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Heterogeneous currents and algal resources mediate in situ foraging activity of a mobile stream grazer

N. LeRoy Poff and J. V. Ward

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The importance of spatial heterogeneity in near-bed currents and algal resource patchiness in regulating the movement patterns, foraging activities, and distribution of the mobile stream insect, *Agapetus boulderensis* Milne (Glossosomatidae: Trichoptera) was investigated with field observational studies and field experiments. Near-bed current velocities were characterized for topographically-complex substrata concurrently with spatial patterns of algal density and taxonomic composition. Activities of self-marked mobile larvae were examined in relationship to mapped current and algal resources. Near-bed currents alone influenced the distribution and local abundance of individuals in a size-dependent fashion – fifth (final) instar larvae occurred across a velocity range of < 5 to 50 cm s^{-1} , while smaller third and fourth instar larvae were found only at currents ranging from < 5 to 30 cm s^{-1} . *Agapetus* movement was also constrained by local current. Direction of movement on stone surfaces was significantly into or lateral to oncoming flow. Rate of movement was inversely related to local current speed and positively related both to temperature and to travel in the upstream direction. *Agapetus* movement and foraging were also related to algal density and taxonomic composition. Movement rate was inversely correlated with estimated diatom density but positively correlated with densities of green and blue-green algae for larvae on one stone. Gut analysis revealed a significant positive preference by *Agapetus* for diatoms, particularly *Cocconeis placentula*, which was overrepresented in the gut relative to other diatoms or to blue-green algae. Together, patterns of local current and of algal distribution and composition were important descriptors of movement and foraging activity of this mobile grazer under naturally heterogeneous field conditions. A field experiment under controlled conditions of current and algal density showed both factors were independent and non-interactive determinants of grazer movement rates. This study supports previous research showing the importance of algal patchiness in mediating grazer foraging activity and distribution, but it further indicates that patterns of resource use by grazers may be constrained by heterogeneous local currents, independent of the effects of food distribution and abundance.

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A major concern of ecology is understanding how environmental heterogeneity mediates animal distribution and resource use. Patchiness is a key feature of ecological systems (e.g., Wiens et al. 1985), and animal use of patchy resources has long been of interest (e.g., MacArthur and Pianka 1966). Analysis of the behavior of mobile animals has provided insight into how individu-

als acquire resources in heterogeneous environments (see Stephens and Krebs 1986 for numerous examples). Identification of constraints on resource use is a central component of this approach, and many studies have clearly demonstrated the importance of biotic constraints such as predation risk (e.g., Sih 1980, Gilliam and Fraser 1987). Recently, less effort has been directed

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at identifying abiotic limitations on resource use. Yet, physical features of the environment can constrain ecological processes and patterns as diverse as habitat use in anoline lizards (Moermond 1979), foraging efficiency of centrarchid fishes (Werner and Hall 1979), dispersal of littorinid snails (Underwood and Chapman 1989), and home range size in iguanid lizards (Christian and Tracy 1985). Physical environmental constraints have important implications for animal energetics and for detection of food and predators and may therefore mediate not only patterns of resource use and distribution, but also interactions among species.

In stream ecosystems, the action of flowing water is a dominant physical feature. Flow influences rates of food/nutrient delivery and gas exchange, and it exerts erosive shear stresses on organisms exposed to it (e.g., Statzner 1988). The heterogeneous spatial distribution of current over a topographically-complex streambed may generate physically-separated patches (cf. Wiens et al. 1985, Pringle et al. 1988), within which demonstrable variation in magnitudes of ecological processes can occur (e.g., predation – Peckarsky et al. 1990, Hansen et al. 1991). Indeed, near-bed currents influence the distributions and abundances of many lotic organisms, including attached algae (e.g., Blum 1960, Poff et al. 1990) and sedentary invertebrates (e.g., Edington 1968, Alstad 1982). However, little is known about how current influences mobile benthic animals, which can potentially experience a wide range of shear stresses during their normal activities. For mobile larval insects that graze on attached algae (periphyton), resource use and distribution may be mediated by flow heterogeneity in at least two ways. First, near-bed current can directly influence movement (cf. Bournard 1974) and/or foraging success (cf. Calow 1974, Hansen et al. 1991). Second, current may indirectly influence grazer resource use by mediating distribution and abundance of algal resources. While the distribution of mobile grazers has often been related to algal densities (e.g., Lamberti and Resh 1983, McAuliffe 1984), only one study (Vaughn 1986) has related mobile grazer distribution to both near-bed currents and algal abundances. Further, the movement and foraging patterns of mobile grazers in heterogeneous stream environments have never been examined with respect to current – all previous studies on movement and foraging have focused solely on algal resource availability (e.g., Hart and Resh 1980, Hart 1981, Kohler 1984, 1985, Wiley and Kohler 1984).

In this paper, we examine how naturally-heterogeneous algal resource distributions and near-bed currents interact to influence the movement, foraging, and distribution of a mobile stream grazer. This is the first study to characterize these environmental features at a spatial scale small enough to explore how natural heterogeneity influences grazer activity in a complex natural environment. In an observational field study, we related the movements and distribution of self-marked, individual grazers on natural substrata to spatially-variable

near-bed currents and algal resources. In a field experiment, we further explored the relative importances of current and algal resources in regulating larval movement and foraging patterns.

Materials and methods

Study organism and study site

Agapetus boulderensis Milne is a glossosomatid caddisfly (Trichoptera: Insecta) that hatches from the egg stage in late spring, grows through five instars over the next three months, enters the pupal stage and emerges relatively synchronously over a period of ca. one month's time. At maximum size, larvae are ≤ 3 mm in total body length. Their pebble cases, constructed from streambed mineral particles at each ecdysis, reach maximum dimensions of ca. 5 mm length, 3 mm width and 3 mm height. These saddle cases are open ventrally at both ends along the long axis, and the larva extends its legs and anal claws through these openings to grasp the substratum while feeding on attached algae. Glossosomatid larvae travel at maximum rates on the order of centimeters per hour across substratum surfaces (cf. Oemke 1984) in relatively straight paths (see below), and they do not actively enter the water column, making their movements relatively easy to follow. Diel foraging activities of glossosomatids are poorly documented, but Castro (1975) found a population of *Agapetus fuscipes* consumed twice as much periphyton during equal daylight and nocturnal periods throughout larval development. *Agapetus* larvae should be at low relative risk to predation by benthic-feeding fishes (Kohler and McPeck 1989), and, because potential invertebrate predators are rare on upper stone surfaces at the study site (N.L. Poff, unpubl.), their movement activities and distribution should primarily reflect factors other than risk of predation.

Work was conducted in the upper Colorado River, at a site 7 km below a hypolimnial release reservoir and at an elevation of ca. 2500 m. Natural substrata consisted primarily of cobble and boulder, with interspersed gravel and sand. *Agapetus* occurs at densities of up to 3000 m^{-2} during summer and is a dominant component of the guild of grazing insects at this location. Larvae can be observed across a wide range of microhabitats ranging from calm, unsilted shallow zones to deep, fast-flowing sites.

