Nonconcordance of Drift and Benthic Activity in Baetis

Margaret A. Wilzbach

Nonconcordance of drift and benthic activity in *Baetis*

Abstract—Simultaneous collection of stream drift and observations of epibenthic activity of *Baetis* nymphs (Baetidae: Ephemeroptera) from within a field enclosure were made over 24-h periods. A fiber-optic observation system that enabled night viewing of animals in unexposed locations supplemented observations. Drift was out of phase with epibenthic density and total number of movements of *Baetis,* which were greater during the day. Numbers of individuals on tops of stones were often insufficient to account for numbers in the drift. Individuals from exposed and unexposed locations fed continuously, and little difference existed in gut fullness between drifting and benthic animals. Observations do not support a hypothesis that *Baetis* drifts at night because it is hungry and in search of food.

Diel periodicity in the drifting behavior of many stream insects has been substantiated numerous times since its original description, generally with higher drift occurring at night (e.g. Waters 1972). There is little consensus regarding diel periodicity in substrate positioning and activity of stream insects, however, and the relationship of these behaviors to drift. As reviewed by Casey (1987), field and laboratory studies have variously found greater densities and activities of insects on stone tops at night, during the day, or with no diel changes in positioning exhibited.

Conclusions regarding the fundamental cause of drift, i.e. whether it represents an active or passive phenomenon, have been based on the correspondence found in diel timing between drift and benthic activity; thus it is important that inconsistencies in findings be resolved. Allan et al. (1986), for example, maintained that a positive relationship between activity on stone top surfaces and drift is the underlying basis of a passive drift model, and that the results of their study, which showed a lack of correspondence between drift and epibenthic activity, rejected this premise.

Contradictory results concerning diel patterns of benthic activity and its relationship with drift may occur for several reasons. As reviewed by Statzner et al. (1984), a complex array of physical and biological factors influences the occurrence and magnitude of invertebrate drift, and the manner in which they interact is poorly understood. Thus, varying environmental conditions under which studies were conducted probably contributed to the discrepancy in results.

A second reason for the discrepancy in results undoubtedly reflects differences among taxa. Because stream invertebrates differ, e.g. in mode of locomotion and attachment, morphobehavioral mechanisms of acquiring food, drift propensity, and susceptibility to predation, it is reasonable to assume that benthic activity patterns will vary in relation to other aspects of their ecology (Corkum 1978; Wilzbach et al. 1988). Conflicting results concerning benthic and drift activity have been reported, however, even within genera or species. This diversity of reported behaviors is particularly true for *Baetis,* a ubiquitous mayfly genus that exhibits a pronounced diel drift periodicity. It could result from geographic or individual variation due to size or instar, or from some other factor.

Allan et al. (1986) suggested that a third reason to explain the discrepancy in results involves methodological differences. Many field studies based conclusions on the removal or scraping of stones, which could alter animal positions during the disturbance. Studies of Statzner and Mogel (1984, 1985), Allan et al. (1986), and Casey (1987) are unique in that they included systematic observations of animals in the field without removal or disturbance of stream sediments.

Even these studies are limited, however,

by lack of information on the density and activity of animals underneath the substrate. For example, to be certain that diel differences in density on the tops of stones represent vertical position changes of the same individuals rather than immigration of different individuals from surrounding areas, visual observation of both top and bottom surfaces is required; if observations are made on tops of stones alone, the total substrate density of individuals should be known and should not change over the course of the study (Kohler 1983).

The objective of this study was to determine the diel periodicity of insect epibenthic activity in relation to drift. The methodology of Allan et al. (1986) was followed closely to facilitate comparison with their results, but two major modifications were instituted. The first is that drift was collected and observations were conducted simultaneously from within a field enclosure to prevent immigration and emigration (other than via drift) and to enable determination of total substrate density. The second is that a fiber-optic observation system was developed and used to supplement observations on tops of substrate surfaces with remote observations of insect activity in substrate crevices and on bottom surfaces. Interfaced with a light source supplying long-wavelength red and infrared light, to which aquatic insects are apparently not sensitive (Chapman 1982; Casey 1987), the fiber-optic system is capable of providing enlarged images of insects in concealed locations even at night.

