Research Article

Current velocity and spatial scale as determinants of the distribution and abundance of two rheophilic herbivorous insects

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Abstract

Organisms frequently show marked preferences for specific environmental conditions, but these preferences may change with landscape scale. Patterns of distribution or abundance measured at different scales may reveal something about an organism's perception of the environment. To test this hypothesis, we measured densities of two herbivorous aquatic insects that differed in body morphology and mobility in relation to current velocity measured at different scales in the upper Colorado River (Colorado, USA). Streambed densities of the caddisfly larva *Agapetus boulderensis* (high hydrodynamic profile, low mobility) and mayfly nymph *Epeorus* sp. (low hydrodynamic profile, high mobility) were assessed at 3 spatial scales: whole riffles, individual cobbles within riffles, and point locations on cobbles. Riffles were several meters in extent, cobbles measured 10–30 cm in size, and the local scale was within a few centimeters of individual larvae (themselves ca. 0.5–1.0 cm in size). We also quantified the abundance of periphytic food for these herbivores at the cobble and riffle scales. *Agapetus* favored slow current (<30 cm s^{-1}) across all scales. *Epeorus*, by contrast, favored fast current (60–80 cm s^{-1}) at the local and riffle scale, but not at the cobble scale. Only *Agapetus* showed a significant relationship to current at the cobble scale, with greatest larval densities occurring at velocities near 30 cm s^{-1}. We had predicted an inverse correlation between grazer density and periphytic abundance; however, this occurred only for *Agapetus*, and then only at the cobble scale. These data suggest that organisms respond to environmental gradients at different spatial scales and that the processes driving these responses may change with scale, e.g., shifting from individual habitat selection at local and cobble scales to population responses at the riffle scale. This study also highlights the importance of using the appropriate scale of measurement to accurately assess the relationship between organisms and environmental gradients across scale.

Introduction

Organisms frequently show marked preferences for specific environmental conditions in nature. As environmental conditions vary along gradients across the landscape, natural selection will favor organisms that distribute themselves within environmental ranges that favor growth and reproduction. The scale at which environmental gradients are important to organisms, however, will vary across taxa (Lima and Zollner 1996). Even when organisms have similar resource requirements, they may use the landscape at different spatial scales to attain them (Menge and Olson 1990). For example, both grazing ungulates and herbivorous insects may feed on the same types of food plants, but the ways in which these herbivores perceive and use landscape scales will differ greatly (Kolasa and Rollo 1991). An individual plant, for instance, may be of much greater 'relevance' to an insect than to an ungulate. Whereas an insect may spend its entire larval

existence feeding on a single plant, the same plant may represent only a mouthful of food to the large ungulate. Size is not the only consideration, mobility is likewise important. Some insect herbivores restrict their movement to plants spaced only a few centimeters apart while others range between plants that are spaced by kilometers (Strong et al. 1984). Hence, the scales that are most 'relevant' to organisms are those having ecological importance.

It is not surprising, then, that imposing an arbitrary scale (e.g., quadrat size) on a species' pattern of distribution and abundance may result in an inaccurate picture of that organism's response to environmental gradients. Similarly, altering the scale of observation may alter inferred species environment patterns. For example, the abundance of two species competing for the same food resource can be negatively correlated at some local scale, but positively correlated at larger scales if both competitors have similar environmental requirements (Cooper et al. 1998). Thus, a challenge facing ecologists is appropriately characterizing environmental gradients that are relevant to the organism and then accurately measuring the organism's response to those gradients across the landscape.

One approach to understanding the scale(s) at which species respond to environmental variability is to conduct investigations at multiple scales (Wiens 1989; Levin 1992; Cooper et al. 1998). Organisms frequently show marked preferences for specific environmental conditions, but these preferences often change with landscape scale. Patterns of distribution or abundance measured at different scales, then, may reveal something about an organism's perception of the environment, and hence provide clues as to which scales are most ecologically relevant to the organism.

A defining environmental gradient in stream ecosystems is current velocity. Organisms as diverse as fish, macroinvertebrates and algae all respond to its influence, and current is often a prime descriptor of stream organism distributions (Hynes 1970; Allan 1995). Stream current varies at many spatial scales, including longitudinal (headwaters to lower reaches), horizontal (bank to mid-channel), and vertical (surface to streambed), and the influence of current on species distributions and abundances can be multiscalar (Hart and Finelli 1999). At the spatial scale of riffles, current can influence immigration and emigration rates within benthic populations (Ghosh and Gaur 1991; Rader 1997). At smaller scales, such as the surfaces of cobbles, current velocity can influence the positioning and movement rates of individual benthic organisms (Poff and Ward 1992, 1995). Current velocity is of particular importance to stream herbivores because they forage on surfaces exposed to flow. Herbivore attributes such as body shape (Statzner and Holm 1982), mode of movement (Frutiger 1998) and respiratory requirements (Ericksen et al. 1996) constrain herbivore performance under different flows, and hence, stream 'grazers' often show distinct current preferences (Hynes 1970). Moreover, flow can configure the taxonomic and physical structure of algal assemblages (McIntire 1966; Poff et al. 1990) which grazers are thereby able to differentially harvest depending on their mouthpart form and function (Arens 1989; Wellnitz and Ward 1998). Thus, current may directly or indirectly influence stream herbivores independently of other factors (but see Statzner et al. 1988), either by influencing their ability to move and forage across substrata or by altering the physiognomy of algal assemblages on which they can efficiently feed.

