

Effects of substrate and predator type on microdistributions and drift of a lotic mayfly

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Abstract. This study examines the effects of substrate and predator type on microdistributions and drift responses of nymphs of the mayfly *Heptagenia hebe* in a warmwater sandy stream in northern Michigan. Nymphs were significantly more abundant on cobble/boulder substrates than on gravel/pebble or woody debris. Mayfly densities among these substrates were unrelated to densities of predaceous stoneflies (perlids) and hellgrammites (*Nigronia serricornis*). Nocturnal drift, measured instream from enclosed substrates, was significantly lower from cobble/boulder substrates (0.1%) than from gravel/pebble and woody debris. Drift rates were unrelated to stonefly, crayfish, or fish (mottled sculpin and hornyhead chubs) densities, but were positively correlated with hellgrammite densities. However, experiments in artificial stream channels revealed that propensity to drift was strongly linked to substrate type, not predator type (hellgrammites and/or stoneflies). Cobble/boulder substrates apparently function as sinks (where immigration > emigration) for dispersing *H. hebe* nymphs in sandy streams with limited suitable habitat.

Key words: *Heptagenia hebe* nymphs, substrate, drift, predator type, instream enclosures, experimental stream channels.

Elucidation of factors that determine patch-use and drift decisions of lotic macroinvertebrates is critical to understanding benthic community structure and dynamics. Patch-use patterns may be determined by many interacting factors such as substrate type, size, and condition (e.g., Giller and Cambell 1989, Holomuzki and Messier 1993, Rader and McArthur 1995), current velocity (e.g., Bergey and Ward 1989, Poff et al. 1991), food (e.g., Palmer 1995), competitor densities (e.g., Lancaster et al. 1988, Hemphill 1991), or predation risk (e.g., Scrimgeour et al. 1994, Kratz 1996). Spatio-temporal variation in these factors creates habitat patches with varying microhabitat physical characteristics, resource profitability, and predation risk. Interplay between these resultant effects influences relative suitability of patches and hence distributional responses of the zoobenthos (Townsend 1989, Lancaster et al. 1991).

Predators can have particularly strong effects on emigration behaviors, and thus on local densities and patch-use patterns of lotic mayflies. Many mayfly larvae drift to escape or avoid encounters with predatory vertebrates (fish) (Allan 1978, Kohler and McPeck 1989, Williams 1990, Culp et al. 1991, Forrester 1994) or invertebrates (e.g., stoneflies) (Corkum and Clifford 1980, Peckarsky 1980, 1987, Malmqvist and Sjöström 1987). However, drift responses to predator risk

may be influenced by juxtaposition and availability of suitable habitat patches. For example, in sandy streams suitable microhabitats are disconnected isolated patches separated by uninhabitable stretches of sand. Drift is the key way of moving between patches. Relatively long times spent in the water column and scarcity of suitable habitat are added costs to interpatch movements, and may thus affect the triggering of predator-induced drift responses.

Here, I describe microhabitat distributions and drift responses of nymphs of the mayfly *Heptagenia hebe* McDunnough in a sandy-bottom stream in northern Michigan, USA. Heptageniids are scrapers and gatherers (Shapas and Hilsenhoff 1978, Edmunds and Waltz 1996) commonly found in rocky substrates in small streams to rivers (Flowers and Hilsenhoff 1975). Overall their propensity to drift is relatively low (Forrester 1994). However, determinants of their microhabitat distributions and drift response are poorly known. I combine correlative observations from field enclosures with data from artificial stream experiments to examine how substrate and predator type interplay to affect drift decisions. The influence of a particular predator on mayfly drift responses may be substrate-specific, considering that predators differ in foraging efficiency, and hence pose different threats, in different substrates (Fuller and Rand 1990). I

also studied microdistributions of other heptageniid nymphs (*H. diabasia* Burks and *Stenonema* spp.) to address their potential effects on patch use and drift of *H. hebe*. Because heptageniids are abundant and play a dual role as grazer and detritivore in northern Michigan streams, evaluating the effects of substrate and predator type on their microdistributions and emigration rates is important to understanding system function.