The fiber-optic observation system consisted of a Diaguide (RTM) silica fiberscope and an infrared-enhanced xenon light source, interfaced with a video-recording system comprising a TV camera, monitor, and time-lapse VCR. The fiberscope has a forward field of view of 45° and an adjustable focus, with an objective lens that provides 7× magnification. The semiflexible fiberscope, 2-mm o.d., can be maneuvered readily underneath stones or into crevices. The observation system was set in place along the stream bank in a glass-sided housing that shielded the equipment from moisture. The fiberscope was long enough (3 m) to manipulate from the bank or from a location downstream from the enclosure without disturbing stream sediments in the area around the enclosure.

Observations were taken in an enclosed area of stream bottom to prevent immigration of animals into the observed area and to enable determination of the benthic density that served as the source of the measured drift. The enclosure was a Plexiglas box, 30 × 30 × 21 cm, open at the bottom and top and divided by a plastic partition into two longitudinal sections (each 450 cm^2) that provided for paired samples. Panels of 250-μm-mesh Nytex (RTM) allowed flow through the front and sides of the enclosure. Nytex panels may have reduced water velocity in the enclosed area, but current speeds in the enclosure (0.20–0.36 cm s^{-1} at the mouths of the drift nets near the bottom) were in the same range as flows in the surrounding riffle. Clogging of the nets was not a problem, as particle transport was minimal during this time of low and stable flow. In each left and right section of the enclosure, water exited the box through a downstream port to which a drift net could be attached. Each port (and drift net) had a circular mouth opening 10 cm in diameter and was situated so that the opening was several centimeters above the level of the substrate. The drift nets attached to each port were 0.8 m long and made of 250-μm net.

Drift was sampled and paired observations were made from the left and right sides of the field enclosure on each of three dates (28 July, 3 and 11 August 1988) to provide six data sets. The enclosure was inserted 10 cm into the stream bottom with the exit ports open (drift nets not attached) for a minimum 3-h equilibration period before the beginning of a 24-h observation session. Observations were made for a 1-h period at 3-h intervals over 24 h (at 0300, 0600, 0900, 1200, 1500, 1800, 2100, and 2400 hours) with the time of initiation varying among dates (2100, 1200, and 1500 hours, respectively). Drift originating from the enclosed area was sampled over the same 1-h period in which observations were made. Drift was sampled again over the 2-h period preceding the next set of observations so that all of the drifting animals over each 24-h session were collected.

Benthic samples were collected at the

conclusion of the last observation period by reattaching the drift nets and washing each cobble and agitating the gravel in the enclosed area of bottom sediments so that dislodged organisms were washed into the drift nets. Drift and benthos samples were live sorted, measured, and identified immediately after collection. Live individuals were examined under a dissecting microscope at $12\times$ or greater magnification to estimate the degree of gut fullness, assessed as regions of opaque gut contents in the otherwise transparent digestive tract readily seen through the body wall. Percent fullness of the foregut, which indicates recent feeding, and of the total digestive tract was recorded to the nearest 25% (i.e. 0, 25, 50, 75, 100% full). Visual scoring of gut fullness was also used by Williams and Levens (1988) on preserved specimens. Use of live specimens greatly facilitates the technique, as preservatives usually make body tissue opaque.

During an observation period (1 h), all individuals visible on the top surfaces of stones in the enclosed area (left or right side of enclosure) were observed during a 30-s interval. Observations were repeated at 1-min intervals for 10 successive observations. In each 30-s observation, the number of individuals and the number of movements, defined as changes in position, were recorded. Each individual was counted as moving a maximum of once in the 30-s interval. Observations were made through a small glass or plastic lens placed on the water's surface. Observations at night were made with a flashlight fitted with a red filter. Sediments in the area of the enclosure were not disturbed. Water temperature and surface illumination above the enclosure were measured at the start of each observation period. Illumination was measured with a LiCor (RTM) photometer.

