 of 13 cases), although they were significantly greater only for *Baetis intercalaris* in September ($p < 0.05$). Overall, individuals tended to occur more on top surfaces in September than in August. These differences were significant for *Baetis intercalaris* ($p < 0.05$) and *Baetis* spp. ($p < 0.001$), and marginally significant for *B. flavistriga* ($p < 0.1$).

General positioning behavior was quite consistent for each taxon over the two sampling dates. Furthermore, no taxon was distributed randomly ($P_t = 0.5$) on artificial substrates on either date. This was generally true for all invertebrates colonizing the substrates (Kohler 1979). Individuals appear to have surface preferences that are highly consistent over time. *Baetis* were found largely on top surfaces while the remaining taxa occurred largely on bottom surfaces (Table 1).

Drift

Drift nets undoubtedly did not sample only animals drifting from the artificial substrates. Because of the pool immediately upstream of the study area and because of short drift distances (McLay 1970; Elliott 1971), drift sampled, however, was probably derived from the immediate vicinity of the substrate configuration. I have assumed that positioning behavior on artificial substrates is representative of that on adjacent natural substrates.

All taxa exhibited greater drift density at night than during the day on both dates. The magnitude of difference between nocturnal and diurnal drift density, however, varied considerably among taxa and between

TABLE 2. Spearman rank correlation coefficients between P_t and drift density

Taxon	August	September
Baetis flavistriga	0.76*	0.06
Baetis intercalaris	0.27	0.49
Baetis tricaudatus	—	0.43
Baetis spp.	0.94**	0.19
Ephemerella spp.	0.43	0.43
Paraleptophlebia mollis	0.17	0.64
Heptageniidae	0.51	0.17

*$p < 0.1$.
**$p < 0.01$.

dates. In general, this difference was greatest for *Baetis* species and least for taxa dominated by early instars (e.g., *Baetis* spp., *Ephemerella* spp., and Heptageniidae).

P_t and drift density were positively correlated for all taxa on both dates (Table 2). However, for only 2 of 13 cases were the correlations significant or marginally significant. Examination of drift-positioning relationships representative of those observed on both dates (Fig. 1) helps to explain these results. For the one case where P_t and drift were highly correlated (*Baetis* spp., August), drift was nearly aperiodic (Fig. 1C). Drift-positioning relationships were generally not consistent for a given taxon between dates (Table 2).

Drift density varied considerably between taxa within dates and between dates within taxa. To standardize drift densities so that they may be compared within and between dates, I calculated the instantaneous proportion of animals in the water column using Elliott's (1967a) method:

$$P(\text{drift}) = \frac{(\text{drift density})(\text{water depth})}{(\text{benthic density}) - (\text{drift density})(\text{water depth})}$$
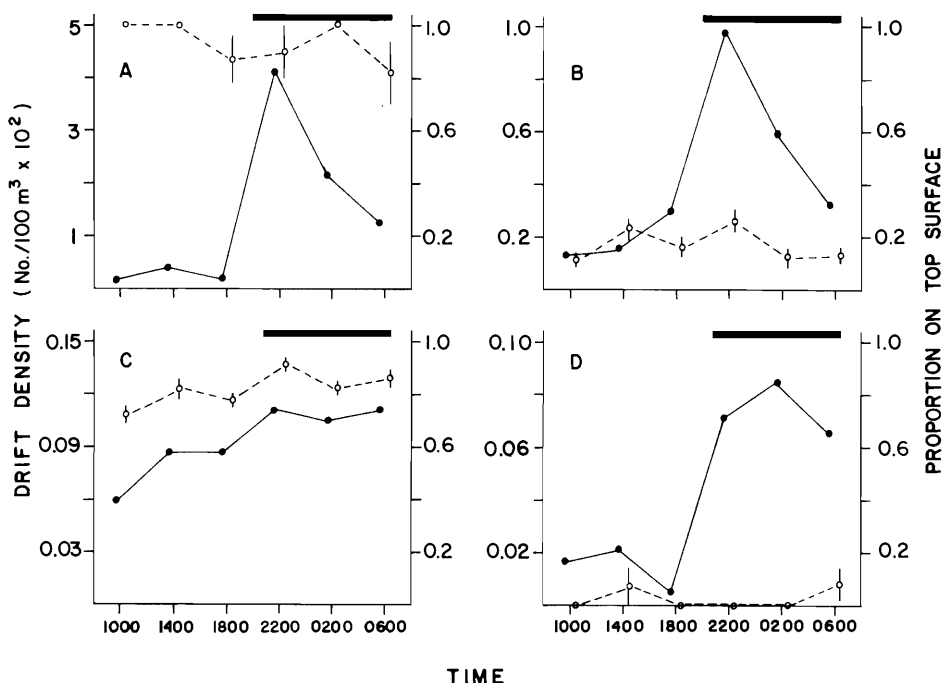
FIG. 1. Diel relationships between proportion (± standard deviation) of individuals on the top surface of artificial substrates (O---O) and drift density (●—●). (A) *Baetis flavistriga*, September. (B) *Ephemerella* spp., September. (C) *Baetis* spp., August. (D) *Paraleptophlebia mollis*, August. Drift density is the mean of two replicates. Dark bars denote time after sunset.

where P(drift) is considered the instantaneous proportion of animals drifting or, equivalently, the instantaneous probability of an individual entering the drift. For each date, benthic densities were estimated from densities on artificial substrates averaged over all sampling times. These density estimates agreed quite well with those reported elsewhere for the same taxa on natural substrates and other artificial substrates in the Pigeon River at the same time of year (Kovalak 1978a, 1979). To simplify presentation, only day and night instantaneous drift probabilities were determined. Since drift density was fairly constant during the day, P(drift) values were obtained using the mean day drift density. Peak night drift density was used to calculate night P(drift).

