



## Effects of structural habitat on drift distance and benthic settlement of the caddisfly, *Ceratopsyche sparna*

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### Abstract

We conducted two experiments in flow-through, artificial streams to examine how habitat structure affected drift and benthic resettlement of larval hydropsychid caddisflies (*Ceratopsyche sparna*). In the first experiment, we quantified drift distance and the number of times larvae re-entered the drift in  $9.0 \times 0.51$ -m channels with contiguous patches (ea. 2.5-m long) of biofilm-covered gravel, biofilm-covered cobbles (– *Cladophora*), and *Cladophora*-covered cobbles (+ *Cladophora*). In the second experiment, we tracked nocturnal movements of larvae after benthic settlement in  $2.8 \times 0.1$ -m channels, each containing one of the three habitat types. In experiment 1, drift distance was (1) greatest in gravel and lowest in cobbles + *Cladophora*, (2) inversely related to hydraulic roughness of habitats, (3) independent of body size, and (4) similar for live and dead larvae. Average drift distance was relatively short (<2.5 m), regardless of habitat type. Number of drift re-entries also varied among habitats, being greatest in gravel and lowest in cobbles + *Cladophora*. No larvae re-entered the drift after settling in *Cladophora* patches. Results from experiment 2 revealed that drift propensities were higher for larvae in biofilm-covered gravel and cobbles than in cobbles + *Cladophora*. Larvae remaining in substrate patches (i.e. not drifting) laid fewer draglines in biofilm-covered stones than in *Cladophora* patches. Extent of benthic movement (i.e., crawling) by non-drifting larvae did not differ significantly among habitats. However, distance moved did differ with flow direction, being 4× greater downstream than upstream. These results highlight how local substrate and hydraulic conditions interact to affect small-scale movements of caddisfly larvae.

### Introduction

Movements by organisms are often influenced by the spatial and temporal heterogeneity of environments. Spatio-temporal variability in habitat physical characteristics, resource profitability, and (or) predation risk creates habitat patches that differ in suitability. Movement in response to patch variability has important implications for many ecological processes, including population spread and redistribution, local population and metapopulation dynamics, and strengths of social and species interactions (e.g. Hanski, 1998; Gilliam & Fraser, 2001).

Many lotic macroinvertebrates move among habitat patches by drifting, the downstream transport of individuals by water flow (Brittain & Eikeland, 1988). The focus of many drift studies has been the identification of environmental cues that synchronize the drift of a large portion of the benthos, e.g. nocturnal drift periodicity (e.g. Waters, 1962; Haney et al., 1983) or drift in response to predators (e.g. Allan, 1978), flow disturbance (e.g. Cobb et al., 1992; Lancaster et al., 1996) or toxicological perturbations (e.g. Schulz & Liess, 1999). Estimates of transport distance from such mass movements suggest that macroinvertebrates may drift substantial distances (10–60 m per drift)

(McLay, 1970; Elliot, 1971; Neves, 1979; Larkin & McKone, 1985). According to studies of drift at the level of species or individual, drift entry appears largely determined by food abundance (e.g. Kohler, 1985), predation risk (e.g. Forrester, 1994; Peckarsky, 1996), or accidental dislodgement (Elliot, 1967). Moreover, drift distances appear to be highly variable, depending largely on current velocity and the organism's ability to regain the bottom (i.e. swimming ability) (Cibrowski, 1983; Campbell, 1985; Allan & Feifarek, 1989; Kerans, 1992). Understanding how environmental variability affects the movements and distributions of benthic animals will require more data on how physical habitat features affect drift responses of individuals. Habitat structure in streams is a complex amalgam of sediment size and shape, epilithic cover, and flow forces over sediment surfaces. Together, these features can influence drift behaviors of individuals by affecting their hydraulic environments, predation risk, and food availability.