In this study, we examined the responses of two rheophilic ('current-loving') herbivorous insects to current velocity measured at three scales. The spatial scales examined were (1) whole riffles, (2) individual cobbles within riffles, and (3) point locations on cobbles. These scales ranges from ca. 100 m^2 for riffles to $< m^2$ for cobbles to ca. 1 cm^2 for point locations and are commonly recognized by stream ecologist as being relevant to a variety of lotic insect taxa (Newbury 1984; Allan 1995). The herbivorous insects were a caddisfly larva (*Agapetus boulderensis* Milne) and a mayfly nymph (*Epeorus* sp.), insects that differ greatly in their body morphology and mobility and are thus likely to respond differently to current across different scales. *Agapetus* larvae construct and live inside 'tortoise shell' sand grain cases that produce substantial hydraulic drag which causes *Agapetus* to move slowly in high current and to cover <1 m a day in their foraging activities (Poff and Ward 1992). *Epeorus* and other heptageniid mayflies, by contrast, have a flattened morphology that minimizes drag forces and maximizes lift (Statzner and Holm 1982), but they are nonetheless able to cling to, and crawl quickly across, substrate exposed to fast current (T.A. Wellnitz, pers. obs.). In addition, *Epeorus* has the ability to enter the water column and 'drift', which allows it (unlike *Agapetus*) to potentially move many meters downstream in a single day (Rader 1997).

We hypothesized that there would be a significant association between current and abundance at the local scale for both insects because of their need to

negotiate and maintain position while foraging on algae attached to exposed substrates. At the two larger scales, the cobble and the riffle, we hypothesized that *Agapetus* and *Epeorus* would respond differently because of their relative mobilities. We predicted that *Agapetus* abundance would be more closely associated with current at the cobble scale because this scale circumscribed its daily foraging movements. At the riffle scale, however, we predicted only a weak relationship between *Agapetus* and current. Compared to cobbles, riffles would have less ecological relevance to this slow-moving caddisfly. Limited mobility restricts *Agapetus* foraging to the surfaces only a few cobbles for much of their larval existence (Poff and Ward 1992), consequently, we hypothesize that this caddisfly is less able to perceive heterogeneity at the riffle scale and its response to riffle current would be weak. By contrast, we predicted that the more mobile *Epeorus* would respond most closely to current at the riffle scale. The riffle scale would encompass this mayfly's drift movements and its ability to locate preferred flows, whereas the cobble scale would be less important to an organism that could move across several cobbles in a day.

In addition to assessing the densities of *Agapetus* and *Epeorus*, we also measured periphytic abundance in relation to current at the cobble and riffle scale. Periphyton is comprised primarily of algae and is the main food of grazers (Lamberti and Moore 1984). Periphyton was measured to see whether *Agapetus* and *Epeorus* abundance were responding to periphyton, current alone, or the interaction between these factors. Periphyton was not measured at the local scale.

Another question we examined was how the different methods of measuring current velocity compared in describing insect distributions at different scales. Coarse scale measurement at the riffle and cobble scale are often used to characterize benthic habitats and we were interested in how well, if at all, this scale of measurement corresponded to local conditions.

Materials and methods

Study site

This study was conducted in a 2 km section of the upper Colorado River in Grand County, Colorado, USA. The stream section consisted of a series of riffles and runs with depths ranging around 0.5 m making the entire streambed accessible by wading. In our study section stream width was approximately 10 m across. The streambed was comprised primarily of large (ca. 15–25 cm in diameter), closely packed cobbles with a surrounding gravel and sand matrix. The upper Colorado is a regulated river and temporal variation in stream flow at this site is highly predictable (Poff et al. 1990). Thus, the distribution of current velocity over substrate does not vary greatly over time, allowing instream examination of the current effects on the spatial distribution of benthic insects.