Rock observation study

Eight months before the observation period, five representative stones (upper surface area range ca. 200–300 cm^2) were removed from the stream, cleaned with a wire brush, gridded with 3 mm diameter dots of yellow marine paint at 2–3 cm intervals, and returned to vari-

ous locations across the streambed, where they were colonized with periphyton (primarily algae and associated entrained detritus). The stable hydrograph at the site and the large sizes of the stones ensured that physical disturbance of the substratum did not occur over that time period. On 9 July 1987, two rocks (R1 and R2) were randomly selected for two days of observation through two 25 × 25 cm clear plexiglass boxes situated to just break the plane of the water surface ca. 25 cm above the streambed. Each viewer was mounted on a thin steel frame, the four legs of which were positioned to prevent interference with natural flow patterns over the rock surface. The yellow dots on the rock surfaces served as permanent reference points, where local current was measured with a Nixon Instrumentation Ltd. meter (propeller diameter = 13 mm), which integrates instantaneous velocity over 1-s intervals. This meter, while not designed to determine instantaneous velocity readings at a very fine spatial or temporal scale, is appropriate for estimating average point velocities in the direct vicinity of foraging *Agapetus* larvae. For each point on the surface, a grand mean velocity was calculated from ≥ 20 1-s readings at the beginning of the observation period for the 70 reference points on R1 and the 43 points on R2, by holding the meter perpendicularly to the rock surface and rotating it until a maximum reading was obtained. Because streamflow did not change over the course of the two-day observation period, local currents were presumed to have remained constant; therefore, no additional measurements were taken. Stream discharge had been relatively constant at ca. $1.8 \text{ m}^3 \text{ s}^{-1}$ for 10 weeks before the study (U.S. Bureau of Reclamation, unpubl.).

The positions of all *Agapetus* larvae on the rock surfaces were recorded on pre-marked acetate sheets placed in the bottom of the viewer and aligned with the permanent reference points. Larval positions were recorded on day 1 at 0900, 1020, 1135, 1240, 1400, 1520, 1655, and 1920 h, and on day 2 at 0830, 0950, 1155, 1300, 1600, and 1800 h. Nocturnal observations could not be made reliably through the viewer. Water temperature was measured concurrently with each observation. Permanent photographic records were also made with a 35 mm camera to facilitate later identification of individual larvae. The sequential static positions of individual larvae were recorded for those individuals that had incorporated into their cases painted pebbles seeded on the stream bottom two weeks before the observational study. Individually-marked larvae were occasionally observed during the ca. 15 min period required to record all larval positions on an acetate sheet. Because movement of individuals was rarely discernible, the observation intervals given above allow for reasonable estimation of *Agapetus* movement behavior.

At 1800 h on the second day, the two rocks were removed from the water. Larvae were individually collected and preserved in a carbonated formalin solution to reduce regurgitation of gut contents (Shapas and

Hilsenhoff 1976). Algae were then collected from locations scattered randomly across the surface of each rock (R1 = 31, R2 = 28). A 50 mm² circular brass tube was placed on the surface and its base sealed with soft eraser putty. The 8 mm diameter of this sampler falls near the mid-point of the range of distances moved by larvae over one hour (see below). A dense wire brush was inserted into the tube and algae were dislodged with a vigorous stirring action, removed with a pipette and stored in 2% formalin. Locations of periphyton samples were recorded on acetate sheets. (Two samples were omitted for each rock due to leakage from the base of the brass tube.) In the laboratory, individual samples were brought to standard volume and at least 200 algal cells were counted using standard strip-count methods (see Poff et al. 1990). Cells were identified to lowest practicable taxon and \log_{10} densities determined for predominant taxa at each of the sampled points.

Spatial coordinates (X,Y) for points of velocity measurement, periphyton samples and larval positions on each rock were determined by digitizing data from individual acetate sheets on a graphics tablet. Using a computer interpolation routine, contour maps of equal mean velocity ("isovels") were generated for each rock surface. Similarly, isopleths of "equal" algal density were generated by interpolating between sampled periphyton points. Analysis of larval movement was restricted to self-marked larvae. Direction of movement over the observation intervals was determined from X-Y spatial data; however, rate of movement was calculated in 3-dimensional space, because the rock surfaces had considerable topographic relief. After removal from the stream, each rock was restored to its original streambed orientation and Z-coordinates (height) were measured for corresponding X-Y positions of the permanent yellow dots to mathematically generate a synthetic topographic surface, from which larval Z-positions could be estimated. The difference between beginning and ending position of an individual larva for each observation interval (see above) was used to calculate Euclidean distance: $[(X_i - X_{i-1})^2 + (Y_i - Y_{i-1})^2 + (Z_i - Z_{i-1})^2]^{0.5}$. Net movement rate was calculated as distance moved divided by time elapsed in the interval. For each coordinate position of an individually identified larva, approximate current velocity and algal density values were visually interpolated from the velocity and algal contour maps described above. Average values over the interval between two consecutive observations were then used as independent variables in a multiple linear regression model using movement rate during the interval as the dependent variable (see Results).

The sizes of all collected larvae were determined by measuring maximum head capsule width with a binocular microscope at 40×. Width, length and height of larval cases were also measured as another index of size.

The gut contents of larvae collected within 5 mm of actual periphyton sampling locations on R1 and R2 were extracted from the foregut and midgut, which

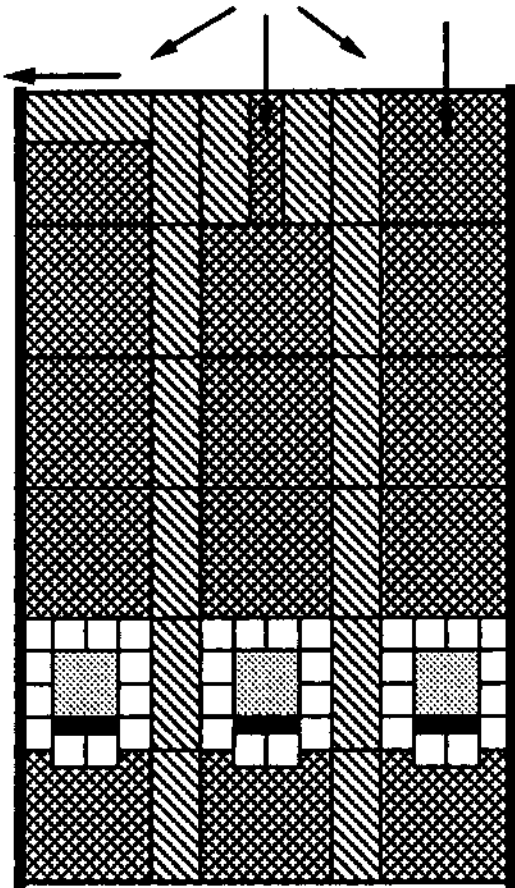


Fig. 1. Plan-view diagram of trough design used in field foraging experiment. Large cross-hatched squares are $10 \times 10 \times 3$ cm bricks that pave the bottom of the trough. Diagonally-shaded rectangles are bricks set on their sides (extending through water surface) to divide the trough into three 10 cm wide channels, through which flow (and current velocity) is regulated by bricks (rectangles) at the upstream end of the trough. Arrows indicate that no flow passes through the channel on the left (slow velocity treatment, $< 1 \text{ cm s}^{-1}$), full flow passes through the channel on the right (high velocity treatment, $\bar{x} = 38.5 \text{ cm s}^{-1}$) and partial flow passes through the middle channel (medium velocity treatment, $\bar{x} = 18.2 \text{ cm s}^{-1}$). Small white squares are $2.3 \times 2.3 \times 0.5$ cm tiles permanently affixed to brick surfaces to create a template into which $4.9 \times 4.9 \times 0.5$ cm foraging tiles (light stippled squares) are placed. The small black, rectangular space between the permanent template tiles and the foraging tile represents the space into which *Agapetus boulderensis* larvae were placed and from which they crawled onto the surface of the foraging tiles during the experimental observations.

were dissected under a binocular microscope. The gut contents were vigorously dispersed on a microscope slide, combined with a 40% sucrose medium, covered, and allowed to harden (cf. Stevenson 1984). For each larval sample, at least three transects were taken across the width of the cover slip at $500\times$ and algal taxa identified. Preference for dominant taxa was assessed by calculating Jacobs' (1974) electivity index, D , a measure

that compares proportion of a prey item in the gut vs proportion in the environment, and a measure that is independent of relative abundances of prey items in the environment. Jacobs' D was transformed to Chesson's (1983) α to test the null hypothesis of no preference ($\alpha = 0.5$) for dichotomous food choices (see Chesson 1983). To compare the relative contribution of specific algal taxa to grazer diet, biovolumes of three major taxa found in the gut were estimated by measuring dimensions of three cells per taxon.

