



Current velocity and invertebrate grazing regulate stream algae: results of an *in situ* electrical exclusion

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Received 4 June 2002; revised 21 January 2003

Key words: benthic algae, current velocity, stream herbivory, environmental gradients, electrified substrates, algal-grazer interactions

Abstract

Current velocity is a pervasive feature of lotic systems, yet this defining environmental variable is rarely examined as a factor for regulating stream herbivory. To investigate how current modifies herbivory in the upper Colorado River, U.S.A., loops of electrified fencing wire were used to reduce *in situ* grazer densities on 30 × 30 cm tile substrates. After 45 d, electrified tiles had significantly fewer grazers ($P = 0.03$) and >2X more algal biomass than controls ($P = 0.0002$). Reduced grazing on electrified tiles yielded periphytic assemblages having more diatoms and chlorophytes, as well as greater algal species richness. Current velocity effects alone did not significantly regulate algal abundance; however, the interaction between current velocity and grazer exclusion resulted in more algae in slow vs. fast current ($P = 0.02$). Grazer abundances were similar between fast and slow current velocities, suggesting that grazers in the Colorado River differ in their ability to regulate algae across the current velocity gradient. Our results indicate that stream current-mediated herbivory in streams may be more important than is generally recognized.

Introduction

Since the recognition that autotrophic production could equal or exceed detrital energy inputs in streams (Minshall, 1978; Gregory, 1983), numerous observational and experimental studies have demonstrated that herbivores exert strong control over the distribution and abundance of stream algae (Steinman, 1991; Feminella and Hawkins, 1995; Lamberti, 1996). Despite this wealth of information, little is known about the *extent* to which herbivores control the distribution, abundance, and accrual rates of algae across the range of physical conditions typical of streams during normal flow.

Current velocity is a defining environmental parameter that can potentially influence algal-grazer interactions in streams and may impose strong energetic

and ecological constraints on both algae and herbivores (Hart & Finelli, 1999). Despite its perceived importance, however, current velocity is seldom examined as an experimental variable in studies of stream herbivory (see Feminella & Hawkins, 1995 for review). In studies that have examined the influence of current velocity on herbivores, the focus is typically on a single herbivore species or the studies are conducted within artificial mesocosms. To date, no study has examined the way in which an invertebrate grazing assemblage in a natural stream responds to variation in near-bed current velocity. By contrast, the relationship between algal biomass and stream current has been described in numerous studies, and often with contradictory results (see Biggs, 1996; Stevenson, 1996; Biggs et al. 1998 for reviews). The model that most succinctly describes periphytic re-

sponses to stream current is the 'subsidy-stress model' of periphytic accumulation proposed by Biggs et al., (1998, after Odum et al. 1979). These authors point out that current velocity can shape periphytic communities through its antagonistic influences on algal biomass accrual; positively, via nutrient uptake subsidy; and negatively, via shear stress. The degree to which periphyton will respond to these divergent forces will depend on periphytic architecture. Adherent benthic assemblages, for example, are more resistant to sloughing and will benefit from increased mass transfer with increasing current velocity. Filamentous assemblages, by contrast, will exhibit high rates of diffusion at slow velocities while being more susceptible to shear, and hence, will respond negatively to increased current velocity. An implicit assumption of this model is that herbivory does not vary across the velocity gradient. Given the major significance grazers have in controlling periphyton in many streams (Feminella & Hawkins, 1995; Steinman, 1996), this approach may over-simplify the many factors that are responsible for shaping periphytic communities in nature by placing too much emphasis on abiotic processes alone.

There are many reasons for thinking that current velocity can mediate herbivory. Current velocity has been shown to affect herbivore movement rates (Poff & Ward, 1992; Palmer, 1995), patterns of immigration and colonization (Poff & Ward, 1991; Swan & Palmer, 2000), and may control herbivore distribution across the streambed (Hart, 1992; Wellnitz et al., 2001), as well as determine the taxonomic and architectural composition of their benthic algal food (Poff et al., 1990; Biggs & Hickey, 1994; Passey, 2001). This last reason is important because many herbivores exhibit specialized mouthparts for feeding on particular kinds of periphyton, and thus, periphytic structure can influence herbivore consumption of benthic algae (Arens, 1989; Steinman, 1996; Wellnitz & Ward, 1998, 2000). Given the level of attention paid to the relationship between current velocity and periphyton, it seems only logical to extend this focus to algal-grazer interactions.