Insect grazers

Agapetus boulderensis and *Epeorus* sp. are common grazers in the upper Colorado river in mid-summer. Mean ($\pm$ 1 SE; n = 12) streambed densities for *Agapetus* and *Epeorus* on 16 July 1998 were 83.3 ($\pm$ 25.3) and 95.1 ($\pm$ 27.0) individuals m^{-2}, respectively. These insects were chosen for study because (1) they were abundant at our study site, (2) field observations (Poff and Ward 1992) and laboratory studies (Palmer 1995) indicate they exhibit distinct, small scale velocity preferences, and (3) they differ in mobility (Merritt and Cummins 1996). It was also important that both insects were sufficiently resistant to observer disturbance to maintain their position on substrates so locations of individuals could be determined before current velocity was measured. We checked our assumption that *Epeorus* was not disturbed by the presence of an observer by locating an individual nymph on the streambed, waiting several minutes for it to acclimate to the observer's presence, then having a second observer approach the nymph until it was caused to move. In many instances, *Epeorus* nymphs would not shift position until the observer's hand was within 10 cm of its location.

Measuring current velocity

Current was measured using a current probe and digital readout manufactured by Schiltknecht Messtechnik AG, Zürich, Switzerland. The probe's propeller (diameter = 8 mm) is mounted in a 10 mm diameter plastic housing, and the instrument has a temporal resolution of 1 s. Each measurement of current velocity was the mean of 6 readings spaced 1 s apart.

Current was measured in a different manner for each of the three stream scales. Local current was measured by placing the probe directly on the substrate surfaces and adjusting the probe's horizontal and vertical angle of orientation until maximum current for a point location was attained. A meter stick attached

to the probe's handle facilitated depth measurement after current velocity was measured. Cobble current was measured at 0.4 stream depth directly above the cobble's midpoint, a standard method current measurement for this scale (Gordon et al. 1992). Riffle current was measured in a manner similar to that for cobbles, but this scale's larger spatial extent required that several readings be taken instead of just one (the procedure is detailed below).

It is important to note that this study did not employ a strict nested design, because we did not measure local current on all sampled cobbles. Our intent, rather, was to asses the relationship between current and benthic organisms using means commonly employed by stream ecologists at each of these 3 different scales of spatial resolution. We restricted the local scale to point location measurements of individual grazers on cobble surfaces to get the most precise measure obtainable of the insect-current relationship. Cobble and riffle scales, by contrast, were deliberately measured at courser levels of resolution above the streambed because this method is most commonly employed by stream ecologists (Gordon et al. 1992).

Stream surveys

Between 22 July and 13 August 1998 we surveyed the streambed for *Agapetus boulderensis* and *Epeorus* sp. density, periphytic abundance, and measured depth and current velocity at 3 spatial scales: whole riffles, individual cobbles within riffles, and point locations on cobbles. Riffles were several m^2 in extent, cobbles measured 10–30 cm in diameter, and the local scale was within a few centimeters of individual larvae (themselves ca. 0.5–1.0 cm in size).

We selected seven riffle or runs, hereafter to be called 'riffles', that showed homogeneous stream flow as defined by uniformity in their surface current. Each riffle measured 10–20 m in length and had comparable substrates and bottom topography. After the extent of a riffle was determined by eye, it was divided into a 4×4 grid of 16 cells having approximately equal area. Mean depth and current in each cell were determined by recording the average taken from the four quarters of the cell. Current was measured using the Schiltknecht current probe held at 0.4 stream depth above the bottom (Gordon et al. 1992). Whole riffle current was taken as the grand mean of the 16 cell velocities. It should be noted that riffles having a mean current velocity of less than 15 cm s^{-1} were

not found within our study section because it exhibits a moderately steep gradient.

To sample insects from riffles, a single cobble was selected from the approximate center of each cell, rolled into a kick net and carried to shore. Sixteen cobbles comprised the insect sample for each riffle. *Agapetus*, *Epeorus* and other macroinvertebrates were removed by hand from the cobble surface that was exposed to streamflow (as determined by the extent of periphytic cover) and preserved in 5% formalin for later counting in the laboratory. After removing insects, periphyton was removed with a toothbrush and squirt bottle and preserved in 5% formalin. Surface area was quantified by wrapping the sampled cobble surface with aluminium foil and trimming off the excess material (Steinman and Lamberti 1996). The foil was air-dried, weighed and a mass/area relationship was used to determine the sampled surface area of the cobble.

Individual cobbles were sampled from a heterogeneous stream section at 0.4 depth having velocities that ranged from < 5 to > 80 cm s^{-1}. A line transect was established across the stream in order to span the full range of current velocities. Cobbles were randomly selected from points along the transect until a minimum of 5 cobbles were selected from each of 3 ranges: 0–20 cm s^{-1}, 30–50 cm s^{-1}, and 60–80 cm s^{-1}. After a cobble was selected, stream depth and current velocity were measured at 0.4 depth directly over the cobble and then the cobble was rolled into a kick net and carried to shore. Macroinvertebrates and periphyton were sampled as described above.