Study Site

The study was conducted along a 800-m stretch of the East Branch of the Maple River during summer 1995. The East Branch of the Maple River is a permanent, warmwater 2nd-order stream that drains Douglas Lake. The study stretch runs by the Experimental Stream Facility of the University of Michigan Biological Station, ~3 km east of Pellston, Emmet Co. Early summer temperatures range from 15 to 23°C, but temperatures may exceed 25°C in August. Discharge (0.463 m³/s) varied little during the study.

The East Branch flows through a mixed conifer and birch-aspen forest underlain with sand soil. The predominant riparian shrubs are speckled alder (*Alnus rugosa* [Duroi] Sprengel) and sweet gale (*Myrica gale* L.). The river has a sand-dominated substrate (>90%) at the study location, though deposits in the form of woody debris and fine particulate organic matter (FPOM) are abundant along stream margins, particularly where the channel widens. Long reaches of sand, often >50 m, are interspersed with patches of gravel/pebble. Cobble/boulder substrates are rare (<1% of total substrate) and are typically found along vertical or steep banks near bends in the channel.

Heptageniids and *Baetis* spp. are the dominant mayflies at the study site. *Heptagenia hebe* and *H. diabasia* are the only species present within the genus. *Stenonema vicarium* (Walker), *S. modestum* (Banks) and *S. exiguum* Traver are also common, while *Stenacron interpunctatum* (Say) is rare. The perlid stoneflies *Acroncuria abnormis* (Newman), *Agnatina capitata* (Pictet), and *Paragnetina media* (Walker), and the hellgrammite, *Nigronia serricornis* (Say), are common invertebrate predators. *Paragnetina* emerges in late-June to early July; however *A. abnormis* and *A. capitata* are present through July. The crayfish *Orconectes propinquus* (Girard) is also abundant.

Relatively few fish inhabit study sections of the stream. Hornyhead chubs (*Nocomis biguttatus* Kirtland) and mottled sculpin (*Cottus bairdi* Girard) are relatively common, while brook trout (*Salvelinus fontinalis* Mitchell), northern redbelly dace (*Chrosomus eos* Cope), and brook lamprey (*Ichthyomyzon fossor* Reighard and Cummins) are rare.

Methods

Distributions among streambed substrates

I compared distributions of heptageniids, stoneflies, and hellgrammites among 5 substrate types in runs on 4 dates between 28 June and 5 July 1995. Substrates were different sizes of inorganic particles (i.e., sand, gravel/pebble, and cobble/boulder), FPOM, and woody debris. Different collecting techniques were used in different substrates because current velocity and mean particle size varied so widely among substrates. I used a Hess sampler (33 cm diameter, 41 cm height, 1 mm mesh) to sample sand and gravel/pebble substrata from high flow areas ($\bar{x} \pm \text{SE}$; sand: 21 ± 4 cm/s, gravel/pebble: 27 ± 8 cm/s). On each date, 5 samples were randomly taken from 1-m wide transects extending across the main channel (~4–6 m wide). I used a stove-pipe sampler (24 cm diameter, 43 cm high) for FPOM collections in low-flow areas (2 ± 1 cm/s). Five FPOM samples were taken on each date along stream margins from 1-m wide transects that paralleled the stream channel. The sampler was sunk 10–15 cm into the substrate and all animals within were removed by dip net to a depth of 3–4 cm. Sand, gravel/pebble, and FPOM samples were immediately placed in Ziploc[®] plastic bags and preserved with 70% ethanol.

The size and orientation of cobble/boulder substrates and woody debris precluded the use of substrate-penetrating samplers and thus required different sampling techniques. Densities in cobble/boulder areas (flow: 17 ± 3 cm/s) were estimated by lifting rocks into an enamel pan and counting the number of organisms on each rock. A drift net (363 μm mesh) placed 1–5 cm behind each chosen rock captured fleeing animals as rocks were lifted from the water. Ten rocks, each smaller in at least 1 dimension than the width of the enamel pan (22 cm), were chosen from a 1.0-m wide transect that paralleled

the stream channel. Animals were removed from rocks by hand and by gentle splashes with water. To compute densities, bottom surface areas of rocks (i.e., portion resting on streambed) were estimated using areas of simple geometric shapes which approximated that of the rock. Lastly, 2–4 samples of woody debris were collected on each date from 55×55 cm quadrats outlined by wire. All wood was collected by hand and placed in a plastic tub next to the sampling quadrat. Drift nets placed immediately downstream of each quadrat (flow: 9 ± 3 cm/s) captured fleeing animals as sticks were lifted. Animals were immediately removed from samples at the Experimental Stream Facility by hand sorting and by rinsing sticks with water over a 0.5-mm-mesh sieve. Counts from both samples and nets were used to estimate densities.