In the study described below, we investigate the extent to which stream current constrains grazing across a natural streambed. The mat structure exhibited by the algae in the Colorado River at the time of this study can be described as an adherent to moderately adherent mat of periphyton dominated by blue-green algae. According to the subsidy-stress model proposed by Biggs et al. (1998), periphyton having these

characteristics should show an increase of biomass with current velocity, and indeed, this was the pattern seen in the natural stream. We found it intriguing, then, that algae grown in artificial, grazer-free stream mesocosms maintained immediately adjacent to the Colorado River showed the exact opposite pattern of biomass accumulation (T. Wellnitz, unpublished data). These contrasting phenomena led us to hypothesize that current velocity can modify herbivory such that algae removed by grazers in slow current velocity is greater than in fast. Because streambed grazer densities did not differ between fast and slow current speeds, we hypothesized that grazers shape this pattern of periphytic biomass by being better able to remove algae in slow as opposed to fast current velocity.

To test our hypothesis, we conducted an *in situ* grazer exclusion experiment using an electrical field to reduce grazing on artificial substrates situated in slow and fast stream flow. Electrical fields have been used to exclude large-bodied invertebrates in lotic systems (e.g., shrimp, Pringle & Blake, 1994) and have been known to influence small benthic invertebrates during electrofishing (Mesick & Tash, 1980; Taylor et al., 2002). Recently, Brown et al. (2000) used a modified electric fence charger to successfully exclude benthic grazers during laboratory and in-stream trials in Australia. In this study, we expand this technique to directly examine how spatially heterogeneous current velocity and mobile grazers interact to shape algal assemblages in a natural stream.

Methods

Study area

The study was conducted in a 100-m section of the upper Colorado River (2400 m a.s.l.) approximately 7 km below Lake Granby in Grand County, Colorado. The 10-m wide stream section consisted of a series of riffles and runs with depths < 0.5 m, making the entire streambed accessible by wading. The bed was comprised of large (15–25 cm diameter), closely packed cobbles underlain with sand and gravel.

The upper Colorado is a regulated river and temporal variation in flow at this site is minimal, with flows maintained at constant levels for weeks or months at a time (Poff et al., 1990). Thus, the distribution of current velocity over the substrate does not vary for extended periods, allowing in-stream examination of the effects of stream current on the spatial

distribution of periphytic algae and benthic invertebrates. Discharge during this study was $1.29 \text{ m}^3 \text{ s}^{-1}$ from 12 to 31 August 2000 and dropped to $0.80 \text{ m}^3 \text{ s}^{-1}$ on 1 September, where it remained through the end of the study (30 September 2000). Water temperature ranged from $6.4 - 16.7^\circ\text{C}$ in August to $5.6 - 9.8^\circ\text{C}$ in September. During the same period, electrical conductivity measured (mean \pm S.D.) $81.7 \pm 8.5 \mu\text{S cm}^{-1}$ and total dissolved solids averaged $42.4 \pm 4.4 \text{ mg l}^{-1}$. Nutrient levels measured on 3 August 2000 were: $0.04 \text{ mg l}^{-1} \text{ NO}_3\text{-N}$; $0.18 \text{ mg l}^{-1} \text{ PO}_4^{3-}\text{-P}$; and 0.25 mg l^{-1} total P. Midday irradiance measured with a LiCor spherical quantum sensor ranged from 850 to $1500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and did not differ between the fast and slow flowing sections of the stream where the study was conducted. Periphyton in the upper Colorado River during late August and September is dominated by blue-green algae (Cyanobacteria), particularly colonies of *Nostoc parmelioides*, many of which are inhabited by the symbiotic midge, *Cricotopus* sp. (Diptera; Chironomidae) (Dodds & Marra, 1989). *Nostoc* comprised 50–90% of the algae on streambed cobbles; however, these colonies were large, clustered and patchily distributed. Consequently, other algae such as *Draparnaldia*, *Chorella*, *Ulothrix* spp. (Chlorophyta), and diatoms (Bacillariophyta) were common across whole cobble surfaces.

Common grazing invertebrates in the upper Colorado River during August and September were mayflies of the genera *Baetis* (Baetidae), *Drunella* (Ephemeroidea), *Paraleptophlebia* (Leptophlebiidae); and glososomatid and *Lepidostoma* caddisflies; chironomids, predominantly *Pagastia sabulosa* and symbiotic *Cricotopus* sp. (J. Monroe, unpublished data). Abundant, non-grazing invertebrates include *Brachycentrus* sp. and *Hydropsyche* sp. caddisflies, and large perlid stoneflies of the genus *Claassenia*.