Point locations on cobbles were sampled from a single riffle by selecting points using a 'random walk' technique. Starting from the approximate center of the riffle, pairs of random numbers were used to determine the distance and direction of each sampling point. If the walk brought the sampler to shore, random number pairs were generated until sampling points were returned to the stream. Once a point was selected, the nearest *Agapetus* or *Epeorus* individual to that point was located, and after removing the insect, the stream depth was recorded and current was measured at the collection point with the Schiltknecht current probe (within 10 mm of the bed). Care was taken to hold the current probe perpendicular to the surface and in the direction of the maximum flow. Periphyton was not sampled at this scale.

To assess the relationship between current measured at the two finer scales (local and cobble) we measured current at 45 randomly selected point loca-

tions on cobbles and at 0.4 depth above these points (following the method for cobble measurement). Linear correlation was used to assess the relationship between current measured at these two scales.

Statistical analysis

We analyzed the relationship between current velocity, depth, and periphytic AFDM on the abundance of *Agapetis* and *Epeorus* at the riffle and cobble scales using the regression module in Statistica™ software (StatSoft Inc., Tulsa, OK, USA). Data were log-transformed as necessary to meet the assumptions of parametric regression analysis. We used current as a predictor variable, rather than more synthetic variables that combine current and depth (e.g., Reynolds number and Froude number – see Statzner et al. 1988), for two reasons. First, at the cobble and riffle scales, depth did not vary appreciably among samples, resulting in a high colinearity between measures of current and related synthetic variables. At the local scale there was some variation in depth among sampling locations; however, interpretation of results did not change depending on whether current or more synthetic variables were used. Second, because *Agapetis* and *Epeorus* are known to be rheophilic, we preferred to interpret our results in terms of the more direct variable of current velocity

To analyze cobble-scale data we performed two regression analyses: one on all cobbles sampled, and one on only those cobbles having *Agapetus* or *Epeorus*. This was done because several cobbles sampled had neither grazer present and these cobbles did not cluster around slow or fast current but were spread across the measured range. That some cobbles sampled had neither grazer present is not unusual, because benthic organisms in streams are notorious for their patchy distributions and variable abundances (Allan 1995). Indeed, some studies suggest that the number of samples necessary for attaining accurate estimates of benthic abundance may be prohibitively high (Benke 1984).

Local scale current data were frequency counts based on point velocities and, therefore, not density measurements. To determine whether *Agapetis* and *Epeorus* showed a preference for current, we tested the null hypothesis of no preference (i.e., uniform distribution across current). A Chi-square test for goodness of fit was computed to determine if the observed frequencies deviated significantly from those expected in a uniform distribution.

Results

Each insect exhibited distinct current velocity preferences at different scales. In general, *Agapetus* preferred slow current whereas *Epeorus* preferred fast current (Figures 1 and 2). Periphytic ash-free dry mass (AFDM) showed a significant relationship to current, but only at the cobble scale (Figure 3). Multiple regression models that incorporated current, depth and periphytic AFDM to predict insect abundance at different scales showed that only current was a significant factor.

At the local scale the null hypothesis of no preference was rejected for each grazer ($P < 0.001$). *Agapetus* appeared to select slow currents, with more than half of individuals sampled (57%) occurring at currents < 20 cm s^{-1} (Figure 1a). Frequency peaked between 5–15 cm s^{-1} and dropped off sharply at very slow and fast current, giving the distribution a 'hump' that was skewed towards slow current. *Epeorus*, by contrast, preferred fast current, with 53% of individuals sampled occurring above 50 cm s^{-1} (Figure 2a). These mayfly nymphs were not collected at velocities < 10 cm s^{-1} and numbers tended to increase gradually as current velocity increased.

At the cobble scale, *Agapetus* and *Epeorus* did not exhibit a significant relationship to current when cobbles having no insects were included in the analysis. However, when zero values were removed from the analysis, a significant quadratic relationship resulted for *Agapetus* (Figure 1b; $P = 0.006$; $r^2 = 0.57$), but not for *Epeorus* (Figure 2b; $P > 0.10$). The peak in *Agapetus* abundance was slightly greater than for the local scale. Periphyton also showed a quadratic relationship to current, but it was the *opposite* of that seen for *Agapetus* (Figure 3a). These inverse patterns suggest a relationship between *Agapetus* and periphyton, and regression of log periphytic AFDM on *Agapetus* abundance did indeed show a significant, if weak, relationship ($F_{1,10} = 4.40$, $P = 0.05$, $r^2 = 0.20$).