To report mayfly and predator abundances consistently across substrates, regardless of sampling technique, I present all densities on the basis of number/m². Log ($\times + 1$) transformed densities were analyzed using single factor ANOVAs followed by Tukey's msd tests with $\alpha = 0.05$ (SYSTAT Version 4.0, Evanston, Illinois). Homoscedascity of transformed data was confirmed by Bartlett's tests. I used Pearson-product correlation analyses to compare densities of mayflies to densities of predators in different substrates.

Substrate effects on drift in artificial streams

Drift rates of *H. hebe* were compared among 4 predator-free substrates in artificial stream channels at the University of Michigan Experimental Stream Facility. Water in the 32 vinyl gutters (each 2.8 m long, 0.1 m wide, 7 cm high) used as channels was drawn from the East Branch of the Maple River by a Monarch® pump with 2.54-cm holes in the impeller. Valves at the head of each channel regulated discharge in the flow-through channels. Water in each channel first flowed through a "pool" section that collected FPOM, then through a section containing substrate and mayflies (Fig. 1). A 1.3-m long section of channel from the valve heads to a dam of clay tiles (5 × 5 cm) stacked on end collected incoming FPOM. Nylon screening (0.5-mm mesh), supported by galvanized hardware cloth (1.2-cm mesh) and glued with silicon sealant to the bottom and sides of channels im-

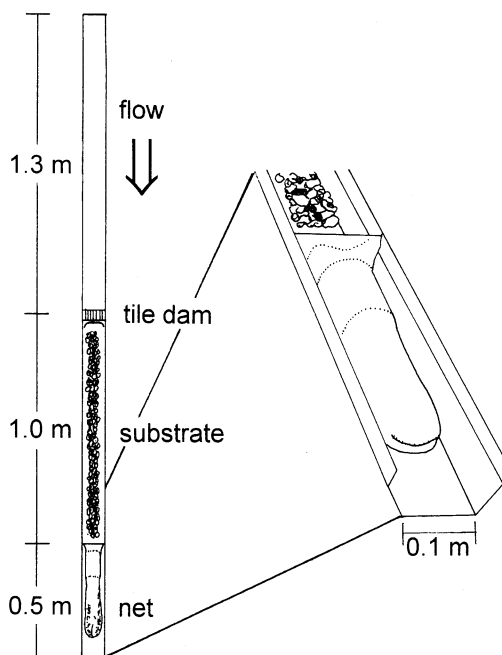


FIG. 1. Schematic of an artificial stream channel for measuring drift.

mediately below the tile dams, restricted mayflies to the substrate-containing section. A drift net placed 1 m downstream from the nylon screening captured drifting mayflies from the substrate section. Drift nets consisted of knee-high nylons (K-mart® brand) supported by an inserted piece of PVC pipe (8–10 cm long, 6-cm diameter). The mouth of the net was supported and expanded by hardware cloth (1.27-cm mesh) and glued with silicon sealant to the bottom and sides of channels, conforming to the rectangular shape of channels.

On 14 July, 1 d after drift nets were glued in place, substrate was added to each 1-m section of channel between the nylon screening and drift net. Eight channels each received 1 substrate type: sand, gravel/pebble, cobble, or woody debris. Sand and gravel substrates were washed and placed in a layer ~2 cm deep. Cobble treatments had 10 small cobbles with diameters (7–9 cm) slightly less than the channel width. Enough washed sticks (~500 g dry mass), collected from the East Branch, were added to cover ~90% of the bottom of channels in woody debris treatments. Discharge (0.2 L/s) and temperature (21°C) were uniform among channels.