Electrical exclusion experiment

For the 7-week study, one ca. $6 \text{ m} \times 6 \text{ m}$ reach was identified that contained both slow ($20\text{--}30 \text{ cm s}^{-1}$) and fast ($45\text{--}55 \text{ cm s}^{-1}$) regions of stream current as measured using a Flowmate 2000TM (Marsh-McBirney, Inc., Frederick, Maryland, U.S.A.) portable flow meter at 0.6-total-depth (Gordon et al., 1992). This reach was sub-divided into 20 'cells' of slow and fast flow (10 fast, 10 slow) measuring approximately 0.5 m^2 into which experimental tiles could be placed. Six, $30 \text{ cm} \times 30 \text{ cm}$ unglazed, ter-

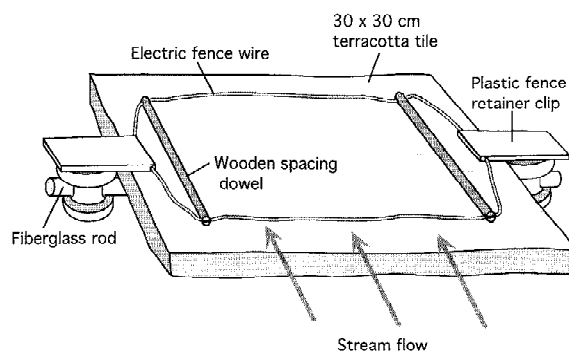


Figure 1. Schematic of the wiring harness fitted to each $30 \times 30 \text{ cm}$ unglazed, terracotta floor tile used in the streambed manipulation. A loop of 17-gauge electric fence wire was suspended approximately 3 mm above the tile surface by two electric fence retainer clips and two wooden spacing dowels. The retainer clips were fitted to a 40 cm fiberglass rod that ran beneath the tile allowing the wiring harness to be clamped to the tile. The assembly was placed on the streambed so that flow was parallel to the wooden spacing dowels to minimize hydraulic turbulence on the experimental substrate.

racotta tiles were randomly assigned to 6 of the 10 cells within each velocity regime. Cobbles immediately below each tile were removed so tiles could be laid flush with the streambed to allow crawling grazers access to tile surfaces. After tiles were placed on the streambed, near-bed current velocities across tile surfaces were checked with a Schiltknecht current meter (Schiltknecht Co., Zürich), which has a temporal resolution of 1 s and a spatial resolution of 10 mm. Tile angles were adjusted and upstream cobbles were manipulated until velocities of 25 ± 5 and $50 \pm 5 \text{ cm s}^{-1}$ were attained for slow and fast current velocities, respectively. For each velocity regime, three of the six tiles were randomly selected to be electrified and the remaining three were left as controls.

The tiles had been exposed to natural grazing levels for 12 months and, prior to placement, were brushed lightly with a nylon-bristled brush to create similar initial conditions. At the start of the experiment, periphyton on tiles had $1.02 \pm 0.12 \text{ mg cm}^{-2}$ ash-free dry mass (AFDM) and $5.48 \pm 2.28 \mu\text{g cm}^{-2}$ chlorophyll *a* (mean \pm S.E., $n=12$). When stream discharge dropped on 1 September from 1.29 to $0.80 \text{ m}^3 \text{ s}^{-1}$, cobbles upstream of tiles were repositioned to enhance flow over tiles and maintain surface velocities within the established $20\text{--}30 \text{ cm s}^{-1}$ and $45\text{--}55 \text{ cm s}^{-1}$ ranges. Electrical service was available on site, allowing the use of two, 110V AC, low-impedance electric fence chargers (Red Snap'r LI-100TM, North Central Plastics, Inc. Ellendale, Minnesota, U.S.A.) to exclude invertebrates from the six treatment tiles

(3 tiles per charger, randomly assigned). A 14 cm × 25 cm loop of 17-gauge electric fence wire was suspended ca. 3 mm over each experimental tile using two 15 cm × 0.75 cm diameter wooden spacing dowels secured by two electric fence retainer clips attached to a 40 cm fiberglass rod that ran beneath the tile (Fig. 1). The treatment tiles were connected to the fence chargers using 16-gauge, double-insulated, underground electric fence wire. Control tiles were also fitted with fencing wire, but were not connected to chargers. The manufacturer's rated output of the chargers was 2800–4000V DC and 8J, transmitted at one pulse per second; the measured output directly at the chargers was 2500–3000V DC, with 200–600V DC delivered to each tile.

