DISSERTATION

THE IMPORTANCE OF CURRENT VELOCITY, SCALE, AND PATCHINESS FOR AQUATIC INVERTEBRATE MOVEMENT AND COLONIZATION

Submitted by

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY AARON HOFFMAN ENTITLED "THE IMPORTANCE OF CURRENT VELOCITY, SCALE, AND PATCHINESS FOR AQUATIC INVERTEBRATE MOVEMENT AND COLONIZATION" BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

THE IMPORTANCE OF CURRENT VELOCITY, SCALE, AND PATCHINESS FOR AQUATIC INVERTEBRATE MOVEMENT AND COLONIZATION

The field of landscape ecology focuses on spatial patterns of heterogeneity and their effects on ecological processes. Another main focus is on scale, and how the interplay between patterns and processes changes with scale. Landscape ecology has traditionally been concerned with terrestrial heterogeneity, particularly how the arrangement of vegetation affects ecological processes. This dissertation, however, focuses on streambed landscapes, which, though largely unexplored, represent an excellent opportunity to study landscape ecology concepts such as heterogeneity, scale hierarchy and the effects of landscape structure at various scales.

Chapter 1 uses percolation theory as a framework to examine how the proportion of useable habitat in a streambed landscape interacts with current velocity to affect the movement patterns of two benthic grazers. The physical structure and arrangement of patches in a landscape can influence animal movement. Most movement studies have occurred in terrestrial landscapes, though aquatic landscapes are equally heterogeneous and animals living there encounter patches differing in movement resistance. Furthermore, the pervasive and variable effects of unidirectional flowing water are unique in streambed landscapes, and the constraints imposed on animal movement by this factor are poorly understood.

Using percolation theory as a framework, this study asks how the proportion of useable habitat in a streambed landscape interacts with current velocity to affect movement patterns of two benthic grazers that differ in body size and habitat preferences. Ten experimental streambed landscapes of varying proportions of two algal types were constructed: tall, structured filamentous stands engineered by the chironomid larva *Pagastia sp.,* and low, smooth diatom turfs. Movement paths of larval glossosomatid caddisflies (*Agapetus boulderensis*) and pulmonate snails (*Physa sp.*) were recorded on these plots at two current velocities, and analyzed their movement patterns using four metrics: net displacement, movement rate, mean vector length, and upstream orientation.

Both landscape structure and current velocity affected animal movement. *Agapetus* net displacement, movement rate, and upstream orientation were significantly related to the proportion habitat, current velocity, and their interaction; mean vector length was affected by proportion habitat and its interaction with current velocity. Specifically, *Agapetus* 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, yet only in completely smooth landscapes. *Agapetus* movement paths showed increasing straightness with proportion habitat at both flow levels. *Physa* movement rate and mean vector length were affected by proportion habitat, current velocity, and their interaction; net displacement was affected by proportion habitat; and upstream orientation was affected by proportion habitat and current velocity. Increasing proportions of smooth habitat allowed *Physa* to travel farther using more

upstream-oriented paths. Faster flows caused *Physa* to move faster, a pattern demonstrated only in the smoothest landscape. *Physa*'s mean vector length indicated a straighter path at the slow current velocity than at the faster velocity, but again only in the smoothest landscape. Landscape ecology has mainly remained above the water's surface, and this study is a first step towards understanding the interactions between habitat heterogeneity, animal movement, and fluid media.

Chapter 2 broadens the extent of Chapter 1, employing invertebrate community measures to focus on three major spatial scales of the study stream. Hierarchical ANOVA and multiple regression with response variables species richness, species diversity, invertebrate abundance, and faunal ash free dry mass (AFDM) were used. These analyses helped determine how the aquatic invertebrate community responds to multiple scales of patchiness and habitat structure, as well as the spatial scales at which landscape heterogeneity is most important to the distribution of these animals. Experiments were performed over approximately one month, with invertebrate measurements taken from observations spaced three times over the course of the experiment, as well as from a final destructive sampling of the study stones.

In general, results from the multiple regression indicated that percentage and AFDM of algae were the best predictors of species richness and diversity, invertebrate abundance, and faunal AFDM. Specifically for the multiple regression by time, percent algae was significant at all three time intervals for species richness, species diversity and for time steps 2 and 3 for invertebrate

abundance. Other variables in the regression, such as mean depth, were significant for species richness and diversity at time step 1, and also for invertebrate abundance at time step 2. Mean current velocity was significant for species diversity at time step 1, and habitat (riffle vs. run) was significant for invertebrate abundance at time step 3. Results from the final multiple regression based on the destructive sampling indicated similar results: AFDM of algae was a significant predictor of species richness and species diversity, as were habitat and mean current velocity. Invertebrate abundance was significantly affected by mean depth and habitat, while none of the variables measured was a significant predictor of AFDM fauna.

Results from the hierarchical ANOVA generally show that of the variables measured, those at the surface scale were the best predictors of species richness, species diversity, and invertebrate abundance. Specifically, in the analysis by time, the finest (surface) scale was significant for species richness, diversity, and invertebrate abundance at all time steps. The intermediate (stone) scale was significant at time step 2 for species richness but not significant for species diversity or invertebrate abundance. The broadest (channel unit) scale was only significant for invertebrate abundance at time step 3. In the final analysis of destructive sampling, the surface scale was significant for species richness, diversity, faunal AFDM and invertebrate abundance. The stone scale was only significant for species richness and diversity, while the channel unit scale only significant for species diversity.

This study integrates fine-scale stream ecology with the landscape ecology principle of scale-dependence to indicate the scales most important to benthic invertebrate distribution. While the distribution of invertebrates on the streambed can vary significantly between spatial scales, this study indicates that the fine scale explains the most variation in the response variables.

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DEDICATION

This dissertation is dedicated to those family members unable to see its completion. To my great-grandparents Stephen and Rose Biros, my great-grandfather Tom Ruiter, my grandmother Mildred Ruiter, my grandparents Albert and Leona Hoffman, and my grandmother-in-law Edwina Ford.

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CHAPTER 1:
CURRENT VELOCITY AND HABITAT PATCHINESS SHAPE STREAM HERBIVORE MOVEMENT.

Introduction

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, With et al. 2002, Jonsen and Taylor 2000). 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 (but see Poff and Ward 1992).

Percolation theory, which provides the basic framework for this study, has been adapted from the physical sciences (Stauffer 1985) for quantifying the effect of landscape structure on terrestrial animal movement (Gardner et al. 1987, O'Neill et al. 1988, Gardner et al. 1989, Wiens et al. 1997, With et al. 1997, With et al. 1999, With et al. 2002). Generally, percolation 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. The proportion and arrangement of these habitat patches dictates the connectivity of a landscape to animal movement (Wiens et al. 1997). Theoretically, when the average proportion of suitable habitat (p_h) in a landscape equals or exceeds a certain critical threshold (p_{crit}), animals can traverse, or permeate, the entire landscape (Gardner et al. 1987). However, predictions of permeability can vary depending on several factors, including the "movement rules" of the organism (Stauffer and Aharony 1994), the validity of the patch

suitability assumptions (Wiens et al. 1997), the contagion and fragmentation of patches (With et al. 1997, With et al. 2002), and food availability (Goodwin and Fahrig 2002).

Most animal movement models focus only on the importance of patch structure in influencing animal movements, without regard for environmental gradients that may act independently or interactively on movement patterns. Application of movement models in streams, however, requires incorporation of the pervasive and variable effects of water flow. 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 in the shear stress experience by the organisms exposed to it (Statzner et al. 1988, Poff and Ward 1992). Current, 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 (Fausch and White 1981, Kuhara et al. 2000), and movement of aquatic invertebrates (Poff and Ward 1992, Huryn and Denny 1997, Poff and Nelson-Baker 1997). Moreover, the directional nature of current may affect the fluxes of streambed processes (Wiens 2002).

The use of a percolation theory framework in streambed environments affords us a means to examine how flow interacts with habitat patchiness to shape animal movement. This application further allows us to evaluate the general applicability of the percolation approach in a novel setting characterized

by the environmental "forcing function" of flow. Indeed, other landscapes may variably express similar strong forcing functions, such as wind (Schooley and Wiens 2003).

Using primarily an artificial stream experiment, we compared the movement patterns of two herbivorous benthic invertebrates (the glossosomatid caddisfly *Agapetus boulderensis* Milne, 1936 and the pulmonate snail *Physa sp.*) across a range of current velocities and habitat patchiness. We described their movements by calculating four movement metrics (net displacement, movement rate, mean vector length, and upstream orientation) and expected movement patterns for these two species to reflect largely their contrasting behaviors and body morphologies, which are known to significantly influence behavior in flowing waters (e.g. Statzner et al. 1988, Poff and Ward 1992, 1995, Hart and Finelli 1999).

Materials and Methods

Study site and organisms

The study was conducted during the summers of 2001 and 2002 in and alongside the upper Colorado River (Grand County, Colorado, 40°11'N, 105°52'W, elevation 2420 m). The reach runs through a shrubland valley approximately 7 km downstream from 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* (Roback, 1957)(Diptera: Chironomidae; hereafter referred to as *Pagastia*) (Fig.

1.1). 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. The smooth surfaces host inconspicuous biofilms that contain diatoms and other microscopic components. An instream survey of naturally occurring *Pagastia* retreats on stones in the stream indicated that the average proportion suitable smooth habit (p_h) was 0.84 (n=180, SD=0.14) (Monroe 2002).

In this study we examined the movement of two non-drifting (crawling) benthic grazers (Fig. 1.1), the glossosomatid caddisfly larva *Agapetus boulderensis* (only fifth instar animals were used) 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 constructed at each ecdysis (mean length 4.5 mm, mean width 3.0 mm, mean height 2.2 mm, n=80) that are constructed of sand grains and silk with ventral openings at both ends. While the case provides protection from predators (Otto and Svensson 1980, Kohler and McPeek 1989), 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 microhabitats ranging from calm, unsilted shallow water to deep, fast-flowing areas with near-bed current velocities ranging between 5 and 30 cm/s; they are rarely found at current velocities exceeding 50 cm/s (Poff and Ward 1992, Wellnitz et al. 2001). They do not actively enter the water column, which makes them ideal for tracking movements.

The freshwater snail *Physa* is an armored grazer whose shell length varies in length from approximately 9 to 15 mm. *Physa* is most often found crawling on stones along calm stream margins and eddies; current velocity is the primary factor in determining the distribution of these species, and like *Agapetus*, they do not actively enter the drift (Dillon 2000). Also like *Agapetus, Physa* feeds preferentially on diatoms (Dillon and Davis 1991, Lombardo and Cooke 2002). Unlike *Agapetus*, *Physa* is able to negotiate stands of thick filamentous algae using its large muscular foot, which allows the snail to achieve relatively uniform distribution in complex, structured landscapes (Gotoh and Kawata 2000).

Experimental landscapes

The movement response of *Agapetus* and *Physa* to current 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. 1.2A), over the experimental landscapes, and returned to the river. Valves at the top of the flume allowed for the control of current velocity. Experimental landscapes placed in the flume measured 35.5 cm x 35.5 cm and consisted of 196 unglazed ceramic tiles (2.54 cm x 2.54 cm) arranged in 14 rows and 14 columns (Fig. 1.2B). The size of the experimental landscapes was based on pilot studies that indicated the movement rates and distances of *Agapetus* and *Physa*. Since 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 arrays of 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, 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 tiles 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 from smooth and *Pagastia*-colonized tiles confirmed important structural differences between the two habitat types; AFDM of structured tiles was an order of magnitude greater than smooth tiles ($\overline{X}$ = 0.0173 g vs. 0.0014 g, n = 4). Food availability was comparable between tile types, with both containing substantial diatom proportions (Olden et al. 2004*a*); however, food accessibility varied because diatoms on the structured tiles were epiphytic and thus largely inaccessible (particularly to *Agapetus*, which "scrape" diatoms from smooth surfaces using specialized mouthparts).

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 (p_h) at 0.20, 0.40, 0.60, 0.80, and 1.0 (Fig. 1.2B). Two randomly arranged landscapes served as replicates for each p_h. The range of p_h in our experimental

landscapes matched that found in the stream (see "Stream surveys of *Agapetus* movement", below). We recorded movement patterns at each of these p_h levels under two current velocity treatments, as measured within 1 cm of the tiles with a current probe (Schiltknecht Messtechnik AG, Zurich, Switzerland): "fast" (20-30 cm/s) and "slow" (5-15 cm/s). These current velocities commonly occur in the study system, and are well within the range of current velocities at which *Agapetus* reaches the highest densities at this study site (Wellnitz et al. 2001). *Physa*, however, primarily inhabits slower margins and eddies, and is more constrained to slower current velocities (Dillon 2000, A. Hoffman, pers. obs).

On each of the five experimental landscapes (p_h =0.20 to 1.0), two replicates of each landscape, and two current 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). Based on the results of a pilot study and the differential movement speeds of each species, we started each trial by placing an individual near the center of the experimental landscape and recording the *x,y* location of *Agapetus* every 3 min for 1 h and *Physa* 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.).

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 on 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 (Swihart and Slade 1985). Only 9 out of 200 *Agapetus* and 5 out of 200 *Physa* individuals exhibited independence between successive positions. 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 parameters. *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. *Mean vector length* is a measure of overall path tortuosity, and is a unit vector measure of the dispersion of turning angles (Batschelet 1981, Wiens et al. 1993b). It varies between 0.0 (uniform or nondirectional) to 1.0 (perfectly directional). Finally, a measure of *upstream orientation*, or homeward component (Batschelet 1981), was used to determine how close the mean path

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) to test for the effects of smooth habitat, current velocity and replicate landscapes on the four movement metrics, and used water temperature as a covariate. 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).

Percolation theory

In the strictest percolation models, movement from cell to cell is limited to each of the four cardinal directions, and the threshold value (p_{crit}) at which animals can traverse the landscape is on average equal to 0.5928. More complex models allow movement to the "next nearest" neighbor (diagonal moves), and p_{crit} averages 0.4072 (Stauffer and Aharony 1994). These models, however, are limiting in real-world landscapes due to the difficulties of finding habitat patches of binary (all-or-none) permeability. Because natural habitat patches often exhibit varying degrees of permeability, previous studies have shown that the threshold to connectivity in more natural systems can be lower than the theoretical p_h, ranging from p_{crit} <0.20 (Wiens et al. 1997), 0.20-0.50 (With et al. 1999), and 0.29-0.50 (With et al. 1997). To determine whether there was a critical habitat threshold for the movement behaviors of *Agapetus* and

Physa, we graphed the proportion of experimental animals "percolating" (i.e. moving off the experimental landscape) during their movement trials versus p_h.

Stream surveys of *Agapetus* movement

To explore the movement dynamics of *Agapetus* in relation to *in situ* habitat patchiness and current velocity, a second survey was performed in August 2002 (Appendix 1.A). We randomly selected 60 stones in riffle and run habitats and marked the initial location of a single unsystematically-selected *Agapetus* larva on each, measured near-bed current velocity, and estimated the percentage of *Pagastia* retreat coverage. After 3 h, we marked the final location of each larva, and calculated net displacement rate (i.e., net displacement divided by the total time).

Results

Movement metrics: *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. Temperature was a non-significant covariate; however, because of its importance in influencing *Agapetus* movement rate (Poff and Ward 1992) we retained it in the analyses to control for temperature effects regardless of the small amount of variation it explained.

Both p_h and current velocity had significant effects on *Agapetus* movement across the experimental landscapes (Table 1.1). The ANCOVA tests indicated

significant effects of p_h, current velocity, and their interactions for net displacement, movement rate, and upstream orientation. The effects of p_h and the interaction between current velocity and habitat were significant for mean vector length. Post-hoc tests revealed differences in the habitat-flow interactions for net displacement, movement rate, mean vector length, and upstream orientation (Appendix 1.B).

For the slow current velocity treatment, *Agapetus'* net displacement increased linearly with p_h, but it remained relatively constant as p_h increased in fast velocities (Fig. 1.3A). Likewise, movement rate showed a general increase with p_h at slow velocity and was lower and more constant at fast velocity (Fig. 1.3B). Path tortuosity, as measured by mean vector length, showed a slight increase (i.e. was straighter) with increasing p_h, but there were no significant differences between slow and fast velocity treatments (Fig. 1.3C). Upstream orientation at slow velocity was low, yet positive, at low p_h, peaked at p_h =0.40, and then decreased with increasing p_h (Fig. 1.3D). At fast velocity, upstream orientation started low, showed a small rise at p_h =0.40 and then increased.

Movement metrics: *Physa*

Proportion habitat and current velocity also had significant effects on *Physa's* movement (Table 1.2). *Physa's* movement rate and mean vector length were significantly affected by p_h, current velocity, and their interaction. Both p_h and current velocity had significant effects on upstream orientation, but net displacement was only significantly affected by p_h. Further results of the post-hoc

tests of the significant flow-habitat interactions in movement rate and mean vector length are given in Appendix 1.C.

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 p_h (Fig. 1.3E). Movement rate at slow velocity peaked at p_h=0.60, while at fast velocity exhibited a small peak at p_h=0.60, a small drop at 0.80, and an increase to p_h=1.0 (Fig. 1.3F). *Physa's* movement paths were fairly straight at all p_h levels in both the fast and slow velocity treatment levels, and there was a significant difference between fast and slow velocity at p_h=1.0 (Fig. 1.3G). Finally, while *Physa* always exhibited positive upstream orientation, there was a general increase in upstream homing with p_h in both the fast and slow current velocity treatments, though movement was consistently more upstream-oriented in slow current velocity (Fig. 1.3H).

Percolation theory

The plot of the proportion of percolating individuals (those reaching the outside boundary of the experimental landscape) against proportion smooth habitat is shown in Fig. 1.4. *Agapetus* individuals did not percolate in the fast velocity treatment, but in slow velocity began to show an increase in percolating movement at p_h=0.60. *Physa* showed a low proportion of percolating individuals at p_h=0.20 in the fast current velocity treatment, but a sharp increase at p_h=0.40 with general increase thereafter. In the slow current velocity treatment, *Physa*

again exhibited a low proportion of percolating individuals at p_h=0.20, but percolation increased with p_h up to 0.80, at which point it remained constant.