Heptagenia hebe nymphs were collected between 1600 and 1800 h on 14 July from cobble/boulder substrates and randomly sorted in groups of ten into plastic cups. Each group was then randomly assigned to a channel. Mayflies (4.0–6.0 mm lengths, excluding caudal filaments) were poured gently from cups at sunset (2100 h) at the head of each 1-m section, but behind a hand-held tile (5×5 cm). The tile served as a baffle to prevent rapid displacement by the current and was removed only after all mayflies settled on substrates. All channels, but particularly those with sand, were checked over the next 30 min to note whether mayflies became established on substrates. After 12 h (0900 h), number of mayflies captured in drift nets and remaining in substrates were counted in each channel. Percent drift in each channel was computed by dividing the number of animals captured in nets by the total number recovered from each channel. Percent drift was arcsine-transformed to meet normality and homoscedasticity assumptions and analyzed using single factor ANOVA (SYSTAT Version 4.0). Differences among treatments were determined by using Tukey's msd tests.

Substrate, predator type, and drift in instream enclosures

I also compared nocturnal drift rates of *H. hebe* among enclosed substrates of gravel/pebble, cobble/boulder or woody debris in the East Branch of the Maple River from 5 to 31 July. Enclosures consisted of 2 sides of solid aluminum sheeting supported by rebar, with upstream and downstream ends blocked by drift nets. Sides of enclosures (0.91 m high) paralleled the current and were sunk 5–10 cm into the substratum to prevent animals from entering or escaping. Areas of enclosures (cobble/boulder: 3.9–7.7 m², gravel/pebble: 2.5–3.8 m², wood: 0.8–1.6 m²) varied with patch size of substrates. To minimize substrate disturbance, areas to be enclosed were not trampled during construction, and drift nets were not placed at ends until ~36 h after construction of sides. Drift nets (mouth 47×33 cm) were placed at upstream and downstream ends at sunset to capture all animals entering and leaving the enclosed area. Current velocity, as measured by a Marsh-McBirney meter 2 cm from the bottom, was taken in enclosed substrates to assess its

effect on drift. Inflow nets at the head of enclosures gradually accumulated FPOM, which reduced current velocity (~25%) in enclosures. Downstream nets did not clog over the 12 h sampling period.

Animals were removed from nets at 0900 h and immediately preserved in 70% ethanol. Densities of heptageniids, perlid stoneflies, and hellgrammites within enclosed substrates were then estimated following the previously described methods. Calculating densities enabled me to estimate the total number of study organisms in enclosures and hence compute percent drift from each substrate. Percent drift was arcsine-transformed and analyzed using single factor ANOVA followed by Tukey's test. In addition, I visually estimated densities of two other potential predators, fish (sculpins and chubs) and crayfish, in enclosures. About 1 h after drift nets were positioned at ends (~2200 h), when sculpins and crayfish were active, I slowly walked along a side of an enclosure and recorded the number of fish and crayfish observed with a narrow beam headlamp. Individual fish and crayfish did not seem disturbed by brief exposures (2–3 s) to the light. Counts were converted to number per m². Correlation analyses were used to determine whether drift rates of *H. hebe* were related to densities of particular predator types.

Substrate, predator type, and drift in artificial streams

The influence of particular predators on nocturnal drift of *H. hebe* in different substrates was also examined in a 2-factor factorial design experiment in artificial stream channels. Specifically, I measured drift rates in 3 different substrates (gravel/pebble, cobble, or woody debris) with different predator types/combinations (perlid stoneflies present, hellgrammites present, or both predators present). Both predators generally hunt at night and feed on heptageniids (e.g., Pritchard and Leischner 1973, Stewart et al. 1973, Johnson 1981). Each of the 9 treatment combinations was replicated 5 times, resulting in 45 separate experimental units (channels).