Here, we explore the effects of habitat structure on drift responses and resettlement behaviors of the hydroptychid caddisfly, *Ceratopsyche sparna*. The species is often an integral part of food webs of small streams to rivers across eastern North America (Schuester & Etnier 1978; Wiggins, 1996). Larval hydroptychids are net-spinning filter feeders, eating mainly small sestonic algae (e.g. diatoms) and leaf detritus (Fuller & Mackay, 1980). Many species construct retreats (i.e. immovable cases) of tiny stones or plant material on the tops of stones in rapid flows (riffles) (e.g. Malas & Wallace, 1977). Retreats serve a dual role as a refugium from predators (Fuller & Rand, 1990) and as a substrate to attach a food-capturing net. Dispersing individuals may leave the retreat to drift, constructing a new retreat upon resettlement in a suitable benthic patch. A variety of factors have been reported to affect hydroptychid drift. Abiotic factors include substrate availability and texture (Benke et al., 1991; Kerans, 1996) and flow disturbance (Williams, 1990); whereas biotic factors include predation risk (Michael & Culver, 1987; Holomuzki et al., 1999), food availability (Williams & Levens, 1988), intraspecific aggressive encounters (Glass & Bovberg, 1969) and life stage (developmental) changes (Kerans, 1992). Yet we know little about the role of habitat structure in affecting interindividual variation in drift entry, drift distance, and benthic resettlement, all of which can influence population spread and dynamics.

In this study, we conducted two experiments to evaluate how stone size and epilithic algal cover, and

hydraulic environments associated with these substrate conditions, influence drift and resettlement by *C. sparna* larvae. In the first experiment, we quantified drift distance and the number of times larvae re-entered the drift in artificial stream channels with contiguous sections of gravel covered with a thin biofilm (mostly prostrate diatoms [*Cocconeis* spp., *Achnanthes amphora*]), cobble covered with a thin biofilm, and cobble covered with the macroalga *Cladophora glomerata*. We varied the order of these substrates between channels to evaluate how juxtapositioning of substrate types might affect drift distance and drift re-entry of larvae. However, an unexpected result of this experiment was that drift did not exceed the 2.5-m long initial substrate sections in each of the artificial channels. Thus, analyses focus on drift responses in the different substrates. In the second experiment, we examined nocturnal movements of larvae after benthic resettlement in each of the substrate types. In nature, densities of *C. sparna* are positively related to particle grain size and are higher on *Cladophora*-covered stones than on biofilm-covered stones (Fairchild & Holomuzki, in press). This study addresses whether drift responses contribute to this spatial variance in densities.

## Methods

### *Experiment 1: habitat effects on drift distance and drift re-entry*

We studied drift distance and re-entry of larvae in different habitats in three experimental channels (Fig. 1) at the University of Michigan Experimental Stream Facility, located ~3 km east of Pellston, Emmet County, in northern Michigan. Water in channels was drawn with a Monarch pump from the East Branch of the Maple River. The East Branch is a warm-water, second order stream that drains Douglas Lake (45.35° N, 84.40° W). Each channel (9.0 m-long, 0.51 m-wide, 0.36 m-high) was constructed of concrete blocks lined with clear plastic (8 mil) and spaced 1 m apart. A valve on the inflow pipe at each channel head enabled us to regulate discharge in the flow-through channels. Netting (200  $\mu$ m mesh) over inflow pipes prevented the introduction of other macrobenthic animals into channels. A 1.5 m-long section of gravel armored by large cobbles helped reduce turbulence of the inflow before reaching connecting patches of different substrates (ea. 2.5 m-long). Substrates were biofilm-

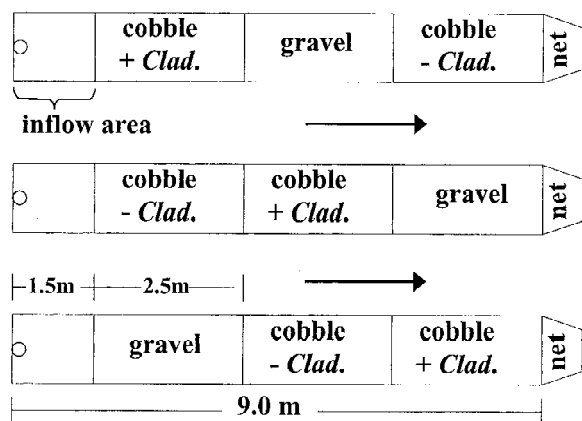


Figure 1. Schematic of the artificial stream channels for measuring drift distance and re-entry in experiment 1. Only substrate sections nearest to inflows in each channel were used in analyses because the average drift distance was no longer than the length of the first substrate-section (2.5 m) in each channel.

covered gravel (1.0–2.5 cm diameter), biofilm-covered cobbles (3.2–13.0 cm diameter), and *Cladophora*-covered cobbles (4.5–17 cm diameter, ~25% *Cladophora* cover), each underlain with coarse sand. Patch order varied between channels (Fig. 1); however discharge ( $\sim 8.5 \text{ l s}^{-1}$ ), depth ( $\sim 13 \text{ cm}$ ), and temperature ( $19\text{--}22 \text{ }^\circ\text{C}$ ) were uniform among channels.