Stream surveys of *Agapetus* movement

At the termination of the in-stream movement survey, 51 out of 60 *Agapetus* larvae remained on the stones. The proportion habitat and current velocity on stones showed an effect on *Agapetus* movement, as net displacement rate increased with p_h and decreased with current velocity (Fig. 1.5). The average in-stream net displacement rate of *Agapetus* individuals was 1.2×10^{-2} cm/s (n=51, SD =0.779). These findings are greater than the *Agapetus* net displacement rate reported by Poff and Ward (1992) on natural stones at a similar site in the same stream, which ranged from 2.5×10^{-6} cm/s to 4.5×10^{-4} cm/s (n=127). Poff and Ward also reported faster rates of 1.38×10^{-5} cm/s to 7.33×10^{-4} cm/s (n=126) for *Agapetus* movement in a separate experiment on porcelain tiles with a current velocity of 40 cm/s. In this separate experiment, larvae were picked from the stream and placed on porcelain tiles in a flow-through trough. The faster movement rates seen in our experiment and that of Poff and Ward (1992) may be as a result of the larvae being physically handled or placed on porcelain tiles.

Discussion

Our study shows that the movement patterns of *Agapetus* and *Physa* responded to both landscape structure and current, and most notably to their

strong interaction. Increasing proportions of smooth 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 current. Swifter currents caused *Agapetus* to move slower using more upstream-oriented paths, yet only in completely smooth landscapes (p_h =1.0). Conversely, swifter currents caused *Physa* to move faster, a pattern also demonstrated only in the smoothest landscape. Clearly, current 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. These interactions will be discussed.

Movement behavior

Differences in *Agapetus* and *Physa* movement patterns reflect, in part, the behavior and morphology of the two grazers (see 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 current changes are more difficult to interpret. Although a slower and more upstream-oriented movement behavior used by *Agapetus* in fast currents has been documented (Olden et al. 2004*a*), *Physa's* faster, less

upstream-directed movements in fast currents suggest that it is "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 current velocity (Levinton et al. 1995, Holomuzki and Biggs 1999, N.L. Poff unpublished data). The natural preference of *Physa* and many other pulmonate snails for areas of little or no current would support this mechanism (Dillon 2000).

The movements of both *Agapetus* and *Physa* exhibited upstream orientation, a pattern that has been examined previously (Clampitt 1974, Poff and Ward 1992). Rheotactic movement behavior has been found in other benthic invertebrates (see Huryn and Denny 1997, Poff and Nelson-Baker 1997), but also found lacking in some (see Hart and Resh 1980, Bird and Hynes 1981), and few have examined animal rheotactic response to different velocities of media. Given the relative scarcity of studies examining such upstream orientation behavior, 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. Indeed, taxis responses have long been known to drive movement (Loeb 1918, Fraenkel and Gunn 1940), and only recently been incorporated into in landscape contexts (Lima and Zollner 1996, Schooley and Wiens 2003, Olden et al. 2004*b*).

Interactive landscapes

Perhaps of greatest interest is how current and landscape structure interacted to influence the movement of these grazers. Our observations provided several insights into the mechanisms of this interaction. By watching visible flow patterns, we noted 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). This mechanism could explain the slight decreases in *Agapetus* net displacement and movement rate between p_h =0.8 and p_h =1.0 in fast current (Fig. 1.3); the smoother landscape contained no slow refuges that allow *Agapetus* local areas of faster movement. Another pattern we observed was the channeling of flows by structured patches, which often "squeezed" currents to create locally elevated flows over smooth patches, particularly at p_h =0.4, which seemed to have the right proportion of smooth patches to create this funnel-like effect. This pattern may strengthen the upstream "signal" to which these animals respond, and it doubtless introduced added variability to our movement data; indeed, we suspect it is responsible for the counterintuitive peak in *Agapetus* upstream orientation at p_h =0.4 in slow flow (Fig. 1.3).

These significant and complex interactions between currents and landscape structure are not uncommon (Poff and Ward 1992, Schooley and Wiens 2003, Olden et al. 2004*a*), 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 flows change, thereby altering the overall perceptual breadth of the animal's perceptual range (Olden et al 2004*b*).

Population implications

Our experimental results are validated by movement and distribution patterns we observed on the streambed. Our reported rates of *Agapetus* movement were considerably faster than those reported by Poff and Ward (1992); however, their *Agapetus* subjects were located in faster currents ranging from 5.1 cm/s – 56.4 cm/s. Our in-stream survey demonstrated that naturally distributed *Agapetus* larvae moved farther on smoother landscapes and in slower currents, and not surprisingly, these larvae were most often found in habitats with these conditions (mean current velocity = 9.51 cm/s; mean p_h =82.49, n=51). We speculate that movement constraints imposed on *Agapetus* by swift currents and high *Pagastia* retreat coverages are energetically costly, 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 they 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 currents and in retreat-structured habitats, which may suggest some unknown benefit of these habitats (See Olden et al. 2004*a*).

These patterns suggest a greater complexity in the dispersal of *Agapetus* and *Physa* in this streambed landscape. Given this heterogeneous habitat template of current and algal 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 directive influences (Poff and Ward 1992, Schooley and Wiens 2003). In an area dominated by smooth patches, in slow currents we would predict elevated dispersal of *Agapetus* and reduced, directed dispersal of *Physa*, while in fast current 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*.

Percolation

In the context of percolation theory, the two species differed in their ability to traverse the experimental landscape. Presumably, the constraining forces of current kept *Agapetus* from moving off the landscape in the fast current velocity treatment within the time allotted. At slow velocity, however, *Agapetus* began to "percolate" and exhibited a p_{crit} at p_h =0.60, with a linear increase in the number traversing the landscape as the proportion smooth habitat increased. These

results are consistent with the predictions of percolation theory in it most strict sense (Gardner et al. 1987, Gardner et al. 1989). Indeed, the textured algal stands we used to mimic *Pagastia* retreats were nearly impermeable to *Agapetus* movement, thus upholding the binary-habitat assumption.

In contrast, *Physa* was less constrained by textured habitat than *Agapetus* and did not exhibit a critical threshold at p_h =0.60. At first glance, this appears to disagree with the expectations of percolation theory. However, in high flow, *Physa* did exhibit a preference for smooth habitat, spending more time there (mean 73% of time, compared to a mean random 50%), and thus indicating that the assumptions of percolation theory are better met in faster flows. Also, in fast current velocity, *Physa* individuals show a sharp increase in traversing the landscape at p_h =0.40 (Fig. 1.5). The p_{crit} in percolation models that allow diagonal movement averages p_h =0.4072 (Stauffer and Aharony 1994), suggesting that *Physa* behavior may more closely follow a "nearest neighbor" percolation model.

The habitat affinities of each grazer, the natural patch types used in the experimental system, and the incorporation of current variability make this a useful application of percolation theory. While our experimental system did not meet the strict assumptions of percolation theory, i.e. animals moving only in the four cardinal directions and only moving in habitat patches and never moving in non-habitat patches (particularly with *Physa*), we recognize that ecological systems will rarely meet these assumptions. Indeed, ecological applications of this model will be somewhat loose interpretations, and will be aided by

recognizing its unrealistic assumptions. Ultimately, percolation theory should continue to be a robust framework for examining animal movement through landscapes, as long as it is applied in biologically appropriate ways.

Conclusions

Our results suggest the effects of smooth and structural habitat patches on animal movement depend on the context of local current 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 the individual level, but it is the individual 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, this structural patchiness is biologically caused and emphasizes the potentially strong role that habitat engineers (here, *Pagastia*) play in landscapes (Jones et al. 1994).

We have demonstrated how the dominant environmental gradient of water current can interact with structural patchiness to influence 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 (Wellnitz et al. 2001).

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. Theoretical models, including movement models such as percolation, will certainly aid these studies by providing not only a framework for investigation, but also means to evaluate differences between natural and modeled patterns. Finally, 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.

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Figure Legends

Figure 1.1: *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: J.B. Monroe*

Figure 1.2: *A*) an artificial streambed landscape; 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 benthic landscapes at varying levels of proportion smooth habitat (p_h): (1) culturing algae on 2.54x2.54 unglazed ceramic tiles, (2) at p_h =1.0, (3) at p_h =0.80, (4) at p_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 p_h levels of the experimental landscapes, which can be compared to the natural benthiscape in Figure 1C.

Figure 1.3: 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. Asterisks indicate significant ($p<0.05$) differences between fast and slow flow treatments. Note dissimilar *y*-axes.

Figure 1.4: Mean values of the proportion of percolating individuals for *Agapetus* (circles) and *Physa* (squares) at slow (5-15cm/s) and fast (20-30 cm/s) treatments. *Agapetus* locations were recorded every 3 minutes for a maximum of 60 minutes; *Physa* every minute for a maximum of 20 minutes.

Figure 1.5: 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.

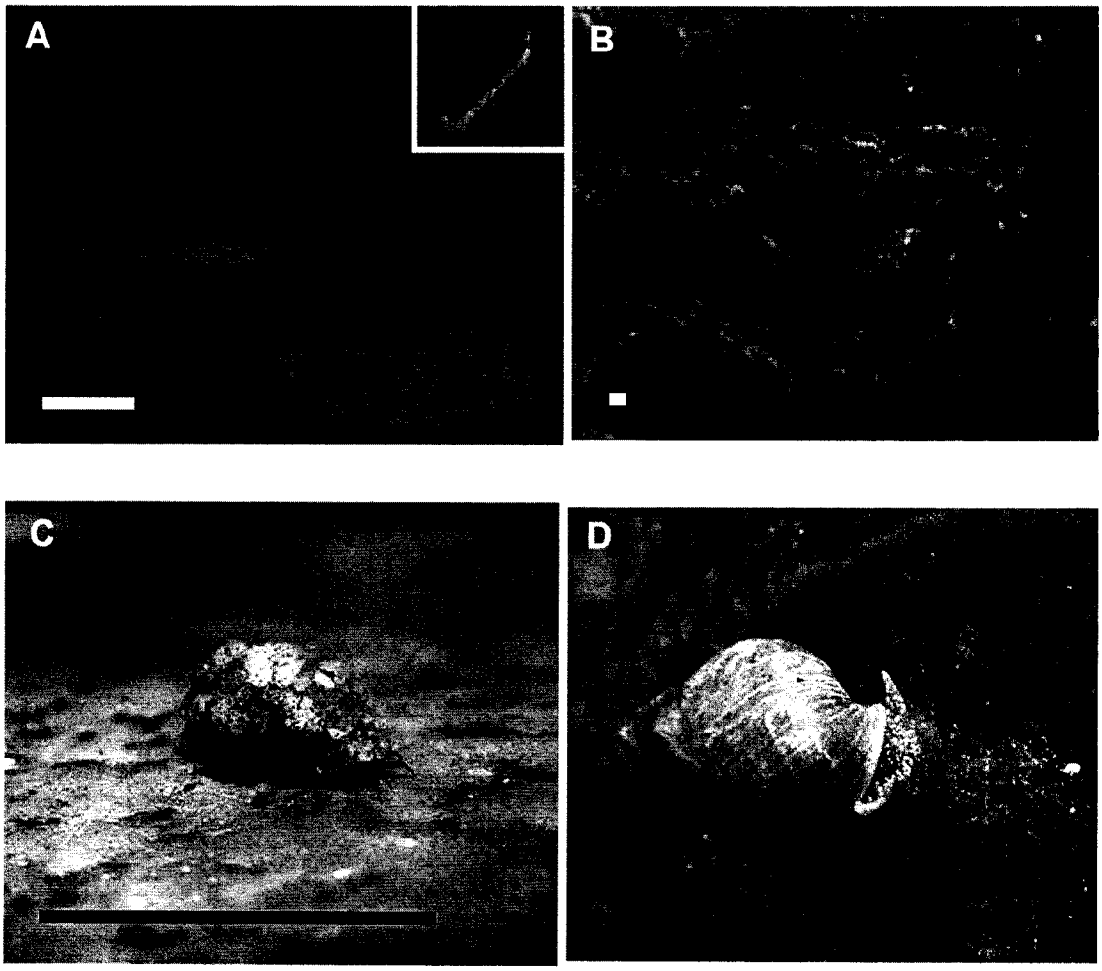
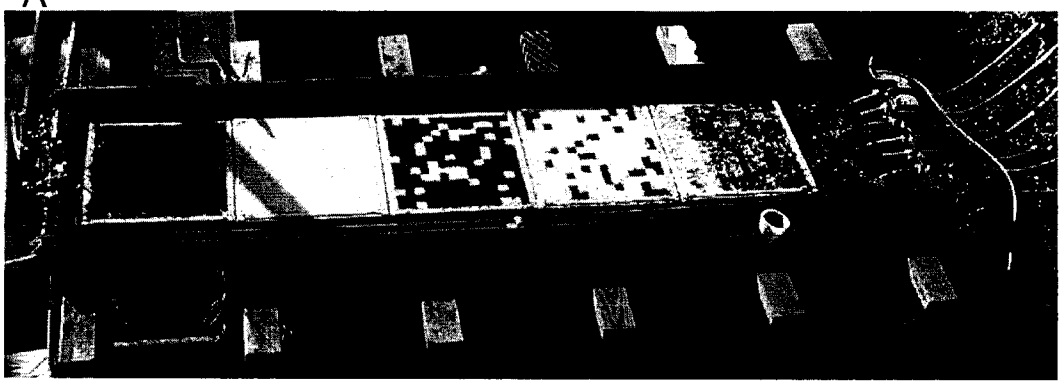


Figure 1.1

A



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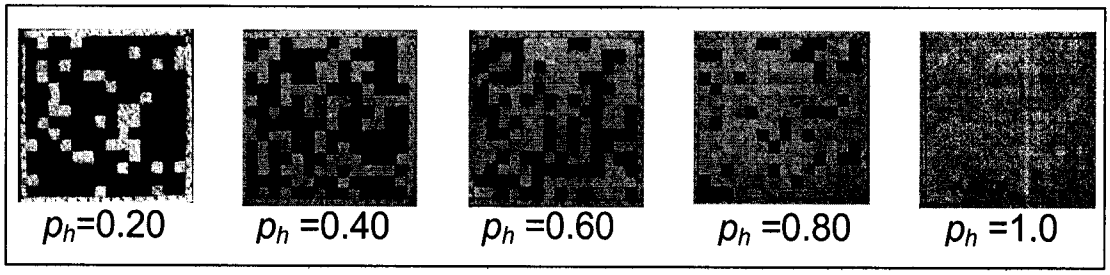


