

# Toward a functional classification of stream invertebrate drift

MARGARET A. WILZBACH, KENNETH W. CUMMINS and ROLAND A. KNAPP

With 5 figures and 3 tables in the text

## Introduction

Rapid advances in stream ecology during the past two decades have proceeded from analysis of community structure alone to a focus on the functional roles played by stream community inhabitants. Conceptual schemes dealing with stream invertebrates have concerned mechanisms of food acquisition (functional feeding groups) and mode of attachment and/or locomotion (functional habit groups). Against a background of functional emphasis on stream systems, we feel it is time for clarification of conflicting views of diel patterns of benthic and drift activity of stream invertebrates, and for integration of such a view with other existing and extensively tested paradigms concerning the functional roles of these animals.

The drifting phenomenon of stream invertebrates is detailed in an extensive but often contradictory literature. Baetid mayflies, for example, have been reported to enter the water column actively (MINSHALL & WINGER 1968, KOHLER 1985) or passively (HYNES 1965, ULFSTRAND 1968, PLOSKEY & BROWN 1980), and to exhibit negative (SCHERER 1962, ELLIOTT 1968) or positive (ELLIOTT 1968) phototaxis. Peaks in diel patterns of drift activity have been found to be generally consistent with (ELLIOTT 1968, WATERS 1972, PLOSKEY & BROWN 1980) or inconsistent with (CORKUM 1978, BAILEY 1981, KOHLER 1985, ALLAN et al. 1986) diel benthic activity. At least some of the seeming contradictions reflect a) generalizations inappropriately extended to taxa other than those studied, b) differing environmental conditions, such as flow or light, under which studies were conducted that affected the results obtained, or c) failure to view drift within the total complex of functional adaptations of the species in question.

A carefully documented and conceptually rigorous classification scheme for stream invertebrates is needed to provide a framework within which various environmental influences can be investigated. This is important for both theory and application: on theoretical grounds, because of the potentially significant role played by drift in downstream dynamics, including as a food source for fish or invertebrate predators; on an applied basis, because the drift is often measured as an indicator of disturbed conditions. For example, the survival rate of drifting animals has been used to evaluate the effectiveness of an insecticide application targeted for blackflies in the U.N.-sponsored onchocerciasis control program in West Africa (CUMMINS 1985).

A basic scheme was provided by WATERS (1965), who distinguished among the three categories of drift: behavioral, constant or accidental, and catastrophic. The behavioral category is comprised of animals that exhibit a diurnal periodicity in activity, with nocturnal generally greater than diurnal drift. Constant drift is aperiodic, and catastrophic drift occurs only during severe disturbances to the benthos. This scheme provides a useful distinction from a fish's point of view: it separates animals which are predictably available as prey from those that are not (WILZBACH et al. 1986). But it does not distinguish among mechanisms of water column entry. Although behavioral drift has often been interpreted as implying an intentional, directed activity, the active vs. passive nature underlying this phenomenon has not been well-established, and remains a controversial subject.

We believe that necessary components of a functional classification scheme focused on drift include the following: 1. that it distinguish among mechanisms that account for drift (active vs. passive) because the fate of drifting animals and the role they play in downstream dynamics are likely to differ with mechanisms; 2. that the timing of drift activity be made explicit — this is particularly important from the point of view of drift-feeding fish and invertebrate predators that may base foraging behaviors on the timing and predictability of drift occurrence; 3. that it distinguish among taxa which differ in the propensity to be passively dislodged at high flows; and 4. that such a

classification scheme should be generally compatible with, or bear some relationship to, other schemes that categorize animals according to feeding strategy (functional feeding groups [CUMMINS 1974, CUMMINS & KLUG 1979]) or habit or mode of locomotion (CUMMINS 1973, MERRITT & CUMMINS 1984). We maintain that propensity to drift should be related generally to other functional roles played by a stream invertebrate.

In this paper we present findings from initial laboratory and field observations and experiments designed to provide information necessary for development of a drift classification scheme. We focus in particular on a) the relationship of drift to flow, b) diel patterns of drift and benthic activity, and c) the survival expectancy of drifting and non-drifting benthic animals.

