

Current velocity and habitat patchiness shape stream herbivore movement

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Animal movements are influenced by the structure and arrangement of patches in a landscape. Most movement studies occur in terrestrial landscapes, though aquatic landscapes are equally heterogeneous and feature patches that differ in resistance to animal movements. Furthermore, the variable and highly directional flow of water over streambed landscapes is a unique environmental element, yet its constraint on animal movement is poorly understood. This study examines how habitat availability in a streambed landscape interacts with current velocity to affect movement patterns of two benthic grazers: glossosomatid caddisfly larvae (*Agapetus boulderensis*) and pulmonate snails (*Physa* sp.). Using experimental streambed landscapes, we found that *Agapetus* traveled farther as availability of smooth habitat (composed of low diatom turfs) increased compared to tall, structured filamentous stands, but only did so in slow current velocities. Swifter flows caused restricted movement of *Agapetus* and more upstream-oriented paths, but only in smooth landscapes where the potential for flow refugia from filamentous stands was minimal. Similarly, increasing proportions of smooth habitat facilitated greater net displacement of *Physa* using more upstream-oriented paths. Higher current velocities caused *Physa* to move faster, a pattern demonstrated only in smooth landscapes.

Our results illustrate a strong interaction between benthic habitat structure and current velocity in shaping patterns of grazer movements in a streambed landscape. Our study also suggests that the flow of water be considered not only a strong environmental gradient in streams, but also an interactive landscape feature that can combine with streambed structure to determine the permeability of patches to the movement of benthic organisms. Landscape ecology has mainly focused on terrestrial environments, and this study offers insight into some of the unique processes that may shape animal movement in aquatic environments.

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The individual movements and behavioral decisions of animals through heterogeneous landscapes scale up to influence many ecological processes and patterns, including metapopulation dynamics, population distribution and dispersal, community composition, and predator-prey interactions (Levin 1992, Wiens et al. 1993a, Fahrig and Merriam 1994, Wiens et al. 1997,

Hanski 1998, With et al. 1999, Malmqvist 2002, Morales and Ellner 2002). Animal movement is strongly dependent on the connectivity of the landscape, which collectively results from the distribution of food resources, the availability of refugia, and the influence of other structured patches (MacArthur and Pianka 1966, Poff and Ward 1992, Wiens et al. 1997, Jonsen and

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Taylor 2000, With et al. 2002). In particular, the degree of structural patchiness in a landscape has been shown to have strong effects on the permeability of that landscape to animal movement (Wiens et al. 1997, With et al. 1999, Goodwin and Fahrig 2002).

Streambeds are a prime example of landscapes with a high degree of structural patchiness, as the nature of substrate size and texture gives rise to diverse arrangements of physical structures through which animals move. The effects of this inherent patchiness on a diverse array of processes have been studied extensively in aquatic systems (Hart and Resh 1980, Hart 1981, Poff and Ward 1992, Palmer 1995, Palmer et al. 2000, Silver et al. 2000), but there have been relatively few studies to document the effects of such patchiness on the movement of aquatic invertebrates across streambed landscapes.

The study of animal movement through highly structured terrestrial landscapes has often been conducted within the framework of percolation theory, originally developed in the physical sciences (Stauffer 1985, Gardner et al. 1987, 1989, O'Neill et al. 1988, Wiens et al. 1997, With et al. 1997, 1999, 2002). In animal movement studies, this theory uses the proportion and arrangement of habitat patches in a landscape to predict the potential for certain animals to move across that landscape (Wiens et al. 1997). In this ecological context, the theory reduces landscapes to two patch types arranged in a simple grid: "suitable" patches through which animals can move, and "unsuitable" patches that are impermeable to movement. However, predictions of landscape connectivity can vary depending on several factors, including the assumptions animal movement behaviors (Stauffer and Aharony 1994, Schooley and Wiens 2003, Olden et al. 2004a), the validity of the patch suitability assumptions (Wiens et al. 1997), the contagion and fragmentation of patches (With et al. 1997, 2002), and food availability (Goodwin and Fahrig 2002).

Most animal movement models focus only on the importance of patch structure in influencing animal decisions on the landscape, without regard for other environmental gradients that may act independently or interactively to shape movement patterns (but see Schooley and Wiens 2003, Olden et al. 2004b). For instance, application of animal movement theories to streambeds requires incorporation of the pervasive and variable effects of water flow (Olden et al. 2004a). Flow has been called "the dominant forcing function to which other stream processes and patterns can be traced" (Hart and Finelli 1999), and the magnitude of water current can reflect forces experienced by the organisms exposed to it (Statzner et al. 1988, Poff and Ward 1992). Flow, like landscape structure, has been shown to affect diverse processes such as animal distribution (Wellnitz et al. 2001), food supply (Nowell and Jumars 1984),

predation (Peckarsky et al. 1990), grazing ability (Poff and Ward 1995, Poff et al. 2003), mediation of competition (Kuhara et al. 2000), and movement of aquatic invertebrates (Poff and Ward 1992, Huryn and Denny 1997, Poff and Nelson-Baker 1997, Olden et al. 2004a). Moreover, the directional nature of flow affects the movement of materials, nutrients, and energy in streambeds (Wiens 2002).