Channel setup was the same as in the first substrate-drift experiment. On 21 July, I added gravel/pebble, cobble, or woody debris to channels ($n = 15$ for each substrate). Mayflies, stone-

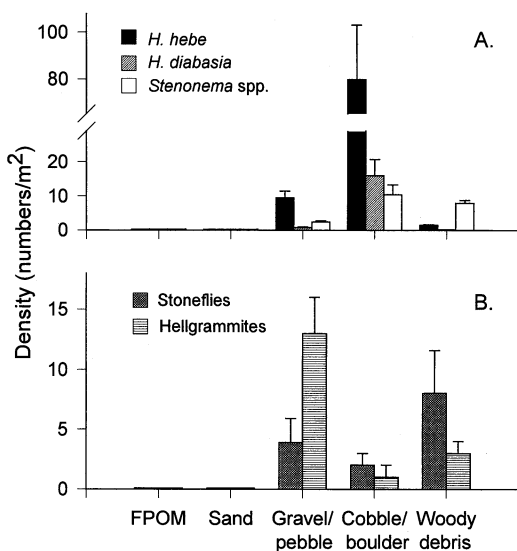


FIG. 2. Grand mean (+1 SE) densities of heptageniids (A) and invertebrate predators (B) in different substrates in the East Branch of the Maple River. Data are from 4 sampling dates for each substrate.

flies, and hellgrammites were collected from the East Branch of the Maple River between 1600 and 1800 h. Mayflies were then sorted into groups of 10, while stonefly larvae and hellgrammites were each sorted into groups of 2. Two stoneflies, 2 hellgrammites or 2 of each predator were randomly assigned to channels. These ratios (5:1 or 5:2) of mayflies to invertebrate predators can be found in substratum patches in the East Branch of the Maple River. Predators and then mayflies were added to channels at sunset following previously described procedures. All animals were collected and counted from drift nets and substrates 12 h later. A 2-way ANOVA was used to assess the effects of substrate type and predator combination on arcsine-transformed drift rates (SYSTAT Version 4.0).

Results

Distributions among streambed substrates

Heptageniid densities differed among substrates. *Heptagenia hebe* was significantly more dense in cobble/boulder than in gravel/pebble or woody debris (Fig. 2A; $F_{2,9} = 50.03$, $p < 0.001$). Densities of *H. diabasias* also differed among substrates ($F_{2,9} = 54.06$, $p < 0.001$), with

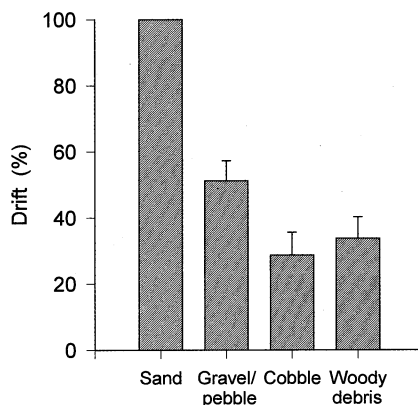


FIG. 3. Mean (+1 SE) percent drift of *H. hebe* from different substrates in predator-free, artificial stream channels ($n = 8$ for each substrate type).

patterns of microdistribution similar to those of *H. hebe* (Fig. 2A). However, densities of *H. hebe* were significantly higher than those of *H. diabasias* in all 3 substrate types (all $p < 0.05$). As for *Stenonema* spp., densities were significantly higher on wood and cobble/boulder than in gravel/pebble (Fig. 2A; $F_{2,9} = 914$, $p = 0.007$). Density distributions of *H. hebe* and *Stenonema* spp. were not related ($r = 0.214$, $n = 12$, $p > 0.75$). No heptageniids were found in sand or FPOM.

Hellgrammite densities also differed among substrate types (Fig. 2B). Hellgrammites were significantly more dense on gravel/pebble than on cobble/boulder or woody debris ($F_{2,9} = 9.27$, $p = 0.007$). Stonefly densities, however, were uniform across these substrate types ($F_{2,9} = 1.47$, $p > 0.25$). *Heptagenia hebe* densities were not correlated with densities of either predator type (stoneflies: $r = -0.331$, $n = 12$, $p > 0.25$; hellgrammites: $r = -0.481$, $n = 12$, $p = 0.11$). Neither stoneflies nor hellgrammites were found in sand or FPOM.