## Methods

A technique developed by VOGEL & CHAPMAN (1966) which VOGEL (1967) used for measuring drag on fruitflies in air, was modified to estimate the drag experienced by macroinvertebrates in running water. A standard microammeter was employed in which an 8 cm section of fine (0.3 mm diameter) piano wire was cemented to the base of the meter needle below the pivotal point. The meter was suspended above a laminar flow tank, as described by VOGEL & LABARBERA (1978), so that the attached fine wire projected through a slot (2 mm wide, 2 cm long) in a plastic plate at the water's surface. An invertebrate to be tested was heat killed, blotted dry, lightly sprayed with clear acrylic resin and cemented to the fine wire with fast drying epoxy cement. The invertebrate was positioned on the wire ventral side up and parallel to the path of movement of the needle with the head facing into the direction of flow. Adjustable clamps allowed the meter to be raised and lowered so that the test animal could be positioned within 1–2 mm of the slotted plate, thus simulating its location on a sediment surface in the current. The distance between the invertebrate and the plate was adjusted to allow for the arc of movement when the wire and attached invertebrate were deflected by the oncoming current. The deflection of the needle on the ammeter scale (graduated in tenths from 0 to 25 milliamps), resulting from rotation of the bearing by the force of the current, was recorded for current velocities ranging from  $05 \text{ cm} \cdot \text{s}^{-1}$  to  $35 \text{ cm} \cdot \text{s}^{-1}$ .

Measurements of the velocity required to dislodge live and heat killed animals were also taken in the laminar flow tank. Current velocities were determined with a Montedoro Whitney (RTM) digital flow meter positioned immediately behind the location of the animal. The flow meter was calibrated with timed release of rhodamine B dye. Live and subsequently heat killed animals were positioned on the upper surface of a ceramic tile placed in the flow tank. Killed animals were arranged into lifelike positions in still water prior to current manipulations.

Animals used in all laboratory studies were collected from Piney Run (Garrett County, Maryland U.S.A.). The ratio of height to width, measured at their widest points, were determined under a dissecting microscope at  $12\times$  to the nearest 0.08 mm; height and width of each animal were measured at the widest part of the body.

A fiber optic observation system was developed for use in behavioral observations of benthic and drifting invertebrates in the field or laboratory. The system allows remote observation of dark or dimly lit, inaccessible microlocations on the bottom surface of sediments or in crevices. It consists of a Diaguide (RTM) fiberscope and light source interfaced with a video recording system (TV camera, monitor, and video cassette recorder) (Fig. 1). The fiberscope is made of pure silica glass, with its coherent image bundle fused over the entire length of 3 m. The diameter of the fiberscope is 2 mm; field of view is 45 degrees. The light source uses a high intensity xenon illuminator with infra-red enhancement. A mechanical shutter allows for switching between visible or infra-red light.

We conducted a preliminary laboratory experiment making use of the fiber optic observation system to investigate benthic and drift activity patterns of two mayfly genera, *Stenonema* sp., a clinger and scarper (MERRITT & CUMMINS 1984), and *Paraleptophlebia* sp. (Leptophlebiidae), a swimmer and collector-gatherer. The experiment provided two levels each of three treatments: light (lighted and dark), current velocity (slow,  $10 \text{ cm} \cdot \text{s}^{-1}$ , and fast,  $50 \text{ cm} \cdot \text{s}^{-1}$ ), and food abundance (no food and abundant food, in which greater than one-third of all substrate — ceramic tiles and small pebbles — provided stream-colonized periphyton). Twenty-five to thirty-five nymphs of each species were introduced into the laminar flow tank in still water maintained throughout the experiment at  $12^\circ\text{C}$ . Current was gradually increased to  $10 \text{ cm} \cdot \text{s}^{-1}$ , and fluorescent overhead lighting was turned on. For a given food abundance level, the order of treatments was as follows: lighted, slow current; dark (lights turned off), slow current; dark, fast current; and