While percolation theory has been a useful construct for examining animal movement, our prior research and observations indicate that the rigid assumptions of percolation theory are unrealistic for the study animals examined in this study (Olden et al. 2004a). However, the general percolation framework can still aid our understanding of animal movement through patchy landscapes by serving as a useful null model of animal-landscape interactions (Gardner et al. 1987). Here, we evaluate the general applicability of such an approach in a novel setting characterized by the environmental "forcing" of water flow, which along with structural landscape elements and individual behavior, has been shown to influence animal movement in this system (Poff and Ward 1992, Olden et al. 2004a). Indeed, other landscapes may similarly express strong and variable forcing functions, such as wind (Schooley and Wiens 2003).

We experimentally compared the movement patterns of two herbivorous benthic invertebrates (the glossosomatid caddisfly *Agapetus boulderensis*, and the pulmonate snail *Physa* sp.) across a range of landscape structure and at two distinct flow velocities. We described their movements in terms of their rate, displacement, tortuosity, and directionality in relation to current to understand the movement dynamics of these two species, and how they might reflect their contrasting behaviors and body morphologies that are known to interact strongly with flowing water (Statzner et al. 1988, Poff and Ward 1992, 1995, Hart and Finelli 1999).

Material and methods

Study site and organisms

The study was conducted during the summers of 2001 and 2002 in and alongside the upper Colorado River (40°11'N, 105°52'W, elevation 2420 m). The reach runs through a shrubland valley approximately 7 km below the deep-release dam that forms Lake Granby. One of the primary sources of late summer, fine-scale heterogeneity in this stretch of the river are the retreats of the chironomid larva, *Pagastia partica* (hereafter referred to as *Pagastia*) (Fig. 1). These conspicuous retreats are largely composed of silk and filamentous algae that are complex, high-profile structures relative to the smooth surfaces that surround them (Monroe et al. 2005). The

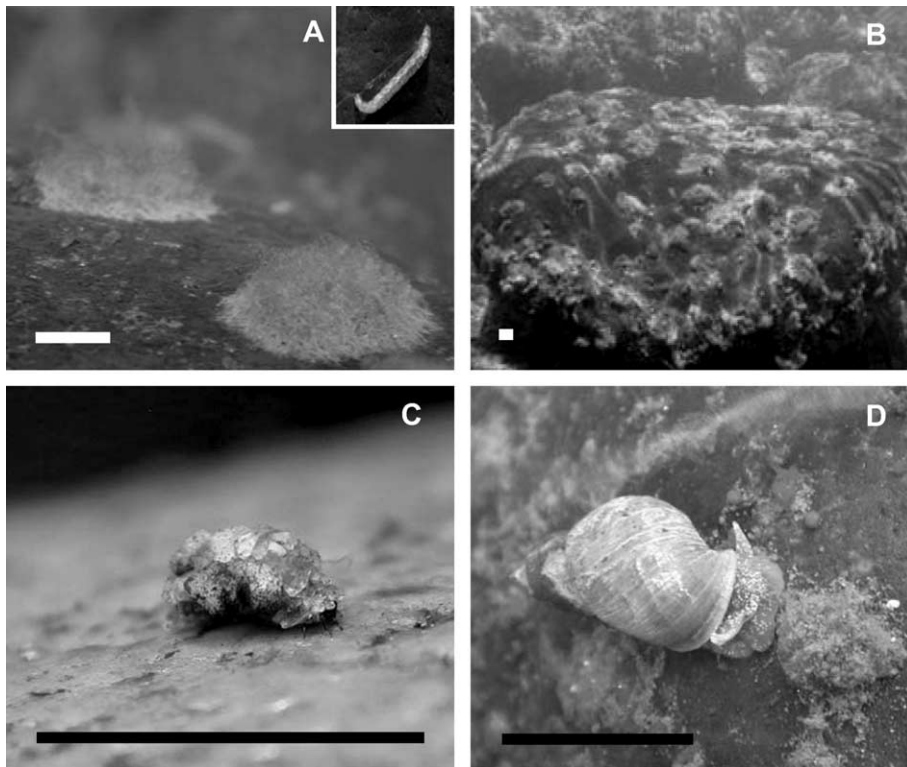


Fig. 1. (A) Retreats woven of silk and algae by the *Pagastia* larva; free-crawling larva shown in inset (B) A stone covered in *Pagastia* retreats, a primary source of fine-scale heterogeneity at the upper Colorado River field site. (C) The glossosomatid caddisfly *Agapetus boulderensis*, shown with legs extending from its hemispherical case. (D) The physid snail *Physa* sp. Scale bars are approximate and each represents 1 cm. Photos courtesy of J. B. Monroe, Freshwaters Illustrated.

smooth surfaces host inconspicuous biofilms that contain diatoms and other microscopic components, though both surfaces contain the diatoms upon which both the study animals graze on (see “Experimental landscapes” below). An instream survey of naturally occurring *Pagastia* retreats indicated that the average proportion of smooth habitat (h) between stones in the stream was 0.84 ($n = 180$ stones, $SD = 0.14$) (J. Monroe, unpubl.).

