Downstream Drift of the Mayfly Baetis flavistriga as a Passive Phenomenon

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ABSTRACT: Drift of *Baetis flavistriga* McDunnough nymphs apparently was a passive process which resulted from increased exposure to water currents during periods of increased foraging. The diel pattern of drift was nocturnal and ecologically significant, with approximately 16.15 kcal of energy drifting daily. Drift was independent of emergence and the density of nymphs in the substrate. Nymphs apparently did not drift because of hunger or long-term food deprivation, since drifting and nondrifting nymphs, collected at the same time of day, had similar gut-content weight and caloric content. A diel pattern of feeding was significantly correlated with diel drift.

INTRODUCTION

Drift of lotic invertebrates has been investigated extensively within the last 25 years *(see* Waters, 1972; Müller, 1974). However, the basic reasons for downstream drift of aquatic invertebrates have not been conclusively determined. Three types of drift, according to cause, have been recognized (Waters, 1965), *i.e.,* constant, catastrophic '(Minckley, 1964) and behavioral. Behavioral drift has been frequently investigated because it involves large numbers and is characterized by diel and seasonal periodicities. The term "behavioral drift" (Waters, 1965) may be misleading. Apparently Waters meant that diel drift was related to diel patterns of activity. Because active organisms were more frequently exposed to currents, they were more susceptible to passive dislodgement which resulted in drift (Waters, 1972). However, Waters (1965) designated constant drift as accidental and thereby implied that behavioral drift may have been more than accidental. Misinterpretation of the term "behavioral drift" may have resulted in the term "drift behavior" (Müller, 1974), which referred to drift as an active process.

Some investigators have indicated that drift may be active. Kroger (1974) suggested that nocturnal drift evolved as a protective mechanism to avoid trout predation. Minshall and Winger (1968) reported that *Baetis* spp. and *Ameletus* spp. (Ephemeroptera) seemed to actively drift. Müller (1974) stated, "The pronounced and recurrent periodicity of drift behavior on both diel and seasonal time scales excludes the interpretation of drift as a passive phenomenon." Corkum (1978), who noted a poor correlation between diel drift and diel activity during the spring and summer, concluded that drift was an innate behavior. The purpose of this investigation was to determine whether the diel drift of *Baetis flavistriga* McDunnough was active or passive. The study assessed diel drift and drift in relation to emergence, benthic density, nutritional condition, patterns of feeding and activity.

DESCRIPTION OF STUDY AREA

The study site was a 19.8 m^2 riffle in Hickory Creek, Benton Co., Arkansas. The creek is a small second-order stream flowing from two cave openings ca. 1.5 km above its entry into Beaver Reservoir. The riffle was located in subclimax forest near the middle of Hickory Creek and exhibited uniform physical characteristics (substrate cobble, depth and flow rate). The riffle was distinctly bounded by two pools.

METHODS

We determined the initial density of *Baetis flavistriga* nymphs, on the riffle in June 1977, by taking three 0.1 m^2 modified-Hess samples (mesh = ca. 0.4 mm). Previous sampling of this species in Hickory Creek had consistently demonstrated that the variance based on three random Hess samples was not significantly reduced when seven additional substrate samples were taken. After 2 days, previously determined to be sufficient time for recolonization of sampled areas, we blocked the upstream pool with netting of the same mesh as that in the Hess and drift samplers. The use of the same mesh size in the block net and samplers should have insured that all losses of early instars were similar. The block net should have virtually eliminated the drift of nymphs onto the riffle from upstream. We drove steel plates (20 $\times$ 70 cm) 15 cm into the substrate at the lower end of the riffle so that they overlapped lengthwise across the entire width. Steel plates should have restricted the immigration of nymphs from downstream areas without seriously impeding drift. Four drift samplers (aperture = 112.5 cm^2) were placed evenly across the riffle and in contact with the upper edges of the steel plates. We collected drift samples at 2000, 0200, 0800 and 1400 hr each day for 4 consecutive days and measured temperature, dissolved oxygen and flow rate every 6 hr. We estimated the final density of nymphs by taking three modified-Hess samples at the end of the 4-day period.

Discharge was calculated as the product of linear flow rate and the cross-sectional area of the riffle. Drift density of nymphs and mature-sized exuviae was expressed as number drifting m^{-3} sec^{-1} day^{-1} and as number drifting per 100 m^3 of water sampled. Drift of mature-sized exuviae (6-7 mm) was used as a relative index to emergence (cf., Cloud and Stewart, 1974). Emergence was expressed as the number emerging m^{-2} 6 hr^{-1}.