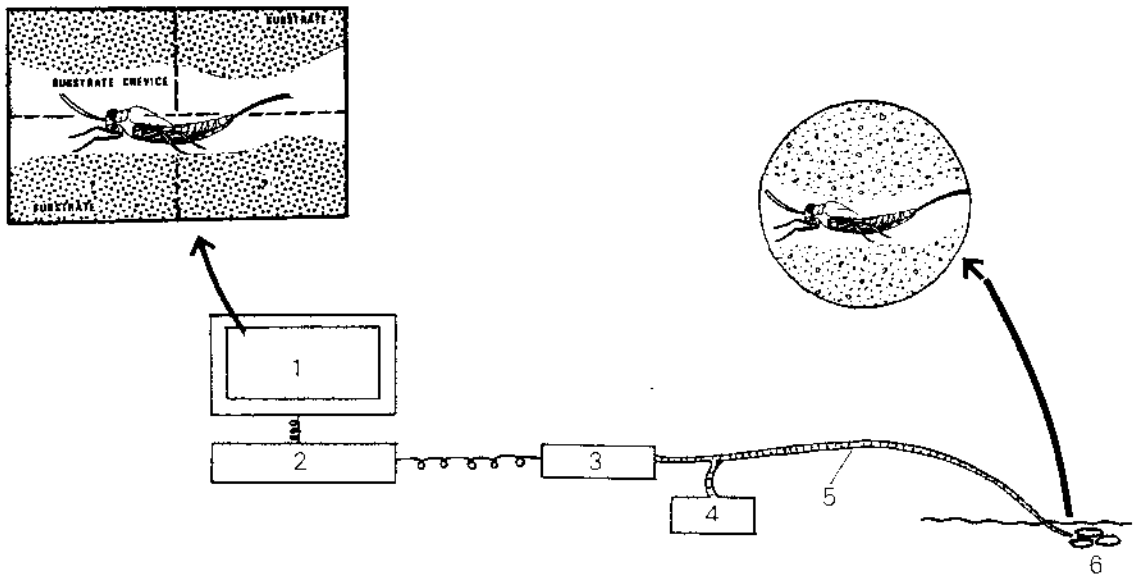


Fig. 1. Fiber optic observation system. Components include: 1, video monitor; 2, video cassette recorder; 3, TV camera with silicon diode array having low light level as well as infra-red sensitivity; 4, variable light source allowing for visible light or infra-red illumination; 5, fiberscope; 6, substrate under observation in the field or in laboratory channels.

lighted, fast current. Each treatment period lasted for one hour and was not replicated. The numbers of animals and their activity on the top and bottom of the substrate were censused every 15 min; drift from the experimental area was collected at the end of the one hour period. Observations in the dark were made with infra-red and near-red illumination. Our predictions were that if the mechanism underlying the drift for a given taxa is active, and assuming that a search for food represents the primary motivation of active drift, the numbers in the drift should be greater under conditions of low than high food abundance, irrespective of current velocity. If the mechanism underlying drift is passive, and assuming a diel benthic activity pattern that brings animals to locations of increased turbulence, numbers in the drift should be greater under conditions of fast than slow current, irrespective of food abundance.

The survival expectancy of drifting and non-drifting benthic animals was assessed in two field and one laboratory experiments as described in CUMMINS & WILZBACH (1987). In all studies, drifting and non-drifting members of the population were separated and animals within each group were held in containers individually, at stream temperatures, without food, for 12 h. Mortality was assessed after this time period, discounting individuals that were physically damaged.

## Results and discussion

### The relationship of drift to flow

Drag, expressed on a relative scale, varied considerably among taxa that differed in body shape (Fig. 2). Increases in velocity increased the drag experienced by an animal in a linear fashion. As demonstrated by large (12 mm in length) and small (6 mm) *Platycentropus* (Limnephilidae) (Fig. 2), an increase in size of individuals within a taxon appeared to increase the drag experienced and the relationship between drag and current velocity may be altered. The relationship between drag and current velocity did not vary in a consistent way with body shape. Chironomini midges, for example, exhibited a drag-velocity relationship very similar to that measured for *Psephenus* (Psephenidae).

Among the taxa that we examined, the velocity required for entrainment of killed animals in the water column was inversely correlated with a ratio of body height to width ( $p < 0.05$ , SPEARMAN rank correlation) (Fig. 3). For passively drifting animals, we suggest