Larval size distribution and current

Additional *Agapetus* larvae were collected from six representative stones on the streambed. A transect was established along the midline of each stone with the plexiglass viewer positioned just beneath the water's surface. Along each transect, local current was measured immediately upstream of individual larvae ($N = 61$), which were collected in situ with a modified forceps and preserved in carbonated formalin. Larval size was determined as described above.

Aggregative response of larvae to algae

To establish larval response to spatially heterogenous algal distribution, a $4.9 \times 4.9 \times 0.5$ cm tile colonized with algae for 30 d was subdivided into 16 equally-sized square patches, half of which were scraped clean to produce a checkerboard pattern of food presence/absence. In calm, oxygen-saturated water, eight larvae starved for 1 h were introduced onto the tile surface at random locations and the time each spent in the two types of patches was recorded.

Field experiment on movement and foraging under different currents and algal abundances

A field experiment was conducted to examine the relationship between larval movement rate, current velocity (three levels) and algal food abundance (three levels) for a total of nine treatment combinations. The three food abundance levels were obtained from periphyton cultured for 0 d (low), 16 d (medium) and 30 d (high) on unglazed porcelain tiles ($4.9 \times 4.9 \times 0.5$ cm) at a depth of 5 cm in a flow-through trough placed in the stream, where current was maintained at ca. 40 cm s^{-1} (see Poff et al. 1990 for details). Algal cell densities at 16 and 30 d were determined from 2.3×2.3 cm tiles collected from the same trough and analyzed as described in Poff et al. (1990). Analyses of untransformed algal data indicated that food quantity was greater on 30 d ($\bar{x} = 121 \text{ cells mm}^{-2}$, $SE = 57$, $N = 2$) than on 16 d tiles ($\bar{x} = 74 \text{ cells mm}^{-2}$, $SE = 12$, $N = 2$).

Current treatments were established by setting a 36

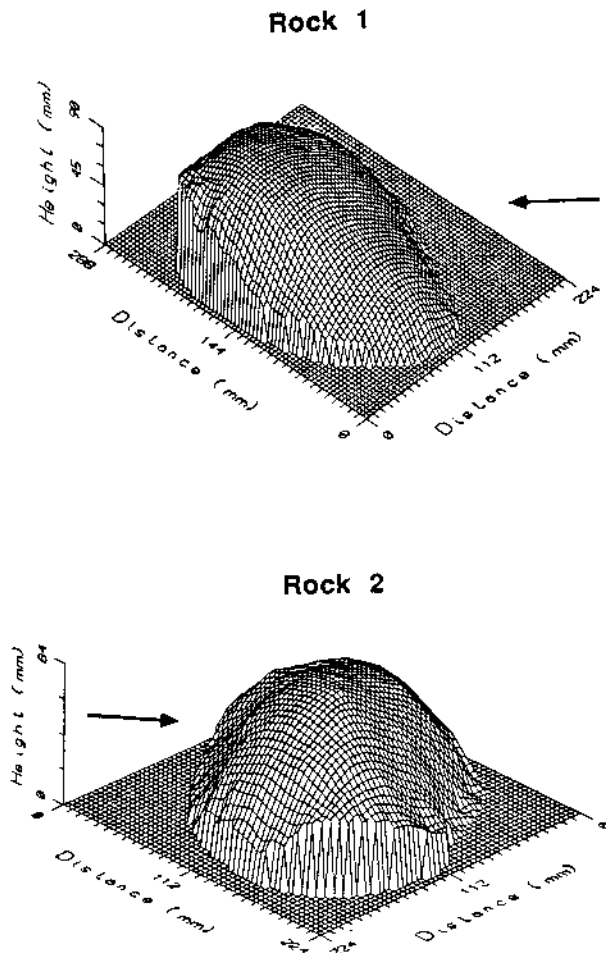


Fig. 2. Reconstructed surfaces for Rock 1 and Rock 2 used in the field observational study. Arrow indicates prevailing direction of streamflow. Axes are arbitrary and are rotated to provide the best view of surfaces.

cm wide \times 10 cm deep \times 61 cm long trough on concrete blocks on the stream bottom (Fig. 1). Unglazed fire-place bricks (10 cm \times 10 cm \times 3 cm) were set on their edges to create three parallel channels (10 cm wide) within the trough. The bottom of each channel was paved with flat bricks. At the upstream ends of the channels, bricks were positioned to create three velocity treatments. Mean current, measured within 13 mm of a foraging arena (see below), were $< 1 \text{ cm s}^{-1}$, 18.2 cm s^{-1} (SD = 2.4), and $38.5 \text{ (SD = 3.6) cm s}^{-1}$, for the slow, medium, and fast treatments, respectively. The downstream-most brick in each channel had its upper surface covered with 0.5 cm thick, bare porcelain tiles, except for a $4.9 \times 5.7 \text{ cm}$ space into which one algal-colonized foraging tile ($4.9 \times 4.9 \times 0.5 \text{ cm}$) could be fitted. Fifth instar *Agapetus* were collected from the stream bottom 1 h before each experimental trial and held in a flow-through container in quiet water without food. Flow through a channel was temporarily blocked and at least

10 larvae were placed into this $0.8 \times 0.5 \text{ cm}$ space remaining along the downstream edge of the foraging tile after it was placed in the template (see Fig. 1). Flow was immediately resumed and, following a period of acclimation, individual larvae began crawling onto the surface of the foraging tile. Larval positions were recorded on data sheets gridded at 1.25 cm intervals at periods as brief as 15 s (depending on movement rate) until larvae departed the tile surface. Larvae moving along the edges of tiles were excluded from analysis. For one replicate, three separate trials (food levels) were performed in each of the three velocity channels. Two of the nine treatment combinations (3 current \times 3 food levels) were simultaneously observed in two channels, until all nine combinations were completed. This procedure was repeated on three successive days (18–20 July 1987) for a total of three replicates per treatment combination. To avoid thermal influences, experimental runs were restricted to afternoon hours at water temperature ranged from 12 to 16°C. Treatment observations lasted from 0.5–1 h each, and new animals were used for each of the 27 runs. The average movement rate for each larva on the foraging tile was used to calculate a mean value for all larvae on each of the 27 tiles. The number of individual larvae observed on each tile ranged from 2 to 7. Foraging tile means were analyzed with a two-way ANOVA (Steel and Torrie 1980) on SPSSX. Pairwise comparisons between treatment effects were made with the LSD test ($\alpha = 0.05$). We examined the effects of flow on larval movement in only three channels because it was not feasible to replicate identical flow conditions, though this would be statistically desirable (Hurlbert 1984). However, we have confidence that our results would be consistent with those from truly replicated channels, because the flow regimes we used were clearly categorically dissimilar.