On 9 July 1999,  $\sim 300$  larvae were collected from the East Branch and placed in a fourth channel (not used in the experiment). This channel was similar in design to our experimental channels, with conditions (i.e. predator-free, currents of  $\sim 30 \text{ cm s}^{-1}$ , mix of gravel to boulders with  $\sim 15\%$  *Cladophora* cover) that promoted retreat construction. On 6 dates between 22 and 31 July, a total of 104 larvae of varying size (limits: head capsule, 0.80–1.45 mm; damp mass, 3.8–29.3 mg) were collected from this channel and released one at a time in experimental channels. A larva was randomly assigned to a channel for release; thus number of releases varied among channels ( $n = 35$  in channel 1,  $n = 36$  in channel 2, and  $n = 33$  in channel 3). Immediately before release, a larva was marked with a quick-drying ( $\sim 1 \text{ min}$ ) pink acrylic paint on each thoracic sclerite. Sclerites were first blotted dry with a cotton swab, then paint was applied with a fine-tipped paintbrush. The paint mark greatly increased visibility, and hence tracking of larvae when released in experimental channels. Pilot work showed that the paint spot, when confined to thoracic sclerites, did not affect drift and resettlement of larvae.

Each larva was released 1.5 m from channel heads near the upstream edge of the first experimental substrate patch between 0930 and 1530 h. The larva was hand-held over a patch of small gravel and released  $\sim 1 \text{ cm}$  from the bottom. Two individuals observed the drift and benthic settlement of each larva. Upon settlement, we counted the number of times the animal re-entered the drift. Five min after release, the larva was removed from the channel and preserved in 70% ethanol. We recorded drift distance as the distance from the point of release to the final point of benthic settlement. Thus, for animals re-entering the drift, drift distance was the total distance traveled from the release point. Nets at the end of channels captured those larvae that drifted the full distance of the channel. About half (53) of the 104 larvae released were killed by freezing before mark and release to determine whether benthic resettlement was active or passive. A two-way MANOVA (SYSTAT version 7.0) was used to assess the effects of substrate type and larval condition (alive or dead) on the interdependent response variables drift distance and number of drift re-entries (both rank-transformed). Significant results were then interpreted employing univariate ANOVAs and LSD multiple comparisons. Head capsule width and damp mass of all larvae were measured to examine the effect of larval size on drift distance. Head capsule width was measured using an ocular micrometer, while damp mass was measured by placing a larva on a paper towel for 5 s, then immediately weighing it on a Mettler<sup>®</sup> AE 163 balance. Spearman's rank correlation coefficient ( $r_s$ ) was used to test whether drift distance was related to larval size.

We calculated roughness Reynolds numbers ( $Re_*$ ) in each substrate section to characterize the hydraulic roughness of habitats close to the bed. These numbers are considered good habitat descriptors because they combine the effects of both current velocity and particle grain size (Davis & Barmuta, 1989).  $Re_*$  was calculated using the equation:

$$Re_* = V_* k / \nu,$$

where  $V_*$  is shear velocity (m/s),  $k$  is particle roughness height (diameter [m] along the c-axis) at  $d_{84}$  (i.e. diameter at which 84% of the particles are smaller), and  $\nu$  is kinematic viscosity ( $1.007 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$  at  $20 \text{ }^\circ\text{C}$ ). On 30 July, we visually quartered each habitat section in each channel and measured current speeds 2 cm from the bottom, at  $0.6 \times$  depth, and 2 cm from the surface near the center of each quarter with a Marsh-McBirney flow meter. Shear velocities

were estimated from slopes of regression lines, fitted to the relationship between current velocity and log-transformed depth, divided by 5.75 (Gordon et al., 1992). The  $d_{84}$  in each quarter was determined by measuring roughness heights of 8–16 stones. ANOVA followed by LSD multiple comparisons were used to compare  $Re_*$  (rank-transformed) among habitats.