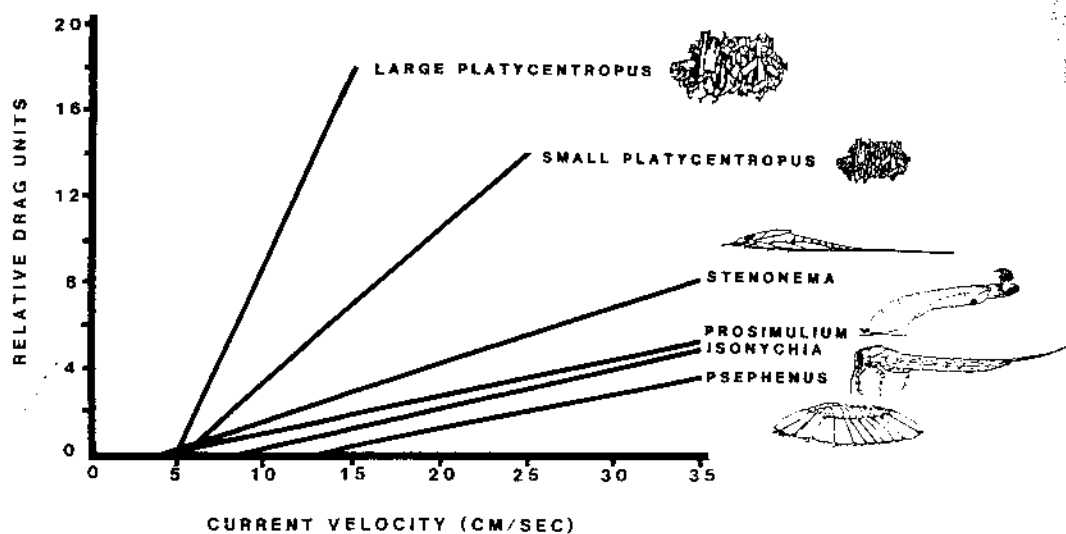


Fig. 2. Relationship between current velocity and drag, expressed in relative units, experienced by invertebrate taxa differing in body shape. Measurements of drag were taken in a laminar flow tank on animals coated in acrylic resin that were held stationary in a lifelike position.

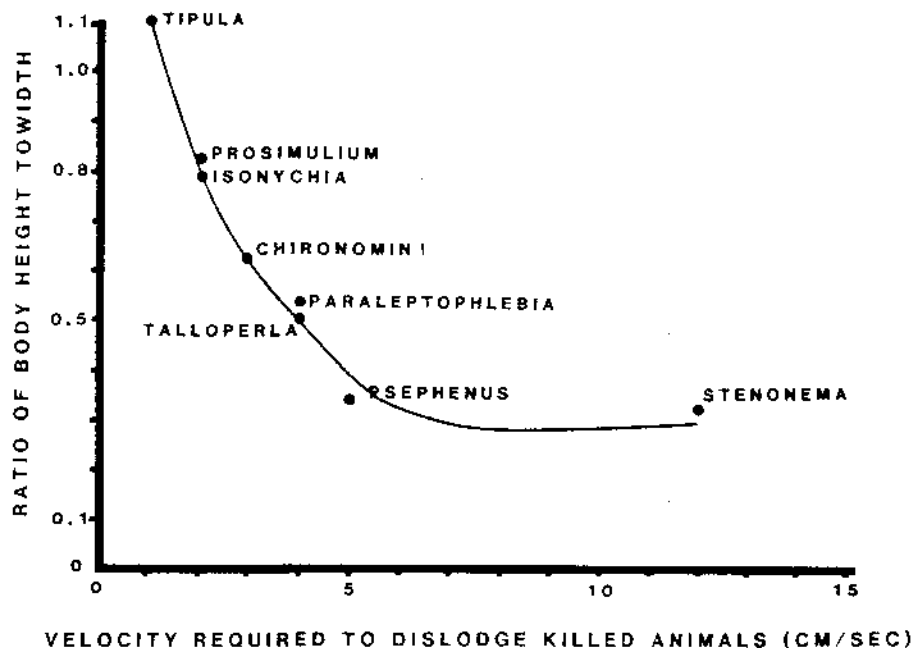


Fig. 3. Ratio of body height to width and the velocity required to dislodge killed individuals from substrate placed in a laminar flow tank. Height to width ratio was based on maximum body dimensions.

that a height to width ratio is a reasonable index of propensity to become dislodged with high flow.

The current velocities we determined that were required to dislodge live or dead drifting animals are within the range reported by other authors. BENGTTSSON (1984) reported that *Nemoura cinerea* (Nemouridae) are dislodged at velocities greater than  $30 \text{ cm} \cdot \text{s}^{-1}$ , which is roughly similar to the velocity required to dislodge live *Tallaperla* (Peltoperlidae) (Fig. 4), also a shredder-stonefly. Live *Taeniopteryx* (Taeniopterygidae), another shredder-stonefly, were dislodged in our studies at a mean velocity of  $65 \text{ cm} \cdot \text{s}^{-1}$ . DORIER