After the series of censuses in each observation period, the fiberscope was used to film the activity of at least five randomly selected individuals in varying substrate locations. Observations at night were made with infrared light. It was not possible to use the fiberscope to conduct an accurate census of animals in unexposed locations because of difficulty in determining whether the total unexposed area had been scanned. The usefulness of the fiberscope was in providing an enlarged image of individuals for observation of detailed behavior. Videotapes were analyzed to determine allocation of time by individuals among three activity categories (holding, feeding, and movement) in concealed and exposed locations. Because individual animals were observed for differing lengths of time, construction of time budgets was based on analysis of a standardized number of frames, representing a mean of 12 min of observation.

All observations were from Piney Run, a second-order, low-gradient, brook trout stream in the Youghiogheny River basin of the Ohio River drainage system in Garrett Co., Maryland (Appalachian highlands ecoregion, Omernik 1987). The enclosure was placed in a different location in the same 7-m-long riffle on each of the three dates, upstream from the location of previous observations. The riffle was in an open section of the largely wooded stream, bordered by grasses and herbaceous vegetation (largely jewelweed, *Impatiens capensis*; asters, *Aster* spp.; and goldenrod, *Solidago* sp.), with some shading provided by red maple (*Acer rubrum*). Stream width at the site was 2 m (bankful width is 3 m) and depth was 10 cm. Discharge at summer base flow averaged $0.1 \, \text{m}^3 \, \text{s}^{-1}$.

Nymphs of *Baetis* spp. were the most abundant insect present and contribute the only data presented here. *Baetis intercalaris*, *Baetis flavistriga*, and *Baetis brunneicolor* were present but could not be reliably distinguished during rapid censuses, so observations were combined. *Baetis brunneicolor* slightly outnumbered the *fuscatus* group (*B. intercalaris* and *B. flavistriga*) in both benthic and drift collections. These species were easily observed and did not seem to react to the approach or presence of observers. Allan et al. (1986) and Casey (1987) reported similar insensitivity of *Baetis bicaudatus* to human observation (*but see* Statzner and Mogel 1985 regarding European *Baetis*).