Results

Rock observation study

Topography, near-bed current and algal heterogeneity. The two rocks observed were similar in size but different with respect to shape, surface relief, and orientation to streamflow (Fig. 2). Mean 1-s current velocities measured at the reference points ranged from $5.1\text{--}56.4 \text{ cm s}^{-1}$ on R1 and from $5.7\text{--}38.3 \text{ cm s}^{-1}$ on R2. Maximum 1-s velocities recorded at each reference point were highly correlated with mean velocities ($r = 0.98$ for both rocks); therefore, isovel maps were constructed only for mean velocity distributions. The topographic differences between the two rocks (Fig. 2) may have presented additional spatial constraints on larval movements (cf. Underwood and Chapman 1989), microdistribution and resource use. For example, the shape of R2 and its orientation to flow afforded low velocity access points on both upstream and downstream edges

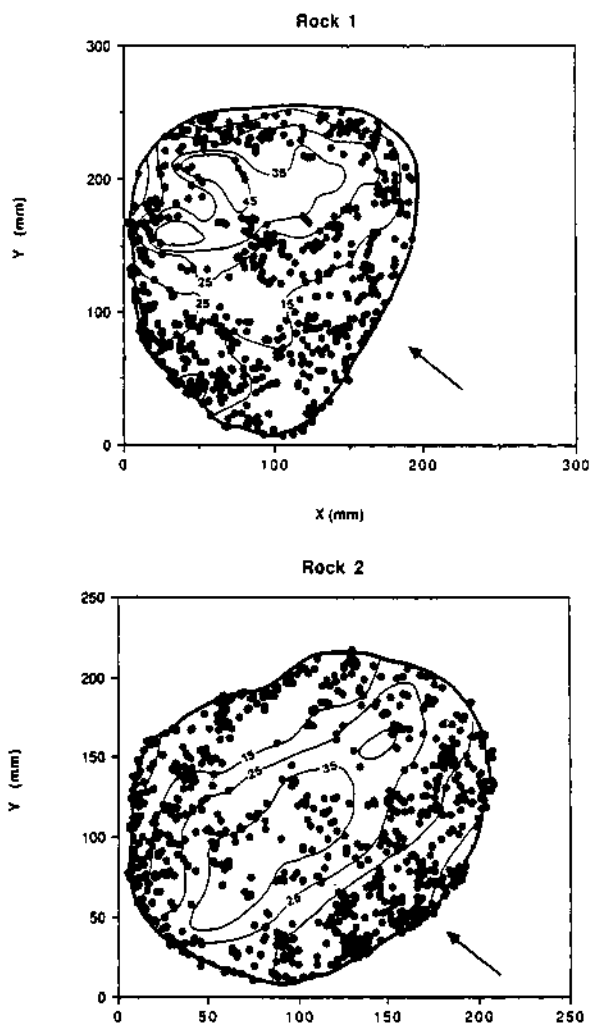


Fig. 3. Plan-view of Rock 1 and Rock 2 used in the field observational study, showing contours of equal mean velocity (cm s^{-1}) and combined distribution of *Agapetus boulderensis* larvae. Each circle represents the position of an individual larva at one of the 14 observation times. Arrows indicate prevailing directions of streamflow.

of the rock for *Agapetus* larvae crawling up from the the stream bottom. By contrast, access to the surface of R1 on upstream vs downstream edges was highly asymmetrical with respect both to local current conditions and to elevation above the stream bottom (cf. Figs 2 and 3).

A total of 22 and 38 taxa of algae was collected from R1 and R2, respectively (Table 1). Diatoms (Bacillariophyta), and blue-green algae (Cyanophyta) were relatively more abundant than were green algae (Chlorophyta) on both rocks. Contour maps for \log_{10} densities of total diatoms and blue-green algae were constructed for both rocks, but densities of green algae were sufficient for map construction on R2 only. Mean densities of diatoms and blue-green algae did not differ

among rocks (t-test, $P > 0.10$ for both taxa), although green algal density (Chlorophyta) was statistically different between the two rocks (Mann-Whitney U test, $P = 0.01$). However, qualitative differences in algal flora were observed. For example, R1 was less speciose than R2, and 94% of the total diatoms on R1 was comprised by the species *Achnanthes lanceolata*, *A. minutissima* and *Cocconeis placentula*, versus only 46% for R2. There were no significant correlations between density and mean local current for any of the three major algal taxa or for individual species in the 50 mm^{-2} samples using either univariate correlation or multivariate principle correlation analysis. However, combined densities of green and blue-green taxa showed an inverse relation to current velocity ($R = -0.22$, $P = 0.09$, $N = 59$), a finding consistent with previous work at this site (Poff et al. 1990).

Larval distribution – response to current velocity. Fig. 3 shows the combined distribution of all larvae observed on the surfaces of the two study rocks over the two day observation period. All larvae collected from both rocks were 5th instar, with the exception of one 4th instar larva. The rock surfaces were divided into 10 cm s^{-1} velocity regions and the average number of larvae observed in each region over the 2-d period was calculated. The association between average larval density and proportion of surface in the velocity intervals for each rock was tested with a χ^2 test. On both rocks, larvae tended to occur at less than expected densities in higher current areas. However, the overall larval-current relationship was significant only on R2 ($\chi^2 = 14.5$, $DF = 3$, $P < 0.005$), not R1 ($\chi^2 = 5.2$, $DF = 4$, $P > 0.10$). Johnson and Zimmer's (1985) index of dispersion (I) was used to determine whether pattern of larval distribution on stone surfaces was uniform ($I = 2$), random ($I \ll 2$) or clumped ($I \gg 2$). The average value of I for all larvae observed at each of the 11 observation times was 2.53 for R1 and 2.98 for R2, indicating an overall tendency toward clumping. Dispersion was significantly different from random ($p < 0.05$) in 7 of 11 cases on R1 and in 8 of 11 cases on R2.

Larval movement – independence of animal observations. On both stones, 13 individually-marked larvae were observed beginning on day 1. On day 2 numbers observed were 5 for R1 and 12 for R2, as some individuals from the first day moved off the rocks and some new individuals moved onto the rocks. Because movements of individuals observed on consecutive days were separated by ca. 13 h, total numbers observed were tallied as 18 for R1 and 25 for R2. Our ability to identify sequential point locations for marked individuals on the photographic records varied both among days and among larvae for a total of 101 and 134 interval observations for R1 and R2, respectively.

For the purposes of constructing a multiple linear regression model of the effects of microhabitat hetero-

Table I. Summary of major algal groups collected at locations on the two stones used in the analysis.

	Rock 1	Rock 2
Number of locations samples	31	28
Diatoms		
no. species	15	24
no. genera	9	13
density (\log_{10} (cells 50 mm ⁻²)) \bar{x} (SE)	2.30 (0.15)	2.27 (0.12)
proportion of locations with diatoms	0.94	0.96
with <i>Cocconeis placentula</i>	0.39	0.21
with <i>Achnanthes</i> spp.	0.81	0.69
proportion of all diatoms comprised by <i>C. placentula</i> and <i>Achnanthes</i>	0.94	0.46
Green algae		
no. species	3	7
no. genera	3	6
density (\log_{10} (cells 50 mm ⁻²)) \bar{x} (SE)	0.14 (0.77)	0.76 (0.21)
proportion of location with green algae	0.10	0.38
Blue-green algae		
no. species	4	7
no. genera	4	6
density (\log_{10} (cells 50 mm ⁻²)) \bar{x} (SE)	1.82 (0.25)	2.31 (0.25)
proportion of location with blue-green algae	0.68	0.79

generality on *Agapetus* movement and foraging patterns, it was necessary to consider the individual interval observations as independent data points. Movement of larvae over an entire diurnal cycle would not be appropriate because individuals can encounter a wide range of algal patches and current velocities in 12 h. We statistically examined the assumption of serial independence of larval movement at successive observation times using a runs test (Sokal and Rohlf 1981). Sequential movement rates for individual larvae were not significantly different from random ($P > 0.10$) in all 18 cases for which sample sizes were adequate. Additionally, independence of sequential X-Y observations for an individual larva was examined using the procedure of Swihart and Slade (1985). This test compares the ratio between the mean squared distance between successive observations (r^2) and mean squared distance from the center of animal activity (r_c^2). For animals moving in relatively straight lines (i.e., lacking a "center of activity"), this test is very conservative, because the resulting large r^2 term biases the outcome toward rejection of the null hypothesis of independence of successive observations. Despite this conservatism, independence of sequential observations was accepted ($P > 0.10$) for 12 larvae. Based on the above considerations, we therefore treat individual interval observations as independent for the purposes of the regression analysis.