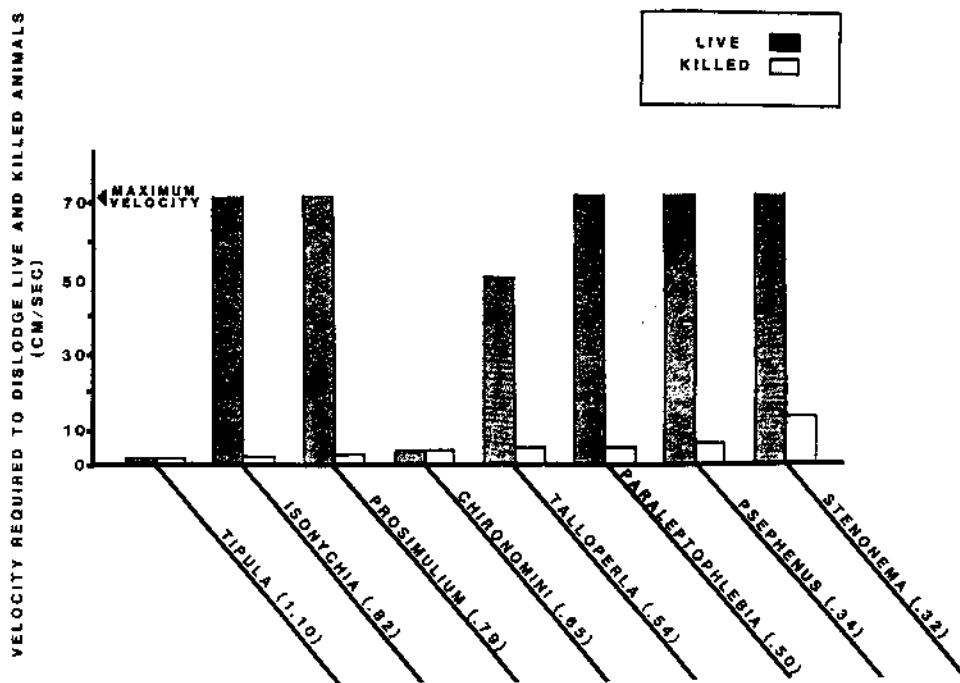


Fig. 4. The velocity required to dislodge live and killed stream invertebrates that were positioned on substrate in a laminar flow tank. The body height to width ratio of test animals is indicated in parentheses.

& VAILLANT (1954) reported that *Baetis rhodani* remained attached to a concrete slab at a current velocity of  $1.77 \text{ m} \cdot \text{s}^{-1}$ .

A large difference in the displacement velocity between live and dead specimens of the same taxon (Fig. 4) gives evidence of morphological and/or behavioral adaptations for maintaining position in the current. Morphological adaptations are apparent in dorsoventrally flattened taxa, such as *Stenonema* and other heptageniid mayflies that exhibit low height to width ratios. In animals that are streamlined and torpedo-shaped and that exhibit height to width ratios approaching unity, as for example in *Isonychia* (Oligoneuriidae), baetids, and other invertebrates whose mode of locomotion is swimming (MERRITT & CUMMINS 1984), a large discrepancy between live and dead animals may also suggest a greater capability for directing movement in the water column. We propose that it is within this group, the swimmers, that drift is generally active. HYNES (1970) maintained that baetids are such strong swimmers that models of their drift activity should not be extended to other taxa. The same is likely true for other swimmers (e.g., most of the Leptophlebiidae and Siphonuridae). This suggestion is based simply on common sense. An animal with morphological and behavioral adaptations for swimming is most likely to resort to water column transport in a search for food or other resources. Further, animals whose predominant means of locomotion are crawling along or burrowing into the substrate are not likely to be found in the water column except as a result of a change in life history stage, by accident, or under abnormal conditions (if the habitat becomes suddenly intolerable, water-borne transport may be the quickest and least costly way out).

For most benthic stream invertebrates, including those in the habit categories of burrower, clinger, and sprawler (CUMMINS 1973, MERRITT & CUMMINS 1984), we propose that drift probably represents an accidental dislodgement from the substrate. This should