A nocturnal increase in drift abundance of *Baetis* is well documented (e.g. Waters 1962), but in this study the diel pattern was only slight. Effect of time of day on drift density of *Baetis* was significant ($P \leq 0.05$, one-sample Kolmogorov-Smirnov test with expected frequencies based on a uniform
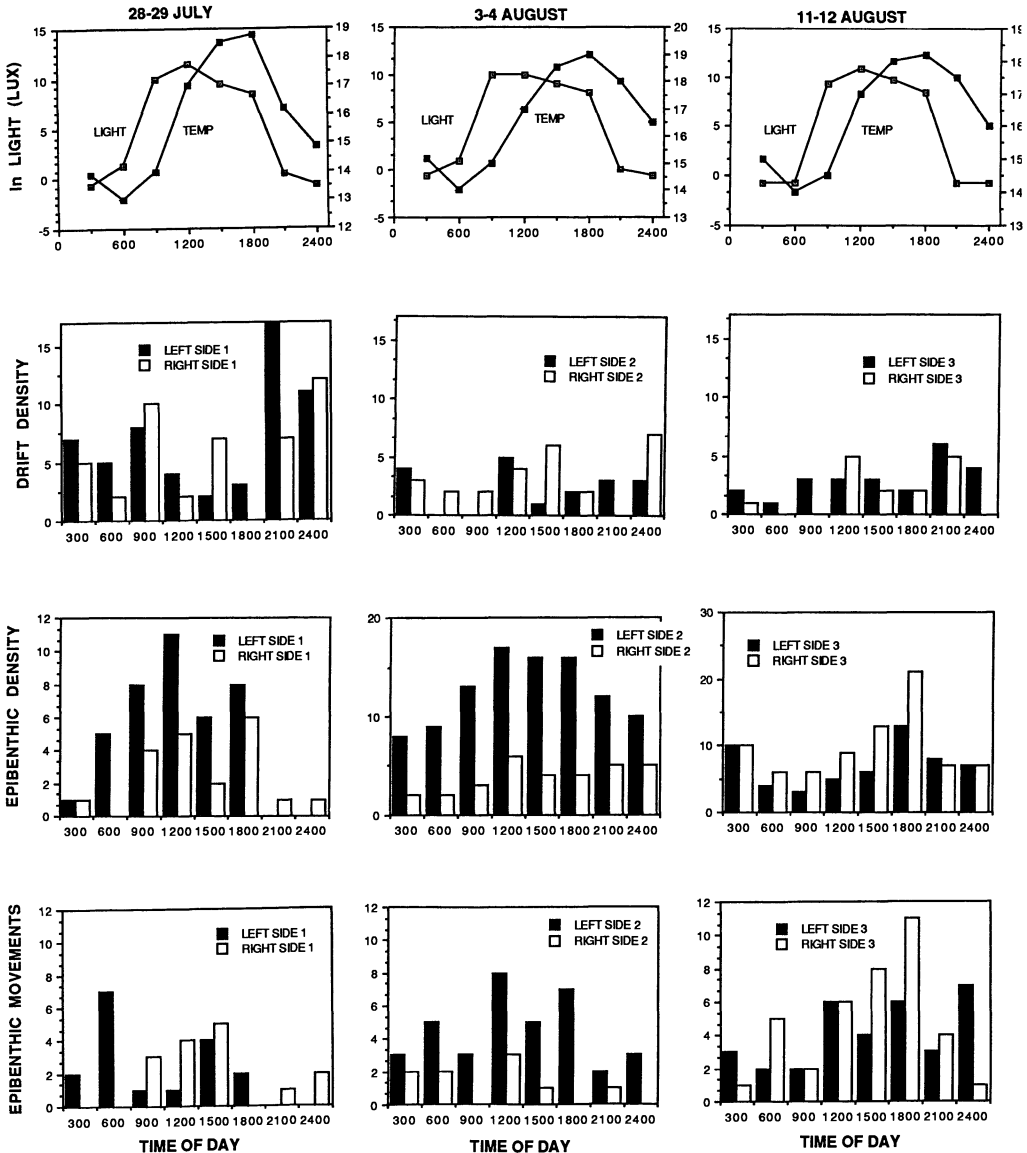
Fig. 1. Changes over 24 h in surface illumination and water temperature, number of drifting *Baetis* exiting per hour from the left and right sides of enclosure, and number and activity of *Baetis* in view on the tops of stones in the enclosure on each of three dates. Epibenthic density represents the maximal number of individuals observed in any of 10 censuses at each observation period. Epibenthic movements represent the total number of movements observed in 10 censuses at each time.

distribution) in all but one data set (left side, 3 August). On all dates, maximal drift density occurred at night or was coequal with drift density at noon (Fig. 1). Hourly day drift, averaged over eight samples on each date, always composed 2% of benthic density; maximal hourly drift at night composed 6% of benthic density (SD = 1%). Drift rates from the benthic sediments in the enclosure were similar to those from the stream bottom. Drift of *Baetis* collected at dusk from the same riffle in summer 1986, which was blocked at its head to prevent immigration from upstream as described by

Wilzbach and Cummins (1989), was similar in density (21 m^{-2}) to that collected from the small enclosure in this study (33 m^{-2}).