Nutritional condition of drifting and nondrifting nymphs, before and 3 hr after sunset, was determined by measuring gut-content weight. Caloric contents of drifting and nondrifting nymphs were also determined. Drifting and nondrifting specimens were collected and immediately frozen in liquid nitrogen to prevent regurgitation of gut contents. They were transported to the laboratory in separate Thermos bottles and later dissected. Gut tubes were removed from some specimens and separately pooled (five tubes per sample) according to time of capture and state at the time of capture (drifting or nondrifting). Samples were then dried to a constant weight in a vacuum oven (20 mm Hg) at 55 C and weighed to the nearest μg on an electrobalance. Remaining drifting and nondrifting nymphs were separately dried at 55 C and weighed $\pm$ 1 mg. Caloric content (cal. g^{-1} ash-free dry weight) was determined by combustion in an adiabatic bomb calorimeter, using the procedure outlined in the Parr manual (no. 130; Parr Instrument Co., 1960).

We quantified the diel activity of nymphs in the laboratory at 16 C, the ambient temperature of water in Hickory Creek, by counting the number of movements exceeding 1 cm in a glass dish (diam = 23 cm, depth = 3 cm), during a 5-min period. All experiments were conducted in still water and no food or substrate was provided. Activity of 4-5 nymphs was quantified each hour beginning at 1700 hr, for 28 consecutive hr. At 0800 hr, fresh nymphs were collected and monitored to insure that any change in activity was the result of a diel rhythm and not due to the fatigue of original specimens.

<center>RESULTS</center>

Diel drift of *Baetis flavistriga* was nocturnal, with a maximum of 330 $\pm$ 12.5 nymphs drifting during the interval 2000-0200 hr. During the next period (0200-0800 hr) significantly fewer nymphs drifted (67 $\pm$ 8.4), but drift still exceeded that which occurred during the 12-hr period 0800-2000 hr (17 $\pm$ 2.4). Sunrise and sunset occurred at approximately 0535 and 1855 hr, respectively.

Nymphs exhibited a diel periodicity of emergence which differed significantly from their diel pattern of drift. Emergence density (no. emerging m^{-2}) was 3.7 (0800-1400 hr), 10.9 (1400-2000 hr), 7.7 (2000-0200 hr) and 0.7 (0200-0800 hr). These data depict a peak in emergence during the afternoon and evening. Although emergence decreased during the 2000-0200 hr interval, it was significantly greater than that which occurred over the next 12 hr (0200-1400).

Percent drifting (the percent of nymphs in the substrate that drifted off the riffle each day) was calculated as:

$$\% \text{ Drift} = (D_i / \Sigma B_d - D_p - E_p) \times 100,$$

where D_i = drift per day, B_d = initial benthos density, D_p = previous drift and E_p = previous emergence. Because the density of nymphs decreased significantly over the 4 days ($t_{(2,0.05)}$ = 7.68), while % drift remained constant (2% per day), drift was considered independent of density, within the density range we observed (983 − 1220 m^{-2}).

Nymphs from the drift and substrate had similar gut-content weights (130.34 and 126.83 μg, respectively) and caloric contents (6465 $\pm$ 147 and 6325 $\pm$ 58 cal. g^{-1} ash-free dry weight, respectively). Gut contents of nymphs collected at night (2200 hr, 132.5 $\pm$ 10.7 μg) weighed significantly more than those of nymphs collected just before sunset (1800 hr, 84.3 $\pm$ 23 μg).

There was a significant correlation between diel activity (Fig. 1) and diel drift. The relation of activity (x) to drift (y) was exponential (y = $0.428e^{0.17x}$, r^2 = 0.96). When activity was low (0330-1800 hr), drift was insignificant, but as activity increased to a maximum between 1900 and 0200 hr, diel drift increased exponentially toward an asymptote (Fig. 2).

Although flow rate remained constant throughout the experiments (ca. 2.73 m^{-3} min^{-1}), temperature and dissolved oxygen concentration exhibited significant diel periodicities. Daily maxima in temperature and oxygen concentration were recorded at 1400 hr (17.3 C and 9.0 mg $liter^{-1}$, respectively) and minima at 0200 hr (14.8 C and 6.7 mg $liter^{-1}$, respectively). Diel drift was not correlated to either of the parameters, but the diel periodicity of emergence was similar to that of temperature and dissolved oxygen.