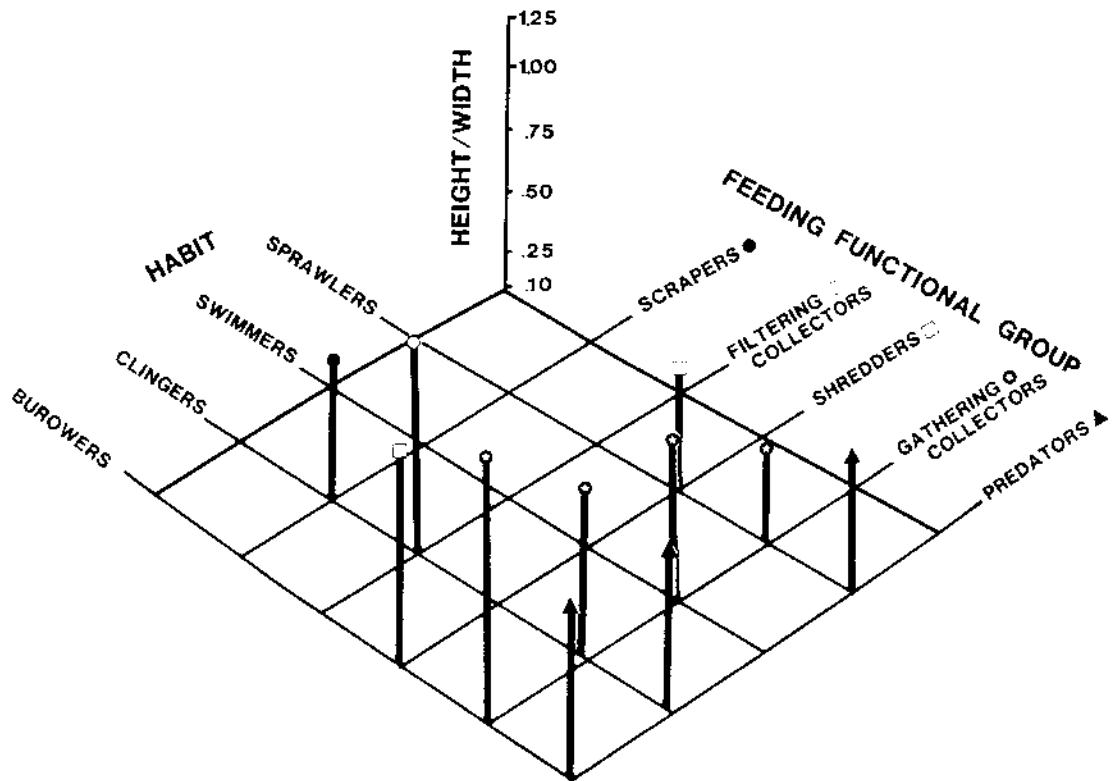


Fig. 5. A three-dimensional matrix relating habits (mode of locomotion and/or attachment), feeding functional groups, and an index of body shape (ratio of maximum body height to width). Values of height: width represent means of measurements made on animals in several taxa belonging to various combinations of feeding and habit functional groups.

occur whenever an animal moves into a region where turbulence is sufficient to lift the animal from the substrate. Turbulence is likely the critical parameter in determining drift magnitude rather than velocity per se. It is more likely to produce the lift required to entrain an animal into the current and it is likely difficult to orient to in a completely safe fashion. Inconsistency in the literature with regard to the influence of current velocity on drift magnitude probably has resulted also from an inability to accurately characterize flow at the actual invertebrate micro-locations, and because measurements of velocity are generally taken at the mouth of a drift net rather than at the point of actual water column entry of the invertebrate.

Proof of an active drift mechanism is difficult. The drift process encompasses two components that should perhaps be distinguished: water column entry, and movement through the water column. An animal, for example, may volitionally enter the water column but be unable to direct its course. Assuming that an animal is not physiologically disabled, an active mechanism of water column entry, we believe, can be inferred if an animal's entry into the water occurs under flow conditions (velocity and turbulence patterns) lower or more calm than those required to entrain an inert particle of equal size, shape, and density. Active drift through the water column can be inferred if an animal exhibits some control over its direction and location of re-settlement. Drift is likely active if, for example, an animal re-settles at a velocity greater than that described for sediments by Stokes Law (INMAN 1949). By these criteria the shorter settling time found by CIBAROWSKI (1983) and CAMPBELL (1985) for live rather than dead *Baetis* would indicate that at

least one component of drift, that is, movement through the water column, is an active process.

As with habit classifications, drift propensity may also vary with functional feeding groups inasmuch as the location, including proximity to turbulent flow, and timing of feeding vary with feeding strategy. For example, with few exceptions, all invertebrates classified as either scrapers or filtering collectors are clingers (MERRITT & CUMMINS 1984). The body shape is either flat (low height to width ratio) or long and streamlined (high depth to width) (Fig. 5). Gathering collectors are found among every habit category, and exhibit the greatest range in height to width values of the animals measured (Fig. 5).