Each tile was sampled weekly for periphytic AFDM and chlorophyll *a* concentrations. Four random points on each tile surface were sampled: 2 for periphytic AFDM and 2 for chlorophyll *a*. After collection, the two samples for each parameter were combined. Samples were taken with a 3 cm length of copper tubing having a 1 cm diameter opening and a rubber gasket fitted to one end. During periphytic sampling, each tile was carefully lifted out of the water to disturb periphyton as little as possible, and the copper tube was held to the tile's surface making a watertight seal with the rubber gasket. One ml of filtered water was then added to the tube and a battery operated, high-speed (7500 rpm) rotary tool (Dremel®, Racine, Wisconsin, U.S.A.) equipped with a 4.5 mm diameter brass-bristled brush was used to dislodge all periphyton within the 0.8 cm² sampling area enclosed by the tube. The resulting algal slurry was removed using a glass pipette, filtered through a glass-fiber filter, and frozen with dry ice. All samples were frozen on dry ice within 10 min of collection. Laboratory analyses of chlorophyll *a* and AFDM followed procedures outlined by the American Public Health Association (1992). The extraction medium for chlorophyll *a* was 90% acetone with 10% saturated MgSO₄ solution as recommended by Steinman & Lamberti (1996).

Invertebrates were sampled from the tiles at the mid- and end-point of the experiment (9 and 30 September 2000, respectively). During sampling, the rim of a D-frame kick net (1 mm mesh) was held flush with the downstream edge of the tile to capture mobile or dislodged invertebrates from the tile's upper surface as it was lifted from the streambed. The detached invertebrates were removed from the net, and those remaining on the tile surface were removed with a forceps and preserved in 75% ethanol.

In addition to sampling the experimental tiles, 3–6 cobbles per flow treatment were randomly selected and sampled, beginning 7 d prior to the initiation of the experiment (12 August), and weekly thereafter, to monitor ambient algal and invertebrate abundance on the streambed. Procedures followed those described above for the tiles, with the difference that AFDM samples were preserved in 5% formalin rather than filtered and frozen. Cobble surface area was determined using the aluminum foil method (Steinman & Lamberti, 1996).

To identify taxonomic composition of algae on tiles, on the final day of sampling a scraping of periphyton 1 cm wide and 5 cm long was removed from each experimental tile and combined according to treatment. The periphyton was preserved in 5% formalin and returned to the lab so relative algal species abundance could be determined. Density estimates of algal taxa were based on counts of intact, protoplast-containing (i.e., 'live') cells using an inverted, phase contrast Leitz microscope. Cell density, and species composition were estimated by counting at least 300 cells from each sample. Cell biovolume measurements followed Hillebrand et al. (1999). Large cells were counted at 125× magnification; Cyanophyta and small diatoms were counted at 1250×. Diatom identifications were made at 1250× magnification on Hyrax-mounted slides from material cleared in 30% hydrogen peroxide before mounting (Dodd, 1987).

Analysis and statistics

For tiles, chlorophyll *a* samples presented a problem because these data were highly variable. This was a consequence of samples being collected both inside and outside the effective zone of the electric field that extended ca. 5 cm from the electrified wires. Log-transformations of the data did not homogenize variance between treatments, so the data were ranked and a non-parametric, two-way (current velocity × electricity), repeated measures ANOVA test was performed (Sokal & Rohlf, 1995). Ash-free dry mass samples were not used in the analysis because of suspected contamination during processing.

For cobbles, invertebrates were identified to the lowest feasible taxonomic level and categorized into two functional groups, grazers and non-grazers (Merritt & Cummins, 1996). These data, along with periphytic AFDM and chlorophyll *a*, were log-transformed to meet homogeneity of variance and

normality assumptions prior to performing ANOVA (as determined by Bartlett's & Shapiro-Wilk's test, respectively). Sample replicates were averaged for each sampling date (once a week for 8 weeks) at each current velocity (slow or fast) giving $n = 16$, and a one-way, repeated measures ANOVA was performed on each cobble parameter.

Invertebrate abundance data from control tiles on 9 and 30 September 2000 were compared with cobble data on these dates to assess the differences between the two substrates over time using a repeated measures one-way ANOVA. Invertebrate abundance on tiles was analyzed using a repeated-measures, two-way ANOVA. In each case, the data were log-transformed prior to analysis to meet parametric assumptions.

Results

Electrical exclusion of grazers from tiles had a marked effect on algal accumulation. A thick mat of periphyton extended 3–5 cm either side of the electrified wire loop and was easily distinguished from the non-electrified controls because algal biomass appeared to be an order of magnitude or more greater (Fig. 2). Across the entire electrified tile surface, chlorophyll *a* showed a two to three-fold increase (Table 1, Fig. 3) regardless of current velocity. There was a significant interaction between current velocity and electric treatment, with more algae accumulating on electrified tiles in slow than fast current velocity (Table 1, Fig. 3).