Figure 1.2

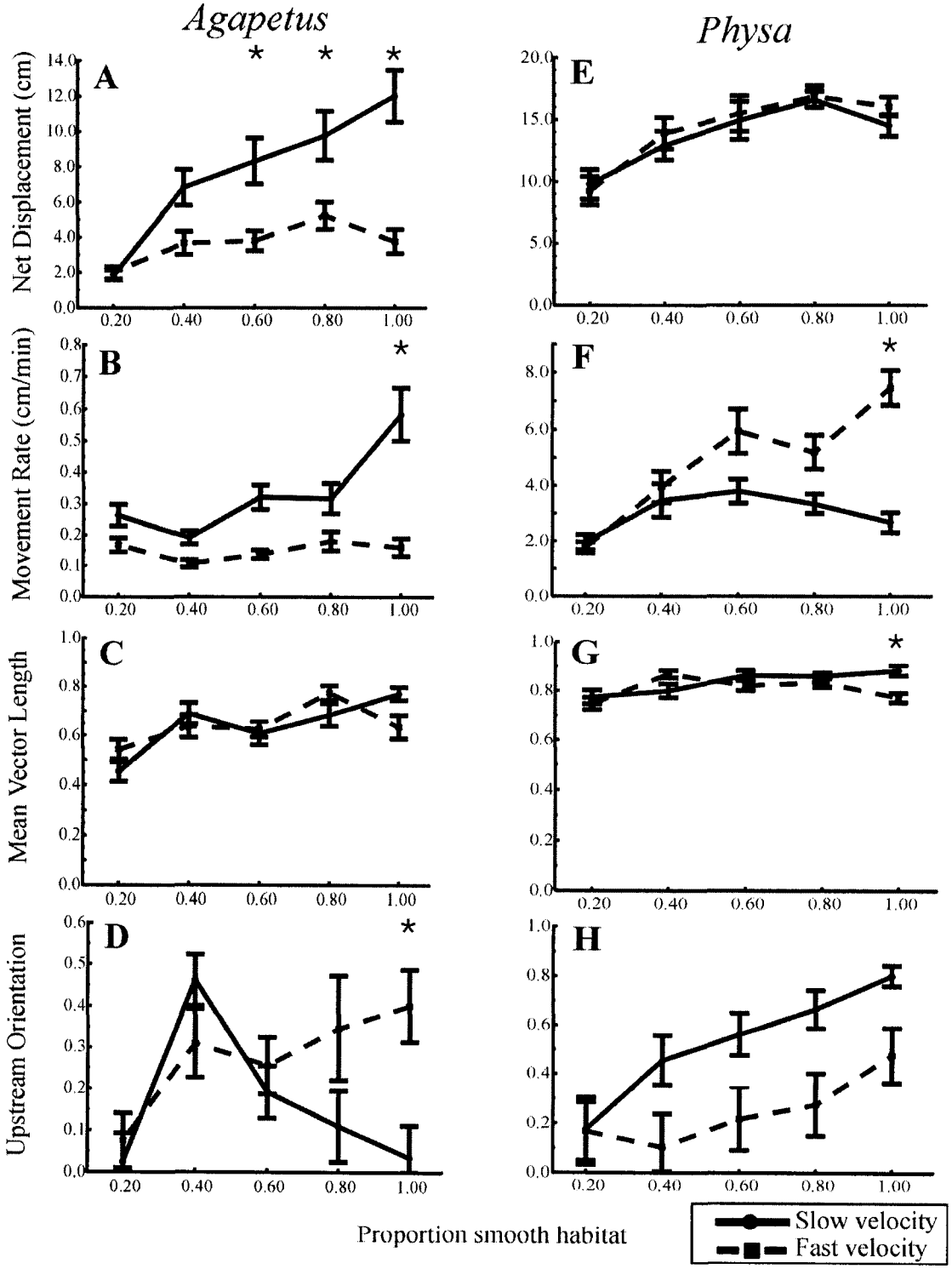


Figure 1.3

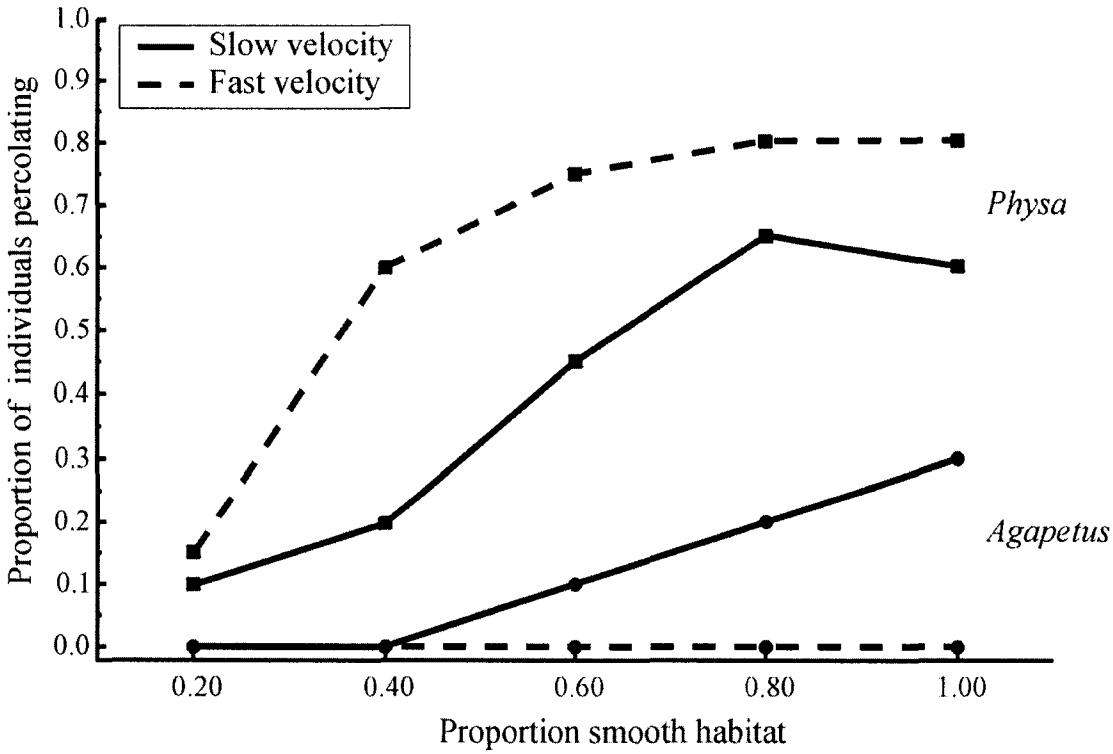
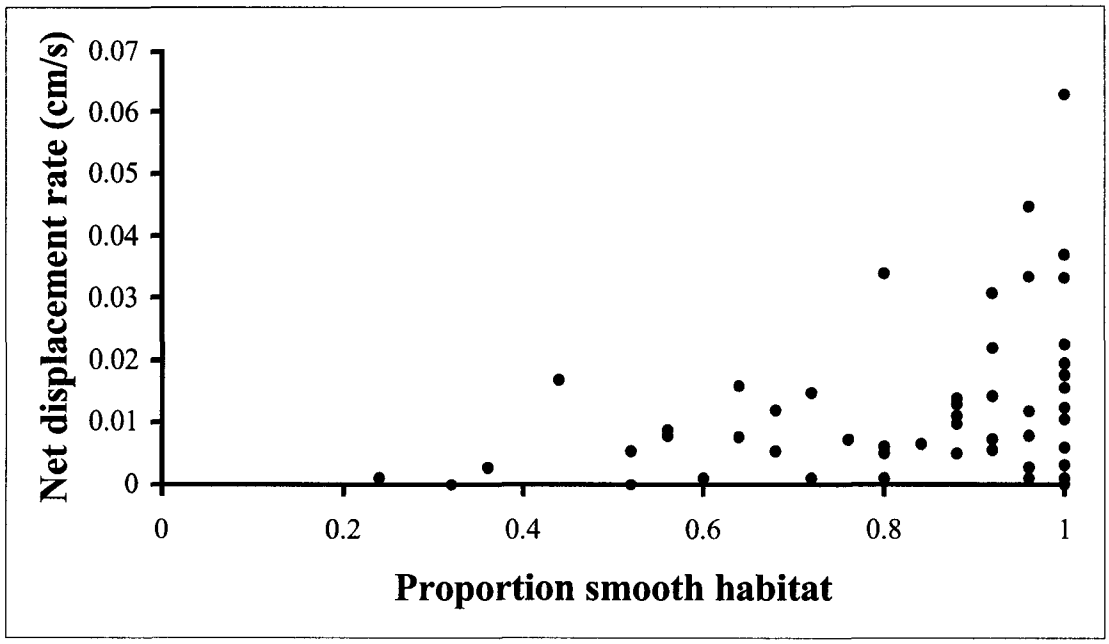


Figure 1.4



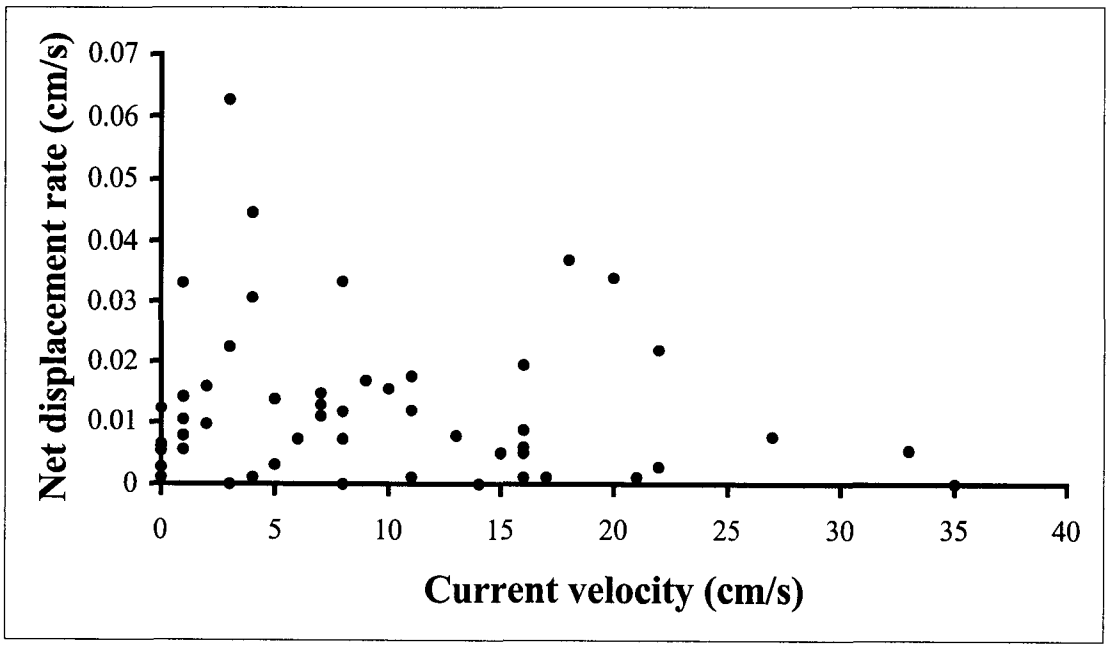


Figure 1.5

Table 1.1: Analysis of covariance for the movement parameters from *Agapetus boulderensis* pathways. Twenty replicate pathways (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 and 20-30 cm/s). Each movement parameter was analyzed separately using water temperature as a covariate.

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		

Table 1.2: Analysis of covariance for the movement parameters from *Physa* sp. pathways. Twenty replicate pathways (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 and 20-30 cm/s). Each movement parameter was analyzed separately using water temperature as a covariate.

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 – 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 – Flow	4	34.92	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 – 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 – Flow	4	0.26	1.06	0.377
	Error	179	0.25		

Appendix 1.A – Results of the stream survey of *Agapetus* movement.

Stone number	Stone depth (cm)	Current velocity (cm/s)	Proportion habitat	Net displacement (cm)	Start time	End time	Elapsed time (hrs)	Movement rate (cm/s)
1	15.0	13	96	1.5	1342	1655	3.22	0.00776
2	14.5	5	100	0.6	1345	1656	3.18	0.00314
3	12.0	10	100	3.0	1346	1659	3.22	0.01553
4	9.5	8	76	1.4	1348	1702	3.23	0.00722
6	11.5	0	68	1.0	1355	1702	3.12	0.00534
7	10.0	14	100	0.0	1400	1704	3.07	0.00000
8	7.0	7	72	2.7	1403	1706	3.05	0.01475
10	10.5	11	68	2.2	1405	1708	3.05	0.01202
11	7.5	11	72	0.2	1410	1711	3.02	0.00110
12	17.5	22	96	0.5	1411	1712	3.02	0.00276
13	10.0	1	100	1.9	1413	1714	3.02	0.01049
14	10.0	1	100	6.0	1414	1715	3.02	0.03311
15	11.5	0	84	1.2	1415	1717	3.04	0.00658
16	13.5	16	100	1.1	1418	1720	3.04	0.00603
17	11.0	3	100	4.1	1419	1721	3.04	0.02248
18	15.0	0	80	1.1	1420	1721	3.02	0.00607
19	12.5	1	92	1.0	1424	1724	3.00	0.00556
20	14.0	6	92	1.3	1427	1725	2.96	0.00732
21	22.0	7	88	2.0	1426	1727	3.02	0.01104
22	16.0	8	100	0.0	1431	1728	2.95	0.00000
23	7.0	3	52	0.0	1433	1729	2.93	0.00000
24	7.5	0	100	2.2	1434	1732	2.96	0.01239
25	10.5	2	64	2.8	1436	1733	2.95	0.01582
26	21.5	11	100	3.1	1437	1735	2.96	0.01745
27	8.5	0	36	0.5	1439	1737	2.96	0.00282
28	6.5	1	56	1.4	1440	1739	2.98	0.00783
29	1.0	17	24	0.2	1441	1741	3.00	0.00111
30	2.0	15	88	0.9	1442	1742	3.00	0.00500
31	23.5	4	96	7.9	1450	1748	2.96	0.04448
32	14.5	2	88	1.8	1453	1758	3.08	0.00974
33	21.0	3	100	0.0	1452	1750	2.96	0.00000
34	10.0	22	92	4.0	1455	1757	3.04	0.02193
35	8.0	20	80	6.4	1456	1805	3.15	0.03386
36	14.5	4	92	5.7	1459	1805	3.10	0.03065
37	6.5	35	32	0.0	1500	1805	3.08	0.00000
38	1.5	18	100	6.8	1502	1807	3.08	0.03680
39	7.5	33	52	1.0	1503	1809	3.10	0.00538
41	14.0	8	96	2.3	1253	1608	3.25	0.01179
42	22.0	5	88	2.7	1256	1611	3.25	0.01385
43	18.5	0	80	0.2	1300	1615	3.25	0.00103
44	19.5	7	88	2.5	1302	1617	3.25	0.01282
45	10.0	27	64	1.5	1305	1620	3.25	0.00769
46	10.0	8	96	6.5	1308	1623	3.25	0.03333
47	13.0	4	100	0.2	1310	1625	3.25	0.00103
49	10.5	16	96	0.2	1314	1627	3.22	0.00104
50	5.5	16	56	1.7	1316	1631	3.25	0.00872
51	11.5	1	92	2.8	1317	1633	3.27	0.01427
52	8.0	9	44	3.3	1319	1635	3.27	0.01682
53	2.0	3	100	12.3	1321	1637	3.27	0.06269
54	10.0	16	100	3.8	1322	1638	3.27	0.01937
56	18.0	16	80	1.0	1326	1642	3.27	0.00510
57	7.0	21	60	0.2	1330	1644	3.23	0.00103
60	8.0	13	96	1.5	1336	1650	3.23	0.00774

Appendix 1.B – Post-hoc Tukey Honest Significant Difference Tests for ANCOVA: *Agapetus boulderensis*. Reported are *p*-levels for differences among habitat-flow treatments for net displacement (upper matrix, upper diagonal), movement rate (upper matrix, lower diagonal), mean vector length (lower matrix, upper diagonal), and upstream orientation (lower matrix, lower diagonal). Numbers across the top and along the sides are proportion habitat (0.2 to 1.0); "Low" and "High" are the current velocity treatments nested within each habitat treatment.

Net Displacement (cm)

Habitat / Velocity		*0.2*		*0.4*		*0.6*		*0.8*		*1.0*	
		Low	*High*	*Low*	*High*	*Low*	*High*	*Low*	*High*	*Low*	*High*
0.2	*Low*	-	1.00	**0.01**	0.93	**0.00**	0.91	**0.00**	0.23	**0.00**	0.91
	High	0.74	-	**0.01**	0.96	**0.00**	0.94	**0.00**	0.29	**0.00**	0.94
0.4	*Low*	0.94	1.00	-	0.31	0.98	0.37	0.43	0.97	**0.00**	0.35
	High	0.10	0.98	0.86	-	**0.01**	1.00	**0.00**	0.97	**0.00**	1.00
0.6	*Low*	0.99	0.12	0.32	**0.00**	-	**0.02**	0.98	0.34	0.13	**0.02**
	High	0.35	1.00	0.99	1.00	**0.02**	-	**0.00**	0.99	**0.00**	1.00
0.8	*Low*	0.99	0.14	0.37	**0.00**	1.00	**0.03**	-	**0.02**	0.79	**0.00**
	High	0.87	1.00	1.00	0.94	0.20	0.99	0.24	-	**0.00**	0.98
1.0	*Low*	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	-	**0.00**
	High	0.65	1.00	1.00	0.99	0.08	1.00	0.10	1.00	**0.00**	-

Movement Rate (cm/min)

Mean Vector Length

Habitat / Velocity		*0.2*		*0.4*		*0.6*		*0.8*		*1.0*	
		Low	*High*	*Low*	*High*	*Low*	*High*	*Low*	*High*	*Low*	*High*
0.2	*Low*	-	0.87	**0.00**	**0.04**	0.18	0.08	**0.00**	**0.00**	**0.00**	**0.04**
	High	1.00	-	0.24	0.82	0.98	0.91	0.29	**0.00**	**0.00**	0.85
0.4	*Low*	**0.00**	**0.02**	-	0.99	0.92	0.98	1.00	0.91	0.92	0.99
	High	0.26	0.55	0.94	-	1.00	1.00	0.99	0.34	0.38	1.00
0.6	*Low*	0.90	0.99	0.33	0.99	-	1.00	0.94	0.11	0.12	1.00
	High	0.57	0.85	0.72	1.00	1.00	-	0.99	0.23	0.25	1.00
0.8	*Low*	0.99	1.00	0.06	0.76	0.99	0.96	-	0.87	0.89	0.99
	High	0.12	0.33	0.99	1.00	0.94	0.99	0.53	-	1.00	0.31
1.0	*Low*	1.00	1.00	**0.01**	0.31	0.93	0.63	1.00	0.15	-	0.35
	High	**0.03**	0.11	1.00	0.99	0.71	0.96	0.23	1.00	**0.04**	-

Upstream Orientation

Appendix 1.C – Post-hoc Tukey Honest Significant Difference Tests for ANCOVA: *Physa sp.* Reported are *p*-levels for differences among habitat-flow treatments for movement rate (upper diagonal), mean vector length (lower diagonal). Numbers across the top and along the sides are proportion habitat (0.2 to 1.0); "Low" and "High" are the current velocity treatments nested within each habitat treatment.

Movement Rate (cm/min)

Habitat / Velocity		*0.2*		*0.4*		*0.6*		*0.8*		*1.0*	
		Low	*High*	*Low*	*High*	*Low*	*High*	*Low*	*High*	*Low*	*High*
0.2	*Low*	-	1.000	0.528	0.145	0.237	**0.000**	0.645	**0.000**	0.993	**0.000**
	High	0.997	-	0.347	0.072	0.127	**0.000**	0.456	**0.000**	0.962	**0.000**
0.4	*Low*	0.998	0.782	-	1.000	1.000	**0.020**	1.000	0.317	0.985	**0.000**
	High	0.060	**0.003**	0.410	-	1.000	0.145	0.998	0.773	0.749	**0.000**
0.6	*Low*	0.102	**0.006**	0.543	1.000	-	0.083	1.000	0.632	0.865	**0.000**
	High	0.885	0.321	1.000	0.856	0.929	-	**0.011**	0.990	**0.000**	0.509
0.8	*Low*	0.117	**0.007**	0.583	1.000	1.000	0.945	-	0.228	0.995	**0.000**
	High	0.663	0.138	0.987	0.973	0.992	1.000	0.995	-	**0.016**	0.050
1.0	*Low*	**0.012**	**0.000**	0.151	1.000	1.000	0.545	0.999	0.803	-	**0.000**
	High	1.000	0.999	0.995	**0.044**	0.077	0.839	0.090	0.593	**0.008**	-

Mean Vector Length

CHAPTER 2:
THE EFFECTS OF MULTIPLE-SCALE PATCHINESS ON AQUATIC INVERTEBRATE COLONIZATION IN THE UPPER COLORADO RIVER

Introduction

Landscape ecology focuses on spatial patterns of heterogeneity, their effects on ecological processes, and how these processes change at different spatial scales. Landscape ecology has traditionally been concerned with terrestrial heterogeneity, particularly how the arrangement of vegetation affects ecological processes. Although largely unexplored, streambed landscapes present an excellent opportunity to study the biological effects of landscape structure at multiple scales. Streambed landscape structure and patchiness are expressed at different scales, such as streambed substrate size and texture, water depth, macroalgae, aquatic insect retreats, and current velocity (Minshall 1984, Diamond 1986, Dudley et al. 1986, Hart and Finelli 1999, Ellsworth 2000, Cardinale et al. 2004).

Patchiness in the spatial distribution of animals, their resources, or specific environmental variables is influential in terrestrial and streambed landscapes because of its effects on animal resource acquisition, foraging, behavior and

growth, movement, distribution, and colonization (Hart 1981, Kohler 1984, Diamond 1986, Dudley et al. 1986, Richards and Minshall 1988, Palmer 1995, Wiens et al. 1997, With et al. 1997, Bond et al. 2000, Ellsworth 2000, Jonsen and Taylor 2000, Silver et al. 2000, With et al. 2002). Streambed landscapes are extremely patchy (Poff and Ward 1992, Palmer and Poff 1997, Palmer et al. 2000): Substrate size and texture, the arrangement of algal patches, and the alternation of riffles and runs create varied 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).