Drift probability varied markedly between the two dates (Table 3). In fact, for *B. flavistriga* and *B. intercalaris* drift probability in the day in September was greater than in the night in August. This occurred despite very similar physical conditions on the two dates and similar positioning patterns. In general, the magnitude of nocturnal drift increase (ratio night:day drift probability) was greater in September than August. Day–night positioning changes, however, were more pronounced in August (Table 1).

The interval between sampling dates appeared to be a period of rapid growth for most taxa (Table 3). I calculated specific growth rate (percent body mass per day) for three taxa for which head capsule width (HCW) and mass relationships were available from the Pigeon River (Kovalak 1978b; S. L. Kohler, unpublished data). Specific growth rates were high for *B. flavistriga* (2.53%), *P. mollis* (2.84%), and *Ephemerella* spp. (3.88%). Based on mean HCW, this would not be the case for *B. intercalaris* (Table 3). However, if a portion of the large number of early instar *Baetis* present were *B. intercalaris*, a high growth rate may have also occurred for this taxon.

Drift probability was highly positively correlated with general positioning behavior on substrates (cf. Tables 1 and 3). This is especially evident in September. Taxa occurring largely on top surfaces (e.g., *Baetis*) had high drift probabilities while taxa found largely on bottom surfaces (e.g., *P. mollis*) had low drift probabilities. The only exception to this pattern occurred with early instar *Baetis* (i.e., high P_t, low P(drift)). P_t values were generally greater in September than August (Table 1). This positioning change may also have contributed to the increase in drift probability in September.

Discussion

Diel periodicities in stream drift have been hypothesized to result, in part, from diel changes in invertebrate positioning on stones (Waters 1965; Elliott 1967a, 1967b; McLay 1968; Bishop 1969; Bishop and Hynes 1969). Many stream insects, especially mayflies,

TABLE 3. Drift probability and HCW ($\bar{x} \pm$ SE) of drifting animals. Day drift probability derived from mean of day (1000, 1400, 1800) drift densities; night drift probability derived from mean drift density at time of peak drift (see text for calculation method). HCW is not reported for Heptageniidae as this is a grouping of several taxa (see text)

	August			September		
		Drift probability ($\times 10^{-5}$)			Drift probability ($\times 10^{-5}$)	
Taxon	HCW (mm)	Day	Night	HCW (mm)	Day	Night
Baetis flavistriga	0.535 ± 0.020	14.4	55.3	0.651 ± 0.009	72.7	1508.8
Baetis intercalaris	0.745 ± 0.016	1.3	29.6	0.612 ± 0.009	39.7	841.1
Baetis tricaudatus	—	—	—	0.687 ± 0.021	22.4	192.6
Baetis spp.	0.346 ± 0.006	8.5	12.3	0.389 ± 0.008	9.5	21.0
Ephemerella spp.	0.403 ± 0.006	6.1	13.4	0.570 ± 0.013	7.5	38.2
Paraleptophlebia mollis	0.363 ± 0.008	4.8	28.5	0.464 ± 0.035	3.6	12.1
Heptageniidae	—	5.4	23.3	—	2.4	19.4

are considered to be negatively phototactic and occur largely on the bottom surface of stones during the day (Wodsedalek 1911; Lyman 1945; Scherer 1962; Chapman and Demory 1963). Laboratory studies have shown mayflies to be more active at night than during the day (Elliott 1968; Bailey 1981). It has been suggested that increased activity combined with the lack of a phototactic stimulus results in the movement of individuals to upper, current-exposed surfaces at night where it is more likely that individuals will be dislodged and swept into the water column (Elliott 1967b, 1968). Elliott's (1968) laboratory study showed marked diel positioning changes for five mayfly taxa but drift rate peaks preceded peaks in the number of individuals on the upper surface of stones in most cases. Bailey (1981) reported similar observations on a leptophlebiid mayfly. Results presented here show a marked nocturnal increase in drift in the absence of a significant increase in the proportion of individuals on top surfaces. Similarly, Bohle's (1978) observations on the common European baetid *Baetis rhodani* showed no diel positioning changes while drift had nocturnal maxima. Together, these studies suggest that positioning changes alone are of minor importance in affecting diel changes in propensity to enter the drift. Movements to and from current-exposed surfaces appear not to be "dangerous" (in terms of drift entry). Diel variation in activity levels has also been cited as a potential mechanism influencing diel changes in drift propensity. These results indirectly suggest that activity rates are of primary importance in affecting drift entry, although the mechanisms by which activity and drift entry are associated have not yet been defined (see Elliott 1968; Corkum 1978a; Bailey 1981).