Overall, cyanophytes dominated the benthic algal assemblages, comprising 78–99% of all algal biovolume on treatments. Chlorophytes and diatoms, however, were more abundant on electrified tiles and made up 7–15% of algae as opposed to <1% on controls (Table 2). Electrified tiles also developed a more speciose algal community compared to controls (28 vs. 19 species, respectively). Although algal species richness differed little between electrified tiles in slow and fast current (23 vs. 22, respectively), diatoms were twice as abundant in slow current (Table 2).

Chlorophyll *a* and periphytic AFDM were more abundant on streambed cobbles in fast than in slow current; by contrast, total grazer abundance and richness on cobble surfaces did not differ significantly between current regimes (Table 3). Neither periphytic parameter showed a significant trend over time (repeated measures ANOVA, $df = 7, 28, P = 0.35$ for each parameter); however, grazer abundance did (repeated

measures ANOVA, $df = 7, 28, F_{time} = 2.62, P = 0.03$). Grazer density peaked on 26 August, the third week of the study, reaching 0.132 ± 0.051 individuals cm^{-1} , before dropping to 0.050 ± 0.009 individuals cm^{-1} on 30 September (mean \pm SE for fast and slow cobbles combined; Fig. 4).

Compared to natural substrates, grazer abundance on control tiles were lower by a factor of two (repeated measures ANOVA comparing cobbles and control tiles sampled on 9 and 30 September, $df = 1, 10, F_{substrate} = 18.95, P = 0.001$); however, no time effects were observed between these dates ($df = 1, 10, F_{time} = 1.88, P = 0.20$).

Among tiles, electrified treatments showed a significant reduction in grazer densities compared to controls (Fig. 4; ANOVA, $df = 1, 8, F_{electricity} = 6.90, P = 0.03$). *Baetis* was the most abundant grazer, making up 28% of all invertebrates on tiles, and showed the greatest reduction in density on electrified treatments (Table 4). Current velocity did not influence grazer densities (ANOVA, $df = 1, 8, F_{current} = 0.75, P = 0.41$), nor were there any significant second order interactions between current velocity and electricity on grazer abundance. Particular taxa, however, showed different responses to the electric field. For example, contrary to the trend displayed by *Baetis* and *Drunella* mayflies, *Lepidostoma* sp. caddisflies and chironomids did not decrease in density on electrified tiles (Table 4).

Discussion

Electrical exclusion of grazers from experimental tiles had a marked effect on algal accumulation and taxonomic composition. Most strikingly, algal biomass increased by several orders of magnitude within a zone 2–3 cm on either side of the electrified wire (Fig. 2). Electrified tiles also showed greater algal taxonomic richness, especially with regard to green algae and diatoms, whereas blue-green algae comprised nearly all algae on controls. Diatoms and green algae are considered more palatable and nutritious to stream herbivores than blue-greens (Hart, 1985; Feminella & Resh, 1991), and their increased representation on electrified tiles suggests reduced herbivory. By contrast, the blue-green species that dominated control tiles (e.g., *Homoeothrix* sp. and *Nostoc parmelioides*) were reduced on electrified treatments, perhaps as a consequence of competitive displacement by the green algae and diatoms which received less grazing pres-

Table 1. Treatment and time effects on chlorophyll *a* taken at 8 weekly intervals from experimental tiles between 19 August and 30 September 2000. Three replicates for each current \times electricity treatment combination ($n = 4$) were sampled each week from the second week onwards ($n = 6$; the first week was not used in the analysis, because this was the periphytic growth phase and the only period where time effects were seen). Second and third order interactions between factors are abbreviated with E = Electricity, C = Current and T = Time. *F*-values are from a non-parametric, two-way, repeated measures ANOVA conducted on ranked data for chlorophyll *a*

Factor	df effect	df error	<i>F</i> - value	<i>P</i> - level
Electricity	1	8	39.23	0.0002
Current velocity	1	8	1.83	0.21
Time	5	40	1.96	0.11
E \times C	1	8	8.60	0.02
E \times T	5	40	1.03	0.42
C \times T.	5	40	1.17	0.34
E \times C \times T	5	40	0.45	0.81