In this study we examined the movement of two benthic grazers that crawl across substrates and do not actively enter the drift (Rader 1997, Dillon 2000) (Fig. 1): the glossosomatid caddisfly larva *Agapetus boulderensis* Milne and the pulmonate snail, *Physa* sp. (hereafter *Agapetus* and *Physa*). *Agapetus* feeds on diatoms and fine particulate organic matter on the upper surfaces of stones (Poff and Ward 1992, Wiggins 1996), and builds hemispherical cases (5th instar larvae: mean length 4.5 mm, mean width 3.0 mm, mean height 2.2 mm, $n = 80$) that are constructed of coarse sand and silk with ventral openings at both ends. While the case provides protection from predators (Otto and Svensson 1980), it greatly constricts mobility and maneuverability, and movement is limited mainly to smooth surfaces (Becker 2001). In the upper Colorado

River, *Agapetus* larvae occur in near-bed current velocities ranging between of 5 and 30 cm s^{-1} ; rarely found at current velocities exceeding 50 cm s^{-1} (Poff and Ward 1992, Wellnitz et al. 2001).

The freshwater snail *Physa* is an armored grazer that is most often found on stones along calm stream margins and eddies; current velocity is the primary factor in determining the distribution of these species (Dillon 2000, A. Hoffman, pers. obs.). Like *Agapetus*, *Physa* feeds preferentially on diatoms (Dillon and Davis 1991). Unlike *Agapetus*, however, *Physa* is able to negotiate stands of thick *Pagastia* retreats and filamentous algae using its large muscular foot, which allows the snail to achieve relatively uniform distribution in complex, structured landscapes (Gotoh and Kawata 2000).

Stream surveys of *Agapetus* movement

To explore the daytime movement dynamics of *Agapetus* in relation to *in situ* habitat patchiness and flow velocity, an in-stream survey was performed in August 2002. We haphazardly selected 60 stones in riffle and run habitats and on each stone, marked (with wax crayon) the initial location of a single *Agapetus* larva, measured near-bed

flow velocity, and estimated the percentage of *Pagastia* retreat coverage. After 3 h, we marked the final location of each larva, and calculated within-stone net displacement rate (i.e. net displacement divided by the total time: see “Movement metrics” below). Due to logistical constraints, a similar study was not performed for *Physa*.

Experimental landscapes

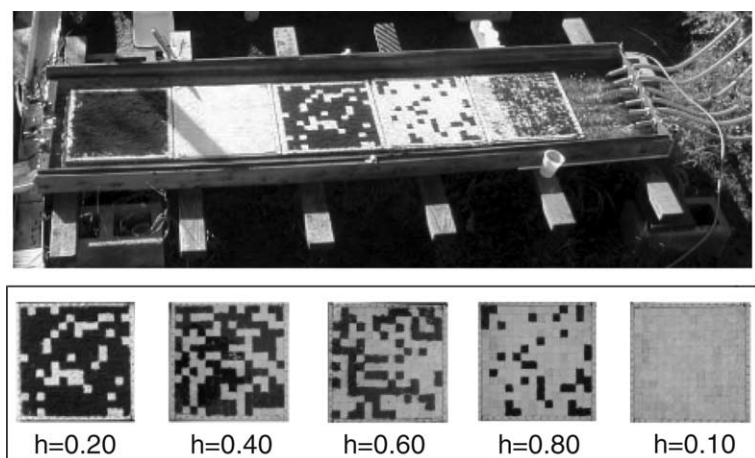
The movement response of *Agapetus* and *Physa* to flow velocity and landscape structure was tested by observing their movement on experimental streambed landscapes in a streamside flume. Water was pumped from the river into the 185 cm long, 60 cm wide and 10 cm high flume (Fig. 2A), over the experimental landscapes, and returned to the river. Valves at the top of the flume allowed for the control of flow velocity. Experimental landscapes placed in the flume measured 35.5 × 35.5 cm and consisted of 196 unglazed ceramic tiles (2.54 × 2.54 cm) arranged in 14 rows and 14 columns (Fig. 2B). The size of the experimental landscapes was based on pilot studies that indicated the movement rates and distances of *Agapetus* and *Physa*. Because both organisms frequently encounter patches of smooth, diatom-inhabited patches and patches of *Pagastia* retreats, we replicated these two habitat types on the experimental landscapes using the unglazed ceramic tiles. Approximately one month before the experiments, one set of tiles was placed in-stream (in the presence of grazers) and colonized with a uniform biofilm (but no *Pagastia*), which provided a smooth surface for movement and diatom foraging for the two grazers (Scott 1958, Poff and Ward 1992, Lombardo and Cooke 2002). We refer to these as smooth tiles. In circular streamside channels (in the absence of grazers), another set of tiles was cultured with a thick algal mat and stocked with *Pagastia* larvae, which modified algal structure by building retreats. These *Pagastia*-colonized tiles are hereafter referred to

as structured tiles. Periphytic ash-free dry mass (AFDM) of algae scraped with a razor blade from smooth and *Pagastia*-structured tiles confirmed important structural differences between the two habitat types: AFDM of structured tiles was an order of magnitude greater than smooth tiles (\bar{X} = 0.0173 g vs 0.0014 g, n = 4), yet food availability was comparable between smooth and structured tiles, with both containing high diatom concentrations (Olden et al. 2004a). This is somewhat contradictory to the results of Pringle (1985), which showed that diatom biovolume was greater on chironomid retreats than off. Regardless, these results establish structural differences between the two tile types, as well as food availability on both tile types. However, food accessibility likely varied, because diatoms on the structured tiles were epiphytic and perhaps less accessible (particularly to *Agapetus*).