Substrate effects on drift in artificial streams

Propensity of *H. hebe* to drift differed among substrates in predator-free experimental stream channels (Fig. 3). Drift rates were significantly higher from gravel/pebble than from cobble and woody debris ($F_{2,21} = 3.27$, $p = 0.05$). Drift rates were 100% from sand. In fact, on average, 76.2% of all *H. hebe* drifted from sand substrates within 15 min after being added to channels.

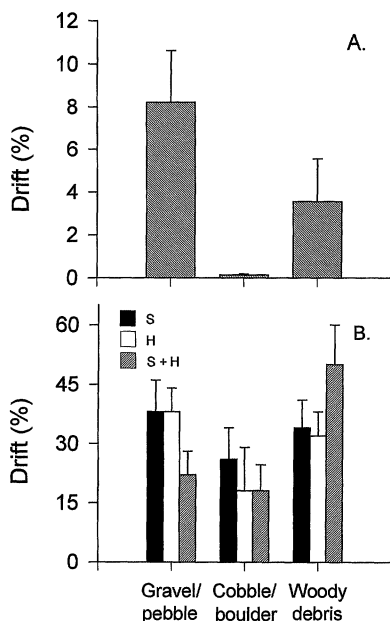


FIG. 4. Mean (+1 SE) percent drift of *H. hebe* from predator-containing substrates in enclosed areas of the East Branch of the Maple River (A) and in artificial stream channels (B). Letters in (B) represent predator combinations in different substrates: stoneflies (S) only, hellgrammites (H) only, and both (S + H) predators present. Replicates (n) were 5 for each substrate in (A) and for each substrate/predator combination in (B).

Drift in instream enclosures

Drift of *H. hebe* from enclosed substrates in the East Branch of the Maple River was significantly greater from gravel/pebble than from other substrates (Fig. 4A; $F_{2,12} = 4.37$, $p < 0.05$). Drift was negligible (0.1%) from cobble/boulder substrates. Drift rate of *H. hebe* was significantly positively correlated with hellgrammite densities among substrates ($r = 0.503$, $n = 15$, $p = 0.056$), but not with stonefly densities ($r = -0.061$, $n = 15$, $p > 0.80$). No hellgrammites were captured in drift nets from any substrate. Although no stoneflies drifted from cobble/boulder substrates, drift did occur from gravel/pebble (4.64%) and woody debris (7.34%).

Crayfish densities in enclosures differed among substrates ($F_{2,12} = 5.86$, $p < 0.05$), being highest in cobble/boulder ($0.9/\text{m}^2$) and similar between gravel/pebble ($0.3/\text{m}^2$) and woody debris ($0.2/\text{m}^2$) (Tukey's msd). Fish densities (0.5 – $0.6/\text{m}^2$) were similar across enclosed substrates

TABLE 1. Results of a 2-way ANOVA comparing drift of *H. hebe* from different substrate types (gravel/pebble, cobble, woody debris) with different predator types/combinations (with stoneflies, with hellgrammites, with both predators).

Source of variation	SS	df	F	p
Substrate type	25.20	2	4.154	0.024
Predator combination	0.93	2	0.154	0.858
Substrate type \times predator combination	19.47	4	1.604	0.194

($F_{2,12} = 0.12$, $p > 0.75$). Drift rates of *H. hebe* were not correlated with densities of either crayfish ($r = -0.413$, $n = 15$, $p > 0.10$) or fish ($r = -0.219$, $n = 15$, $p > 0.25$). In addition, current velocities differed among enclosed substrates (cobble/boulder: 13 ± 1 cm/s, gravel/pebble: 10 ± 2 cm/s, woody debris: 7 ± 1 cm/s) ($F_{2,12} = 4.87$, $p < 0.05$), but were not related to drift of *H. hebe* ($r = -0.05$, $n = 15$, $p > 0.85$).

Few *H. hebe* were caught in upstream drift nets in all substrates ($\bar{x} \pm \text{SE}$: 2.0 ± 0.5 ; limits: 0–6 individuals).

Effects of substrate and predator type on drift in artificial streams

In experimental stream channels, drift of *H. hebe* was not affected differently by stoneflies or hellgrammites alone or combined (Table 1). Instead, drift was strongly linked to substrate type (Fig. 4B), being significantly higher from gravel/pebble than from cobble. This latter result is consistent with data from enclosed substrates in the East Branch of the Maple River. However, overall drift rates were considerably higher in artificial streams than in the East Branch, perhaps because of stress caused by capture and release.