The concept of landscape filters (Poff 1997) is an explicitly hierarchical framework that emphasizes a biologically based approach to determine the occurrence of species at different spatial scale by considering the constraints to their occurrence imposed by hierarchical "filters" at different scales. Streams are innately hierarchical in nature, and the distribution of their biota may be a product of such multiscale filtering (Wiens 2002). Fine-scale and coarser-scale components in streams are linked across a wide range of spatial and temporal scales, and streams exhibit patterns at spatial scales ranging from the surface of a stone to an entire stream network (Frissell et al. 1986, Roth et al. 1996, Lancaster and Belyea 1997). Patchy coarse-scale features such as climate, geology, vegetation, and topographic conditions determine the hydrology of streams, but also act within streams. There, they can affect the position of

depositional and erosional zones and ultimately affect the local distributions of organisms influenced by current, substrate, and depth (Cooper et al. 1998).

Because the animals living in streams differ in mobility, patchiness is likely to be perceived at different scales by different species (Wiens 1989, Schooley and Wiens 2003). We should therefore expect that ecological patterns such as animal distribution to change with scale. Indeed, invertebrate species distribution and abundance in streams often change with spatial scale, and patterns of animal patchiness can occur at spatial scales spanning several orders of magnitude (Downes et al. 1993). We would therefore expect that the processes behind these patterns would be movement (the focus of Chapter 1), animal response to resource distribution, and colonization (Kerans et al. 2000).

I focus here on the process of invertebrate colonization in streams. Colonization studies are an effective way to illustrate the importance of patchiness and scale, because individual species respond to environmental factors operating at different scales (Downes et al. 1993, Wiens et al. 1993). For example, herbivorous larval stream insects may respond at a very fine scale to local algal availability, but at coarser scales they may respond to abiotic variables such as habitat type (Wellnitz et al. 2001). Although there have been numerous studies of lotic invertebrate colonization (e.g. Richards and Minshall 1988, Ellsworth 2000, Kerans et al. 2000) and scale dependency (e.g. Boulton et al. 1988, Downes et al. 1993, Lancaster and Belyea 1997, Downes and Keough 1998, Wellnitz et al. 2001), few studies have used an experimental approach to link fine-scale animal distribution to scale-dependency and habitat patchiness

(but see Johnson and Vaughn 1995). Using invertebrate colonization as a response and identifying the scales at which invertebrate species respond to patchiness will lead to understanding of animal distributions in streams, as well as a bridging of the gap between spatial variation at coarse and fine spatial scales.

Because of the importance of patchy algal distribution in the movement and distribution of larval aquatic insects in streams (Poff and Ward 1992, Olden et al. 2004, Hoffman et al. *in preparation*), the study design is intended to test the effects of different types of fine-scale structural algae (e.g. tall filamentous strands vs. low, smooth diatom "turf") on invertebrate distribution (species richness, Shannon diversity, and abundance) within the natural patch hierarchy found in streams. From previous work on the upper Colorado River (Monroe 2002), we know that the hierarchical structure of the habitat encompasses runs and riffles, various stone sizes within the runs and riffles, and variations in algal structure on stone surfaces. We also know that different insect species vary in their distributions within this hierarchy (Monroe 2002). We therefore have an understanding of the hierarchical structuring of the streambed landscape and the invertebrates found there.

I focus on three spatial scales (Fig. 2.1). At the coarsest, *channel unit scale* habitat spans the entire channel and encompasses a relatively homogeneous length of channel that is relatively uniform in depth, area, and slope, and encompasses a broad range of local current velocity characteristics. Previous work (Carter et al. 1996, Murphy et al. 1998) indicates that many

aquatic invertebrates, particularly more mobile taxa, respond to environmental features at this scale with respect to two major patch components (runs and riffles). The next-finest scale, the *stone scale,* is comprised by the surfaces on individual stones, on which algae grow. Stone size is also important in the context of depth; since larger stones are often found in deeper waters, stone size can act as a surrogate for light intensity, which may influence insect and macroalgal distribution (Wellnitz and Ward 1998, Monroe 2002, Franken et al. 2005, Hillebrand 2005). The finest scale, *surface scale*, is the scale of the experimental measurement and observation. It comprises stone surfaces treated to have high or low levels of algal structure. Many aquatic insects, particularly those with low mobility, respond to environmental structuring and flow conditions at this fine scale (Poff and Ward 1992, Downes et al. 1993, Olden et al. 2004, Hoffman et al. *in prep*). This fine surface scale takes into consideration behavioral and movement scales of individual insects, and places surface-scale algal structure in a testable framework of patch hierarchy.

I address several questions related to stream patchiness, scale, and colonization in this study:

- How do multiple scales of patchiness and habitat structure affect animal distribution?
- How does habitat structure at these spatial scales affect community structure?
- At what spatial scale does landscape heterogeneity most affect animal distribution?

In this experiment, I test the hypothesis that variations in larval aquatic insect colonization and distribution are primarily due to the presence of algal patchiness at fine scales, versus coarser-scale patchiness (size and depth of stones at intermediate scales and depth and velocity at the channel unit scale).

Methods:

Study site

The study was conducted during summer 2003 in three runs (deep areas of a stream where water flows smoothly) and three riffles (shallow areas of a stream where water flows rapidly over the streambed and the water surface is broken) of the upper Colorado River (Grand County, CO, 40°11'N, 105°52'W, elevation 2420 m) near Granby, Colorado. The study reach runs through a shrubland valley approximately 7 km below the deep-release dam that forms Lake Granby. In addition to freestanding algal patches, the retreats of various insect larvae, including the chironomid larva, *Pagastia partica* comprise one of the primary sources of late-summer fine-scale heterogeneity in this stretch of the river. These conspicuous retreats, largely composed of silk and filamentous algae, are complex, high profile structures relative to the smooth surfaces that surround them. The smooth surfaces host inconspicuous biofilms that contain diatoms. A previous instream survey of naturally occurring *Pagastia* retreats indicated that the average proportion of area taken up by the structured *Pagastia* habitat was 0.16 (n=180, SD=0.14) (Monroe 2002); a photographic survey and

image analysis from this experiment placed the average proportion of structural algae at 0.40 (n=144, SD=0.38).

Other common later-summer structural periphyton taxa include cyanobacteria dominated by *Nostoc parmelioides*, many of which are inhabited by the symbiotic chironomid larva *Cricotopus* sp. (Brock 1960). Other algae such as *Draparnaldia*, *Chorella, Ulothrix* spp. (Chlorophyta), and numerous diatoms (Bacillariophyta) also occur (Opsahl et al. 2003).

Experimental design

I used a hierarchical study design to encompass the major scales of the streambed (Figs. 1 and 2). I selected sampling sites in six alternating runs and riffles, each separated by ca. 75-100 m. Mean near-bed current velocity averaged 0.63 cm/s (SD=0.47) in runs and 1.53 cm/s (SD=0.99) in riffles (t=4.04, p<0.001). In each run and riffle, one 3.6m long observation platform was erected approximately 30 cm over the surface of the water (Fig. 2.2). To minimize the effects of the platforms on current dynamics and shading, the supports driven into the bed had a diameter of 3 cm or less, and the platform surface was removed when observations and experiments were not taking place. One month prior to the start of the experiment (August 2003) I selected 48 study stones from under the water near each platform based on their size (large enough to mark a sampling area and small enough to physically remove from the water for destructive sampling). The stones chosen also had a relatively flat upper surface (ranging in area from approximately 100 cm^2 to 250 cm^2), to reduce stream flow

heterogeneity over the stone. If necessary, stones were moved to an area within easy view of each observation platform. A 10x10cm sampling area was marked on the surface of each stone using eight small dabs of marine epoxy. Each stone was labeled with a unique identifier using an embossed metal tag.

In September 2003, stones randomly designated as treatment stones were lightly scrubbed underwater with a nylon brush to remove all visible structural algae and invertebrates. Treatments similar to these are often used to approximate stream disturbance (Dudley et al. 1986, Boulton et al. 1988, Johnson and Vaughn 1995, Matthaei et al. 1996). The algae on the control stones were untouched except for the epoxy used to mark the sampling area. All visible invertebrates were also removed so that both treatment and control stones began the study period without a visible invertebrate community.

For each stone, I measured average current velocity, average depth, and *B*-axis of each stone (the longest axis perpendicular to the longest axis of the stone and an effective estimator of overall stone size, as it determines the size sieve opening the stone could pass through; Wolman 1954). Near-bed current velocity was measured with a probe (Schiltknecht Messtechnik AG, Zurich, Switzerland) and depth was measured using a current probe at nine points bordering and in the center of each 10x10cm sampling area. During the duration of this study the whole channel discharge was maintained at a constant 0.57 m^3/s. Because of the constant flow, current velocity and depth were measured once during the experiment.

Every 2 days on average, I recorded the abundance and taxon of all visible invertebrate individuals within each 100cm^2 sampling area on each stone. Most insects were identified to the genus level; other invertebrates were photographed and recorded as morphospecies to be identified later.

Four algal samples were taken from each stone *in-situ* on September 7, 18, and 30; this sampling schedule was determined to avoid a scheduled decrease in whole river discharge on October 1 that would reduce water levels over the experimental stones. Samples were taken by removing a 1-cm diameter circle of algae with a specially designed algal sampler, consisting of a retractable steel brush housed in a suction device with a rubber gasket. Samples were taken by placing the rubber gasket against the stone, making a seal, extending the brush and vigorously spinning it to dislodge the algae and scrape the stone, retracting the brush, and suctioning the algal-water mixture (~40 mL) into sample containers. Samples were taken from different areas of the sampling area border in order to avoid re-sampling at later dates and to minimize disturbance to algal growth. Algae samples were preserved in 10% formalin for later analysis (see Laboratory Analysis, below). I also photographed the sampling area for later image analysis of algal area on the stones.

On September 30, I performed the final, destructive invertebrate and algal sampling of stones by placing a square, 10x10 cm foam gasket over the sampling area of each stone and removing the gasket-and-stone combination from the water. I picked out all visible invertebrates, then scraped and scrubbed all algae and remaining invertebrate fauna within the gasket into 10% formalin.

This final sampling was used to identify cryptic, retreat-building, and small invertebrate species, and obtain an accurate estimate of algal density.

Laboratory analysis

After sorting, invertebrate samples from the final sampling were counted and identified to genus or species. Ash-free dry mass (AFDM) of invertebrate samples from each sampling area was calculated by drying for 24 h at 100° C, weighing, ashing at 500° C for 2 hrs, and weighing again (American Public Health Association 1988, Steinman and Lamberti 1996). For each of the three non-destructive sampling dates, algae were analyzed by determining the percentage of "structural algae" canopy (composed of green and/or blue-green algae likely along with epiphytic diatoms) covering each 10x10 cm sampling area using ImageJ image analysis software (Rasband 2004). Structural algal canopy cover was determined by visually outlining all algal patches on each 100 cm^2 sampling-area image taken during algal sampling (at all 3 dates) and calculating the percentage of the total image that was covered with these algal patches. I also determined AFDM from both the final algal collection and the three scraping samples for each sampling area at each sampling date, using the same procedures as for the AFDM of invertebrate samples

Data Analysis

Data were separated into two components: "observational" and "final." Observational data included the invertebrate species counts obtained from 13

visual observations between September 7 and 29 and the percent cover of structural algae taken from the 10x10 cm sampling surface and obtained from digital photographs taken September 7, 18, and 29. Final data were obtained when stones were destructively sampled at the end of the experiment, and include the final species counts, AFDM of invertebrates, and AFDM of algae scraped from stones. Environmental data (current velocity, average depth, and *B*-axis) were measured once during the course of the experiments, and therefore are used with both observational and final invertebrate data.

Keeping control and treatment data separate, environmental data (current velocity, average depth, and *B*-axis) and structural algal coverage data were aggregated into surface-, stone-, and channel unit-scale components. At all three scales I calculated species richness (the number of different taxa in a sample), invertebrate abundance and Shannon diversity (which takes into account both the abundance and evenness of the taxa present). I aggregated the sub-samples at the larger stone and channel unit scales so as to avoid the logistics of clearing the algae off *all* the stones in an entire run or riffle.

For observational data, I performed multiple regression with the dependent variables invertebrate species richness, Shannon diversity, and invertebrate abundance from the three time steps nearest to each of the dates that the algae were photographically sampled (September 7, 18, and 29). The independent variables remained constant for all observational models:

$$y = Algae + Mean\ Depth + Habitat + Mean\ Current\ Velocity + B\text{-}axis$$

in which "Algae" is the percent cover of structural algae in the sampling area, "Mean Depth" is the mean depth of each sampling area, "Habitat" refers to either the run or riffle habitat that the sample stone resides in, "Mean Current Velocity" is the mean current velocity of each sampling area, and "B-axis" is the B-axis of the stone on which each sampling area lies.

For the final data, I used final (destructive) species richness, Shannon diversity, AFDM fauna, and invertebrate abundance data as dependent variables in the models. To understand how these variables affected invertebrate functional groups at the study site, I also performed this analysis on the abundance of a group of four representative invertebrate genera. These were the gastropod *Physa* (a low-mobility grazer), the mayfly *Baetis* (a mobile grazer), the caddisfly *Brachycentrus* (a low-mobility nongrazer), and the caddisfly *Lepidostoma* (a mobile nongrazer). Independent variables remained constant for all final models:

y=AFDM algae+Mean Depth+Habitat+Mean Current Velocity+B-axis

In order to determine which habitat scales best explained variation in invertebrate community structure when subjected to structural algae removal, I used a hierarchical analysis of variance (ANOVA) to compare the explanatory variables habitat, *B*-axis, and treatment (Fig. 2.1) for the dependent variables species richness, Shannon diversity, and abundance over time. These

dependent variables (habitat, *B*-axis, and treatment) were used to represent the channel unit, stone, and surface scales, respectively. Fixed effects (which did not represent a random sampling of a population) were riffle and run (channel unit scale) and treatment and control (surface scale); random effects were *B*-axis measurements (stone scale). Current velocity, which can vary greatly at fine scales, was used as a covariate. These analyses indicate the hierarchical structure of the invertebrate response to structural algal removal, if present. For observational data, I used data from the three dates of the photographic algal sampling. For final data, I used only data from final sampling. Species richness, Shannon diversity, and invertebrate abundance were dependent variables, and the independent variables remained constant for all models. Using final sampling data, I also performed the analysis on the abundance same four representative genera listed above. The models used for both observational and final data (using current velocity as a covariate) were:

$$y = habitat + B\text{-}axis + treatment$$

For all ANOVA analyses, factors were considered *significant* if $p<0.05$, and *marginally significant* if $p<0.10$.

Results

Data for all habitat measurements recorded are found in Appendix 2.B

Multiple Regression: observational and final data

In the multiple regressions of observational data by time, the models for species richness and Shannon diversity were statistically significant ($p<0.05$) for the overall models at all time intervals, while the overall model for abundance was insignificant at time 1. The most important factors influencing species richness were percent algae at all three time intervals (richness increased with % algae) and mean depth at time 1 (richness increased with depth) (Table 2.1). Stone size (*B*-axis) was marginally significant at time 2, and showed a positive relationship with species richness. The most important factor influencing Shannon diversity over time was the positive relationship with percent algae at all time steps. Mean depth had a positive relationship with Shannon diversity and was marginally significant at time 1; mean near-bed current velocity was marginally significant at time 2, and had a positive relationship with diversity (Table 2.1). The factors most important to invertebrate abundance were the positive relationship with percent algae at times 2 and 3; mean depth was marginally significant at time 1 and significant at time 2 (abundance increased with depth), and habitat was significant at time 3 (higher abundance in riffles). The results for invertebrate abundance at time 1 should be considered carefully, as the overall model for abundance was not significant.

The overall models using the final destructive data were significant for species richness and Shannon diversity, marginally significant for abundance, and not significant for AFDM fauna (Table 2.2). Both species richness and Shannon diversity were significantly affected by AFDM algae (both were greater

with increasing AFDM algae), habitat (both were higher in riffles), and mean near-bed current velocity (both were negatively affected by mean current velocity). AFDM fauna was not significantly affected by anything, although AFDM algae, habitat, and mean current velocity were marginally significant and exhibited the same trends as did species richness and Shannon diversity. Invertebrate abundance was significantly affected by mean depth (abundance increased with depth) and habitat (abundance was higher in riffles), although these results must be carefully considered given the marginal significance of the overall model. Stone size (*B*-axis) was insignificant in all cases, as was the mean depth of stones (except in the case of invertebrate abundance).

The models focusing on the four functional group representatives were significant ($p<0.05$) for *Physa* (low-mobility grazer), *Brachycentrus* (low-mobility nongrazer), *and Lepidostoma* (mobile nongrazer), and marginally significant ($p=0.10$) for *Baetis* (mobile grazer) (Table 2.3). Mean depth significantly affected *Physa, Baetis,* and *Lepidostoma* abundance, with abundance increasing with depth in the cases of *Lepidostoma* and *Baetis*, but decreasing with depth in the case of *Physa*. Habitat significantly affected *Brachycentrus* and *Lepidostoma* abundance, and was marginally significant for *Baetis* abundance; abundance was higher in riffles for all three genera. Mean near-bed current velocity had a significant negative effect on *Physa* abundance. *B*-axis and AFDM algae had no significant affects on any of the variables.

Hierarchical ANOVA and scaling significance: observational data

The scales at which heterogeneity was most important became evident after analyzing the hierarchical ANOVA for species richness, Shannon diversity, and invertebrate abundance over time. Structural heterogeneity at the surface scale (algal structure treatment and control) was the most important source of variation for species richness and Shannon diversity ($p<0.05$) at all time steps and was also significant at time steps 2 and 3 for abundance (Table 2.4). Richness and diversity were significantly higher on control stones at all time steps, and abundance was significantly higher on control stones at time steps 2 and 3. Species richness, Shannon diversity, and invertebrate abundance at the surface scale showed inconsistent variation with time, but species richness and invertebrate abundance were consistently higher on control surfaces than on treatment surfaces (Fig. 2.3). The covariate near-bed current velocity was not significant at any time step for species richness, Shannon diversity, or invertebrate abundance.