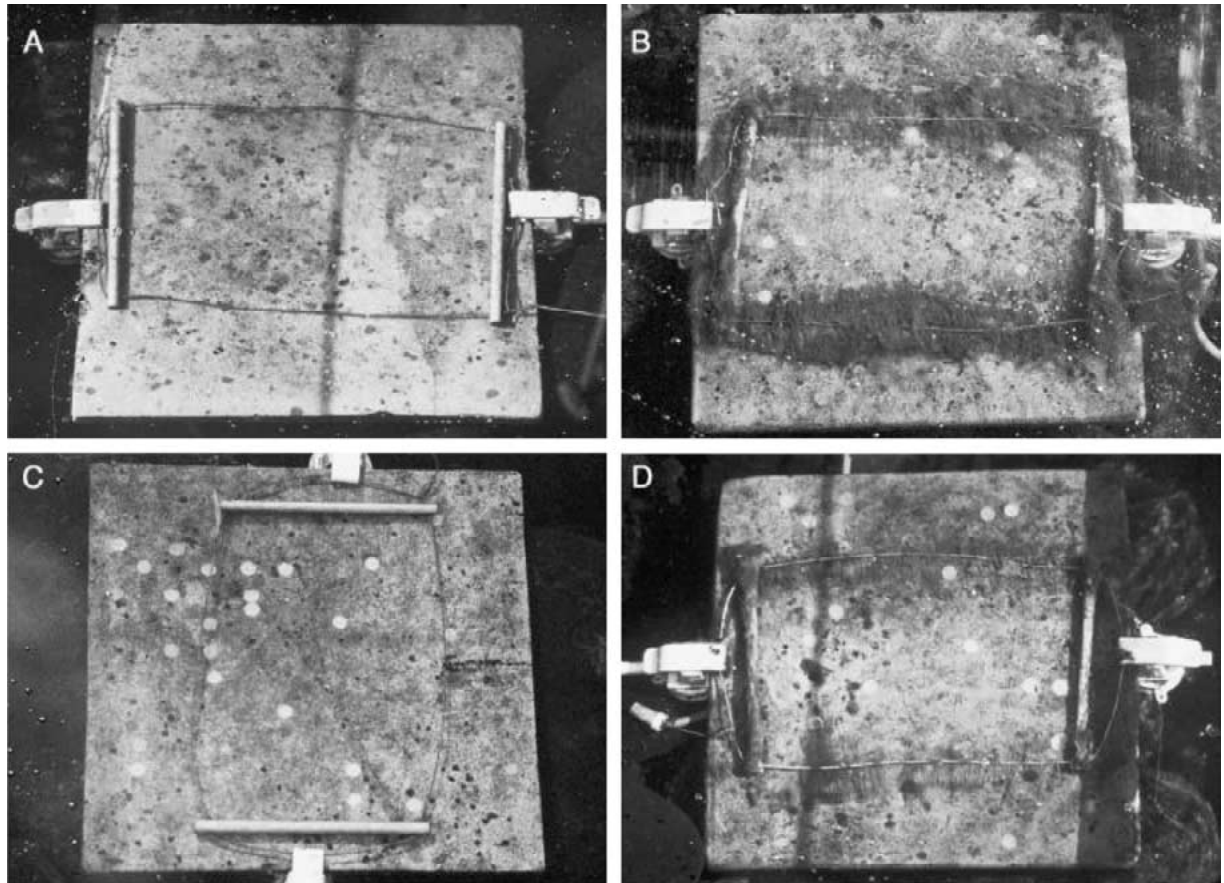


Figure 2. Treatment and control tiles after six weeks of algal colonization: (A) slow velocity, control; (B) slow velocity, electrified; (C) fast velocity, control; (D) fast velocity, electrified. Sampling points are sometimes visible as scraped circular areas. Exclusionary field was most effective to approximately 2–3 cm from the electrified wire.

Table 2. Taxa-specific percent algal biovolume from experimental tiles. Bold numbers within parenthesis are the percent biovolume comprised by each division. Numbers for individual genera and species within each division represent the percent contribution each taxon makes to its respective division