*Experiment 2: benthic movement and behavior after settlement*

We examined nocturnal movements and behaviors of larvae after settlement in artificial channels containing either biofilm-covered gravel, biofilm-covered cobbles or *Cladophora*-covered cobbles. Only nocturnal activity was monitored because hydropsychid larvae are most active at night (Kerans, 1996). Each substrate treatment was replicated 8 times, resulting in 24 separate experimental units (channels).

Water in the 24 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 with a Monarch pump. Stream water was first diverted to three head tanks (eight channels per head tank) before reaching channels. Netting (200  $\mu$ m mesh) over inlets to the head tanks prevented the introduction of macrobenthic organisms into experimental channels. Both the head tanks and valves at the head of each channel allowed us to finely regulate discharge in the flow-through channels. Channels used to assay larval movements were similar to those illustrated in Holomuzki (1996). Water in each channel first flowed through a 0.9 m-long substrate-free section, then through a 1.0-m long section containing substrate and a caddisfly. The substrate-free section collected incoming fine particulate organic matter, which helped prevent downstream nets from clogging. A drift net placed 0.9 m downstream from the substrate-containing section captured drifting caddisflies. The drift net created a  $\sim$ 0.5-m-long standing wave, so the 0.9-m-long gap between substrate and net ensured that any dam effects created by the net did not disrupt flow patterns in substrate-containing sections. Drift nets were knee-high nylon stockings (K-mart<sup>®</sup> brand, 200  $\mu$ m mesh) inserted over the ends of channels.

On 5 August 1999, substrates collected from the East Branch were added to channels. Each channel contained a thin layer of sand (0.5–1.0 cm-deep) armored by either biofilm-covered gravel, biofilm-covered cobbles or *Cladophora*-covered cobbles picked free of macroinvertebrates. In both cobble

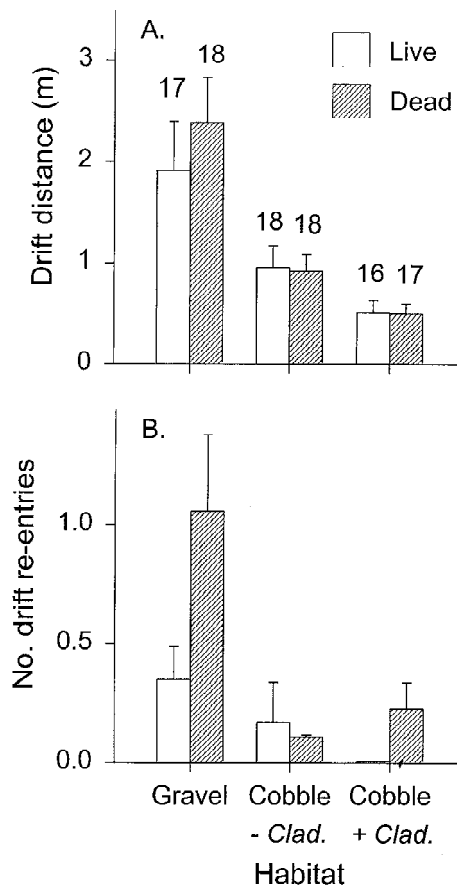


Figure 2. Mean (+1 SE) (A) drift distance and (B) number of drift re-entries of live and dead larvae in different habitats in the artificial channels used in experiment 1. Numbers over bars indicate number of larvae released.

treatments, flat stones ( $\sim$ 3 cm-high, 6–9 cm-wide) were used so that the entire surface of the stone would be submerged, and hence available as potential habitat for larvae. Cobbles in channels were arranged linearly and spaced a few millimeters apart. After rock placements, one caddisfly was added by hand to the center of each substrate-containing section of each channel at 1400 h. Only fifth instars (damp mass limits: 14.7–22.3 mg) from the East Branch were added to channels. Valves at channel heads were momentarily reduced by  $\sim$ 95% to prevent rapid displacement by the current and to facilitate benthic settlement of larvae. Discharge (325 ml  $s^{-1}$ ), current velocity ( $\sim$ 25  $cm s^{-1}$  2–10 mm over rocks, as estimated by pitot tube) and temperature (19.5  $^{\circ}C$ ) were similar among all channels.