Although positioning changes appeared unimportant in producing diel changes in drift density, overall positioning behavior within taxa was positively correlated with differences in drift propensity between taxa. Taxa occurring largely on top surfaces (i.e., *Baetis*) were more likely to drift than other taxa. This correlation probably has little general significance. Several non-baetid mayflies are found largely on top surfaces during the day and night (e.g., the heptageniids *Epeorus longimanus* and *E. grandis* (F. F. Hooper, personal communication); the ephemerellid *Serratella sordida* (Kohler 1979)), but have low drift propensities (see Radford and Hartland-Rowe 1971; Hildebrand 1973). In part, this reflects morphological differences between these mayflies and *Baetis*. Behavioral differences (Corkum et al. 1977) between taxa with similar positioning behavior must also affect drift probability. Lehmkuhl and Anderson (1972) found 8- to 16-fold differences in drift propensity between two *Baetis* species with similar microdistributions, but positioning behavior was not studied. Differences in behavior resulting in between-taxa differences in drift propensity are likely to be more complex and subtle than those suggested by broad behavioral classifications of mayflies (Corkum 1978b). Yet little is known of mayfly behavior beyond casual, anecdotal observations (Edmunds et al. 1976). Quantitative comparative studies relating behavioral observations and drift should prove fruitful in explaining between-taxa differences in drift probability and in helping to identify drift mechanisms.

Positioning on substrates was very consistent for all taxa within and between sampling dates. No taxon was a positioning generalist; all taxa had apparent surface preferences. At any point in time, the position that any individual assumes on a substrate likely reflects a compromise between energetic considerations and risks

associated with occurring on exposed surfaces (e.g., susceptibility to visual predators (Ware 1973) and erosion (Kovalak 1976)). If this conceptual model is valid, positioning behavior within taxa should be fairly plastic, especially for those taxa capable of gill ventilation and having relatively low metabolic rates (Wiley and Kohler 1980). For example, the proportion of the ephemerellid *Drunnella lata* on top surfaces of stones increases with increasing water temperature and, on the same date, varies between streams depending upon stream temperature (D. R. Ottey, personal communication). Apparent surface "preferences" of some taxa considered in this study (e.g., *Baetis*) may more realistically represent positioning restrictions resulting from physiological considerations (Wiley and Kohler 1980). However, our knowledge of factors which may influence positioning behavior (such as respiratory demand versus oxygen renewal rates, food abundance versus demand, diel variation in predation pressure, susceptibility to dislodgement) is too meager to allow for reliable prediction of positioning or even interpretation of observed positioning under certain ecological conditions.

Variation in drift magnitude between dates within a season in this study is among the largest reported (cf. Elliott 1967b; Stoneburner and Smock 1979). Change in physical conditions could not account for this variation. Although individuals tended to occur more on top surfaces in September when drift was greatest, it is unlikely that the increase in drift between dates can be attributed to this positioning change (see above). High drift probability in this study is best associated with high growth rates for most taxa considered. All *Baetis* species considered here had late summer – early fall emerging cohorts. Immature *Baetis* were likely part of these cohorts. High abundance of immature *Baetis* on both dates suggests rapid growth occurred for all three *Baetis* species between August and late September. Rapid growth just prior to emergence occurs commonly in *Baetis* (Waters 1966; Elliott 1967b). *Ephemerella* spp. and *Paraleptophlebia mollis* individuals were immature states of spring emerging cohorts and had high growth rates in August. Correlation between drift magnitude and growth rate has been frequently observed (e.g., Elliott 1967b; Ulfstrand 1968; Otto 1971; Cloud and Stewart 1974). Since food resource availability for these grazer taxa did not increase during August (S. L. Kohler, personal observation), high growth rates should reflect increases in feeding activity intensity. Otto (1971) observed increases in drift of the caddisfly *Potamophylax cingulatus* when larvae were growing rapidly and later (Otto 1976) demonstrated that only the presence of an abundant, high quality food source reduced the rate of downstream movement. These results point to the importance of variation in behaviors

involved in food acquisition resulting from changes in food resource abundance–demand relationships in determining variation in drift probability.

Day drift probability in September was greater than night drift probability in August for *Baetis flavistriga* and *B. intercalaris*. Similar patterns are indicated by data reported by Elliottt (1967b) for *B. rhodani*. Allan (1978) hypothesized that individuals should be more constrained to nocturnal drift as they increase in size since visually feeding fish predators are more selective for large individuals in the drift during the day than at night. Results presented here do not support this hypothesis. Rather they suggest that foraging energetics (and associated behaviors) may override constraints imposed by predation risk in determining drift probability at any point in time. Kovalak (1976) presented a similar argument to account for the positioning behavior of the caddisfly *Glossosoma nigrior* where the constraints on positioning were maximization of oxygen uptake and minimization of erosion probability. In general, both positioning behavior and drift at any point in time should reflect compromises to various constraints upon behavior made by individuals attempting to maximize fitness (see Sih 1980).

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