Algal taxa	Experimental treatments			
	Slow Control (%)	Fast Control (%)	Slow Electricity (%)	Fast Electricity (%)
Cyanophyta	(99)	(99)	(78)	(86)
<i>Anabaena affinis</i>	–	–	3	–
<i>Chamaesiphon</i> sp.	0.5	–	–	–
<i>Clastidium</i> sp.	2	–	–	2
<i>Homoeothrix</i> sp.	49	5	10	35
<i>Leptolyngbya nana</i>	0.5	–	6	46
<i>Nostoc parmelooides</i>	47	95	51	16
<i>Siphononema</i> sp.	0.7	–	4	–
<i>Synechocystis</i> sp.	0.3	–	26	1
Chlorophyta	(0.6)	(0.5)	(7)	(7)
<i>Chlorella</i> sp.	–	–	–	66
<i>Draparnaldia plumosa</i>	100	100	–	27
<i>Oedogonium</i> sp.	–	–	15	–
<i>Scenedesmus communis</i>	–	–	15	–
<i>Spirogyra</i> sp.	–	–	7	–
<i>Tetraedron minimum</i>	–	–	4	–
<i>Ulothrix</i> spp.	–	–	59	7
Bacillariophyta	(0.4)	(0.5)	(15)	(7)
<i>Achnanthes</i> spp.	–	6	–	1
<i>Cocconeis</i> spp.	6	47	4	2
<i>Cymbella</i> spp.	9	4	3	8
<i>Didymosphenia geminata</i>	6	–	–	1
<i>Epithemia</i> spp.	3	–	5	3
<i>Fragilaria</i> spp.	–	–	25	2
<i>Gomphonema</i> spp.	–	4	7	3
<i>Melosira varians</i>	–	–	21	3
<i>Navicula cryptotenella</i>	42	13	16	15
<i>Navicula veneta</i>	6	10	7	10
<i>Navicula</i> spp.	15	4	4	3
<i>Nitzschia paleacea</i>	10	6	5	45
<i>Nitzschia</i> spp.	–	–	1	2
<i>Synedra</i> spp.	3	6	2	2

sure (Stevenson et al., 1991). Indeed, some algae require grazing in order to maintain dominance on streambeds (Rosemond & Brawley, 1996).

The pattern of algal accumulation on tiles where grazers were excluded by electricity – more algae in slow current velocity, less in fast – was not the streambed configuration; however, subsidy-stress mech-

anisms may still account for its occurrence. According to Biggs et al. (1998), moderately coherent periphytic mats – the type that dominated in our study – should increase as a function of increasing current velocity, but only to a point. As current velocity increases, the mass transfer subsidy is eventually overcome by shear stress, leading to sloughing and a subsequent decline

Table 3. Chlorophyll *a*, periphytic ash-free dry mass (AFDM), grazer density and taxa richness from 3 to 6 randomly selected cobbles sampled in regions of fast (47–53 cm s⁻¹) and slow (23–28 cm s⁻¹) current in the upper Colorado River for 8 weeks between 3 August and 30 September 2000. Replicates were averaged for each sampling date (*n* = 8) within each current regime (slow or fast), giving *n* = 16. Values are mean ± 1 standard error. *F*-values are from a one-way ANOVA conducted on each parameter

Parameter	Slow	Fast	df	<i>F</i> -value	<i>P</i> -level
Chlorophyll <i>a</i> ($\mu\text{g cm}^{-2} \times 10^{-3}$)	5.83 ± 0.57	9.64 ± 1.12	1, 14	6.61	0.02
AFDM ($\text{mg cm}^{-2} \times 10^{-3}$)	5.23 ± 0.27	7.09 ± 0.49	1, 14	7.30	0.02
grazer density (individuals cm ⁻²)	0.071 ± 0.011	0.088 ± 0.018	1, 14	0.67	0.43
grazers taxa richness	7.2 ± 0.5	7.0 ± 0.4	1, 14	0.04	0.84

Table 4. The 5 most common taxonomic groups on experimental tiles, their overall percent representation and mean (± 1 S.E.) densities per cm⁻² × 10⁻³. Asterisks indicate significant differences between Control and Electrified treatments (two-way ANOVA, *df* = 1, 8, *P* < 0.05). There was no significant effect of current velocity on the density of any group. The 4 percent of taxa not shown comprised mostly of *Paraleptophlebia* sp. mayflies and glossosomatid caddisflies

Taxon	%	Control	Control	Electrified	Electrified
		Slow	Fast	Slow	Fast
Non-grazers	33	15.7 ± 5.4	17.5 ± 3.7	16.1 ± 4.2	16.8 ± 2.1
<i>Baetis</i> *	28	22.4 ± 5.6	19.6 ± 3.2	5.1 ± 2.0	9.4 ± 0.6
<i>Lepidostoma</i>	20	5.3 ± 0.5	11.3 ± 3.1	7.6 ± 1.9	15.5 ± 6.3
Chironomids	8	3.5 ± 2.5	1.1 ± 0.6	1.9 ± 1.4	9.4 ± 4.3
<i>Drunella</i> *	7	5.7 ± 0.5	5.5 ± 0.8	1.7 ± 0.7	2.3 ± 0.4

in periphytic biomass. The result is a unimodal distribution of biomass across current velocity with peak periphytic biomass occurring at some intermediate near-bed velocity (Biggs et al., 1998). We hypothesize that in our stream, periphytic mass transfer peaked around our slow treatment (25 cm s⁻¹), whereas shear reduced periphyton at 50 cm s⁻¹. If this is the 'true' subsidy-stress influence on periphyton in the upper Colorado – recall that the natural streambed pattern had biomass increasing monotonically with velocity – its effects were clearly masked by herbivory.