Numbers of *Baetis* on the top surfaces of stones tended to be greater during the day, particularly in the afternoon (1200–1600 hours), than at night (Fig. 1). Similarity of the data sets, evaluated by Kendall's coefficient of concordance W, which ranges from 0 to 1 (perfect concordance), was moderate ($W = 0.43$, $\chi^2 = 18.13$, $P < 0.02$). No relationship between diel patterns in epibenthic density and drift was evident. Correlation between drift and epibenthic density was negative in two data sets and narrowly positive in four, but in no instance were correlations significant ($P > 0.05$, Spearman rank correlation). Baetids that were on tops of stones were generally large, ≥ 3 mm long, but it was difficult to be certain that smaller animals were detected. Size of animals on stone tops did not appear to differ with time of day, but this issue was not examined specifically.

Although epibenthic density of *Baetis* was greater in the day than at night, when expressed as a percent of its total benthic density, numbers of *Baetis* on the tops of stones at all times of day were very low, with an overall average of 0.06% of the total population present. The proportion of *Baetis* located on top surfaces differed with time of day ($P \leq 0.05$, Kolmogorov-Smirnov) for both data sets on 3 and 11 August; differences were not significant on the first date. Even at 1800 hours, however, when the proportion of animals on top was greatest, they represented a minor fraction of the benthos. Most animals were in unexposed locations at all times.

Numbers of *Baetis* on the tops of stones were insufficient to account for numbers in the drift in a quarter of 48 cases of concurrent observation and drift collection (Fig. 1), which suggests that drift may occur from locations other than the tops of stones. If true, it calls into question the ability to deduce drift mechanisms (active vs. passive) from the relationship between diel drift and activity on stone tops. The argument has been that lack of correspondence between drift and (epi-)benthic density or activity rules out the possibility of passive drift

(Kohler 1985; Allan et al. 1986). Particularly since turbulent, unpredictable flow conditions resulting from irregular juxtaposition of sediments can also occur underneath stones, insects might become accidentally dislodged from these locations as well.

On the basis of visual censuses, total epibenthic movements of *Baetis* (number of movements summed over all individuals present), like epibenthic density, tended to be greater in the afternoon than at other times of day (Fig. 1). Concordance of data sets, as was the case for epibenthic density, was moderate ($W = 0.40$, $\chi^2 = 16.8$, $P < 0.02$). In contrast to total epibenthic movement, movements per individual (No. movements/No. individuals) on top surfaces were greatest around dusk (2100 hours) and in the early morning (0300 hours). Among the four data sets in which individuals were observed at all time periods (left and right sides on days 2 and 3), the rankings of the data were quite consistent ($W = 0.79$, $\chi^2 = 22.1$, $P < 0.01$). Therefore the finding of greater activity during the day than at night primarily reflects the contribution of animal numbers rather than the number of movements per individual. It should be noted that counts of movement measured only changes in position, which did not reflect feeding per se.

The finding that total epibenthic movements were greater in the day than at night was not substantiated from longer duration observations with the fiberscope. Videotape analysis revealed that the percent of time spent by *Baetis* in movement, and in the activity categories of holding and feeding, did not vary significantly with time of day on either the tops or bottoms of stones on any of the three dates ($P > 0.10$, Friedman test). On the tops and bottoms of stones, movement accounted for <10% of total activity (Fig. 2).

Allocation of time spent by *Baetis* differed among categories of holding, feeding, and moving in both locations ($P < 0.05$, multiple comparisons on data combined over dates and times of day). Both on the tops and bottoms of stones, the greatest proportion of time was spent feeding (mean of 59%), followed by holding (means of 38 and
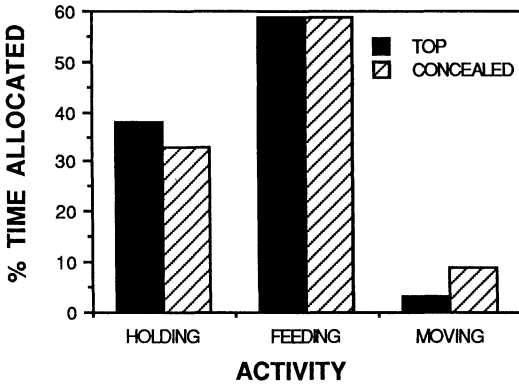
Fig. 2. Percent of time allocated by *Baetis* nymphs in concealed locations and on the tops of stone surfaces among the categories of holding, feeding, and moving. Data represent means from eight observational periods over 24 h; from each observational period, 12 min of videotape footage, which recorded the activities of at least five nymphs, was analyzed. Observations were made with a fiberscope in the field enclosure.