The stone scale was only significant at time 2 for species richness (richness increased with stone size) and was not significant at all for Shannon diversity or invertebrate abundance (Table 2.4). Although species richness, Shannon diversity, and abundance observed at different dates varied at the stone scale, there were no obvious patterns (Fig. 2.4).

At the channel unit scale, habitat (runs and riffles) was not significant ($p>0.05$) for species richness or Shannon diversity at any of the time steps, and the higher abundance seen in riffles was significant for abundance only at time 3

(Table 2.4). There were significant differences in control stones aggregated within riffles and runs in species richness (t=-2.33, p=0.03), Shannon diversity (t=-5.51, p<0.0001), and abundance (t=4.52, p<0.0001) in this instance (Fig. 2.5).

To exclude variation introduced by experimental removal of algae, I also analyzed treatment and control separately at the stone and channel unit scales. None of the variables was significant for control stones as in the hierarchical ANOVA (Table 2.4), but on treatment stones, algae cover (structural heterogeneity) and current velocity were significant variables in contributing to Shannon diversity at time 2 ($p=0.003$ and $p=0.0012$, respectively), as was algal cover at Time 3 ($p=0.0193$).

Hierarchical ANOVA and scaling significance: Final data

As with the observational, time-dependent models, heterogeneity at the surface scale (Treatment) was significant as a predictor of increased species richness, Shannon diversity, abundance, and faunal AFDM on control stones (p=<0.0001 in all cases, Table 2.5, Fig. 2.6). Stone-scale variables (*B*-axis) were not significant predictors of faunal AFDM or invertebrate abundance but were for species richness and Shannon diversity (Table 2.5), which decreased with *B*-axis. Because treatment and control variables at the stone scale would have confounded displaying the differences between species richness and diversity at the continuous range of *B*-axes measured, I graphed only control stones at this scale (Fig. 2.7). Although p values for species richness and Shannon diversity indicated significance (Table 2.5), strong patterns were not clear. Invertebrate

abundance also did not indicate any discernible patterns at the stone scale (Fig. 2.7). Finally, the channel unit scale was not a significant predictor of species richness, faunal AFDM, or abundance although it was for diversity (Table 2.5), which was higher in riffles than in runs. There were no differences for control stones averaged over the channel unit scale between riffles and runs with respect to species richness, Shannon diversity, or abundance (Fig. 2.8).

The hierarchical ANOVA analysis of the final sampling data from four functional groups (Table 2.6) indicated that *Physa* abundance was not significantly affected by the channel unit, stone, or surface scales. *Baetis, Brachycentrus,* and *Lepidosoma*, however, were significantly affected by both the channel unit scale (greater abundance found in riffles) and the surface scale (greater abundance found on control stones).

The five most abundant taxa on control stones were (in order) *Baetis*, *Brachycentrus, Drunella grandis,* chironomids, and the snail *Physa*; treatment stones had an abundance of *Baetis*, *Physa, Drunella grandis, Ameletus, and Brachycentrus* (Appendix 2.A).

Discussion

The effects of spatial scale and environmental heterogeneity on the distribution of stream invertebrates have been emphasized in previous works (e.g. Poff and Ward 1992, Downes et al. 1993, Palmer 1995, Roth et al. 1996, Bond et al. 2000, Ellsworth 2000, Silver et al. 2000, Wellnitz et al. 2001), albeit separately rather than together. For example, Ellsworth (2000) found that

substrate size, caddisfly pupal cases, and algal abundance (*Cladophora*) all had significant effects on colonization by aquatic invertebrates, but the experiment was not performed on natural substrates or at multiple scales. When the issue of scale is combined with an experimental approach, it has often been at very fine spatial scales. For instance, Richards and Minshall (1988) found that *Baetis* mayfly density was affected by periphyton abundance at two spatial scales, but both of the scales were relatively fine (stone and stone surface). Other studies (Statzner and Higler 1986, Minshall et al. 1985) have suggested that fine-scale variation is insignificant and could either be ignored or averaged. This study, like that of Downes et al. (1993), included both fine scales, where biotic interactions are important, and broader scales where abiotic effects may have greater influence, though this study, indicates that variation at fine scales is significant relative to variation at broader scales. Further differences are that this work focuses on finer-scale variation (their smallest scale was the equivalent of my intermediate (stone) scale, and also expands their findings by performing observations over time and including experimental removal of algae and insects. Finally, Downes et. al (1993) show that while some species abundances vary over small scales, others do not, suggesting that some species respond to factors operating at different scales. The current study investigates these other scales in greater detail.

Invertebrate response to algal patchiness

Of all the variables examined, the amount of structural algae present on stones was consistently the most important throughout the study: control stones had consistently higher species richness, Shannon diversity, invertebrate abundance, and ash-free dry mass (AFDM) of invertebrate fauna than did the treatment stones. In this case, the amount of structural algae on stones is clearly important to invertebrate fauna, as has been shown in previous studies (Kohler 1984, Diamond 1986, Dudley et al. 1986, Richard and Minshall 1988, Monroe 2002). Specifically, the results of the ANOVA with observational data at three time steps (Table 2.1) show that percent algae is the most important factor in determining the richness and diversity of the invertebrate community on a streambed landscape, and richness and diversity increased with % algae at all time steps. This is likely because many (though not all) aquatic invertebrates depend on structural algae for either food or for cover from predators. Although the percent algae coverage increased over time (Fig. 2.9), the amount of algae present on stones significantly affected species richness and Shannon diversity at all time steps, underlying the importance of undisturbed structural algae for many aquatic invertebrates. While also important, mean depth, mean current velocity, habitat, and stone size (B-axis) were significant only at certain times, suggesting their importance is more temporally variable.

The results of the final sampling indicated that algal quantities (AFDM), habitat (runs or riffles), and mean near-bed current velocity are important in determining invertebrate species richness and diversity, but they exhibit a lesser

effect on total invertebrate biomass (AFDM fauna). This may be because measuring AFDM fauna is a relatively coarse measure, grouping all taxa together. Higher-resolution models that note differences in abundance among different taxa (such as those for species richness and Shannon diversity) proved significant (Table 2.2). Habitat and mean depth were also important with regards to invertebrate abundance, while AFDM algae was insignificant. Again, the fact that the overall statistical model for AFDM fauna and invertebrate abundance was not significant ($p>0.05$) means that the variables I measured did not account for invertebrate biomass and abundance very well (Table 2.2).

The findings of this part of the experiment agree with previous studies, as most freshwater work in this area has shown that increases in macroalgae and other vegetation are correlated with an increase in invertebrate abundance and taxonomic diversity (Dudley et al. 1986) and that there is no effect of stone size on invertebrate diversity (Khalaf and Tachet 1980). Differences between the results of the observational and final sampling models are likely due to invertebrates being concealed by macroalgae on the control stones, yet observational sampling remains the most practical means of non-invasive sampling. For instance, the last observational sampling on 29 September 2003 detected an average species richness of 1.04 per stone, while the final sampling the next day detected a mean of 5.69 species per stone. Because of these differences, care was taken to analyze final and observational data separately.

The separate analysis of the four functional group representatives (Table 2.3) revealed that mean depth was the most important variable to all but

Brachycentrus, one of two nongrazers (along with *Lepidostoma*). Though depth was significant to these genera, its positive effect on *Lepidostoma* and *Baetis* abundance and negative effect on *Physa* abundance is likely a reflection of the mobility, gas-exchange, and feeding habits of these invertebrates. *Baetis* and *Lepidostoma* are both mobile, which may enable them to move easily through different depths. Despite that one is a grazer and the other a nongrazer, their high mobility should be able to take them to wherever food is located. In general, however, it is not clear why *Baetis* abundance increased with depth, especially given the reduction of algal abundance with depth, particularly at depths greater than 15 cm. (Fig. 2.10). *Physa*'s pulmonate nature may require it to be nearer the surface to obtain atmospheric oxygen (Dewitt 1954), particularly during times of rapid growth (Clampitt 1974). Furthermore there is a general tendency towards less algae with depth (Fig. 2.10) may explain the negative effect of depth on *Physa* abundance.

The habitat variable was important to the nongrazers: In the final sampling there were more than 7 times the *Brachycentrus* found in riffles than in runs, and over 3 times more *Lepidostoma* occurring in riffles than runs. *Brachycentrus* depends on faster currents to support its filter feeding, while *Lepidistoma* is a slow-moving detritovore that might also depend on faster-moving water to provide a food source. Mean current velocity was also important to the pulmonate snail *Physa*, a genus in which current velocity has been shown to be the primary factor in determining distribution (Dillon 2000) because of the difficulty it has moving in high flow areas (Chapter 1).

Scales important to animal distribution

Although many stream studies and models (Vannote et al. 1980, Corkum 1989, Corkum 1991) have focused solely on the coarse-scale features of streams (but see Wellnitz et al. 2001), it is clear that the invertebrate community in this study exhibited strong responses to variables at fine scales. While the landscape filter framework (Poff 1997) indicates that all scales are important to species distribution, the results of this study indicate that the surface scale was particularly important for explaining the species richness, Shannon diversity, invertebrate abundance, and faunal AFDM distribution of macroinvertebrates.

The hierarchical ANOVA of the observational sampling over three time scales (Table 2.4) also showed that algal removal at the surface scale significantly affected the invertebrate community at all time periods except time 1 for abundance. The stone scale (*B*-axis) was also significant for species richness, but only in the second sampling period. This may be because larger stones are often found at deeper depths, which in turn may influence light availability (and therefore algae growth), though I did not see that relationship on these stones (Fig. 2.11). However, because algal growth increased over time (Fig. 2.9), the relative contribution of depth was likely diluted.

The final sampling results also confirm the importance of the surface scale on species richness, diversity, faunal AFDM, and invertebrate abundance, with the strongest model being AFDM fauna (Table 2.5). Stone scale was also important to final richness and species diversity, although it was rarely important

with the observational results (Table 2.4). As with previous results, final results likely differ slightly from those of the observational sampling because of the higher degree of sampling efficiency when using destructive sampling. As with the observational sampling, the scale that this study indicated to be most important to aquatic invertebrates is the same scale at which they carry out their movement and feeding, the surface scale. The fine scale at which aquatic invertebrates operate is simply reflected by the surface scale that, according to this study, is indicative of their distribution.

The analysis of the four functional groups (Table 2.6) indicated that the low mobility grazer *Physa* (also the only non-insect) was the only community member that none of the three habitat scales affected. *Physa*'s low mobility may preclude it from being affected by the channel unit or stone scales, but also by the surface scale, where it may not need the cover provided there (on account of its shell). The other taxa indicated that the channel unit and surface scales were the most important to their distribution. Like the community-wide measures, most of the functional group measures also indicated that the surface scale is very important for invertebrate distribution, almost without regard to the mobility or feeding of the groups involved. Different than the community measures, however, is the importance of the channel unit scale for the mobile and low-mobility grazers and the low-mobility nongrazers, possibly due to the generally faster bulk flow in riffles versus runs (Wellnitz et al. 2001).

Sampling variation

Visual sampling has been used in previous studies for monitoring stream invertebrate populations (Monroe 2002), but it is more commonly used in streams to monitor fish populations (Dudley et al. 1986, Irvine et al. 1992, Ensign et al. 1995). However, observational sampling, while useful for monitoring the changes in invertebrate populations in a defined area over time, does have some limitations. In this case of this experiment, the observation area was relatively small (100 cm^2). Considering the small size of the invertebrates being observed, this was probably an appropriate size, as an area much larger would have been more difficult for a single researcher to observe. There are several potential disadvantages of this type of sampling. First is the inevitability of cryptic species being underrepresented. Second, removal of invertebrates on the control stones in this study presented some potential problems, as the visible invertebrates removed may have been those that colonized. For example, the invertebrates that I observed colonizing may simply have been the ones that I could see and remove easily. Third, the observer should ideally have experience identifying macroinvertebrates without a microscope (and from distances up to 30 cm), and the same person should make all observations throughout the experiment. In general, the limitations and cautions of this type of sampling can be akin to performing visual observations of birds by point counts (Ralph et al. 1995). Despite these potential problems, observational sampling as a means for tracking invertebrate abundances over time was worthwhile (and was really the only way to do such observations), but for the sake of accuracy, observations

should be balanced by a destructive sampling that offsets some of these limitations of observational sampling.

Implications

The invertebrate community is most affected by abiotic and biotic variables at fine spatial scales relative to coarser scales, and the scale that contributed most strongly to invertebrate species diversity and richness in this study was the surface scale, a spatial scale smaller than a stone on the streambed. In effect, it is patch quality at this fine scale that influences invertebrate distribution. It is apparent then when studying streambed communities, fine-scale variables must be strongly considered as primary drivers of spatial variation in the abundance, biomass, and composition of invertebrate communities. If fine-scale variables such as structural algae are not intact, then other scales may become more important. However, it has been shown that heterogeneity at the channel unit scale can directly affect algal growth at smaller scales. Cardinale et al. (2002) performed an experiment to assess the effects of variation in stone size on rates of benthic productivity and respiration, and found that the rates of both processes were elevated in high-heterogeneity arrangements. Furthermore, some grazers can directly influence the spatial arrangement of benthic algal biomass by their grazing habits (Sarnelle et al. 1993). So while this study indicates the importance of fine-scale algal heterogeneity on the invertebrate community, the influence of the invertebrates themselves, as well as that of larger-scale heterogeneity, may in turn affect fine-

scale heterogeneity. The range and heterogeneity of patch types, current velocities, and scales present is also important for the entire community (Poff et al. 2003).

Conclusions

The concept of rivers and streambeds as landscapes (instead of elements within landscapes) is becoming increasingly relevant in the fields of stream ecology and landscape ecology, although the relevant scales vary greatly (Palmer et al. 2000, Wellnitz et al. 2001, Fausch et al. 2002, Malmqvist 2002, Wiens 2002). This study integrates fine-scale stream ecology with the landscape ecology principle of scale-dependence to indicate the scale that is most important to benthic invertebrate distribution. While the distribution of invertebrates on the streambed can vary significantly between spatial scales (Downes et al. 1993, Wellnitz et al. 2001), this study indicates that the fine scale explains the most variation in the response variables, and, within the scope of this study, is the most important scale to lotic invertebrate colonization.

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Figure Legends

Figure 2.1: Conceptual diagram outlining the experimental scheme indicating the three major spatial scales addressed. The major contributors of heterogeneity to each scale are indicated.

Figure 2.2: A depiction of the study area on the upper Colorado River (Grand County, Colorado). Riffle and run sampling areas are separated by ca. 75-100m. Enlargement shows a close-up example of the arrangement of 8 study stones under viewing platforms, 4 cleared of all algae and 4 with algal patches intact (other non-study stones were also present under the platforms). Sampling area is 10x10 cm.

Figure 2.3: Mean species richness, Shannon diversity, and invertebrate abundance of control and treatment stones from observational sampling over all sampling dates.

Figure 2.4: Mean species richness, Shannon diversity, and invertebrate abundance from observational sampling at the range of stone depth encountered in the study. Data are aggregated over all sampling dates at the stone scale.

Figure 2.5: Mean species richness, Shannon diversity, and invertebrate abundance of control stones from observational sampling at all times. Data are aggregated over all sampling dates at the channel unit scale. Error bars represent +/- one standard error. Due to differences in scale of y-axes, invertebrate abundance is graphed separately.

Figure 2.6: Mean species richness, Shannon diversity, and invertebrate abundance of control and treatment stones from final sampling data. Data are from the surface scale. Error bars represent +/- one standard error. Due to differences in scale of y-axes, invertebrate abundance is graphed separately.

Figure 2.7: Mean species richness, Shannon diversity, and invertebrate abundance of control stones from final sampling at the range of stone depth encountered in the study. Data are aggregated at the stone scale. Due to differences in scale of y-axes, invertebrate abundance is graphed separately.

Figure 2.8: Mean species richness, Shannon diversity, and invertebrate abundance of control stones in riffles and runs from final sampling data. Data are aggregated over all sampling dates at the channel unit scale. Error bars represent +/- one standard error. Due to differences in scale of y-axes, invertebrate abundance is graphed separately.

Figure 2.9. Mean algal changes on all stone surfaces over time. Data are derived from digital photographs and analyzed with image analysis software. Error bars indicate one standard error.

Figure 2.10: Algal ash-free dry mass (AFDM) plotted against mean stone depth for each stone used in the experiment. Algal AFDM was determined by scraping the 10x10cm study area for each stone and following the procedure outlined in the Methods section.

Figure 2.11: Mean stone size (as measured by *B*-axis) plotted against mean stone depth for each stone used in the experiment.