Larval movement – orientation with respect to current alone. Travel for larvae was tested for directionality by comparison to a uniform circular distribution using Rayleigh's test (Batschelet 1981). The mean movement vector for individual larvae over an entire diurnal observa-

tion period was calculated by comparing beginning and ending position. Average movement directions (relative to oncoming streamflow) were 94° for R1 and 16° for R2 (Fig. 4). Mean direction of travel for larvae was significantly directional on R1 ($Z = 5.4$, $N = 18$, $P < 0.005$) but not on R2 ($Z = 1.5$, $N = 25$, $P = 0.25$). Movement on R1 was clearly primarily lateral to the oncoming current; however, fewer larvae moved in the downstream (90°–270°) vs upstream direction than would be expected by chance both on R1 ($\chi^2 = 3.6$, $DF = 1$, $P < 0.10$) and on R2 ($\chi^2 = 6.8$, $DF = 1$, $P < 0.01$).

The angle of larval turning during successive time intervals was determined to assess whether larvae moved in straight lines. The observed frequency distribution was compared to null expectation of a uniform probability density function. Larvae tended to travel in straight paths on both R1 ($\chi^2 = 27.7$, $DF = 11$, $P < 0.005$) and R2 ($\chi^2 = 19.0$, $DF = 11$, $P = 0.05$), as indicated by the clustering of turn angles around 0° and the paucity of turn angles near 180° (Fig. 5). For larvae that "reversed" their path of travel during consecutive observations (i.e., 90° < turn angle < 270°) there was no correlation between degree of reversal and local current speed ($P > 0.50$).

Larval movement – rate with respect to current and algae together. The movement of 13 larvae on each of the stone surfaces was further analyzed with respect to the potentially interacting factors of current and algae by using a polynomial multiple linear regression (MLR) technique in which larval movement rate (in X-Y-Z space) in an observation interval was the dependent variable ($N = 91$ for R1, $N = 126$ for R2). Movement

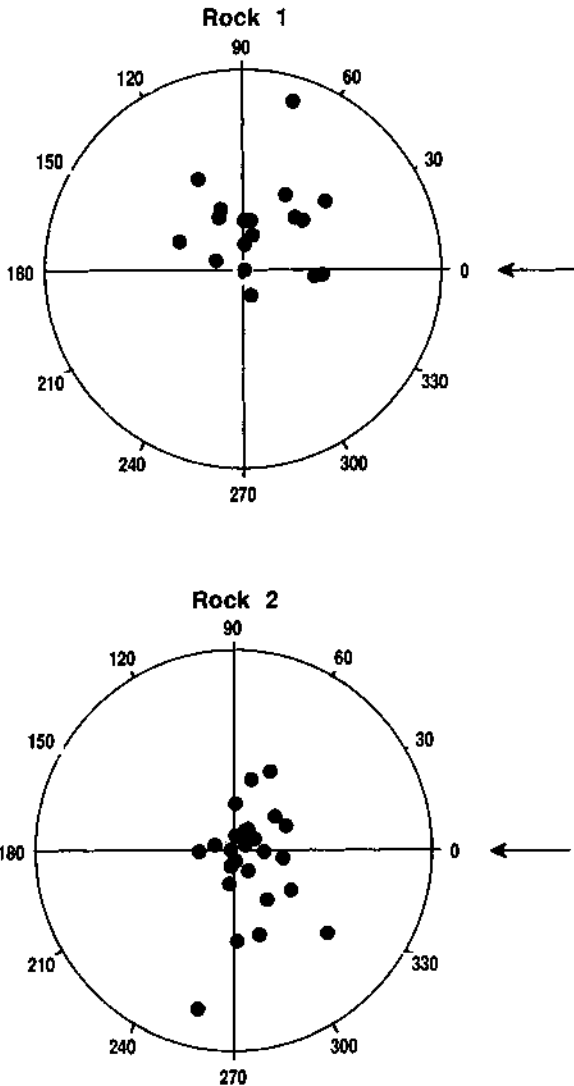


Fig. 4. Circular distributions of movement directions for individual *Agapetus boulderensis* larvae. Each point indicates the distance and direction travelled by one larva over an entire daily period relative to its coordinate position (0,0) at the beginning of the day. Larvae observed on two consecutive days are included twice. Upper graph is Rock 1, where movement is directional (Rayleigh's $Z = 5.4$, $P < 0.005$). Lower graph is Rock 2, where movement does not differ from a uniform circular distribution ($Z = 1.5$, $P = 0.25$). The arrows indicate the direction of prevailing current. Radius for both graphs is 8 cm.

rates ranged from $0.15\text{--}16.2\text{ mm h}^{-1}$ on R1 ($\bar{x} = 5.0$) and $0.09\text{--}16.1\text{ mm h}^{-1}$ on R2 ($\bar{x} = 4.0$). For each larval position, interpolated current velocity and algal density values, as well as temperature and the direction of larval movement relative to current direction (see above) were included as independent regressor variables. In this analysis, we assume that the algal densities and distributions measured after the two diurnal observa-

tion periods were useful descriptors of the conditions experienced by the grazing larvae. About half of the periphyton sampling locations on both stones were not intersected by a mapped larval location over this 2-d period. All linear terms were initially standardized by subtracting the mean for each variable from each observation for that variable to reduce correlations between linear and higher order terms (Damon and Harvey 1987). In addition to linear terms, quadratic terms were used for all independent variables except the angle of movement. Linear interaction terms were used for all combinations of algal type, current velocity and algal