33% on top and concealed surfaces). The mean proportion of time spent in holding and in feeding did not differ between individuals on the tops vs. bottoms of stones ($P > 0.10$, Mann-Whitney). The proportion of time spent in moving was, however, greater for animals on the top vs. bottom ($P = 0.05$, Mann-Whitney). This disparity is likely because food quantity and especially quality in the form of nonfilamentous algae is likely to be lower in concealed locations than on the tops of stones (Cummins and Klug 1979), which necessitates a greater amount of time spent in search.

Use of the fiberscope enabled feeding behavior to be easily distinguished from holding and moving. Feeding was marked by movement of mouthparts and their palps and by a pronounced forward, backward, and upward thrusting of the head and body, often accompanied by slight adjustments in position. These lurching movements of *Baetis* nymphs when feeding gave the impression that attached algae were being ripped loose from the substrate or perhaps that strands of filamentous algae were being combed free of epiphytic or loose algal cells and associated detrital particles. Feeding did not involve mandibular or front-leg scraping of substrate surfaces typical of scraper heptageniid mayflies.
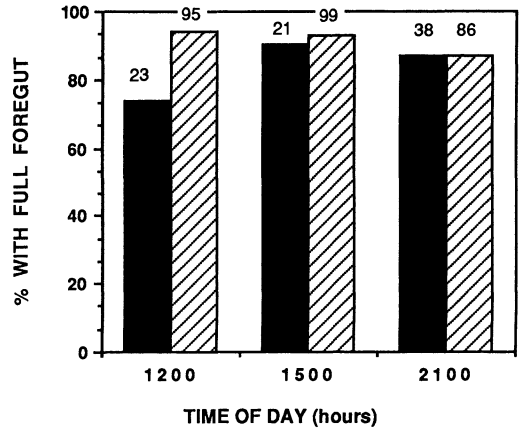

TIME OF DAY (hours)

Fig. 3. Percent of *Baetis* nymphs collected from the drift (■) and benthos (▨) at varying times of day that had foreguts completely full. Sample size given above bar.

Gut fullness data support a conclusion that *Baetis* feeds continuously. Irrespective of time of day, most of the *Baetis* collected from the drift had totally full foreguts, suggesting recent feeding, and total gut length at all times was ≥ 50% full for most animals, as shown in Table 1 for representative periods. Comparisons of gut fullness between drifting and benthic animals were made at 1200, 1500, and 1700 hours and showed only slight differences (Fig. 3). Differences were not significant between 1500 and 2100 hours ($\chi^2 = 0.66$ and 0.11 respectively, $P > 0.10$); at 1200 hours, the proportion of an-

Table 1. Number of *Baetis* collected in the drift that have a given percent of the foregut and total gut length full at different times throughout the day. Numbers at each time are from two drift collections on each of 3 d.

Time (hours)	n	0	25	50	75	100
				(%)		
		Fullness of foregut				
0600	12	8	0	0	0	92
1200	23	17	0	8	0	74
1800	11	18	0	0	0	89
2400	38	5	5	0	0	89
		Fullness of total gut length				
0600	12	8	0	25	25	33
1200	23	0	8	43	39	8
1800	11	0	18	45	27	9
2400	38	2	5	30	49	14

imals with completely full foreguts was greater in the benthos than in the drift (χ^2 = 7.4, $P < 0.05$). Even at this time, however, 82% of drifting animals had completely full foreguts.