At 08:30,  $\sim$ 18 h after larval additions, the presence of retreats, the number of draglines and the length of

Table 1. Two-way MANOVA results for effects of habitat (gravel, cobble – *Cladophora*, and cobble + *Cladophora*) and condition (alive, dead) on drift distance and number of drift re-entries of *C. sparna* larvae in the large, artificial streams used in experiment 1

Source	df	Wilks' $\lambda$	$F$	$P$
Habitat	4, 194	0.637	12.26	<0.001
Condition	2, 97	0.937	3.28	0.042
Habitat $\times$ condition	4, 194	0.971	0.71	0.588

each line were recorded in each channel. Silk draglines laid on benthic surfaces aid movement by decreasing the chance of displacement in fast flows (Holomuzki & Biggs, 2000). Caddisflies were then collected from both drift nets and substrate-containing sections and preserved in 70% ethanol. Linear distance from initial placement of larva to final locality was measured and direction of movement (upstream or downstream) recorded.

We used ANOVA to test whether distance of benthic movement was affected by habitat and flow direction. Larvae that drifted were not included in these analyses. G-tests for goodness of fit (Sokal & Rohlf, 1995) were employed to assess whether direction of benthic movements was independent of flow direction and whether number of larvae constructing retreats and laying draglines was independent of habitat type.

## Results

### Experiment 1: drift distance and drift re-entry

Habitat affected both drift distance and drift re-entry of hydropsychid larvae (Table 1). Drift distance differed significantly among habitats (Fig. 2A) (ANOVA:  $F_{2,101} = 19.51$ ,  $P < 0.001$ ). Rank of drift distances among habitats was gravel > cobbles – *Cladophora* > cobbles + *Cladophora* (LSD comparison). Drift distance was <1 m in cobbles + *Cladophora*. We did not observe any larva grabbing *Cladophora* filaments to facilitate resettlement. The typical response of live, drifting larvae was to point their head toward the streambed and to laterally move their abdomens in a swimming motion. However, drift distance did not differ significantly between live and dead larvae (Fig. 2A) ( $F_{1,102} = 0.51$ ,  $P = 0.477$ ). Consequently, we pooled data from live and dead larvae to assess whether drift distance was a function of body size.

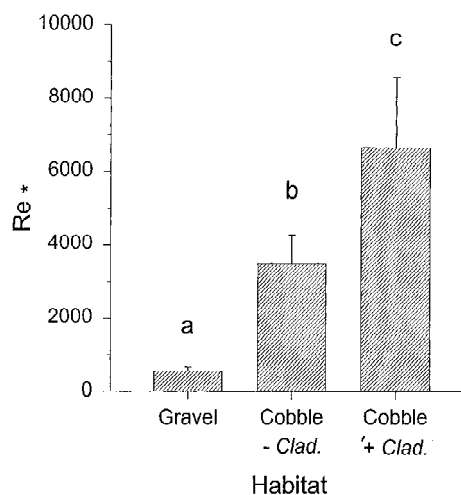


Figure 3. Mean (+ 1 SE) roughness Reynolds numbers ( $Re_*$ ) of different habitats in artificial channels used in experiment 1. Mean  $Re_*$  of only the most upstream habitats of each channel are presented because drift distances did not exceed the length (2.5 m) of these sections. Lowercase letters indicate significant differences between habitat types.  $n = 4$  replicate measurements per habitat.

Based on 89 retrieved animals, drift distance was not related to larval size (head capsule width:  $r_s = -0.045$ ,  $P > 0.50$ ; damp mass:  $r_s = -0.171$ ,  $P > 0.10$ ).

Number of drift re-entries also varied among habitats (Fig. 2B) ( $F_{2,101} = 8.98$ ,  $P < 0.001$ ), being significantly greater from gravel and than from cobbles – *Cladophora* and cobbles + *Cladophora* (LSD). Further, dead larvae made significantly more drift re-entries than live larvae ( $F_{1,102} = 5.35$ ,  $P = 0.023$ ).

Both drift distance and drift re-entry appeared to be related to hydraulic roughness of habitats.  $Re_*$  differed among habitats ( $F_{2,9} = 12.00$ ,  $P = 0.003$ ), being significantly greater in both cobble treatments than in gravel (Fig. 3) (LSD). The smaller, average  $d_{84}$  of gravel (1.2 cm), relative to cobbles – *Cladophora* (6.0 cm) and + *Cladophora* (8.5 cm), contributed to this difference.