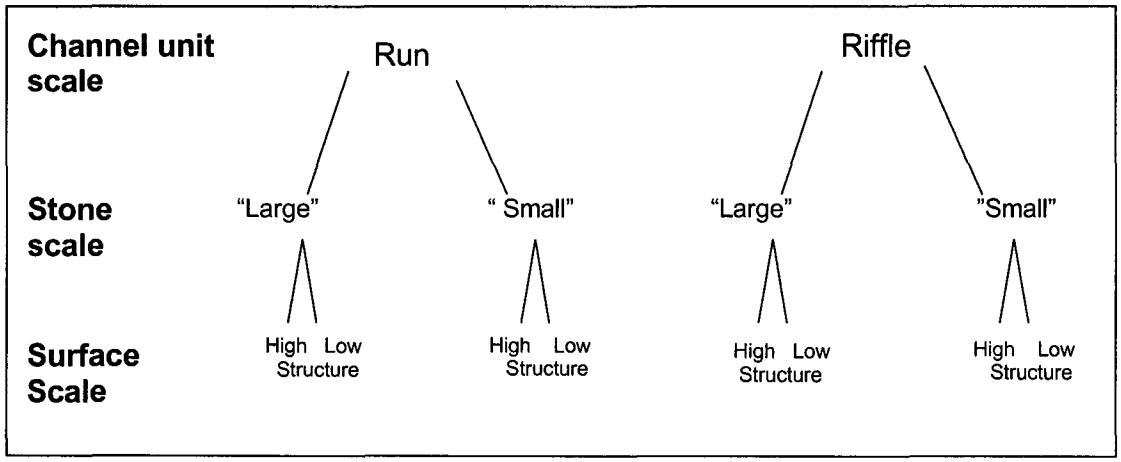


Figure 2.1

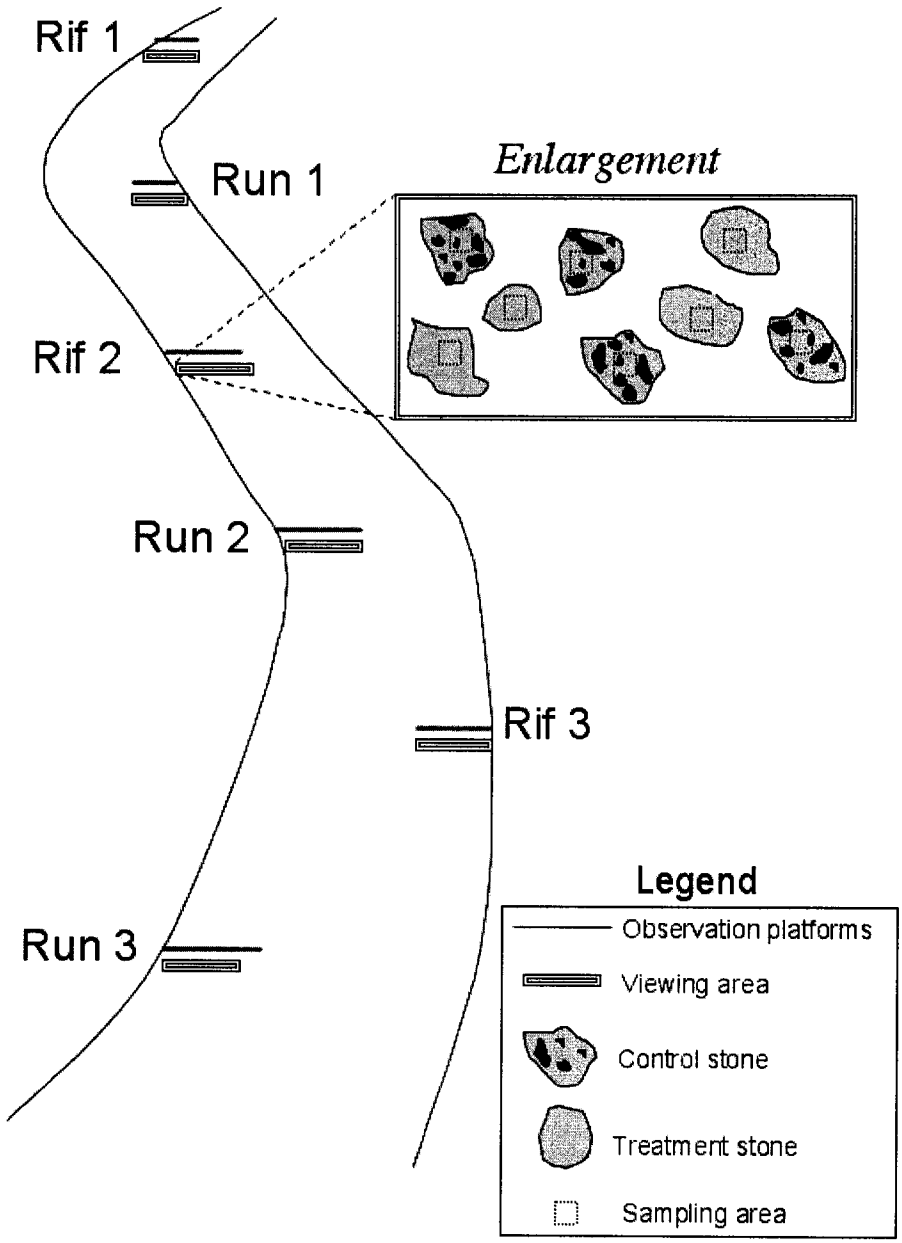
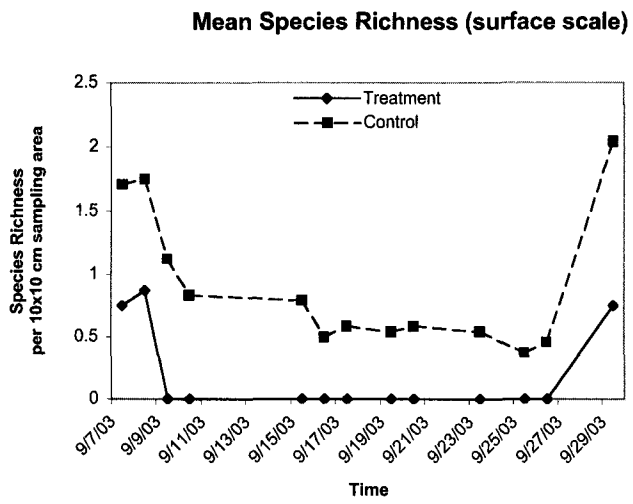
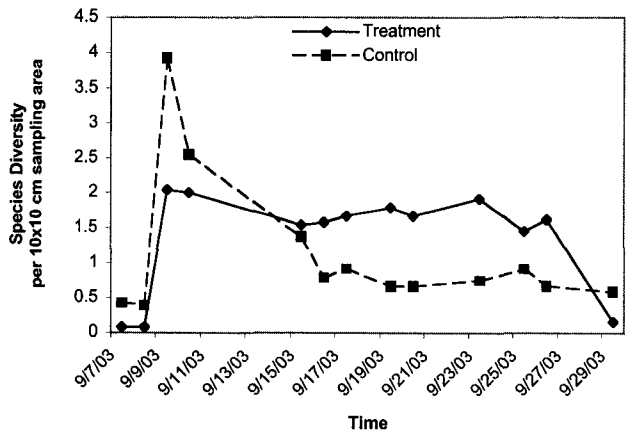


Figure 2.2





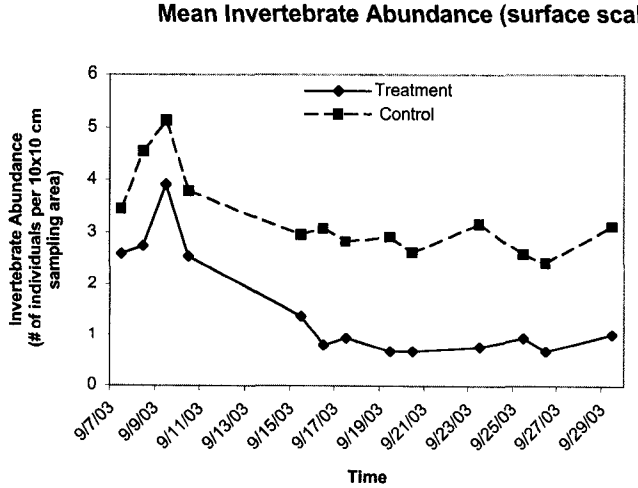
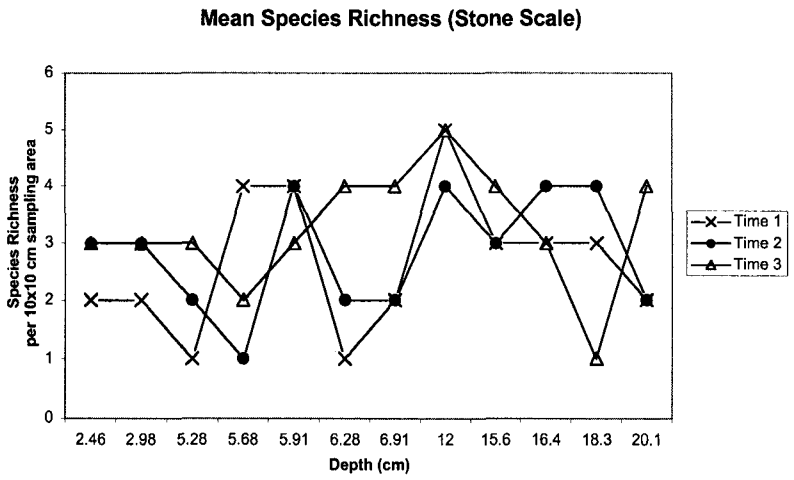
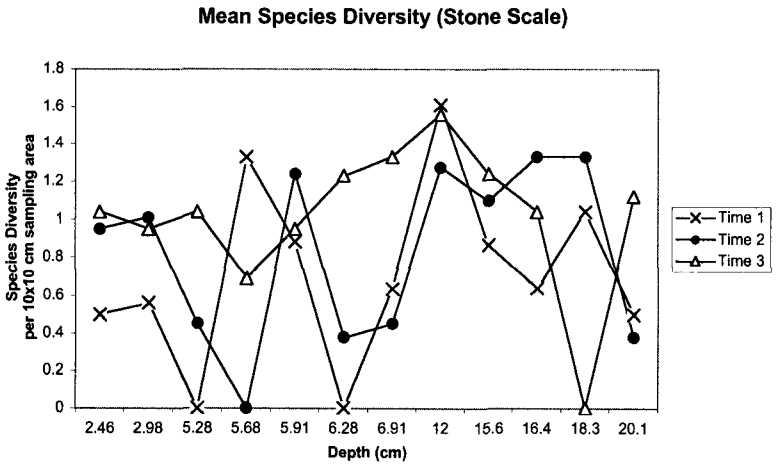


Figure 2.3





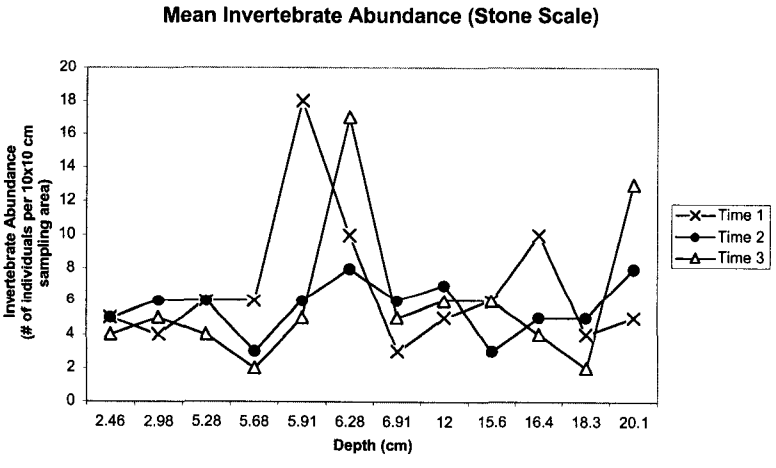
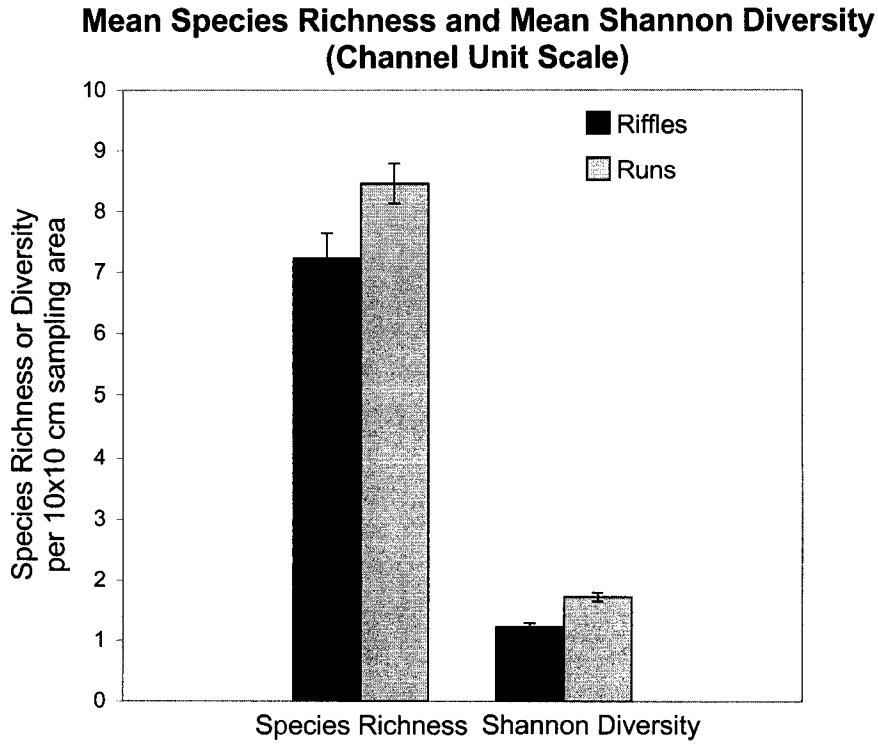


Figure 2.4



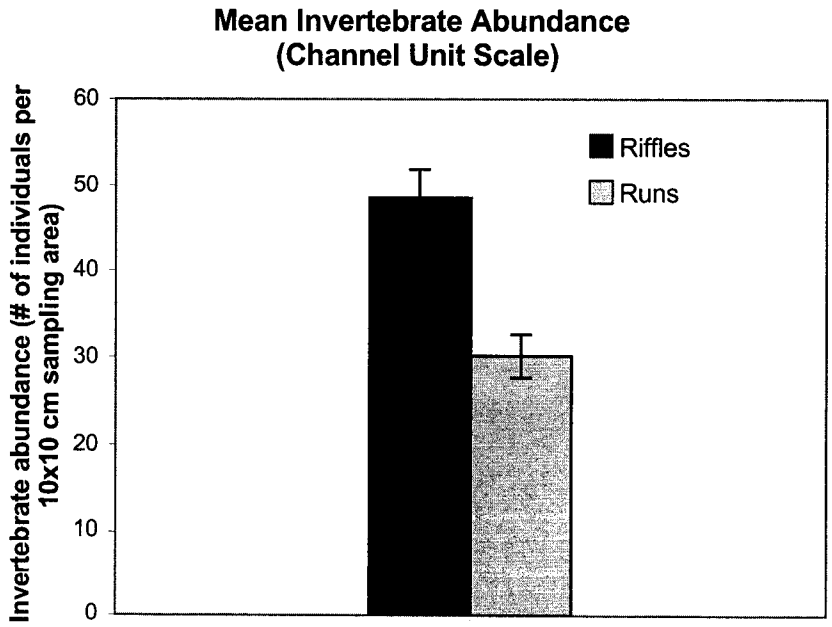
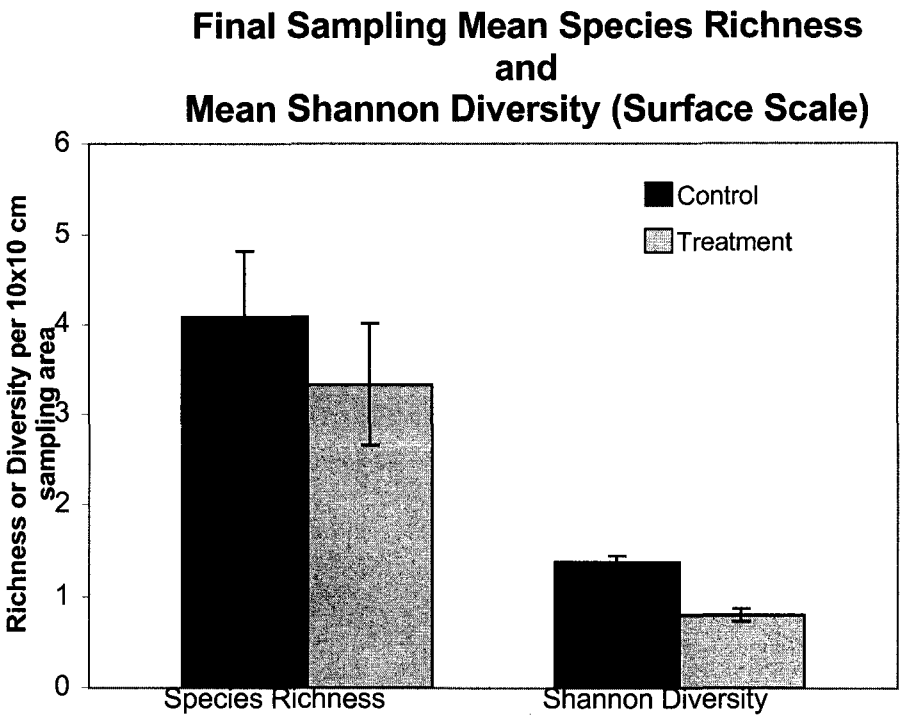


Figure 2.5



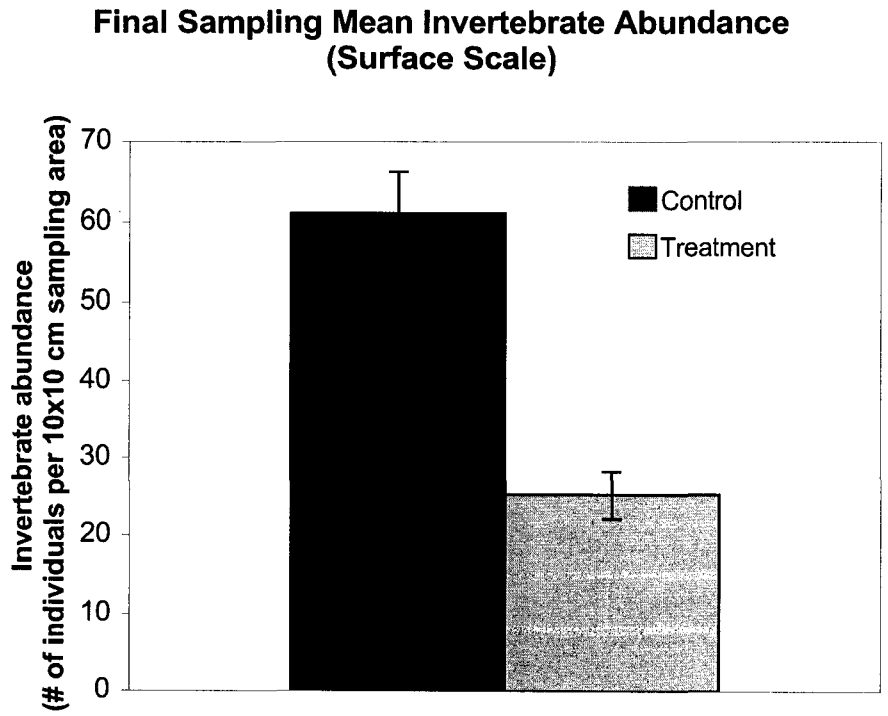
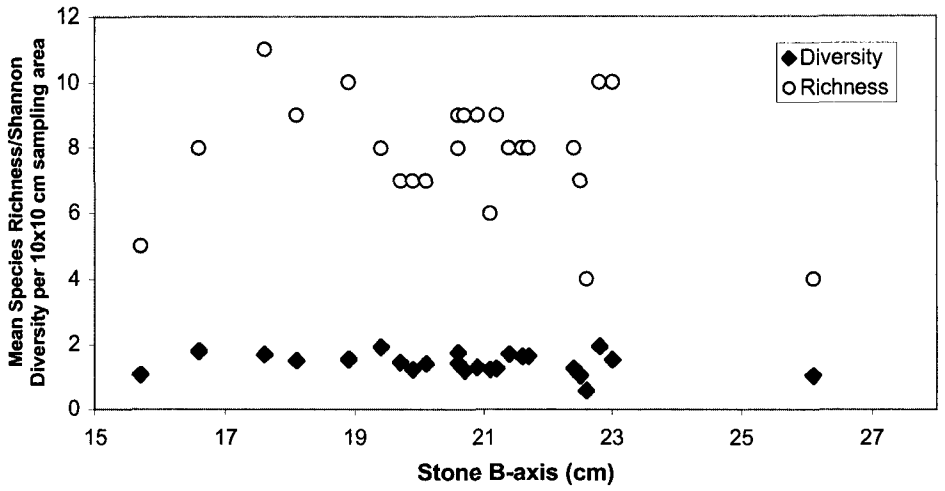