At the riffle scale, *Agapetus* and *Epeorus* distributions across current mirrored their local distributions. *Agapetus* density had a negative relationship to riffle current (Figure 1c; $P = 0.001$, $r^2 = 0.83$), whereas *Epeorus* showed a positive response (Figure 1c; $P = 0.003$, $r^2 = 0.90$). No *Agapetus* were encountered in the two fastest riffles having mean velocities above 75 cm s^{-1}; *Epeorus*, by contrast, were present in all 7 sampled riffles. Periphyton showed no relationship to riffle-scale current (Figure 3b; $P > 0.10$).
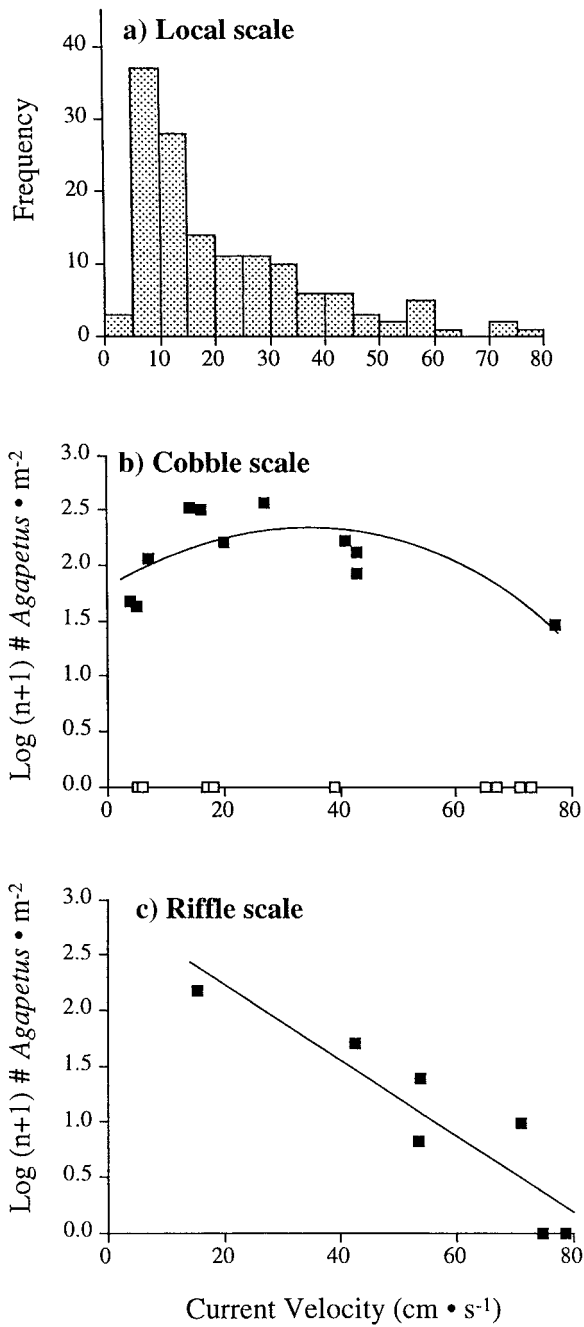
Figure 1.

Figure 2.