### Experiment 2: benthic movement and behavior after settlement

Three (37.5%) and two (20%) larvae drifted from gravel and cobbles – *Cladophora*, respectively, while no larvae drifted from cobbles + *Cladophora*. Distance moved by larvae remaining in substrate patches (i.e. not drifting) did not differ significantly among habitats (Fig. 4) ( $F_{2,16} = 2.028$ ,  $P = 0.16$ ). Further, direction of movement was not biased by flow direction (Fig. 4) ( $G = 1.33$ ,  $P > 0.25$ ). However, degree of benthic

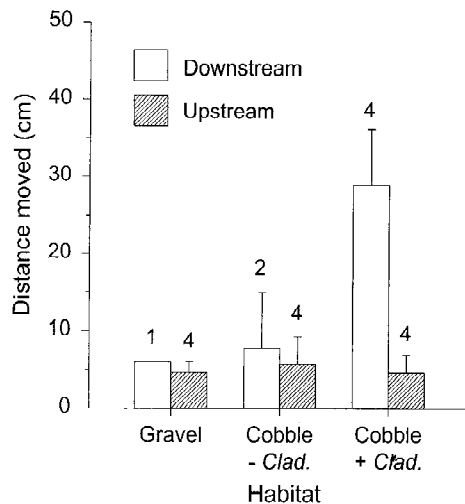


Figure 4. Mean (+ 1 SE) distance moved in upstream and downstream directions by larvae remaining in substrate patches (i.e. not drifting) in experiment 2. Numbers over bars indicate number of larvae moving in each direction in each habitat.

movement (i.e. crawling) did differ with flow direction, particularly in cobbles + *Cladophora*. Distance moved was  $\sim 4\times$  greater downstream than upstream (Fig. 4), and this difference was significant ( $F_{1,17} = 8.974$ ,  $P = 0.008$ ).

Retreat construction was evident in 3 of 8 channels for both gravel and cobble - *Cladophora* treatments, whereas larvae in all 8 channels with cobbles + *Cladophora* began retreat construction. However, this difference was not significant ( $G = 3.32$ ,  $P > 0.10$ ). We were able to detect between-habitat differences in the tendency to lay draglines. Only one and two larvae laid draglines in gravel and cobbles - *Cladophora*, respectively, while all 8 larvae laid draglines in *Cladophora*-covered cobbles ( $G = 7.46$ ,  $P < 0.025$ ). On average, each larva laid 3 draglines (limits: 1–6), and mean ( $\pm 1$  SE) dragline length was 2.07 ( $\pm 0.32$ ) cm.

## Discussion

Our study illustrates the importance of habitat in influencing drift responses and subsequent benthic movements of lotic macroinvertebrates. Drift distance was significantly greater over gravel than over cobbles + *Cladophora* and was related to the habitat descriptor,  $Re_*$  of each substrate type. The comparatively lower  $Re_*$  for gravel indicates that this substrate was hy-

draulically smoother than cobbles. When roughness elements (particles) are relatively close, as they were in gravel sections, flows skim across crests (tops) of bed elements (Davis & Barmuta, 1989). This spacing effect, coupled with more uniform water depths from smaller roughness elements, likely created a hydraulically smoother surface over gravel. Hydraulically smoother conditions may carry larvae further downstream before encountering pockets of slower moving water (e.g. wakes) or bottom-directional eddies that help them regain the bottom.

Drift distance was also significantly greater over cobbles - *Cladophora* than over cobbles + *Cladophora*, and this pattern was related to differences in roughness Reynold's numbers between these habitats. Slower current speeds in the interior of *Cladophora* tufts relative to the surrounding water (Dodds, 1991) may facilitate settlement and hence shorten drift distances over these patches. In addition, the average  $d_{84}$  of cobbles + *Cladophora* was slightly larger than those - *Cladophora*. Higher bed obstruction caused from higher roughness heights may create larger dead-zones around bed elements (Gordon et al., 1992), facilitating settlement. This confounding of rock landscape and local hydraulics highlights the need to carefully map and manipulate hydraulic habitats to verify flow effects on drift, and hence distributional responses of the zoobenthos.