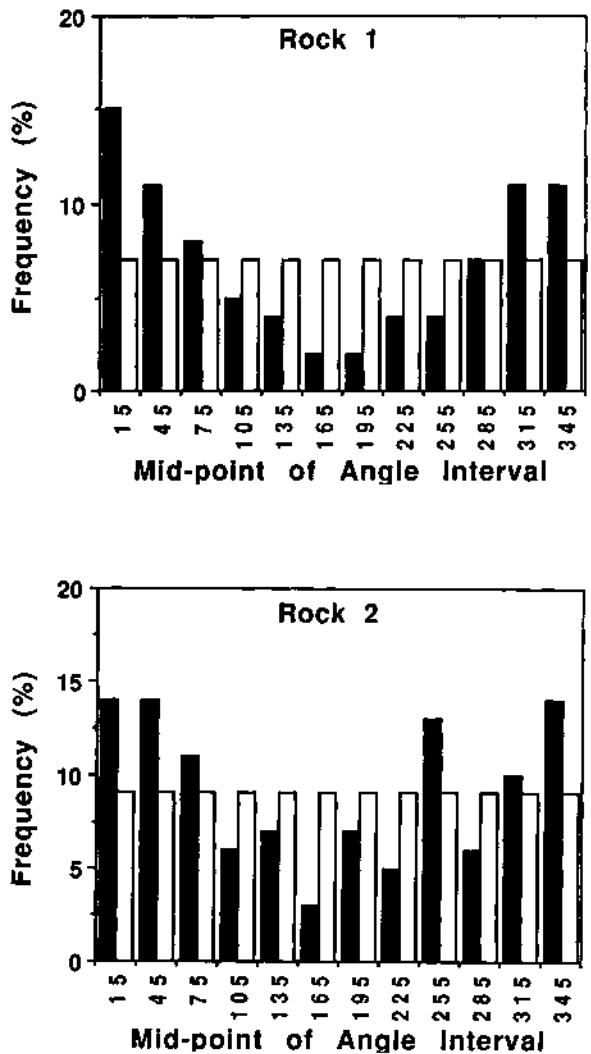


Fig. 5. Frequency distribution of observed turn angles (solid bars) vs frequency expected (open bars) under null hypothesis of random turning (i.e., uniform probability density) for *Agapetus boulderensis* larvae. Data combined over all interval observations show turning is nonrandom both for Rock 1 ($\chi^2 = 27.7$, $DF = 11$, $P < 0.005$) and for Rock 2 ($\chi^2 = 19.0$, $DF = 11$, $P = 0.05$).

Table 2. Regression coefficients and associated t-statistics for a polynomial multiple linear regression model using rate of *Agapetus boulderensis* movement as the dependent variable for Rock 1 (N = 91, R² = 0.19) and Rock 2 (N = 126, R² = 0.36). Independent variables are U (current), T (temperature), A (angle of travel), D (log₁₀ diatom density), G (log₁₀ green algae density), and BG (log₁₀ blue-green algae density). Coefficients for terms in the best-fit model are given, along with associated t-statistics. Terms not included in the best-fit model are indicated by "---". On R1, green algae were too sparse to allow inclusion (denoted by "x"). Significance levels are "*****" (P < 0.001), "****" (P < 0.01), "***" (P < 0.05), and "+" (P < 0.10).

Regression terms	Rock 1		Rock 2	
	Coefficient	t	Coefficient	t
Intercept	5.07	4.89 (***)	6.89	6.77 (***)
Linear terms				
U	-0.06	-2.21 (*)	-0.18	-4.79 (***)
T	---	---	0.14	1.97 (*)
A	-0.57	-1.78 (+)	-0.65	-2.71 (**)
D	---	---	-4.36	-3.77 (***)
G	x	---	2.08	4.27 (***)
BG	---	---	0.41	1.68 (+)
Quadratic terms				
U ²	0.003	1.21	-0.018	-4.07 (***)
T ²	0.02	2.66 (**)	---	---
D ²	---	---	---	---
G ²	x	---	---	---
BG ²	---	---	---	---
Linear interaction terms				
U × T	---	---	---	---
U × D	---	---	0.100	1.81 (+)
U × G	x	---	---	---
U × BG	---	---	---	---
D × G	x	---	-5.30	-4.26 (***)
D × BG	---	---	-2.22	-3.34 (***)
G × BG	x	---	---	---

type, as well as between current velocity and temperature. Data were analyzed with a BMDP all-possible-subsets regression package (BMDP9R) to identify the subset of regressors that maximized overall multiple coefficient of determination, R². All-possible subsets is the most appropriate MLR technique for observational studies with numerous exploratory variables (James and McCulloch 1990).

The results of the polynomial MLR are given in Table 2. For R2, the "best" subset contained 10 regressors. All linear terms were important components in the model. The quadratic velocity term was also included in the model, as were the diatom × current and diatom × other algae linear interaction terms. Of particular interest were the signs of the regression coefficients. For example, the negative value associated with t-statistic for angle of travel indicated that travel upstream on the rock surface was faster than travel downstream, all other factors being held equal. Similarly, the negative signs associated with the current velocity statistics indicated that, as velocity increased, movement rate decreased. Also, as temperature increased during the day,

so did movement rate. Several of the algal food predictors also were important. Larval movement rate declined under conditions of increased diatom density, but increased under higher blue-green and green algal densities. The overall model explained 36% of the variation in movement rate, which reflected both physical variables and food resource variables. For R1, 19% of the variation in movement could be explained by the "best" predictors (Table 2). Interestingly, physical variables alone produced the best model, although associated t-statistics were generally not as large as for R2. The signs on the linear current, direction of travel, and quadratic temperature terms were in the same direction as for R2. The sign associated with the quadratic current term was positive; however, a non-significant t-statistic was associated with this term.

Larval gut contents. Regression results suggested that, because *Agapetus* moved more slowly near areas rich in diatoms (on R2), larvae might be exhibiting preference for certain types of algae. The two major types of algae present in larval guts were diatoms (mostly *Cocconeis placentula*) and blue-green algae (mostly *Chroococcus* sp.). Based on formal measures of electivity (Jacobs 1974, Chesson 1983), *Agapetus* larvae, combined across both rocks, showed positive preference ($\alpha > 0.5$) for diatoms ($\alpha = 0.74$, SD = 0.41, N = 12, P < 0.10) and non-significant negative preference for blue-green algae ($\alpha = 0.35$, SD = 0.48, N = 12, P = 0.30). In terms of biovolume, diatoms were significantly more abundant in the gut that were blue-green algae (paired t-test, t = 2.35, DF = 11, P = 0.038). Moreover, *Chroococcus* sp.

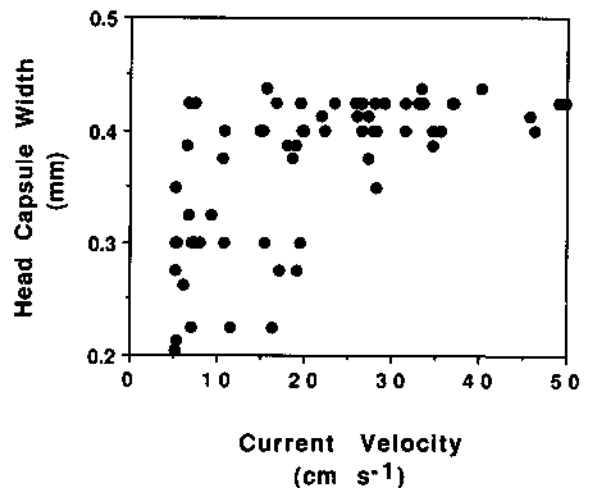


Fig. 6. Plot of body size (head capsule width) of *Agapetus boulderensis* larvae vs the current velocity at the point of larval collection from stone surfaces. The range of currents occupied by larger larvae (5th instar) exceeds that for smaller larvae (3rd and 4th instars). (Bartlett's test for homogeneity of variance: $\chi^2 = 12.4$, DF = 2, P = 0.002) and larger larvae are significantly over-represented at high local currents (≥ 20 cm s⁻¹) ($\chi^2 = 10.4$, DF = 2, P = 0.005).