### Diel Periodicity

A diel pattern of stream drift in which nocturnal abundance usually exceeded that occurring in daylight, often with a sharp peak after sunset and a sharp decrease at sunrise, was first documented by TANAKA (1960) and shortly thereafter by WATERS (1962) and MULLER (1963). This pattern has since been widely described to occur in a variety of insect groups. ELLIOTT (1968) proposed that the light-influenced process which results in nocturnal drift consists of two distinct activities: 1. an increased, non-directional rate of movement by animals on rocks, which represents an endogenous activity triggered by some light cue, and 2. a change in location onto the upper surface of a rock, which represents an activity exogenously controlled by negative phototaxis. HANEY et al. (1983) extended this model with a proposal that a relative change in light intensity is the cue which triggers photokinetic activity, and that phototaxis is regulated by an absolute light intensity. Field data at a lake outlet for two mayfly species on the timing of evening drift initiation relative to the timing of the light stimulus threshold for photokinetic activity supported the predictions derived from his model.

The applicability of the two-component model to describe the drift process for all taxa has not been evaluated. Obviously it should differ at least in detail for animals exhibiting positive or no phototaxis. Animals that are active on a 24 h basis, with no diel peaks in benthic activity, should not exhibit a diel periodicity in drift. Diel changes in rate of movement, the first step in ELLIOTT's model, are likely to occur only in taxa if inactivity during some part of a diel cycle is adaptive, for example, as a means of avoiding

Table 1. Predicted diel activity of stream invertebrates belonging to different combinations of feeding and habit functional groups. Predictions are based on published literature and personal observations of the authors. Because invertebrates probably generally forage on a 24 h basis (KOHLER 1985), only the timing of peak activity is listed below.

	Peak Timing of Benthic Activity	Location of Peak Activity	Diel Change in Location?	Mechanism of Water Column Entry
Scraper - clinger				
stone case caddisflies	24 h	top (of the substrate)	no	passive
mayflies and water pennies	night	top	yes	passive
Shredder - burrower	24 h	inside leaf peak	no	passive
Shredder - sprawler	24 h	outside leaf peak	no	passive
Filtering collector-clinger	24 h	top (some caddisflies may be on sides or bottom)	no	passive/active
Gathering collector-burrower	24 h	within sediments	no	passive
Gathering collector-swimmer	night	top	yes	active
Predator-sprawler (Libellulidae: Odonata)	24 h	top	no	passive
Predator-clinger (stoneflies, <i>Rhyacophila</i> )	day	top	no	passive
Predator-burrower (tanypod midges)	24 h	within sediments	no	passive

visual predators for nocturnally active animals (ALLAN 1978). As with diel changes in rate of movement, diel changes in location to the top of the substrate should occur only if differences in food quality or other resources warrant a change (Table 1). For example, for shredders feeding in leaf packs where food quality is likely as good or better inside as outside of a leaf pack, a diel location change is unlikely to be a necessary part of a process which leads to drift.

ELLIOTT's model, based primarily on observations of *Baetis rhodani*, does not distinguish between mechanisms of water column entry, but only describes the sequence of benthic activities that are associated with, or lead to, drift. Lack of correspondence between timing of diel benthic and drift activity has been used as evidence of active drift (KOHLENER 1985, ALLAN et al. 1986). Correspondence of benthic and drift activity, however, does not seem to be sufficient evidence to preclude active drift, as increased activity and a movement to the top of a rock may also precede volitional water column entry. Findings of ALLAN et al. (1986) that the mayflies *Baetis* and *Cinygmula* (Heptageniidae) exhibit increased nocturnal drift but are more active in the epibenthos in the day than at night are puzzling, particularly since travelling between food patches should involve sampling of the food resource at night in order to determine whether to stay or move on. Although night drift may be a strategy useful in reducing predation, our observations (CUMMINS & WILZBACH 1987) and others (PLOSKEY & BROWN 1980) on gut fullness do not support a general model of predominantly day feeding in a wide range of taxa in all functional groups. GRAESSER & LAKE (1984) argue that animals may appear to be more abundant on the tops of rocks by day only because more of them are drifting at night. We believe that, particularly in an open system where immigration and emigration are not controlled, the numbers present on the top of a rock surface should also be referenced relative to numbers on the bottom both day and night.