Figure 2.6

Mean Species Richness and Mean Shannon Diversity: Stone Scale (control only)



Mean Invertebrate Abundance: Stone Scale (control only)

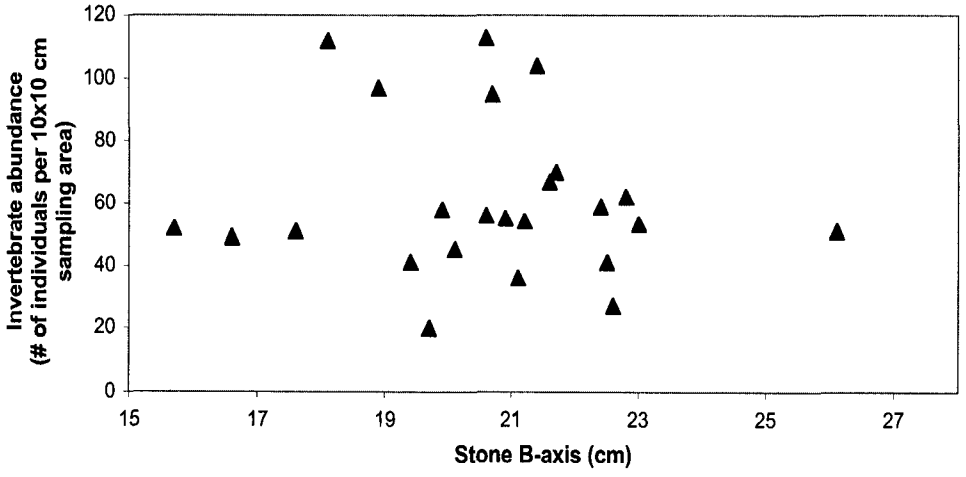
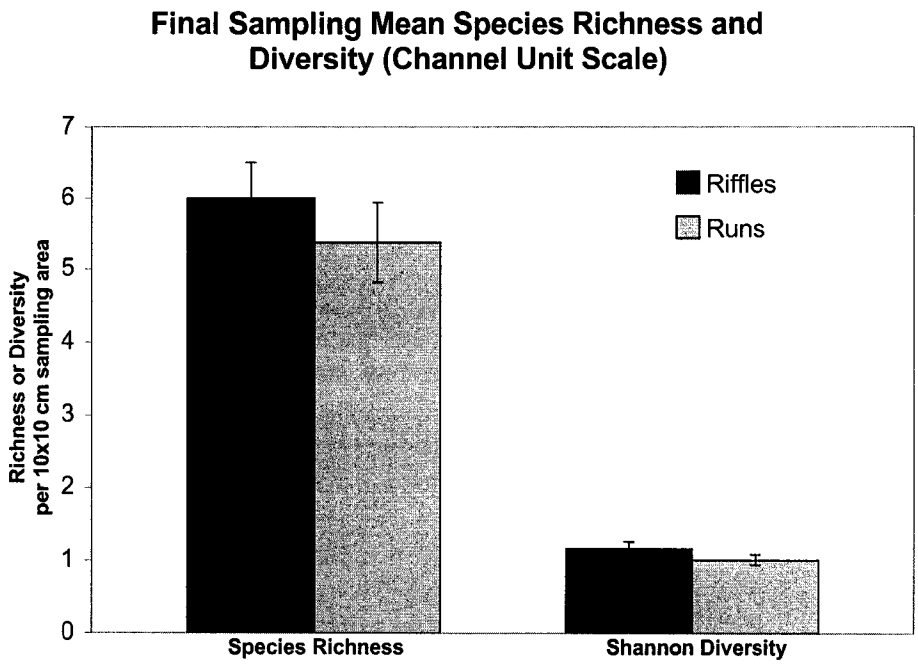


Figure 2.7



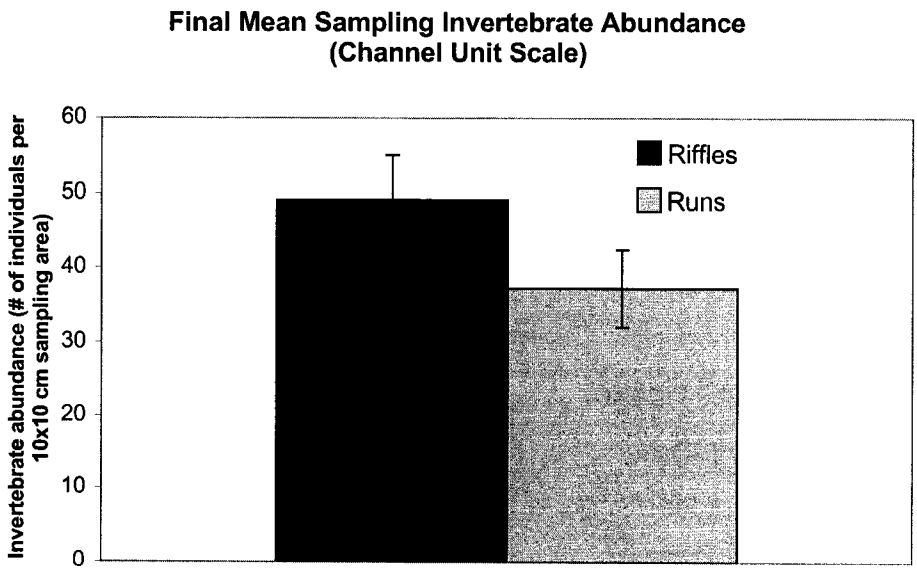


Figure 2.8

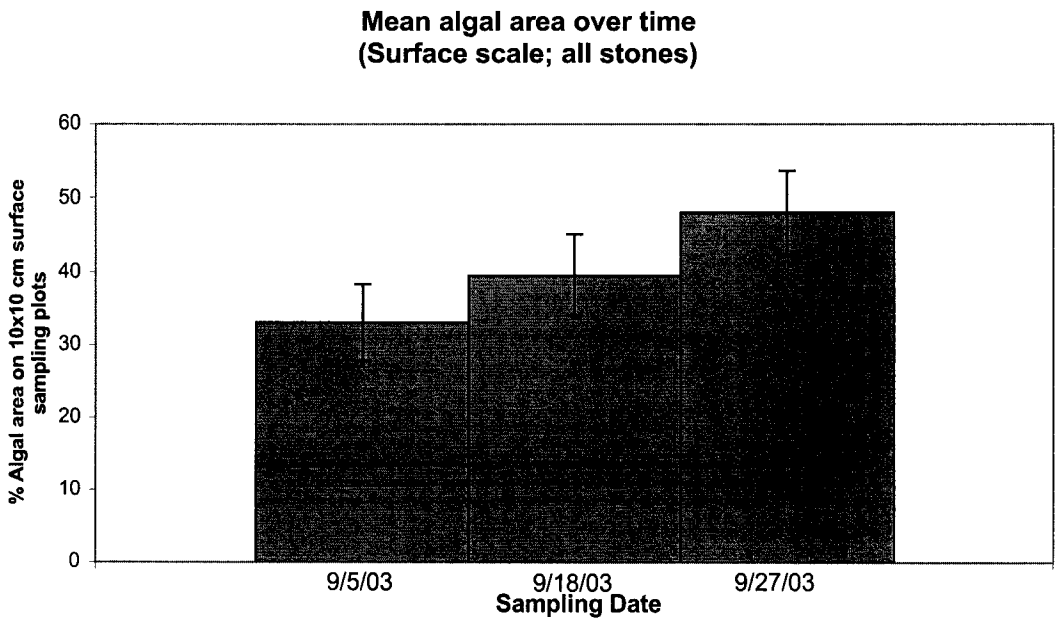


Figure 2.9

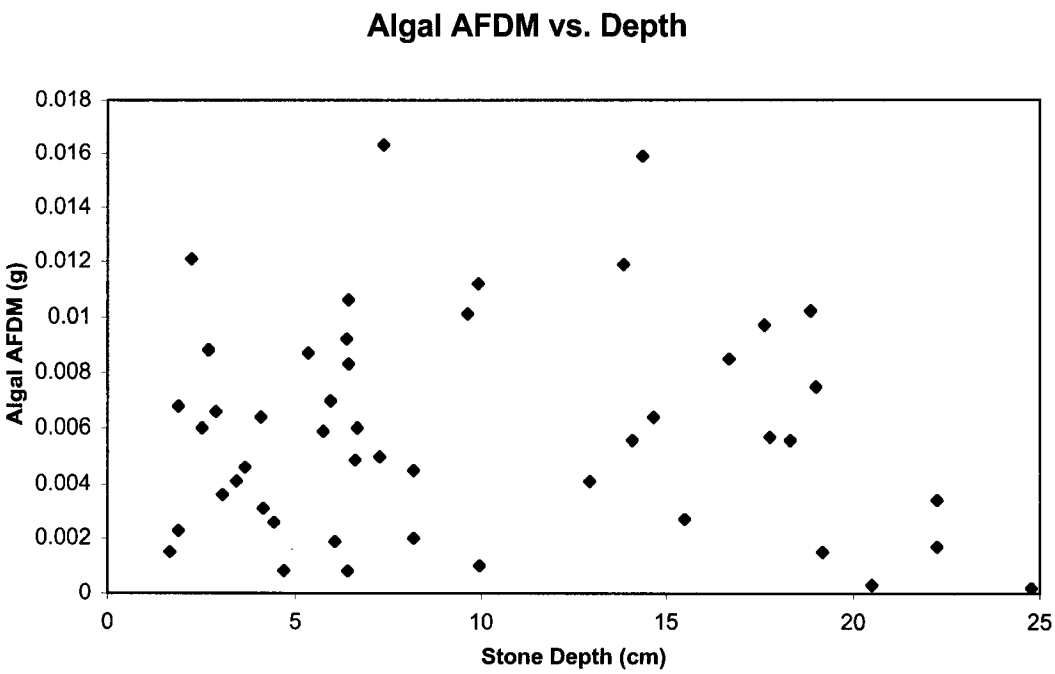


Figure 2.10

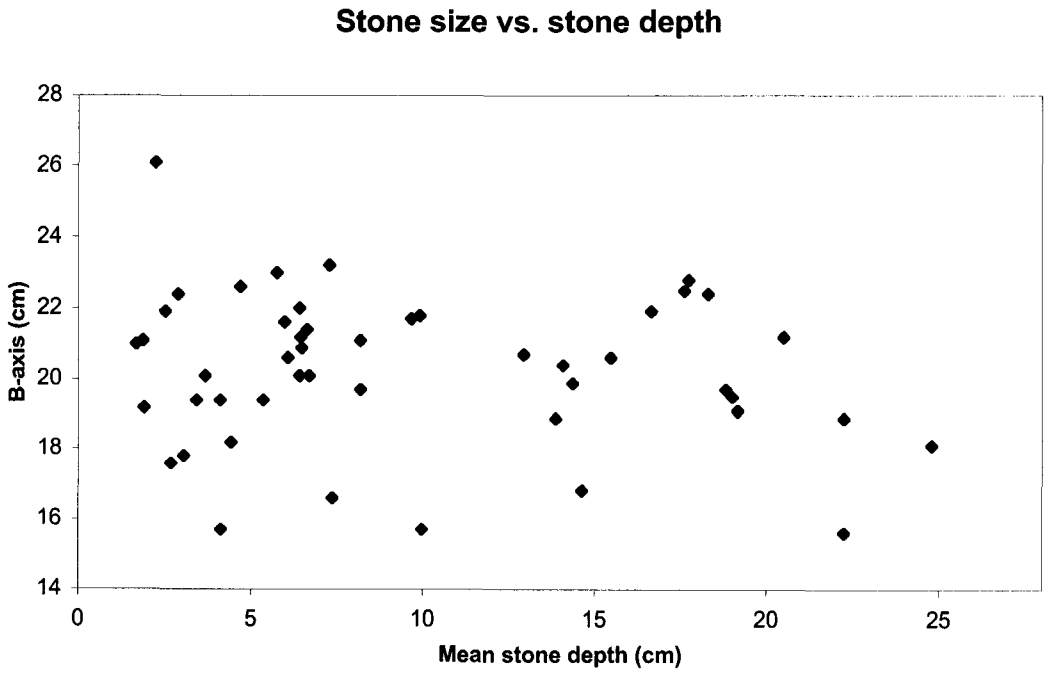


Figure 2.11

Table 2.1: Multiple regression with the response variables species richness, Shannon diversity, and invertebrate abundance (from observational data) at three time intervals on stones in the upper Colorado River. SS=Type III sums of squares, DF=degrees of freedom, MS=mean square, F=F ratio, *p*=level of significance, Model *p*=level of significance for model.

	Source	SS	DF	MS	F	*p*	Model *p*
	RICHNESS						
Time 1	% Algae	9.9369	1	9.9369	17.88	**<0.0001**	**0.0080**
	Mean Depth	2.9569	1	2.9569	5.32	**0.0261**	
	Habitat	0.1215	1	0.1215	0.22	0.6426	
	Mean C.V.	0.4414	1	0.4414	0.79	0.3779	
	B-axis	0.6353	1	0.6353	1.14	0.2912	
Time 2	% Algae	10.9568	1	10.9568	23.88	**<0.0001**	**<0.0001**
	Mean Depth	0.3278	1	0.3278	0.71	0.4028	
	Habitat	0.4052	1	0.4052	0.88	0.3528	
	Mean C.V.	0.3231	1	0.3231	0.70	0.4062	
	B-axis	1.4860	1	1.4860	3.24	*0.0791*	
Time 3	% Algae	14.2652	1	14.2652	14.71	**0.0004**	**0.0092**
	Mean Depth	0.0379	1	0.0379	0.04	0.8441	
	Habitat	0.6574	1	0.6574	0.68	0.4150	
	Mean C.V.	0.2800	1	0.2800	0.29	0.5939	
	B-axis	0.0616	1	0.0616	0.06	0.8022	
	DIVERSITY						
Time 1	% Algae	1.3599	1	1.3599	15.57	**0.0003**	**0.0029**
	Mean Depth	0.2524	1	0.2524	2.89	*0.0965*	
	Habitat	0.0191	1	0.0191	0.22	0.6422	
	Mean C.V.	0.0032	1	0.0032	0.04	0.8483	
	B-axis	0.0126	1	0.0126	0.14	0.7060	
Time 2	% Algae	1.6659	1	1.6659	22.84	**<0.0001**	**0.0006**
	Mean Depth	0.0132	1	0.0132	0.18	0.6733	
	Habitat	0.0000	1	0.0000	0.00	0.9808	
	Mean C.V.	0.2409	1	0.2409	3.30	*0.0763*	
	B-axis	0.0132	1	0.0132	0.18	0.6722	
Time 3	% Algae	1.3589	1	1.3589	9.23	**0.0041**	**0.0488**
	Mean Depth	0.0725	1	0.0725	0.49	0.4867	
	Habitat	0.1633	1	0.1633	1.11	0.2983	
	Mean C.V.	0.0789	1	0.0789	0.54	0.4684	
	B-axis	0.0002	1	0.0002	0.00	0.9705	
	ABUNDANCE						
Time 1	% Algae	5.3511	1	5.3511	0.67	0.4169	0.3164
	Mean Depth	25.2029	1	25.2029	3.17	*0.0824*	
	Habitat	2.6001	1	2.6001	0.33	0.5707	
	Mean C.V.	7.2306	1	7.2306	0.91	0.3460	
	B-axis	3.8742	1	3.8742	0.49	0.4893	
Time 2	% Algae	21.2681	1	21.2681	9.00	**0.0045**	**0.0090**
	Mean Depth	10.3496	1	10.3496	4.38	**0.0424**	
	Habitat	4.4749	1	4.4749	1.89	0.1760	
	Mean C.V.	1.1154	1	1.1154	0.47	0.4958	
	B-axis	3.0071	1	3.0071	1.27	0.2657	
			1				
Time 3	% Algae	39.7911	1	39.7911	9.82	**0.0031**	**0.0100**
	Mean Depth	0.0323	1	0.0323	0.01	0.9292	
	Habitat	18.3784	1	18.3784	4.54	**0.0391**	
	Mean C.V.	0.2049	1	0.2049	0.05	0.8231	
	B-axis	0.3889	1	0.3888	0.10	0.7582	

Table 2.2: Multiple regression with the response variables species richness, Shannon diversity, ash-free dry mass (AFDM), and abundance of invertebrate fauna from final (destructive) sampling of stones in the upper Colorado River. SS=Type III sums of squares, DF=degrees of freedom, MS=mean square, F=F ratio, *p*=level of significance, Model *p*= level of significance for model.