Local current measured within 10 mm of the bed at 45 point locations on cobble surfaces was significantly correlated with flow measurements at 0.4 depth (Figure 4a, dotted line; $P = 0.011$), but the relationship was weak ($r^2 = 0.13$). Cobble scale current consistently under-predicted local scale current (Figure 4a,
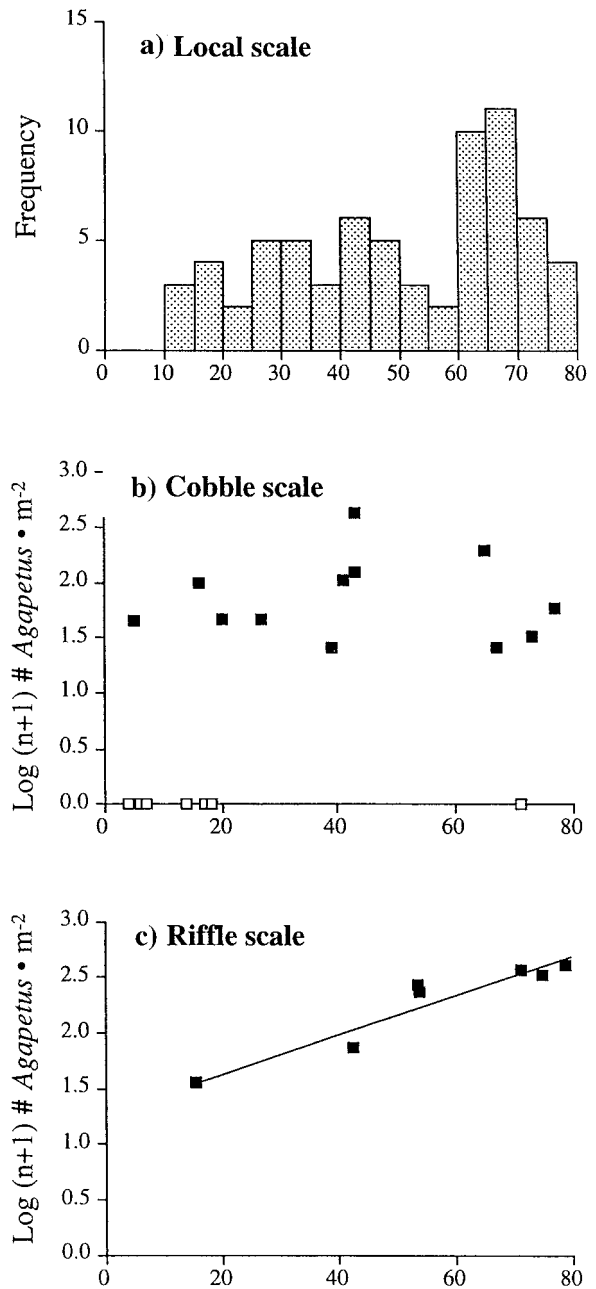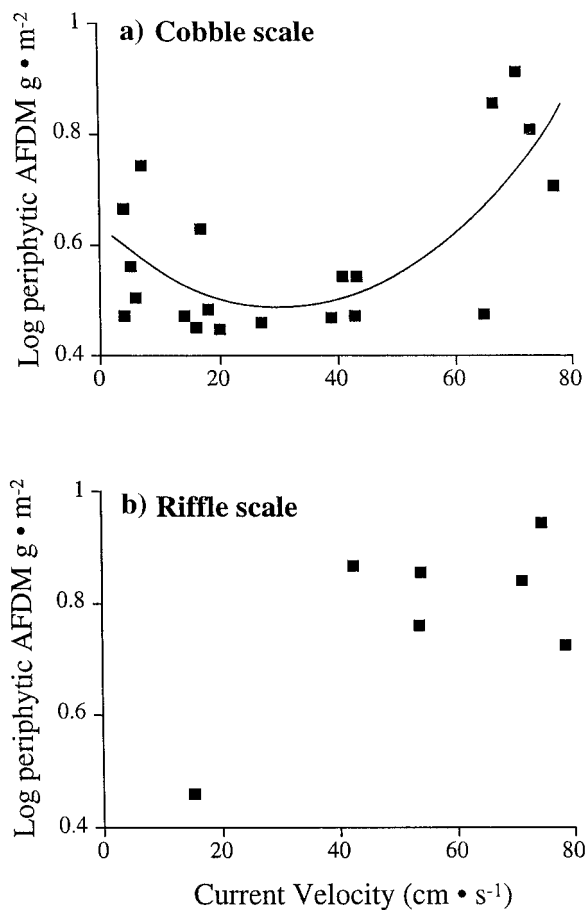
Figure 3.

Figure 4.

solid line), indicating the effect of frictional resistance of the bed and the inability of coarse-scale velocity measurements to predict local velocity.

At the riffle scale, increase in mean current velocity was associated with greater variance (Figure 4b). Current maxima showed a steeper increase than did current minima as mean riffle velocity increased.