Contrary to the findings of ALLAN et al. (1986), we found that an increase in the drift of the mayfly *Stenonema* in the dark in a laboratory stream corresponded with an increase in the percent of animals positioned on the top of the substrate (Table 2). The mean percent of *Stenonema* individuals occurring in the drift was greater in the absence than in the presence of food and was slightly, but not significantly, greater under conditions of fast than slow current. Because the drift response of *Stenonema* was related to food availability to a greater extent than to current speed, these data suggest that the drift mechanism of this animal may be active rather than passive, particularly as the nymphs were capable of maintaining position in extremely fast currents (Fig. 4). However,

Table 2. Response of *Stenonema* and *Paraleptophlebia* to experimental conditions in a laboratory stream channel. Data represent the mean percent of animals present at the beginning of a trial that were observed on the top surface of the substrate during the trial period or that were collected in a drift net at the end of the 1 h period. The results of the three treatments (light, flow, and food), which were tested in combination (each food level in light and dark, each light level at fast and slow flows) were analyzed separately (e.g., total responses in the light, across all flow and food conditions).

	<i>Stenonema</i>		<i>Paraleptophlebia</i>	
	% on top of substrate	% in drift	% on top of substrate	% in drift
Light vs. dark	9 vs. 40	11 vs. 24	2 vs. 1	10 vs. 7
Slow vs. fast flow	25 vs. 24	15 vs. 20	3 vs. 0	3 vs. 14
No food vs. food	22 vs. 27	22 vs. 13	1 vs. 2	6 vs. 11



information on flow and turbulence conditions at substrate locations of the animals are required before a conclusion of active drift can be fully supported.

In laboratory experiments employing the fiber optic observation system to investigate the drifting and benthic activity of *Paraleptophlebia*, a response of the animals to light conditions was not observed (Table 2). Low numbers of individuals occurred at the surface of the substrate in both the light and dark, and numbers of individuals in the drift uniformly low. Drift abundance was greater in the presence than in the absence of food, and was greater under conditions of fast than slow current velocities, but numbers in the drift were not correlated with numbers of animals on the top of the substrate. These findings were contrary to our expectations that the drift activity of *Paraleptophlebia*, because it is a swimmer, would conform to our predictions of a taxon exhibiting active drift (i.e., that the mean percent of individuals in the drift would be greater under conditions of low than high food abundance, irrespective of current velocity). Literature reports that some *Paraleptophlebia* are at least facultative shredders (MERRITT & CUMMINS 1984) and that they exhibit higher growth rates on large than on small particle detritus (unpublished data) indicate that the periphyton, largely diatoms and fine particulate detritus, provided as the food source in this study, may not have represented an optimal food for this animal. The absence of benthic or drifting response of *Paraleptophlebia* to light conditions in this experiment are consistent with the absence of diel changes in benthic locations generally observed to characterize shredders (Table 1). *Paraleptophlebia* may represent a category of animals that exhibits active drift, but without any diel pulse in benthic or drift activity.

#### Survival expectancy of drifting and non-drifting animals

Results from field and laboratory studies support a conclusion that drifting animals experience a lower survival expectancy than their non-drifting, benthic counterparts. Mortality of drifting animals 12 h after collection was three to five times as great as in benthic animals (Table 3). Physical injury was ruled out as a cause of death, and predation and food limitation as causes were not established. In addition to evidence that potential pathogens are present in the animals (CUMMINS & WILZBACH 1987), findings of STATZNER & BITTNER (1983) and WILZBACH et al. (1986) that drifting individuals are more heavily parasitized than the non-drifting population suggests that pathogen loads may play a major role in determining propensity of an insect to drift.

We propose that the fate of drifting animals should vary with drift mechanism. Actively drifting animals should exhibit a similar or greater survival expectancy than the

Table 3. Percent mortality in drifting and benthic insects 12 h after collection. Data are from 2 field studies and a laboratory experiment that are described in CUMMINS & WILZBACH (1987). In all studies, drifting and benthic animals were handled in a similar manner, and were held in the dark at stream temperature without food prior to assessment for mortality. Physically damaged individuals were deleted from calculations.

	% Mortality	
	Drift (n)	Benthos (n)
Field		
Long-term	23 (236)	5 ( 178)
Short-term	24 ( 39)	7 ( 58)
Laboratory	38 (254)	7 (1213)

population at large. Passively drifting animals, on the other hand, may be accidentally dislodged because they are for some reason less tolerant of stress. PETERSEN found, for example, that the drifting amphipod *Gammarus* was more sensitive to lethal concentrations of sodium metaarsenite than were individuals collected from the benthos (Univ. Lund, pers. comm.). This could be the result of pathogenic infection or other physiological stress. Irrespective of the cause, passively drifting animals may exhibit a lower survival expectancy than the non-drifting benthic population. As such, their role in downstream colonization would be greatly reduced.

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Authors' address:

Appalachian Environmental Laboratory, University of Maryland, Frostburg, Maryland 21532, U.S.A.