Experimental design

From the groups of smooth and structured tiles, we created experimental landscapes for each of five treatment levels of increasing proportion of smooth habitat (h) at 0.20, 0.40, 0.60, 0.80, and 1.0 (Fig. 2B). Two randomly arranged landscapes served as replicates for each h. The range of h in our experimental landscapes correspond to that observed in the stream (see “Stream surveys of *Agapetus* movement”, below). We recorded animal movements at each of these h levels under two flow velocity treatments, as measured within 1 cm of the tiles with a Schiltknecht current probe (Schiltknecht Messtechnik AG, Zurich, Switzerland): “fast” velocity averaging 25 cm s⁻¹ (but ranging from 20–30 cm s⁻¹) and “slow” velocity averaging 10 cm s⁻¹ (but ranging from 5–15 cm s⁻¹). Differences in near-bed flows arising from the unique arrangement of each experimental landscape led to the range of ±5 cm s⁻¹ on either side of the average.

Fig. 2. (A) A set of artificial streambed landscapes; water pumped from the stream enters the trough through the 6 parallel hoses on the right. Arranged on the trough from left to right are artificial streambed landscapes (1) culturing algae on 2.54 × 2.54 unglazed ceramic tiles, (2) at h = 1.0, (3) at h = 0.80, (4) at h = 0.20, and (5) culturing algae. Note that at any one time, only one landscape was used to monitor grazer movement; (B) Details each of the h levels of the experimental landscapes, which can be compared to the natural streambed landscape in Fig. 1C.



On each of the five experimental landscapes ($h = 0.20$ to 1.0), both replicates of each landscape, and both flow velocity treatments (fast and slow), the movement of 10 individuals of each species were observed, resulting in 200 movement paths for each species (each individual was used for only one movement path). The replicates were allocated over both space (position in the flume) and time, though only one herbivore was allowed on any experimental landscape at any given time. Based on the results of a pilot study and the differential movement speeds of each species, we started each trial by placing an individual on a smooth tile near the center of the experimental landscape and recording the x, y location of *Agapetus* every 3 min for 1 h and *Physo* every 1 min for 20 min. Each individual was therefore observed for a total of 20 time steps, except those that were dislodged or moved off the surface of the experimental landscape. Water temperature was also recorded at each of the time steps using a Thermochron iButton model DS1921 temperature logger (Dallas Semiconductor, Inc.) to examine the potential influence of temperature on grazer movement. No water temperature effect was observed (results not shown).

Movement metrics

Coordinates of each of the 400 movement paths were scanned, digitized, and imported into Arc View GIS (ESRI v.3.2a 2000). From these, we calculated a series of second-order movement parameters that distill several observations of an individual into a single measure (Batschelet 1981, Wiens et al. 1993b). To test the appropriateness of the use of such second-order statistics, we performed independence tests of successive observations for the movement paths of each individual following Swihart and Slade (1985). Nine out of 200 *Agapetus* and 5 out of 200 *Physo* individuals exhibited independence between successive positions; justifying our averaging over all time steps. These results indicated that in the vast majority of movement paths, the movement from one time step to the next was dependent on the previous time step; in other words, the overall movement path was not just an accumulation of random moves, but was a path dependent on the successive positions making it up. The low number of individuals exhibiting independence between positions justified our averaging over all observations.

We calculated four movement metrics. Net displacement is the net straight-line distance traveled by each individual. Movement rate is the sum of the distances traveled in each time step divided by the total time spent moving (usually 20 minutes, unless the animal moved off the landscape before this time elapsed). Mean vector length is a measure of path tortuosity, and is a unit vector measure of the dispersion of turning angles

(Batschelet 1981, Wiens et al. 1993b) that varies between 0.0 (uniform or nondirectional) to 1.0 (perfectly directional). Lastly, since aquatic invertebrates can exhibit positive rheotaxis (Poff and Ward 1992), we included a measure of upstream orientation, or homeward component (Batschelet 1981), was used to determine how close the mean direction was to the "homeward" (upstream) direction, and it ranges from 1.0 (precisely upstream) to -1.0 (precisely downstream).

We used analysis of covariance (ANCOVA) in the model:

$$y = (\text{smooth habitat}) + (\text{flow velocity}) \\ + (\text{landscape replication}) + (\text{smooth habitat} \\ \times \text{flow velocity})$$

to test for the effects of smooth habitat, flow velocity and replicate landscapes on the four movement metrics. Where significant effects were observed, differences among treatment-factor combinations were tested using post-hoc Tukey honest significant difference tests ($\alpha = 0.05$). Raw data were found to meet the underlying assumptions of ANCOVA (Zar 1999).