Discussion

Agapetus and *Epeorus* exhibited distinct current velocity preferences and showed significant responses to current at different scales. Moreover, the relationship across scales differed for the two grazers. *Agapetus* showed a 'hump-shaped' relationship to current that was skewed towards low velocities at the local and cobble scale, and was very rare at fast current across all three scales. *Epeorus*, by contrast, displayed 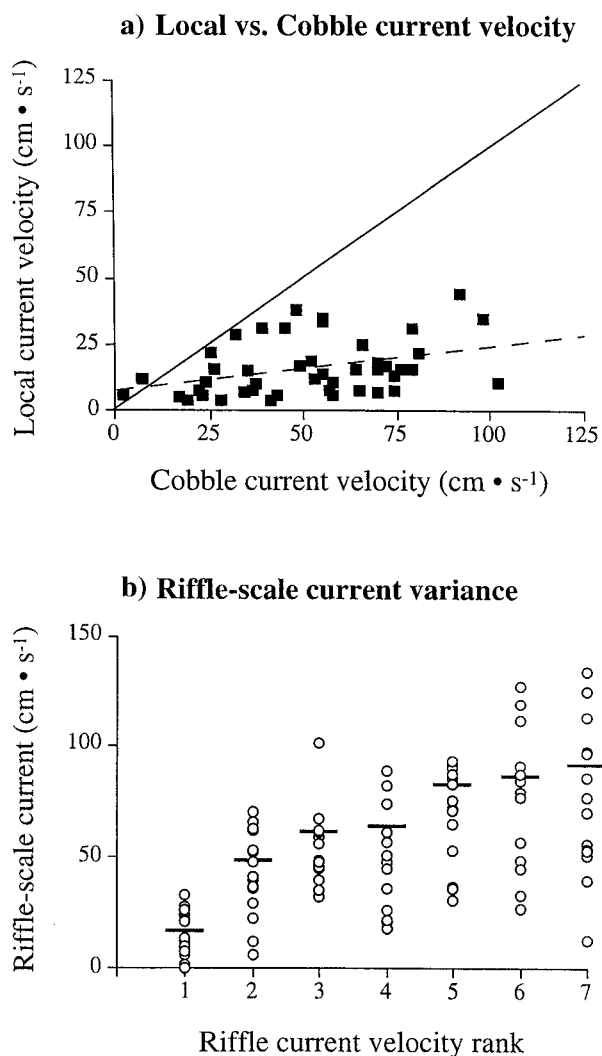a strong positive relationship to current at the local and riffle scales but showed no relationship to current at the cobble scale.

We had predicted that *Epeorus* would not respond to cobble-scale current because of its ability to move easily at the riffle scale (via drift between cobbles) would render the cobble scale 'irrelevant'. Indeed, no relationship to current occurred for *Epeorus* on cobbles. It is important to note, however, that this mayfly was also capable of crawling very quickly across cobble surfaces. If rapid movement within a scale makes heterogeneity at that scale less important, it would follow that the relationship *Epeorus* showed to local current should also be poor. Indeed, *Epeorus* did not show a marked preference across a wide range of local velocity. By contrast, *Epeorus* showed a very good

relationship to riffle current ($r^2 = 0.90$), implying that this scale, the only one to encompass drifting movements, was the most 'relevant' to this mayfly.

Unlike *Epeorus*, *Agapetus* showed a significant relationship to current at each of the three scales. There was a clear preference for slow current over fast, but at very slow velocities abundance of this caddisfly dropped off, resulting in a unimodal distribution pattern for *Agapetus* across local and cobble currents. At the riffle scale, by contrast, abundance declined monotonically with current. This may have been because we were unable to locate 'riffles' at our study site having mean current < 18 cm s^{-1}. Had we been able to find and sample stream sections having such slow velocity, it is likely that *Agapetus* abundance would have been quite low. Indeed, observations in our study section of the upper Colorado indicate this caddisfly is rarely encountered in very slow flowing or depositional areas (N.L. Poff, pers. obs.).

The quadratic relationship *Agapetus* showed to current at the cobble scale was the inverse of that displayed by periphyton, suggesting this caddisfly may have been regulating periphytic abundance. This relationship between *Agapetus* and periphyton was not significant at the riffle scale; however, had we been able to sample more slow-velocity riffles (e.g., < 40 cm s^{-1}, see Figure 3b), we consider it likely that a pattern would have emerged. The hypothesis that *Agapetus* exerted control over periphytic abundance is reinforced by the fact that algae grown and in streamside channels using water pumped from our study reach showed greatest accumulation at ca. 25 cm s^{-1}, the exact opposite pattern observed for algae in the stream (T. Wellnitz and N.L. Poff, unpublished data). *Agapetus* grazers were absent from these channels and we attribute the dramatic differences in periphytic abundance to their influence. Glossosomatids such as *Agapetus* are known to be capable of exerting strong control on benthic algae and periphyton in other streams (McAuliffe 1984; Hart 1987; Kohler 1992), and during the time of this study, *Agapetus* was one of the most abundant grazers at our study site. The quadratic relationship *Agapetus* had to cobble scale current, however, was significantly only when cobbles lacking *Agapetus* were excluded from the analyses.

Benthic organisms inhabiting streams are known for their patchy distributions (Pringle et al. 1988, Allan 1995) and stochastic factors play an important role in determining whether or not a patch will become colonized (Townsend 1989, Hart 1992). Indeed, the likelihood that the macroinvertebrate assemblage on any given stream cobble would be representative of the streambed is extremely low (Allan 1982). In fact, of all the scaling units chosen for the present study, cobbles were the least 'arbitrary' in that they represented discrete units of habitation on the streambed. Our rationale in excluding cobbles lacking *Agapetus* from the analysis, therefore, was that they represented 'empty' patches. By contrast, local scale data were collected in a manner that assured that there would be no zero values because we located individuals nearest to randomly selected points that were 'empty'. Riffles showed zero *Agapetus* abundance in two cases, but riffle samples comprised 16 cobbles instead of just one, decreasing the likelihood that a patch would be empty due to under-sampling.