DISCUSSION

Baetis flavistriga in Hickory Creek, Arkansas, exhibited a nocturnal pattern of drift, with a major peak between 2000 and 0200 hr. The 24-hr drift density (7.69×10^3 m^{-3} sec^{-1}) was low compared to 24-hr rates reported for *Baetis* spp. in the literature (1.1×10^6 m^{-3} sec^{-1}, Waters, 1962; and 14.9×10^6 m^{-3} sec^{-1}, calculated from Pearson and Franklin, 1968). However, the number drifting per 100 m^3 (27.3), during the interval 2000-0200 hr, was approximately equal to that of *Baetis* spp. (ca. 30 per 100 m^3) in the Brazos River, Texas (calculated from data of Cloud and Stewart, 1974). At 6.46 kcal g^{-1} ash-free dry weight, about 16.15 kcal were available daily to fish in the riffle *(e.g., Etheostoma* spp. and *Cottus carolinae)* and downstream pool *(Lepomis* spp. and *Micropterus* spp.).

Diel drift could not be explained in terms of emergence or benthic density, but it did correlate with diel activity. Drifting and nondrifting nymphs, collected at the same time of day, did not differ in gut-content weight or caloric content. These observations indicated that nymphs were not drifting because of hunger or long-term food deprivation. Increased gut contents of nymphs collected during the peak drift period indicated that feeding occurred concomitantly with maximum drift. As herbivores, nymphs move to the upper surfaces of stones to graze algae *(e.g., Baetis rhodani;* Elliott, 1968). Elliott (1968) also observed that foraging of these nymphs was significantly increased after sunset, a periodicity similar to that of drift, though drift was more variable than activity. Thus, increased exposure to and movement in water current may have resulted in the increased passive dislodgement and drift of *Baetis flavistriga* nymphs. Low food levels increased the drift of the mayflies *Ephemerella serrata* and *E. needhami* (Hildebrand, 1974) and of the caddisfly *Potamophylax cingulatus* (Otto, 1976). Increased foraging was suggested to have been the cause of drift in both studies.

The exponential relation of diel drift to diel activity illustrated that low levels of activity resulted in minimal drift. As activity increased to a maximum, drift rates increased exponentially toward an asymptote. This relation may be the most important and yet fundamental explanation for diel drift. After sunset, foraging activity increased, and the greater exposure and movement of nymphs resulted in maximal drift. When foraging subsided at 0200 hr, so did drift.

Corkum (1978), who examined the relation of diel drift to diel activity in mayflies, noted that although the two phenomena occurred in the same light phase, they were poorly correlated. Because nocturnal activity remained constant seasonally, while drift occurred primarily in the
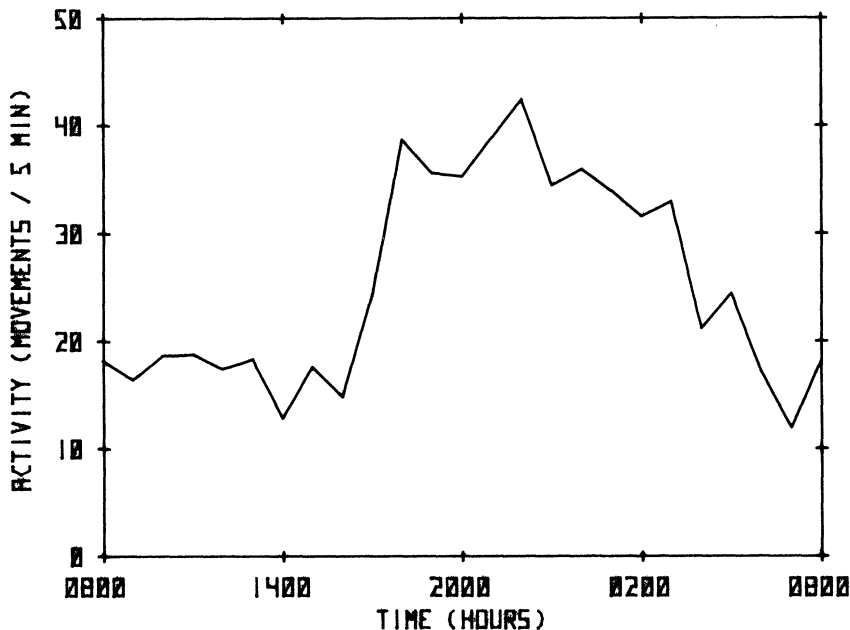

Fig. 1.—Diel activity of *Baetis flavistriga* nymphs quantified in still water at 16 C

spring and summer, she concluded that benthic activity did not result in diel drift. She also hypothesized that the ratio of activity in the dark (D) to that in the light (L) was inversely related to seasonally increased photoperiods. The ratio of activity in the two light phases for *Baetis flavistriga* in early June (photoperiod = 13D : 11L) was 1.96. This ratio is less than Corkum predicted (4.5-13) based on the data of Elliott (1968) and Harker (1953) for a similar photoperiod. More data should be examined before firm conclusions are drawn, especially in light of our strong correlation of diel drift to diel activity in *B. flavistriga.*