Results

Stream surveys of *Agapetus* movement

At the termination of the in-stream movement survey, 51 out of 60 *Agapetus* larvae remained on the stones. These larvae were most often found in habitats with smoother landscapes and in slower flows (mean flow velocity = 9.51 cm s^{-1} , $SD = 8.59$; mean $h = 0.82$, $SD = 0.20$; $n = 51$). Net displacement showed a positive relationship with the proportion of habitat (h) and a negative relationship with flow velocity on the natural streambed (Fig. 4). The average in-stream net displacement rate of *Agapetus* individuals was 0.012 cm s^{-1} ($n = 51$, $SD = 0.779$).

These rates for *Agapetus* net displacement are greater than those reported by Poff and Ward (1992) on natural stones at a similar site in the same stream, which ranged from $2.5 \times 10^{-6} \text{ cm s}^{-1}$ to $4.5 \times 10^{-4} \text{ cm s}^{-1}$ ($n = 127$).

Movement patterns of *Agapetus*

The replicate landscape effect was non-significant ($p = 0.873$), so we pooled the movement pathways across replicates ($n = 20$) in the ANCOVA models. Both h and flow velocity had significant effects on *Agapetus* movement in the experimental landscapes (Table 1). The ANCOVA tests indicated significant effects of h , flow velocity, and their interactions for net displacement, movement rate, and upstream orientation. Net displacement and movement rate increased with higher h and slower flows, whereas upstream orientation showed an

Table 1. Analysis of covariance for the movement parameters from *Agapetus boulderensis* pathways. Twenty replicate pathways (allocated over space and time and pooled across 2 replicates of landscapes for each treatment: see Methods) were measured in each of 5 treatment levels of smooth biofilm habitat (20%, 40%, 60%, 80% and 100%) and 2 treatment levels of flow velocity (5–15 cm s⁻¹ and 20–30 cm s⁻¹). Bold values are significant at the 0.05 level.

Movement parameters	Source of variation	df	Mean square	F	p
Net displacement	smooth habitat	4	230.33	13.70	0.000
	flow velocity	1	856.98	50.99	0.000
	habitat × flow	4	100.88	6.00	0.000
	error	179	16.80		
Movement rate	smooth habitat	4	0.2464	8.70	0.000
	flow velocity	1	1.7707	62.53	0.000
	habitat × flow	4	0.2199	7.76	0.000
	error	179	0.0283		
Mean vector length	smooth habitat	4	0.3319	10.12	0.000
	flow velocity	1	0.0000	0.00	0.985
	habitat × flow	4	0.0916	2.79	0.028
	error	179	0.0328		
Upstream orientation	smooth habitat	4	0.6224	4.94	0.001
	flow velocity	1	0.5558	4.41	0.037
	habitat × flow	4	0.3113	2.47	0.046
	error	179	0.1260		

increase with *h* at fast velocity but exhibited a sharp peak at *h* = 0.40 followed by a decrease at slow flow. The effects of *h* and the interaction between flow velocity and habitat were significant for mean vector length, which increased with *h*. Significant interactions between flow velocity and habitat indicate that flow affected the influence of habitat on *Agapetus* movement, and post-hoc tests revealed differences in the habitat × flow interactions for net displacement, movement rate, mean vector length, and upstream orientation (results not shown).

Specifically, for the slow flow velocity treatment, *Agapetus*' net displacement increased with *h*, but it remained fairly constant as *h* increased in fast velocities (Fig. 3A). Likewise, movement rate showed a general increase with *h* at slow velocity and was lower and more constant at fast velocity (Fig. 3B). Path tortuosity, as measured by mean vector length, showed a general increase (i.e. was straighter) with increasing *h*, but there were no significant differences between slow and fast velocity treatments (Fig. 3C). Upstream orientation at slow velocity was low, yet positive, at low *h*, peaked at *h* = 0.40, and then decreased with increasing *h* (Fig. 3D). At fast velocity, upstream orientation started low and generally increased.

Movement patterns of *Physa*

Proportion of habitat and flow velocity also had significant effects on *Physa*'s movement (Table 2). *Physa*'s movement rate and mean vector length were significantly affected by *h*, flow velocity, and their interaction: movement rate increased with *h* and flow velocity and while mean vector length did not show a difference between slow and fast velocity, there was a

general increase with *h*. Both *h* and flow velocity had significant effects on upstream orientation which increased with *h* and decreased with velocity, but net displacement was only significantly affected by *h*, with which it increased. Significant interactions between flow velocity and habitat indicate that flow velocity affected the influence of habitat on *Physa* movement.

There were no significant differences between *Physa*'s net displacement in slow and fast velocity treatments, but net displacement did show a general increase with increasing *h* (Fig. 3E). Movement rate at slow velocity peaked at *h* = 0.60, while at fast velocity exhibited a general increase from *h* = 0.20 to *h* = 1.0 (Fig. 3F). *Physa*'s movement paths were increasingly straight with *h* in both the fast and slow velocity treatment levels, though there were no significant differences between fast and slow velocity (Fig. 3G). Finally, while *Physa* always exhibited positive upstream orientation, there was a general increase in upstream homing with *h* in both the fast and slow flow velocity treatments, though movement was more upstream-oriented in slow flow velocity (Fig. 3H).