Despite variability in hydraulic conditions, the  $Re_*$  for all three habitats in our experimental streams was  $>70$ , indicating hydraulically rough surfaces over all habitats (Davis & Barmuta, 1989). Rapid flow accelerations and decelerations, toward and away from the bed, are characteristic of these conditions (Kline et al., 1967; Carling, 1992). Thus, the relatively short drift distances ( $<2.5$  m) observed across habitats in our study could be the result of sudden velocity reductions (see Campbell, 1985). Other studies on drift of benthic insects have similarly found that organisms may drift relatively short distances ( $<10$  m) (Waters, 1972; Statzner et al., 1984; Allan & Feifarek, 1989). Short drift distances would be particularly beneficial in sandy northern Michigan streams, where suitable habitat patches (i.e. stony areas) are scarce and isolated by long uninhabitable stretches of sand. Short intrapatch movements would not only likely keep larvae in habitable patches, but also reduce their time spent in the water column, decreasing the threat of predation by drift-feeding fish. Given the extent of habitat isolation and limitation in these streams (Holomuzki, 1996; Holomuzki et al., 1999), studies are needed to deter-

ine the role and consequences of inter-reach drift on population spread and redistribution.

We also found that drift distances were similar between live and dead larvae, suggesting these caddisflies have no special behavior to regain the bottom. This result further emphasizes the importance of hydraulic conditions in affecting distributional aspects of these animals. Many studies have documented that hydropsychid distributions are influenced by substrate roughness and hydraulic conditions (e.g. Osborne & Herricks, 1987; Way et al., 1995; Statzner & Bretschko, 1998; Rempel et al., 2000), which together affect food capture (Fuller & Makay, 1980; Wetmore et al., 1990). However, results of our study suggest substrate morphology and accompanying hydraulic conditions influence hydropsychid abundance by also affecting drift distance and benthic settlement.

Our findings indicate that frequency of drift re-entry also depends on habitat. In experiment one, number of drift re-entries was significantly greater from gravel than from cobbles + *Cladophora*. Once a larva settled in a *Cladophora* section, it did not re-enter the drift. In addition, no larva drifted from *Cladophora* sections in the second experiment. Together, these results may explain the significantly higher densities of *C. sparna* larvae, as well as other hydropsychids, on *Cladophora*-covered stones than elsewhere (Fairchild & Holomuzki, in press). *Cladophora* tends to grow on larger, more hydrologically stable substrates (e.g. large cobbles, boulders, affixed logs) (Dodds & Gudder, 1992; Holomuzki et al., 1999). Thus, *Cladophora*-covered stones may be preferred over gravel because of their stability in higher flows. Sediment stability has been linked to patterns of abundance and within-reach distributions of a variety of lotic, benthic macroinvertebrates (e.g. blackflies [Hart et al., 1996], chironomids [Palmer et al., 1996], mussels [Strayer, 1999], snails [Holomuzki & Biggs, 1999], mayflies [Matthaei et al., 2000]). However, residing in relatively stable *Cladophora* patches may benefit hydropsychid larvae in other ways. The thick, structurally-complex *Cladophora* mats may effectively deter fish or invertebrate predators. Even small amounts (~10% cover) of *Cladophora* on stones can provide enough refuge to significantly decrease predator-induced (i.e. predaceous stoneflies) drift by *C. slossonae* larvae (Holomuzki et al., 1999). Moreover, *Cladophora* filaments provide a building material for retreat construction (Fairchild & Holomuzki, in press) and may affect food availability. Building retreats near the basal thallus may provide

a velocity refuge while still allowing the placement of catch-nets to contact seston-containing flows. Larvae may gather food from catch-nets and from nearby *Cladophora* strands, which often trap fine organic sediments (Holomuzki & Short, 1988) and harbor a dense film of epiphytic diatoms (e.g. Dudley, 1992). Finally, the algal filaments may provide added structure on which larvae lay draglines. In our study, larvae laid significantly more draglines on *Cladophora*-covered stones than in the other two habitats.

We also found that direction of benthic movement (i.e. crawling) was not biased by flow direction. Kerans (1992) similarly reported that *C. slossonae* exhibited no directional bias when crawling on benthic surfaces. However, we found that net upstream movements (~5 cm per night) were considerably shorter than net downstream movements (~20 cm per night). This result implies that population spread by larvae is predominantly in a downstream direction.

Stone size and epilithic cover, and hydraulic environments associated with these substrate conditions, are key factors producing habitat heterogeneity in stream ecosystems. The results of this study further emphasize the role of habitat heterogeneity as a factor affecting small-scale variation in movements of benthic organisms. Understanding linkages between animal movements and habitat heterogeneity will help us better understand and make predictions about population spread in aquatic ecosystems.

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