In addition, feeding methods, as well as activity, may be related to the drift propensity of some insects. How an insect nymph moves over the substrate and how far it must forage to obtain sufficient energy undoubtedly varies with season (as a function of water temperature which affects respiration and leaf fall which influences nutrient and light availability) and determines, in part, the amplitude of drift. In Ozark streams, where leaf fall occurs in October, increasing nutrient input and the light available to periphyton during the winter, nymphs may not have to forage as far to obtain adequate nutrition. This hypothesis may help to explain why drift has been observed to decrease in the autumn and winter, though nocturnal activity (Corkum, 1978) may not. Organisms that move extensively over the substrate and expose themselves to the current during feeding are more likely to be dislodged. Mayflies of the genera *Baetis, Ameletus* and *Paraleptophlebia* are abundant in the drift and exhibit diel periodicities (Adamus and Gaufin, 1976). Needham *et al.* (1935) characterized these genera as free-ranging species that move by quick, minnow-like darts and inhabit rapidly flowing water. By contrast, the megalopteran, *Corydalus cornutus,* does not drift, though it inhabits riffles. Perhaps these nymphs are absent from the drift because they do not search for prey or expose themselves to currents (pers. observ.). Research on feeding methods of other insects may further confirm this suggestion.
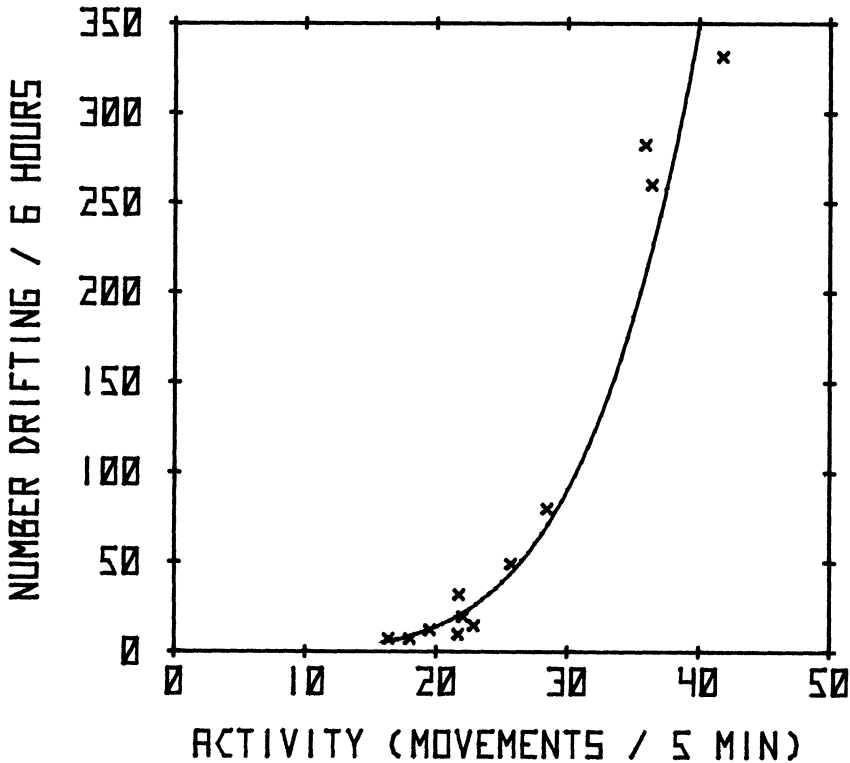

Fig. 2.—Diel drift as a function of diel activity for *Baetis flavistriga* nymphs ($y = 0.428e^{0.17x}$; $r^2 = 0.96$)

Because drift probably increases mortality and yields few obvious benefits to individuals (avoidance of benthic predators may be one benefit), the active entry of nymphs into water currents seems unlikely. Samples from the riffle contained essentially two benthic predators, the megalopteran *Nigronia* sp. and a dipteran of the family Tipulidae. Neither predator was present in densities sufficient to account for increased drift after sunset. Müller (1954) suggested that drift was beneficial to populations, because the attrition prevented crowding in the upstream substrates. However, genes for such altruistic behavior probably would be eliminated from populations by fish predation and nonpredatory mortality incurred when riffle-adapted insects drift into moderate to large pools. Also, drift rates of 2% per day (as in *Baetis flavistriga*) could have no significant regulatory effect. Nymphs in first and second order streams may benefit by drifting downstream to less heavily shaded areas, where periphyton production is greater, at least in streams with small intermittent pools. Whether benefits of such a behavior outweigh the hazards for a particular species would be difficult to quantify and is speculative. Future research should attempt to determine whether drifting insects are displaced significant distances downstream. We believe drift may be a localized phenomenon, compensated for by upstream movements of nymphs (Elliott, 1971).

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