Ploskey and Brown (1980) also found no difference in the weight and caloric content of guts of *B. flavistriga* between drift and benthic samples collected at the same time of day, although they found that guts were fuller after than before dark. Results of their study conflict with those of Williams and Levens (1988), who found that a greater proportion of *Baetis vagans* nymphs on the streambed had guts ¾-full to full than did drifting nymphs during the day. It is important to point out that in both of these studies, benthic samples may have included animals that had recently drifted or for which drift was imminent, and thus there is no assurance that drifting and benthic (nondrifting) components of populations were sampled separately. The enclosure used in the present study helped to ensure that short-term separation of drifting and nondrifting components was effective.

Observations of continuous feeding and gut fullness data do not support a hypothesis that *Baetis* drifts at night because it is hungry and in search of food, which is usually assumed to represent the motivation underlying active drift (e.g. Bohle 1978; Kohler 1985). Although results of this study may not warrant dismissal of an active drift explanation for *Baetis,* it may mean that food quantity is not the critical or the only motivating factor. Perhaps food quality also affects feeding and search behavior, or perhaps factors other than those relating to food availability are required to adequately explain the diel periodicity of drift in *Baetis.* Alternatively, if nocturnal feeding and drifting of nymphs occur in short succession, with animals hopping from place to place as they feed, drift could still be food related but not evidenced in differences in gut fullness between drifting and benthic individuals (J. D. Allan pers. comm.). Gut clearance, however, has been shown to occur within 20 min in at least some aquatic insects (Lacey and Mulla 1979); thus drifting bouts without feeding would have to be quite short. Moreover, in this interpretation, one would expect to find striking differences in gut fullness of benthic animals between day and night because hungry nymphs in the daytime presumably wait until night to drift.

Margaret A. Wilzbach

Department of Biological Sciences
University of Pittsburgh
Pittsburgh, Pennsylvania 15260

References

ALLAN, J. D., A. S. FLECKER, AND N. L. MCCLINTOCK. 1986. Diel epibenthic activity of mayfly nymphs, and its nonconcordance with behavioral drift. Limnol. Oceanogr. **31:** 1057–1065.

BOHLE, H. W. 1978. Beziehungen zwischen dem Nahrungsangebot, der Drift und der räumlichen Verteilung bei Larven von *Baetis rhodani* (PICTET) (Ephemeroptera: Baëtidae). Arch. Hydrobiol. **84:** 500–525.

CASEY, R. J. 1987. Diel periodicity in density of Ephemeroptera nymphs on stream substrata and the relationship with drift and selected abiotic factors. Can. J. Zool. **65:** 2945–2952.

CHAPMAN, R. F. 1982. The insects: Structure and function, 3rd ed. Harvard.

CORKUM, L. D. 1978. The influence of density and behavioural type on the activity entry of two mayfly species (Ephemeroptera) into the water column. Can. J. Zool. **56:** 1201–1206.

CUMMINS, K. W., AND M. J. KLUG. 1979. Feeding ecology of stream invertebrates. Annu. Rev. Ecol. Syst. **10:** 147–172.

KOHLER, S. L. 1983. Positioning on substrates, positioning changes, and diel drift periodicities in mayflies. Can. J. Zool. **61:** 1362–1368.

———. 1985. Identification of stream drift mechanisms: An experimental and observational approach. Ecology **66:** 1749–1761.

LACEY, L. A., AND M. S. MULLA. 1979. Factors affecting feeding rates of black fly larvae. Mosquito News **39:** 315–319.

OMERNIK, J. M. 1987. Ecoregions of the conterminous United States. Ann. Assoc. Am. Geogr. **77:** 118–125.

PLOSKEY, G. R., AND A. V. BROWN. 1980. Downstream drift of the mayfly *Baetis flavistriga* as a passive phenomenon. Am. Midl. Nat. **104:** 405–409.

STATZNER, B., C. DEJOUX, AND J.-M. ELOUARD. 1984. Field experiments on the relationship between drift and benthic densities of aquatic insects in tropical streams (Ivory Coast). 1. Introduction: Review of drift literature, methods, and experimental conditions. Rev. Hydrobiol. Trop. **17:** 319–334.