Discussion

Habitat heterogeneity and near-bed flow velocities affect the behavior, movement and resource use of insects (Hart and Resh 1980, Kohler 1984, Poff and Ward 1992), and thus play important roles in determining the spatial distribution, abundance and community structure of benthic macroinvertebrates in streams (Hart and Finelli 1999). Our study shows that the movement patterns of *Agapetus* and *Physa* responded to both landscape structure and flow, and most notably to their pronounced interaction. Increasing proportions of smooth

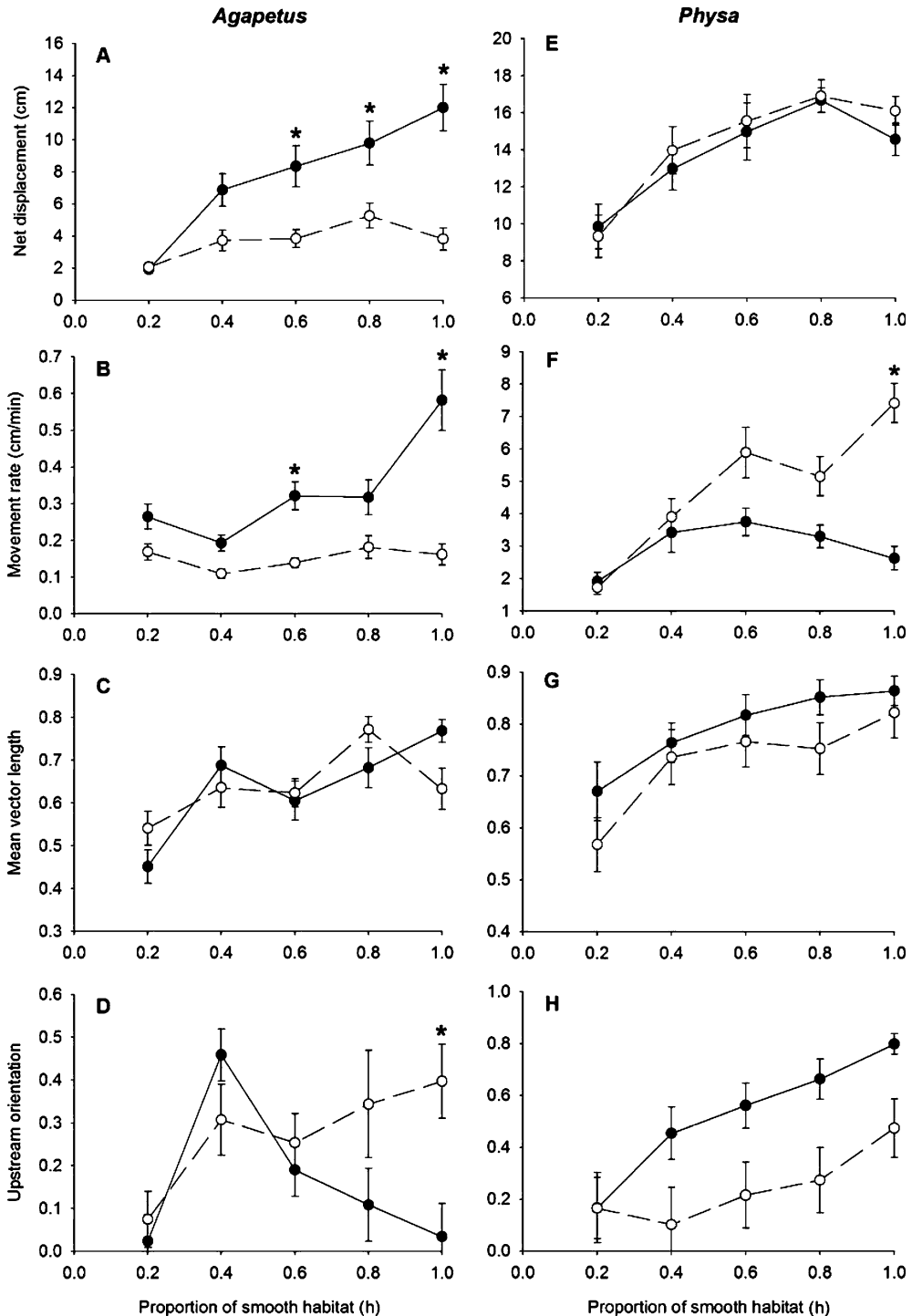


Fig. 3. Mean values (± 1 SE) of *Agapetus* and *Physa* (A,E) net displacement, (B,F) movement rate, (C,G) mean vector length, and (D,H) upstream orientation at fast and slow flows at all treatment levels. Solid lines and ● represent “slow velocity”; dashed lines and ○ represent “fast velocity”. Asterisks indicate significant ($p < 0.05$) differences between fast and slow flow treatments. Note different scales of y axes.