Source	SS	DF	MS	F	*p*	Model *p*
RICHNESS						**0.0302**
AFDM Algae	31.1430	1	31.1430	5.50	**0.0239**	
Mean Depth	5.5203	1	5.5203	0.97	0.3293	
Habitat	37.2681	1	37.2681	6.58	**0.0140**	
Mean C.V.	41.0546	1	41.0546	7.25	**0.0102**	
B-axis	0.4899	1	0.4899	0.09	0.7702	
DIVERSITY						**0.0093**
AFDM Algae	0.6090	1	0.6090	4.22	**0.0463**	
Mean Depth	0.0010	1	0.0010	0.01	0.9336	
Habitat	1.2610	1	1.2610	8.73	**0.0051**	
Mean C.V.	1.5313	1	1.5313	10.60	**0.0022**	
B-axis	0.0904	1	0.0904	0.63	0.4333	
AFDM FAUNA						0.1624
AFDM Algae	0.0001	1	0.0001	3.29	*0.0767*	
Mean Depth	0.0000	1	0.0000	0.14	0.7074	
Habitat	0.0001	1	0.0001	3.42	*0.0716*	
Mean C.V.	0.0001	1	0.0001	3.69	*0.0616*	
B-axis	0.0000	1	0.0000	1.35	0.2518	
ABUNDANCE						*0.0840*
AFDM Algae	1528.35	1	1528.35	2.26	0.1405	
Mean Depth	3789.52	1	3789.52	5.60	**0.0227**	
Habitat	3997.78	1	3997.78	5.90	**0.0195**	
Mean C.V.	704.17	1	704.17	1.04	0.3137	
B-axis	364.69	1	364.69	0.54	0.4671	

Table 2.3: Multiple regression with the response variables abundance of four representative study area genera: *Physa* (a low-mobility grazer), *Baetis* (a mobile grazer), *Brachycentrus* (a low-mobility nongrazer), and *Lepidostoma* (a mobile nongrazer). Abundances of invertebrate fauna are from final (destructive) sampling of stones in the upper Colorado River. SS=Type III sums of squares, DF=degrees of freedom, MS=mean square, F=F ratio, *p*=level of significance, Model *p*= level of significance for model.

Source	SS	DF	MS	F	*p*	Model *p*
***Physa* abundance**						
AFDM Algae	0.0264	1	0.0264	0.00	0.9661	**0.0326**
Mean Depth	60.5225	1	60.5225	4.20	**0.0467**	
Habitat	27.9737	1	27.9737	1.94	0.1709	
Mean C.V.	109.4510	1	109.4510	7.60	**0.0086**	
B-axis	1.8073	1	1.8073	0.13	0.7250	
***Baetis* abundance**						
AFDM Algae	0.3203	1	0.3203	0.01	0.9438	*0.0688*
Mean Depth	428.7393	1	428.7393	6.72	**0.0130**	
Habitat	233.0048	1	233.0048	3.65	*0.0627*	
Mean C.V.	1.9525	1	1.9525	0.03	0.8619	
B-axis	23.8303	1	23.8303	0.37	0.5442	
***Brachycentrus* abundance**						
AFDM Algae	5.8713	1	5.8713	0.41	0.5240	**0.0373**
Mean Depth	9.8659	1	9.8659	0.69	0.4096	
Habitat	110.4698	1	110.4698	7.77	**0.0079**	
Mean C.V.	7.2241	1	7.2241	0.51	0.4799	
B-axis	7.2790	1	7.2790	0.51	0.4783	
***Lepidostoma* abundance**						
AFDM Algae	30.9794	1	30.9794	0.98	0.3287	**0.0333**
Mean Depth	137.9050	1	137.9050	4.35	**0.0432**	
Habitat	353.3622	1	353.3622	11.14	**0.0018**	
Mean C.V.	55.3452	1	55.3452	1.74	0.1937	
B-axis	14.5770	1	14.5770	0.46	0.5016	

Table 2.4: Hierarchical ANOVA at three time periods from observational sampling of stones on the upper Colorado River. Results from this ANOVA address the importance of channel unit (CU), stone, and surface scales. 48 stones were sampled for each scale, and current velocity was used as a covariate. In a separate analysis, control stones only (n=24) were tested for habitat and *B*-axis, but the results were similar to those shown here. Richness=species richness, Diversity= Shannon diversity, Num DF =numerator degrees of freedom, Den DF=denominator degrees of freedom, F=F ratio, *p*=level of significance. Degrees of freedom were calculated using Satterthwaite's approximation (Neter et al. 1996).

	Source	Num DF	Den DF	F	*p*
	RICHNESS				
Time 1	Habitat (CU scale)	1	46.1	1.62	0.2091
	B-axis (stone scale)	1	46.1	0.21	0.6459
	Treatment (surface scale)	1	46	24.18	**<0.0001**
Time 2	Habitat (CU scale)	1	48	0.01	0.9183
	B-axis (stone scale)	1	48	4.04	**0.0502**
	Treatment (surface scale)	1	48	31.36	**<0.0001**
Time 3	Habitat (CU scale)	1	48	0.40	0.5299
	B-axis (stone scale)	1	48	0.15	0.6992
	Treatment (surface scale)	1	48	17.33	**0.0001**
	DIVERSITY				
Time 1	Habitat (CU scale)	1	46.1	1.12	0.2964
	B-axis (stone scale)	1	46.1	0.03	0.8716
	Treatment (surface scale)	1	46	16.66	**0.0002**
Time 2	Habitat (CU scale)	1	48	0.33	0.5691
	B-axis (stone scale)	1	48	0.63	0.4314
	Treatment (surface scale)	1	48	24.88	**<0.0001**
Time 3	Habitat (CU scale)	1	48	0.61	0.4375
	B-axis (stone scale)	1	48	0.01	0.9049
	Treatment (surface scale)	1	48	12.50	**0.0009**
	ABUNDANCE				
Time 1	Habitat (CU scale)	1	46.1	0.10	0.7539
	B-axis (stone scale)	1	46.1	0.18	0.6744
	Treatment (surface scale)	1	46	1.92	0.1725
Time 2	Habitat (CU scale)	1	48	0.16	0.6938
	B-axis (stone scale)	1	48	0.47	0.4968
	Treatment (surface scale)	1	48	23.80	**<0.0001**
Time 3	Habitat (CU scale)	1	48	4.44	**0.0404**
	B-axis (stone scale)	1	48	0.16	0.6929
	Treatment (surface scale)	1	48	13.81	**0.0005**

Table 2.5: Hierarchical ANOVA from final (destructive) sampling of stones on the upper Colorado River. Results from this ANOVA address the importance of channel unit (CU), stone, and surface scales. 48 stones were sampled for each scale, and current velocity was used as a covariate. In a separate analysis, control stones only (n=24) were tested for habitat and *B*-axis, but the results were similar to those shown here. Richness=species richness, Diversity= Shannon diversity, AFDM Fauna=ash-free dry mass of invertebrate fauna, Abundance=abundance of invertebrate individuals. Num DF =numerator degrees of freedom, Den DF=denominator degrees of freedom, F=F ratio, *p*=level of significance. Degrees of freedom were calculated using Satterthwaite's approximation (Neter et al. 1996).

Source	Num DF	Den DF	F	*p*
Final Richness				
Habitat (CU scale)	1	48	0.94	0.1202
B-axis (stone scale)	1	48	7.11	**0.0202**
Treatment (surface scale)	1	48	99.91	**<0.0001**
Final Diversity				
Habitat (CU scale)	1	48	1.72	**0.0154**
B-axis (stone scale)	1	48	6.73	**0.0309**
Treatment (surface scale)	1	48	53.73	**<0.0001**
AFDM Fauna				
Habitat (CU scale)	1	48	0.36	0.3658
B-axis (stone scale)	1	48	0.14	0.6090
Treatment (surface scale)	1	48	34.80	**<0.0001**
Abundance				
Habitat (CU scale)	1	48	3.86	0.2512
B-axis (stone scale)	1	48	0.39	0.4285
Treatment (surface scale)	1	48	41.57	**<0.0001**

Table 2.6: Hierarchical ANOVA from final (destructive) sampling of stones on the upper Colorado River. Results from this ANOVA address the importance of four representative invertebrate genera: *Physa* (a low-mobility grazer), *Baetis* (a mobile grazer), *Brachycentrus* (a low-mobility nongrazer), and *Lepidostoma* (a mobile nongrazer). Results from this ANOVA address the importance of channel unit (CU), stone, and surface scales. Abundance=total number of individuals found in the final sample, Num DF =numerator degrees of freedom, Den DF=denominator degrees of freedom, F=F ratio, *p*=level of significance. Degrees of freedom were calculated using Satterthwaite's approximation.

Source	Abundance	Num DF	Den DF	F	*p*
***Physa* abundance**	93				
Habitat (CU scale)		1	44	0.10	0.7477
B-axis (stone scale)		1	44	0.18	0.6721
Treatment (surface scale)		1	44	0.15	0.6960
***Baetis* abundance**	352				
Habitat (CU scale)		1	44	4.16	**0.0475**
B-axis (stone scale)		1	44	0.10	0.7522
Treatment (surface scale)		1	44	6.61	**0.0136**
***Brachycentrus* abundance**	110				
Habitat (CU scale)		1	44	11.06	**0.0018**
B-axis (stone scale)		1	44	3.54	*0.0666*
Treatment (surface scale)		1	44	11.08	**0.0018**
***Lepidostoma* abundance**	209				
Habitat (CU scale)		1	44	8.95	**0.0045**
B-axis (stone scale)		1	44	0.21	0.6526
Treatment (surface scale)		1	44	17.29	**0.0001**

Appendix 2.A: Listing of taxa found on control and treatment stones over all sampling dates. "Observe sum" refers to the sum of each taxon found over all sampling dates. "Final sampling" refers to the number of each taxon found in the final sampling on September 30 2003.

Control Stones	9/7 2003	9/8 2003	9/9 2003	9/10 2003	9/15 2003	9/16 2003	9/17 2003	9/19 2003	9/20 2003	9/23 2003	9/25 2003	9/26 2003	9/29 2003	Observe Sum	Final Sum
Baetis	53	77	73	58	43	46	39	30	27	27	16	12	14	515	293
Brachycentrus	2	2	3	3	2	3	3	11	10	14	25	19	21	118	89
Drunella grandis	14	8	19	7	7	4	7	2	3	3	5	3	4	86	5
Chironomidae	6	6	2	13	4	10	5	12	8	8	1	6	4	85	830
Physa	4	7	11	3	2	2	4	4	10	3	3	6	7	66	42
Lepidostoma	1	2	5	1	5	3	4	4	2	9	7	7	15	65	174
Corixidae		2	1		2	2	4	5	1	8	2	4	1	32	
Hydropsychidae		1	2	1	1	1	1	1	1	1	1		1	12	
Amaletus	1	1	3	1	1	2			1				1	11	
Drunella doddsi		2	4	2	1									9	1
Lymnaea					1			1		2	2	1	2	9	11
Ephemerella	1			1	1	1				1			1	6	
Hyalella azteca		1											2	3	10
Water mite							1						2	3	
Simuliidae				1										1	
Plecoptera					1									1	
Tipulidae	1													1	
Leech															1
Arctopsyche															
Polycentropodidae															
Tricorythodes minutus															30
Gyraulus sp.															9
Ostracoda															2
Heterlimnius															16
Muscid larva															30
Empidid larva															21

Appendix 2.A, continued

Treatment Stones	9/7 2003	9/8 2003	9/9 2003	9/10 2003	9/15 2003	9/16 2003	9/17 2003	9/19 2003	9/20 2003	9/23 2003	9/25 2003	9/26 2003	9/29 2003	Observe Sum	Final Sum
Baetis	55	48	63	56	23	15	11	10	3	4	4	1	3	296	59
Brachycentrus			1	1		1	1	2	3		1		6	16	21
Drunella grandis			17			1						1		19	
Chironomidae									2			1	2	5	420
Physa	1	4	8	2	4	1	6	1	4	9	13	6	7	66	51
Lepidostoma						1	1	1		2		1	2	8	35
Corixidae															
Hydropsychidae			1				1	2	2	2	2	2	2	14	
Amaletus	2	11		1			1		1					17	
Drunella doddsi															
Lymnaea			2	1			1		1	1	2	4	2	14	
Ephemerella					1									1	
Hyalella azteca															2
Water mite															
Simuliidae	3	3	2		5									13	
Plecoptera															1
Tipulidae															1
Leech															
Arctopsyche															1
Polycentropodidae															1
Tricorythodes minutus															3
Gyraulus sp.															4
Ostracoda															6
Heterlimnius															
Muscid larva															
Empidid larva															

Chironomidae pupae and larvae added together for final sampling results.

Appendix 2.B: A datasheet of all habitat measurements made, including community measures such as species richness, species diversity, faunal ash-free dry mass (AFDM) and algal AFDM. In "Treatment" column, "C"=control and "T"=treatment. In "Habitat" column, "Rif"=riffle and "Run"=run

Stone #	Treatment	mean CV (cm/s)	mean Depth (cm)	B axis (cm)	Habitat	% Algae Time 1	% Algae Time 2	% Algae Time 3	Final Richness	Final Diversity	Algal AFDM (g)	Faunal AFDM (g)
5	C	1.14	4.13	15.7	Rif	51.47	57.40	82.62	5	1.06	0.0031	0.0071
6	T	0.42	3.04	17.8	Rif	0.00	4.42	13.21	5	1.46	0.0036	0.0017
7	T	1.65	4.42	18.2	Rif	0.00	1.23	0.54	3	0.61	0.0026	0.0006
8	C	1.65	6.43	21.2	Rif	43.69	82.49	83.68	9	1.09	0.0083	0.0112
9	C	1.72	24.79	18.1	Rif	49.58	38.48	44.67	9	1.50	0.0002	0.0065
10	T	1.00	22.24	15.6	Rif	0.00	1.43	12.27	6	1.12	0.0017	0.0029
11	C	2.37	15.49	20.6	Rif	82.86	80.11	83.01	9	1.74	0.0027	0.0206
12	T	1.59	19.18	19.1	Rif	0.00	0.87	7.19	3	0.71	0.0015	0.0008
17	C	0.00	2.68	17.6	Run	86.57	62.77	87.97	11	1.14	0.0088	0.0148
18	T	0.26	8.17	19.7	Run	0.00	28.19	15.49	3	0.23	0.0045	0.0044
19	T	0.18	2.88	22.4	Run	0.00	10.20	19.54	3	0.00	0.0066	0.0045
20	C	0.55	2.23	26.1	Run	79.97	98.15	98.30	4	1.04	0.0121	0.0049
21	T	0.82	14.08	20.4	Run	0.00	2.11	6.96	2	0.59	0.0056	0.0006
22	C	0.56	18.84	19.7	Run	94.05	93.11	96.20	7	1.31	0.0102	0.0133
23	T	0.65	22.23	18.9	Run	0.00	2.83	18.06	4	0.66	0.0034	0.0003
24	C	0.53	17.76	22.8	Run	43.94	87.43	96.05	6	1.01	0.0057	0.008
29	T	0.21	3.66	20.1	Rif	0.00	5.15	26.07	6	1.12	0.0046	0.0074
30	C	0.36	1.88	21.1	Rif	80.68	95.26	95.36	6	0.98	0.0068	0.0072
31	T	0.66	1.89	19.2	Rif	0.00	4.77	16.99	5	0.82	0.0023	0.0031
32	C	1.41	4.09	19.4	Rif	75.06	92.84	94.53	8	1.77	0.0064	0.0118
33	C	0.64	5.76	23	Rif	64.38	84.69	92.81	10	1.32	0.0059	0.0049
34	C	1.14	6.06	20.6	Rif	33.29	17.33	35.96	8	1.20	0.0019	0.0067
35	T	1.84	9.96	15.7	Rif	0.00	0.98	6.68	6	0.92	0.0010	0.0006
36	T	2.59	6.40	20.1	Rif	0.00	0.22	5.85	3	0.89	0.0008	0.001
41	T	0.08	1.67	21	Run	0.00	10.31	6.68	3	0.41	0.0015	0.0061
42	T	1.08	2.51	21.9	Run	0.00	1.06	9.05	4	0.70	0.0060	0.0055
43	C	0.83	4.69	22.6	Run	27.33	72.93	87.41	4	0.43	0.0008	0.0014
44	C	0.40	6.67	20.1	Run	83.62	91.27	95.70	7	1.32	0.0060	0.0085
45	T	1.14	8.18	21.1	Run	0.00	2.68	10.20	3	0.64	0.0020	0.0015
46	C	0.85	12.93	20.7	Run	89.68	85.00	93.87	9	1.10	0.0041	0.0188
47	C	0.32	18.31	22.4	Run	81.54	96.77	94.03	8	1.25	0.0056	0.0112
48	T	0.18	20.49	21.2	Run	0.00	13.89	18.37	2	0.45	0.0003	0.001
53	C	0.68	6.61	21.4	Rif	48.39	37.38	82.76	8	1.69	0.0049	0.0072
54	T	2.97	3.43	19.4	Rif	0.00	3.03	9.72	3	0.52	0.0041	0.0018
55	C	1.83	5.96	21.6	Rif	82.49	85.41	89.72	8	1.61	0.0070	0.0175
56	T	3.86	7.26	23.2	Rif	0.00	1.35	8.16	5	1.07	0.0050	0.0031
57	C	0.63	9.64	21.7	Rif	50.24	69.00	76.73	8	1.58	0.0101	0.0311
58	C	1.11	14.36	19.9	Rif	85.74	50.71	80.43	7	1.16	0.0159	0.0062
59	T	3.69	9.91	21.8	Rif	0.00	0.74	3.74	1	0.00	0.0112	0
60	T	1.60	16.67	21.9	Rif	0.00	1.19	7.95	3	0.31	0.0085	0.0013
65	C	0.00	6.44	20.9	Run	44.46	55.75	79.23	9	0.99	0.0106	0.0144
66	T	0.76	5.34	19.4	Run	0.00	15.05	3.53	4	0.30	0.0087	0.0011
67	C	0.72	7.37	16.6	Run	91.79	93.91	95.32	8	1.49	0.0163	0.0062
68	T	2.02	6.39	22	Run	0.00	2.93	5.90	2	0.55	0.0092	0.0025
69	C	0.92	13.86	18.9	Run	84.56	78.33	92.73	10	1.47	0.0119	0.0063
70	T	1.31	14.64	16.8	Run	0.00	2.17	2.30	3	0.68	0.0064	0.0008
71	C	0.80	17.63	22.5	Run	32.74	68.58	92.91	7	0.61	0.0097	0.0066
72	T	0.08	19.00	19.5	Run	0.00	6.99	16.32	6	0.96	0.0075	0.002