Discussion

Substrate type significantly affected microdistributions of *H. hebe*. Nymphs were more abundant on cobble/boulder than on gravel/pebble and woody debris. The congener *H. diabasias* was similarly distributed among substrates, though its densities were 4–11 \times lower than those of *H. hebe*. In contrast, *Stenonema* spp. were abundant on woody debris, where *Heptagenia* were least abundant. Predator distribu-

tions, at least those examined in this paper, cannot clearly explain this difference in heptageniid microdistributions. A possible explanation is that interspecific competition structures distributions of heptageniids among suitable substrate types. The potential for this interaction may be strong considering the limited habitats available to mayflies in sand-dominated reaches of this stream.

No heptageniids, or other macroinvertebrates, were sampled from sand substrates. Downstream transport of sand in midchannel at the study site is considerable, causing abrasion and constant changes in sediment distribution. Moreover, open sandy stretches offer little protection from predators (Kershner and Lodge 1995). Heptageniids were also absent from FPOM patches. Although fine detritus is a food source for heptageniids (McShaffrey and McCafferty 1986, Edmunds and Waltz 1996), the FPOM in the East Branch is largely refractory material high in lignin and cellulose and of little nutritive value (R.J. Stevenson, University of Louisville, personal communication, see also Peters et al. 1989). Additionally, FPOM patches were in warm, marginal areas with little, if any, flow, and are likely oxygen-poor relative to other substrates (Madsen 1968). Heptageniids are often found in fast-flowing areas (Unzicker and Carlson 1982, Ward 1992, Edmunds and Waltz 1996) where oxygen replenishment is continual. Thus, concomitant effects of reduced foraging profitability and oxygen stress may explain the absence of heptageniids from FPOM patches.

My results suggest that propensity to drift by *H. hebe* is strongly linked to substratum type. All nymphs drifted from sand substrates in the artificial stream experiment. This behavior further explains the absence of mayflies from sand substrates instream. Moreover, drift rates were significantly lower from cobbles than from other substrates both in instream enclosed substrates and in artificial channels. Predator type was not a determinant of drift, as shown by results of the factorial design experiment in artificial channels. This latter result is consistent with findings from a few other studies indicating that heptageniids crawl away from predators rather than drift (Peckarsky 1980, Williams 1987, Forrester 1994). In contrast, it appears baetid mayflies generally drift to escape predators (e.g., Allan 1978, Peckarsky 1987, Lancaster 1990, Culp et al. 1991), as do siphonurid mayflies (McIn-

tosh and Townsend 1994). Better knowledge of species-specific responses to predator attacks will contribute to our understanding of benthic community structure and patch dynamics.

The relatively high densities and negligible drift from cobble/boulder patches suggest that propensity to drift is not density-dependent and that these substrates function as sinks for within stream dispersal. Sink is referred to here as an area in which immigration exceeds emigration. Cobble/boulder substrates can provide refugia from the abrading effects of sand (Minshall 1984) and from many insect and fish predators (e.g., Holomuzki and Messier 1993, Hill and Lodge 1994). Moreover, cobble/boulder patches may be good microhabitats for food. Detritus (FPOM) can accumulate in interstitial spaces, and algae can grow on rock surfaces. However, studies are needed that detail the extent of detritivory and grazing by different heptageniid species (see McShaffrey and McCafferty 1986). Considering that diet can influence aquatic insect life-histories (Sweeney 1984), relating feeding habits to habitat-specific life-history traits (e.g., growth, development, time of emergence) will increase our understanding of patch-use patterns and dispersal dynamics of these mayflies.

In summary, my study shows that substrate type strongly affects microdistributions and drift responses of *H. hebe*. Drift rates were unaffected by predator type. This latter result differs from many studies that show that predatory invertebrates generally increase the drift rates of prey (reviewed by Wooster and Sih 1995). Substrate type and patchiness must be considered when assessing how dispersal shapes mayfly distributions in streams.

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