habitat allowed *Physa* to travel farther using more upstream-oriented paths. *Agapetus* likewise traveled farther as smooth habitat increased, but did so only in

slow flow conditions. Swifter flows caused slower *Agapetus* movement using more upstream-oriented paths, but only in completely smooth landscapes

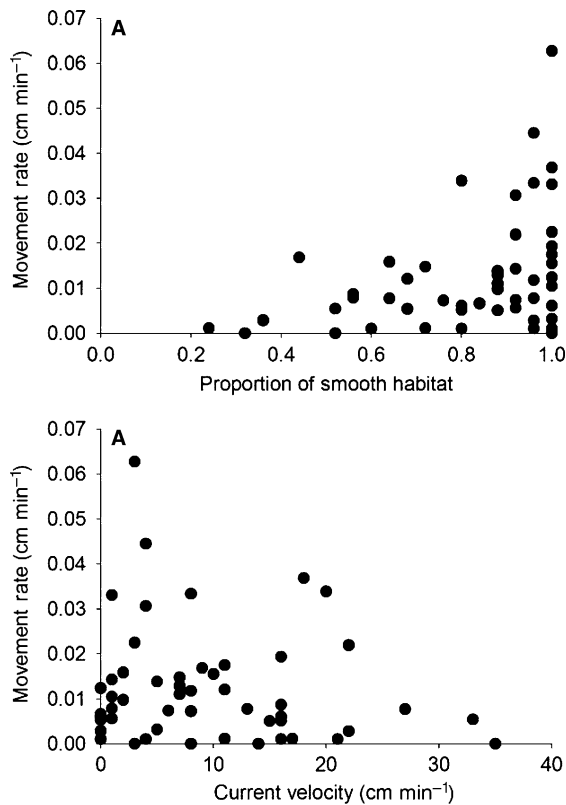


Fig. 4. In-stream survey results indicating the net displacement rate of 51 *Agapetus* individuals on natural stones as a function of (A) proportion smooth habitat and (B) current velocity.

($h = 1.0$). Conversely, swifter flows caused *Physa* to move faster, a pattern also demonstrated only in the smoothest landscape. Clearly, flow and landscape structure had strong individual influences on movement paths, yet more often than not, the two components interacted to shape the movement of these two grazers.

Movement behavior

Differences in *Agapetus* and *Physa* movement patterns reflect, in part, the behavior and morphology of the two grazers (Materials and Methods). The movement styles of *Physa* and *Agapetus* were best suited to smooth habitat patches, however *Physa*'s continuous movement (aided by its muscular foot) was far less impeded by structured patches than was the movement of *Agapetus*. In fact, our observations revealed that *Physa* could often maintain a straight course by moving over a structured patch, whereas *Agapetus* would have to adjust its course around those patches. The two grazers' contrasting responses to flow changes are more difficult to interpret. We have documented a slower and more upstream-oriented movement mechanism ("pivoting") used by *Agapetus* in fast flows (Olden et al. 2004a). *Physa*'s muscular foot might have enabled it to more easily traverse structural barriers compared to *Agapetus* (Fig. 3), but its much larger size might have left it less influenced by micro currents formed by landscape obstacles, resulting in fewer significant velocity \times habitat interactions than *Agapetus*. *Physa*'s faster and less upstream-directed movements in fast current velocities suggest that it may be "escaping" these stressful conditions. This behavior is congruent with other studies in which snails have been shown to move to low-velocity patches or to lodge themselves in sand or gravel to evade fast flow velocity (Levinton et al. 1995, Holomuzki and Biggs 1999, N. L. Poff unpubl.). The natural preference of *Physa* and many other snails for areas of little or no current supports this explanation (Dillon 2000).

The movements of both grazers exhibited upstream orientation, a pattern that has been examined previously. Rheotactic movement behavior has been found in some benthic invertebrates (Poff and Ward 1992, Poff and

Table 2. Analysis of covariance for the movement parameters from *Physa* sp. pathways. Twenty replicate pathways (allocated over space and time and pooled across 2 replicates of landscapes for each treatment: see Methods) were measured in each of 5 treatment levels of smooth biofilm habitat (20%, 40%, 60%, 80% and 100%) and 2 treatment levels of flow velocity (5–15 cm s^{-1} and 20–30 cm s^{-1}). Bold values are significant at the 0.05 level.

Movement parameters	Source of variation	df	Mean square	F	p
Net displacement	smooth habitat	4	303.28	11.87	0.000
	flow velocity	1	15.88	0.62	0.432
	habitat \times flow	4	6.28	0.25	0.912
	error	179	25.56		
Movement rate	smooth habitat	4	67.92	13.22	0.000
	flow velocity	1	162.21	31.56	0.000
	habitat \times flow	4	34.9	6.79	0.000
	error	179	5.14		
Mean vector length	smooth habitat	4	0.05	5.55	0.000
	flow velocity	1	0.04	4.46	0.036
	habitat \times flow	4	0.04	4.60	0.001
	error	179	0.01		
Upstream orientation	smooth habitat	4	1.29	5.25	0.000
	flow velocity	1	4.04	16.40	0.000
	habitat \times flow	4	0.26	1.06	0.377
	error	179	0.25		

Nelson-Baker 1997), but not in others (Hart and Resh 1980, Bird and Hynes 1981). Given the scarcity of studies examining upstream orientation behavior in a landscape context, we suspect its occurrence may be understated. Our results demonstrate not only the occurrence of rheotaxis across taxa and current velocities, but also its consequent constraint of organism movements (Olden et al. 2004a). Indeed, taxis responses have long been known to drive movement (Loeb 1918), and only recently been reconsidered in landscape contexts (Lima and Zollner 1996, Olden et al. 2004b).