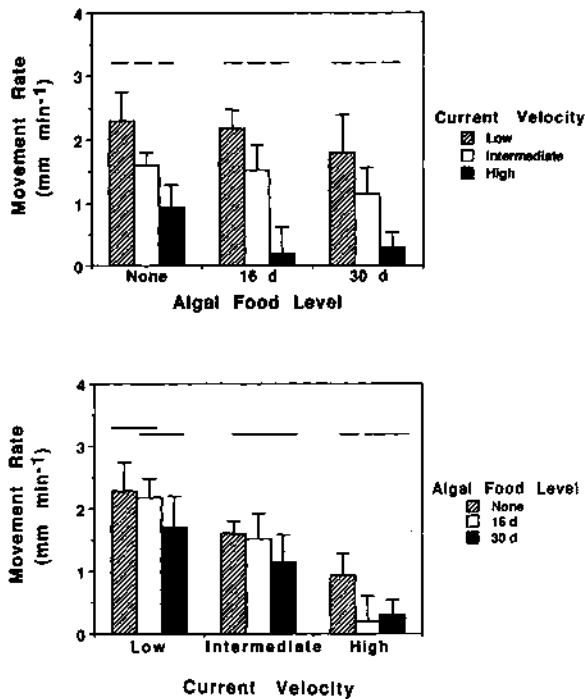


Fig. 7. Movement rate of *Agapetus boulderensis* larvae as a function of three densities of food and three levels of current velocity. Bars are $\bar{x} + 95\%$ CI. Current treatments are low ($< 1 \text{ cm s}^{-1}$), intermediate (ca. 20 cm s^{-1}), and high (ca. 40 cm s^{-1}). Algae were grown on ungrazed tiles at ca. 40 cm s^{-1} . Horizontal lines connect treatments that are not significantly different from one another ($\alpha = 0.05$).

was frequently not digested, as indicated by the visible chlorophyll pigments in the cells. With respect to two major diatom groups, *Agapetus* showed a positive preference for *Cocconeis placentula* ($\alpha = 0.87$, $SD = 0.26$, $DF = 5$, $P = 0.02$) but not for other diatoms combined ($\alpha = 0.19$, $SD = 0.40$, $DF = 5$, $P = 0.10$).

Size distribution and current

Additional larvae collected from haphazardly selected rocks ranged from 3rd ($N = 5$) to 4th ($N = 15$) to 5th ($N = 41$) instars. Two size-related patterns in *Agapetus* distributions were observed. First, as larval size increased, a greater range of current velocities was occupied (Fig. 6). Bartlett's test for homogeneity of group variances (Sokal and Rohlf 1981) indicated that the three size classes of larvae differed with respect to range of currents occupied ($\chi^2 = 12.4$, $DF = 2$, $P = 0.002$). Second, only fifth instar larvae were collected at higher local currents. Velocities as high as 70 cm s^{-1} were measured on the rocks but no larvae were collected above 50 cm s^{-1} . Of the 27 individuals collected at "fast" velocities (i.e., $\geq 20 \text{ cm s}^{-1}$), 5th instar larvae were significantly over-represented ($\chi^2 = 10.4$, $DF = 2$, $P = 0.005$).

Aggregative response to algae

Larvae introduced onto the tile in a bare patch generally moved immediately until they encountered a food patch, at which time they virtually stopped. Larvae spent 70–100% of their time ($\bar{x} = 92\%$) in algal patches, clearly indicating an aggregative foraging response.

Field experiment on movement and foraging under different currents and algal abundances

To examine further how current velocity and algal food density together affected movement rate, a field experiment was done in which the movements of 126 larvae were recorded on experimental foraging trials over a three day period. Movement rates ranged from $0.5 - 26.4 \text{ mm min}^{-1}$ over all treatments. Larval movement rates were log-transformed and an initial split-plot analysis (Steel and Torrie 1980) indicated that the day \times current interaction term (which might reflect between-day differences in food levels among replicates) was small and could therefore be included in the overall error term. A two-way ANOVA blocked by day revealed that both main effects were significant (current: $F_{2,16} = 28.4$, $P < 0.001$; food density: $F_{2,16} = 3.8$, $P = 0.046$) but the interaction was not ($F_{4,16} = 0.56$, $P = 0.70$). The blocking factor was also not significant ($F_{2,16} = 0.65$, $P = 0.54$). Pairwise comparisons (LSD test) indicated that larval movement rate significantly decreased with increasing current for each algal abundance category (Fig. 7), a pattern consistent with the rock observation study. Larvae always moved headward or lateral to the current except in the zero flow treatment, when they turned frequently on the tile surface. Movement also tended to be slower as food quantity increased within a current level (Fig. 7), a pattern also consistent with the rock observation study. Thus, while larvae moved at higher average rates on the artificial substrata relative to the natural ones, the results of the field experiment were generally consistent with those of the rock observation study.

Discussion

This study showed that both near-bed currents and algal patchiness influence the movement pattern, foraging activity, and local distribution of a mobile grazer in a naturally heterogeneous habitat. Most previous work in streams, carried out under more uniform physical conditions, has shown grazer sensitivity to algal densities alone. Our work supports these studies, but expands upon them by indicating that spatial heterogeneity in near-bed currents is a potentially important constraint on resource use by mobile grazers.

When considered independently, current velocity af-

fecting larval microdistribution on natural substrata in two ways. First, larvae tended to be less abundant in areas of higher current on both observed stones (though results were significant only on R2). Other workers have also shown that the abundance of mobile grazers declines at high current (e.g., Scott 1958, Williams et al. 1983, Vaughn 1987). Second, we observed a size-dependent distribution of *Agapetus* larvae (Fig. 6). Smaller individuals occupied less exposed surfaces, whereas larger individuals could be found in currents up to 50 cm s^{-1} , which may represent an upper limit in the microdistribution of this species. A possible explanation may be provided by Vaughn (1987), who found that larger larvae of *Helicopsyche borealis* (Hagen) were more abundant in locations with high (50 cm s^{-1}) vs low (5 cm s^{-1}) current than were small larvae, which were physically displaced at the higher velocity under experimental conditions. Similar, size-dependent relative abundances along velocity gradients have been observed for the mobile grazers *Glossosoma verdoni* (N. L. Poff, pers. obs.) and *G. nigrior* (S. L. Kohler, pers. comm.), as well as for sedentary, net-spinning hydropsychid caddisflies (Osborne and Herricks 1987) and filter-feeding simuliids (D. D. Hart, pers. comm.). These observations run counter to the prediction that larger individuals within a species should be absent from higher current micro-environments due to their experiencing presumably greater drag forces (cf. Statzner 1988, Statzner and Holm 1989). However, drag is but one factor influencing an organisms' potential susceptibility to displacement by shearing flow. Other important animal features (e.g., mass, morphology, behavior) may interact to generate differences within and among species in terms of size-dependent displacement by current (e.g., see Poff et al. 1991).

Some components of larval movement pattern were also explicable in terms of local micro-current velocity conditions alone. For example, most larval movement was biased against the downstream direction, being oriented mostly into or lateral to the main flow (Fig. 4). This same trend was observed on experimental foraging tiles where larvae always moved in an upstream and/or lateral direction except under low current ($< 1 \text{ cm s}^{-1}$), when frequent turning and downstream movement occurred. Similarly, larvae also tended to move faster in the upstream vs downstream direction. Further, rate of larval movement was inversely related to magnitude of near-bed current, as indicated by results from the multiple linear regression analysis for both rocks (Table 2) and from the experimental foraging trials (Fig. 7).