———, AND R. MOGEL. 1984. No relationship between the substrate surface densities and drift of the stream caddisfly *Micrasema longulum* McL. (Brachycentridae, Trichoptera), p. 383–389. *In* Proc. 4th Int. Symp. Trichoptera. Junk.

———, AND ———. 1985. An example showing that drift net catches of stream mayflies (*Baetis* spp.,

Ephemeroptera, Insecta) do not increase during periods of higher substrate surface densities of the larvae. Int. Ver. Theor. Angew. Limnol. Verh. **22:** 3238–3243.

WATERS, T. F. 1962. Diurnal periodicity in the drift of stream invertebrates. Ecology **43:** 316–320.

———. 1972. The drift of stream insects. Annu. Rev. Entomol. **17:** 253–272.

WILLIAMS, D. D., AND G. P. LEVENS. 1988. Evidence that hunger and limb loss can contribute to stream invertebrate drift. J. N. Am. Benthol. Soc. 7: 180–187.

WILZBACH, M. A., AND K. W. CUMMINS. 1989. An assessment of short-term depletion of stream macroinvertebrate benthos by drift. Hydrobiologia **185:** 29–39.

———, ———, AND R. A. KNAPP. 1988. Toward a functional classification of stream invertebrate drift. Int. Ver. Theor. Angew. Limnol. Verh. **23:** 1244–1254.

Epibiotic euglenoid flagellates increase the susceptibility of some zooplankton to fish predation

Abstract—The phototrophic flagellate, *Colacium vesiculosum* (Euglenophyceae), lives externally on freshwater zooplankton. In experimental tanks with supplemental nutrients, epibiotic prevalence (% zooplankters infested with epibionts) was not consistently different from control. Experimental reduction of the zooplankton population did not reduce epibiont frequencies; no substrate limitation is suggested. In tanks with planktivorous fish, *Menidia beryllina,* prevalence was significantly reduced on *Daphnia, Ceriodaphnia,* and cyclopoid copepods. The pump-filter-feeding fish, *Tilapia aurea* and *Dorosoma cepedianum,* reduced prevalence on *Ceriodaphnia* and copepod nauplii, but only *Dorosoma* reduced prevalence on cyclopoids. Impacts of fish predation appear to be related to the effects of *Colacium* on visibility and escape efficiency.

Planktonic rotifers and crustaceans often have small organisms, called epibionts or ectosymbionts, attached to their external surfaces. Some epibionts, such as fungi and microsporidians, affect their host populations by increasing egg and adult mortality and reducing clutch size (e.g. Brambilla 1983; Burns 1980; Green 1974). Little is

known of the interactions between other epibionts, such as ciliates and algae (some of which are photosynthetic), and their substrate organisms (rather than hosts, after Whitfield 1979). Epibionts may affect the life history of their substrate organisms by competing for food, hampering locomotion, or leading to reduced brood size or increased susceptibility of the substrate organism to predation (Kankaala and Eloranta 1987; Green 1974). We present here the fortuitous combination of an experimental evaluation of the effects of planktivorous fish predation on a zooplankton community (Threlkeld 1987) with observations on the prevalence of an epibiont, *Colacium vesiculosum,* on members of that community.

Colacium vesiculosum is a phototrophic, epiplanktonic, euglenoid flagellate (Rosowski and Kugrens 1973). It is found on the surface of freshwater zooplanktonic crustaceans, rotifers, ostracods, and mites. Free-swimming cells are rarely reported (Green 1974; Rosowski and Kugrens 1973). Under laboratory conditions, the cells grow without their substrate organisms in a suitable medium with suitable surfaces for attachment, making the association facultative. Reproduction is nonsexual and restricted to the attached phase (unpubl. obs.). As in the better known *Colacium libellae* (Willey and Giancarlo 1986), the cells of *C. vesiculosum* attach to a substratum by a carbohydrate-containing stalk which is se-