Interactive landscapes

Perhaps of greatest interest is how flow and landscape structure interacted to influence the movement of these grazers. Our observations provided several insights into the mechanisms of this interaction. We observed the tendency of high profile structured patches to interrupt near-bed flows, thus creating hydraulic dead zones in smooth patches directly downstream of them (Davis and Barmuta 1989). Another pattern we observed was the channeling of flows by structured patches, which often “squeezed” currents to create locally faster flows over smooth patches. This pattern can strengthen the upstream “signal” to which these animals respond and likely added variability to our movement data; indeed, we suspect that this pattern may be responsible for the counterintuitive peak in *Agapetus* upstream orientation at $h = 0.4$ in slow flow.

These significant and complex interactions between flow and landscape structure are not uncommon, and our results may have important ramifications for the role of abiotic factors in the traditional view of landscape connectivity. Recently, wind has been shown to interact with landscape patches to influence insect movement, resulting in asymmetrical connectivity between patches, depending on which is upwind from the other (Schooley and Wiens 2003). We have likewise shown that aquatic invertebrates can respond to the direction and force of moving water, and therefore create a similar asymmetry in connectivity between upstream and downstream habitat patches. Furthermore, like wind, this connectivity may exhibit temporal variability as turbulence patterns and stream flow changes. This variability might also be affected by temporal changes in the abundance of *Pagastia* and filamentous algae. In short, the influence of directional environmental gradients in shaping animal movement behavior deserves greater attention (Olden et al. 2004b).

Population implications

Our experimental results are in part validated by movement and distribution patterns we observed on the

natural streambed. Our in-stream survey demonstrated that naturally-distributed *Agapetus* larvae moved farther on smoother landscapes and in slower flows. We speculate that movement constraints imposed on *Agapetus* by swift flows and high *Pagastia* retreat coverages are energetically costly as well as hydraulically constraining, perhaps due to increased movement labor and reduced foraging time. These costs may limit the distribution of *Agapetus* to smoother, slower patches of the streambed landscape, and appear to shape the distributions of other glossosomatid species similarly (Monroe 2002). Competing with this explanation, however, are the *Agapetus* larvae we found, albeit infrequently, in swift flows and in retreat-structured habitats, which may suggest biotic interactions or some unknown benefit of these habitats (Olden et al. 2004a).

These patterns suggest a greater complexity in the dispersal of *Agapetus* and *Physa* populations in this streambed landscape. Given this heterogeneous habitat template of flow and structure, and its consequences for movement, we expect the dispersal probabilities of these grazers to reflect not only differential structural and hydraulic permeabilities, but also differential susceptibility to direction of flow. In an area dominated by smooth patches, we would predict elevated dispersal of *Agapetus* and reduced, directed dispersal of *Physa* in slow flow, while in fast flow we would expect reduced, directed dispersal of *Agapetus* and elevated, less directed, dispersal of *Physa*. Areas dominated by *Pagastia* retreats would likely reduce dispersal of both *Agapetus* and *Physa*.

Conclusions and implications

Our results suggest the effects of smooth and structural habitat patches on insect movement depend on the context of local flow velocity. Directional biases in these aquatic herbivores are also important, as connectivity in a streambed landscape may be uneven depending on whether a patch is upstream or downstream of an individual.

Our approach emphasizes individual-level movements and behavioral decisions that scale up to influence processes at coarser-scales and higher levels of organization, such as population dispersal and distribution (Levin 1992, Fahrig and Merriam 1994, Malmqvist 2002, Morales and Ellner 2002). In contrast to much of landscape ecology, which tends to focus on coarser, “landscape scales”, we have shown the importance of fine-scale structural patchiness in a non-terrestrial environment. Furthermore, the structural patchiness we examined is biologically caused, and emphasizes the strong role that habitat engineers play in landscapes (Jones et al. 1994, Cardinale et al. 2004).

We have demonstrated how the dominant environmental gradient of water flow can interact with structural patchiness to influence animal movement in complex ways. Such gradients are ubiquitous in nature (e.g. wind, temperature, altitude), and can interact with the structural landscape to influence animal movement in a variety of settings (Whicker and Tracy 1987, Davis et al. 1999, Schooley and Wiens 2003). These gradients should be more explicitly incorporated into studies of movement, dispersal, and distribution, as they provide the context in which animal-environment interactions produce the most insightful results (Olden et al. 2004b).

Future studies should take into account the differential mobility of animals in landscapes, as well as the differential permeability of landscape patches, to provide biological realism and interpretability. In the continued effort to understand and explain the relationship between animals and landscapes, we encourage researchers to embrace a broader definition of landscape, which includes both aquatic and terrestrial environments, as well as their interfaces.

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