A problem intrinsic to scaling studies is that patterns evident at smaller scales may not be detected at larger scales because the resolution of measurement fails to discern them (Allen and Starr 1988; Wiens 1989). The riffle-scale data in the present study comprised only 7 points and riffles in the lower velocity range were under-represented because they were rare in our study section. Nevertheless, significant trends were seen for *Agapetus* and *Epeorus* distribution at the riffle scale and these trends reflected local preferences (i.e., *Agapetus* was more abundant at slow current, *Epeorus* in fast). We had not predicted this, hypothesizing rather that *Agapetus* moved too slowly to assess current at large spatial scales and so would seek low velocity patches within fast-slowing riffles. Thus, we expected the relationship to riffle current would reflect the availability of low flow cobble patches. Contrary to expectations, the relationship *Agapetus* had to riffle current was quite good ($r^2 = 0.83$).

Surprisingly, however, *Agapetus* was not encountered in the two fastest riffles, despite the fact that both of these riffles possessed cobbles situated in relatively slow current (Figure 4b). Riffles were composed of cobble-scale units and cobbles exhibited a wide range of flow, the variability of which clearly increased with mean current speed. Minimum current increased more gradually than maximum currents, indicating that even fast flowing riffles had cobble-scale patches of slow current. We hypothesized that the pattern for *Agapetus* observed across riffles would reflect the number of slow current 'refugia' where this slow-moving, case-bearing caddisfly possessing an unfavorable hydrodynamic profile could persist and forage. This begs the question, however – why were *Agapetus* not found in the slow velocity 'refugia' that existed within the two fastest riffles (Figure 1c)?

Fast riffles contained regions of slow current, but these favorable habitat patches were far fewer and more isolated than in slower riffles. It is possible that these isolated patches were inaccessible to larval emigration and that mortality within these remote patches was high. Consideration of these vacant patches of slow current leads us to speculate that factors besides individual selection were operating on *Agapetus* abundance at the riffle scale. Distribution patterns at larger spatial scales may be a function of the population response as well individual habitat selection (Menge and Olson 1990). *Agapetus* and other stream insects with winged adult stages may be found within a particular stream riffle not only because of environmental factors important to the larvae, but because adult oviposition placed them there (Wallace and Anderson 1996). Unlike the more mobile *Epeorus*, *Agapetus* may not be able to disperse far beyond locations from which they hatched. Riffle-scale patterns for *Agapetus* (and other sedentary organisms) may represent population-level factors of natality and differential survivorship in riffles of different speed. Alternatively, ovipositing *Agapetus* females may simply avoid riffles exhibiting fastest current. Similar population-level processes would also factor into the distribution and abundance of *Epeorus*, but this mayfly nymph is probably mobile enough to disperse quickly after hatching and distribute itself in regions of preferred flow.

Just as the underlying processes that shape patterns of abundance can shift with scale, so might the relevant scale for measuring environmental gradients change. Moving water slows as it approaches a solid surface (Vogel 1994), and this probably accounts for *Agapetus*' apparent preference for higher velocities on cobbles as compared to the local scale current. In general, however, local current was poorly predicted by cobble scale measurements (Figure 4a). This result has particular relevance to stream studies that attempt to characterize current preferences for benthic species using a cobble-scale of resolution. The rationale for this technique may rest on the assumption that current velocity decreases in a predictable manner as it approaches the streambed. Were this the case, then cobble-scale measurements would be a good approximation of near-bed flows and a valid method of describing the relationship between current and benthic organisms. However, heterogeneous streambeds are dominated by turbulent rather than uniform, laminar flows and current velocity profiles above streambeds can be highly unpredictable (Davis and Barmuta 1989; Hart et al. 1996). Thus current mea-

sured at the cobble scale should not be expected to describe the local current velocity preferences or habitats of benthic organisms in streambeds having great topographic heterogeneity, where local currents can vary by an order of magnitude over a few centimeters (e.g., Poff and Ward 1992). Accordingly, it was not surprising that the relationship between current and grazers was either poor (*Agapetus*) or non-existent (*Epeorus*) on cobbles.

In conclusion, our data suggest that organisms may not only respond to environmental gradients at different spatial scales, but that the scale of measurement must be an appropriate match to the scale of investigation to in order correctly assess the relationship between organisms and environmental gradients. Our findings lend support to the developing consensus among ecologists that habitat relations of organisms need to be quantified at multiple scales to better understand their ecology (Wiens 1989; Levin 1992; Cooper et al. 1998), and that the scale of measurement may influence how patterns in nature are perceived.

Acknowledgements

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