The tendency of *Agapetus* to be less abundant in areas of high velocity on stones could result as a simple, direct consequence of constraints imposed by current on larval movement. For example, if larvae turned more frequently in low velocity areas while travelling more directionally under high currents, average density in slow microhabitats would increase. Although we found no correlation between degree of turning and local cur-

rent for larvae observed on stone surfaces, we did note that under experimental conditions, larvae reversed directions frequently at low flow but rarely at intermediate (18.2 cm s^{-1}) and high (38.5 cm s^{-1}) flows. Further, the absence of *Agapetus* at velocities exceeding 50 cm s^{-1} suggests that larvae either "turned back" when encountering high flows or were displaced from the surface. We cannot use our data to test the former possibility, but erosion of individuals from the surface at high currents was likely. For example, several larvae moving on experimental foraging tiles were directly observed to be eroded at both the intermediate and high current treatments before leaving the tile surface. Also, the occasional "disappearance" of larvae from the upper surfaces of stones between successive observation times suggests that larval distribution was at least partially influenced by near-surface erosive forces (cf. Vaughn 1987). However, the large amount of unexplained variation in larval movement direction and rate in our observations indicates that factors other than local current are important in regulating movement pattern.

Algal resource distribution was clearly a determinant of *Agapetus* activity and distribution, independent of current. Larvae were found to be responsive to algal resource abundance in three separate situations: 1) aggregation on artificially-created patches, 2) reduced movement on artificial substrata under experimental conditions of increased food abundance (Fig. 7), and 3) movement rates on natural substrata that varied depending on algal compositional structure and abundance (Table 2). The aggregation of larvae observed here has been frequently found both among stones (e.g., Lamberti and Resh 1983, McAuliffe 1984) and within stones (e.g., Kohler 1984, Ogilvie 1988) where algal densities vary. Under experimental conditions, larval movement rate declined as algal food density increased, suggesting *Agapetus* uses the behavioral mechanism of area restricted search (see Krebs 1978), as do many other grazing stream insects (Wiley and Kohler 1984). The absence of a significant current-algal interaction term in these experiments suggests that larvae responded to algal density similarly regardless of the current velocity in which they found it and that current does not indirectly influence grazer foraging by controlling algal distributions (but see below). Consistently greater mean larval movement rates on the experimental foraging substrata compared to natural substrata suggests that larvae were perhaps suffering residual disturbance associated with handling. Nonetheless, the results indicate that larvae were sensitive to food densities and that larval movement was increasingly constrained as local velocity increased.

Movement on the surface of one of the natural stones was related to algal density, as indicated by the negative correlations between movement rate and diatom density and by the positive correlations between rate and both blue-green and green algal densities. These data suggest larvae reduced their movement rate as they

encountered diatom-rich patches, and they increased their speed when blue-green and/or green algae were encountered. The expectation would be larval "preference" for diatoms over blue-green and green algae, a finding corroborated by analysis of larval gut contents. Recent work indicates that diatoms and perhaps green algae are higher quality food resources than are blue-green algae. For example, Vaughn (1986) found growth and emergence of the caddisfly *Helicopsyche* to be reduced for larvae fed monocultures of blue-green algae vs either diatoms or green algae. Larval gossosomatids are typically described as feeding on diatoms and detritus in proportion to environmental availability, though some ingestion of filamentous algae occurs (e.g., Mecom 1972). The significant over-representation of the diatom *Cocconeis* relative to the blue-green algae and other diatoms suggests selective foraging (see also Oemke 1984). However, the mechanism by which *Agapetus* would selectively forage for *Cocconeis* in this system is not clear. Food selection is a function of both grazer feeding morphology (e.g., Lamberti et al. 1987) and algal growth form or size (e.g., Gregory 1983), thus it is possible that the generalized scraping mouthparts of *Agapetus* larvae (Wiggins 1984) may simply have a higher removal efficiency for relatively large (e.g., *Cocconeis*) vs small diatoms (e.g., *Achnanthes*) or blue-green algae (e.g., *Chroococcus*).

In this study, we found little evidence for indirect effects of current in mediating grazer foraging activity through influencing algal distributions. With the marginal exception of combined green and blue-green algae, there was little relationship between local current speed and algal densities. However, in the absence of *Agapetus* grazers, algal assemblage structure does reflect local current speed, with the relative abundances (and biomass) of green and blue-green algae and the absolute abundance of diatoms decreasing along a low to high velocity gradient (Poff et al. 1990). Additional experiments conducted at the time of this study further indicate that *Agapetus* foraging at normal field densities can induce convergence in algal assemblage structure under intermediate and high current speeds by increasing the relative abundance of diatoms (Poff and Ward, unpubl.). Thus, antecedent grazing on stone surfaces, not accounted for during the present study, could mask current-algal interactions that might otherwise result in indirect effects of current on grazer activity. Our findings cannot eliminate the potential of an indirect current-algal effects, however. For example, because algal biomass accumulates at a higher rate under low vs high currents at this study site (Poff et al. 1990), grazers could derive an advantage by returning often to locations with high resource renewal rates (see Hart 1981, Power 1984), thus leading to an increased local density.

Theoretically, patterns of movement are expected to differ with patterns of resource dispersion (Pyke 1978); however, characterization of both resource distribution and movement patterns are sensitive to observational

scale (cf. Kotliar and Wiens 1990). In this study, we could only characterize algal "patches" as measured in 50 mm^{-2} samples from locations where we had only an interpolated estimate of local current. A finer degree of spatial and temporal resolution may be needed to characterize flow environments relevant for algae growing on topographically and hydraulically complex surfaces (e.g., Stevenson 1983). Similarly, *Agapetus* larvae were observed at 1–2 h intervals, during which their movement rates ranged from 1–200% of the diameter of the "patches." Thus, sequentially observed larval positions probably resulted from both within- and among-patch movements, and these cannot be easily separated in this study. These constraints probably contributed to the relatively poor fit of the multiple regression model, and they point to some of the limitations of conducting field studies in complex, heterogeneous habitats.

Other studies, however, have clearly shown epilithic grazer movement patterns to vary within and among patches. Individuals often move slowly within a patch and turn back into a patch when a boundary is encountered, but once patch departure occurs, animals tend to move more rapidly and in a relatively straight path (e.g., Hart and Resh 1980, Kohler 1984, Wiley and Kohler 1984). If grazers consistently depart patches in random directions, over time movements can appear non-directional, a pattern that has been observed both for a stream grazer (Hart and Resh 1980) and an intertidal gastropod (Underwood 1977) foraging under relatively homogeneous low current conditions. Our findings show that both direction and rate of *Agapetus* movement are strongly influenced by current and that in physically-heterogeneous stream habitats, local current may directly constrain movement patterns of epilithic grazers. These observations are consistent with Hutchinson's (1953) argument that "vectorial" patterns (here, of movement) reflect organism responses that are constrained by strong external physical gradients (here, current). Similar vectorial patterns have been observed elsewhere along strong physical gradients such as temperature (Riechert and Tracy 1975) and wave motion (Gendron 1977).

The ability of animals to utilize resources efficiently or optimally is a central tenet of behavioral foraging theory (e.g., Stephens and Krebs 1986). Animal movement and distribution patterns are generally considered as indicative of foragers' abilities to track resources successfully. For stream grazers, Hart (1981) suggested that non-directional, among-patch movements may increase efficiency of resource use by minimizing path recrossings. Although we did not assess efficiency of patch use per se, our findings suggest that, insofar as local current constrains forager movement, current may also constrain efficiency of resource use by mobile grazers foraging in physically-heterogeneous habitats. Despite the conspicuous flow heterogeneity in stream habitats, the role of current in mediating resource use has received little attention, though a few recent studies

have shown that local current can influence higher-level trophic interactions among mobile prey and predators (Peckarsky et al. 1990, Hansen et al. 1991). Addressing the broader question of how current constrains efficiency of resource use by consumers in streams will require not only precise description of resource distributions but also quantification of the cost/benefit relationships for the consumer of using spatially-variable resources, including the energetic costs of movement under the range of local currents encountered in natural stream habitats.

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