Grazing efficiency, that is, a grazer's ability to remove a unit of algal biomass per unit time or per calorie of energy expenditure, may vary across current velocity in response to either biotic or abiotic constraints, such as predation and hydraulic shear, respectively (Hansen et al., 1991; Hart, 1992; Wellnitz & Poff, 2001). In our study reach, for example, predaceous *Claassenia* sp. stoneflies are 3–5 times more

abundant in regions of fast flowing water (T. Wellnitz, unpublished data), and this could potentially cause vulnerable grazers (e.g., *Baetis* spp.) in fast current velocities to be less capable of removing benthic algae because of risk-sensitive foraging (Kohler & McPeck, 1989; Peckarsky, 1996). Regarding shear, Poff and Ward (1992) showed that foraging behavior of glossosomatid caddisflies was restricted by fast stream current, presumably because increased shear makes it more difficult for these case-bearing larvae to maneuver, maintain position, and feed. Under slow velocities, by contrast, glossosomatids are better able to move against and perpendicular to flow, and thus, can better track algae on cobbles.

Many grazers are known to show distinct preferences for current (DeNicola & McIntire, 1991; Gawne, 1997; Wellnitz et al., 2001), and although not examined in the present study, this preference may reflect the fact that grazer species in a stream

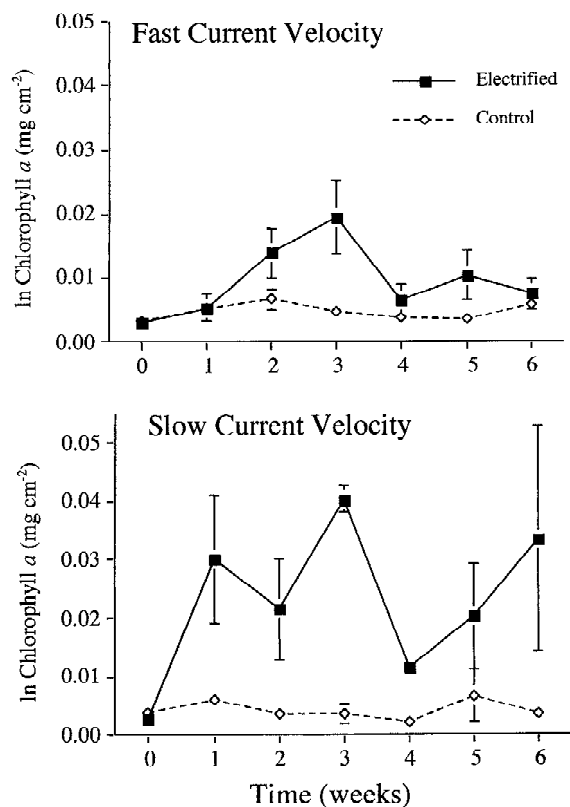


Figure 3. Chlorophyll *a* concentrations from weekly samples taken from treatment and control tiles in slow and fast current ($n = 3$ per time step and treatment) between 19 August and 30 September 2000. Error bars indicate ± 1 S.D.

do not persist, thrive and perform equally well across the whole range of available current velocities (Hart & Finelli, 1999). Other work with grazers from the upper Colorado River has shown that an herbivore's ability to remove periphyton can vary with current velocity. In particular, removal of algae by *Baetis* maintained within streamside mesocosms, was found to peak between 30 and 40 cm s^{-1} (Poff et al., 2003), a range that lays intermediate between our slow and fast velocity treatments. *Baetis* was the most abundant grazer in our study and the one most strongly affected by stream current (Table 4). We speculate that in the natural stream, *Baetis* removes more periphyton in the slower than the faster range of near-bed current velocity examined in this study. We further speculate that this differential performance across stream current is due to a combination of biotic and abiotic factors, such as predation pressure and shear stress. The strengths of these factors can vary over time (Power, 1992), as do the dominant grazers in this stream (Rader & Ward,

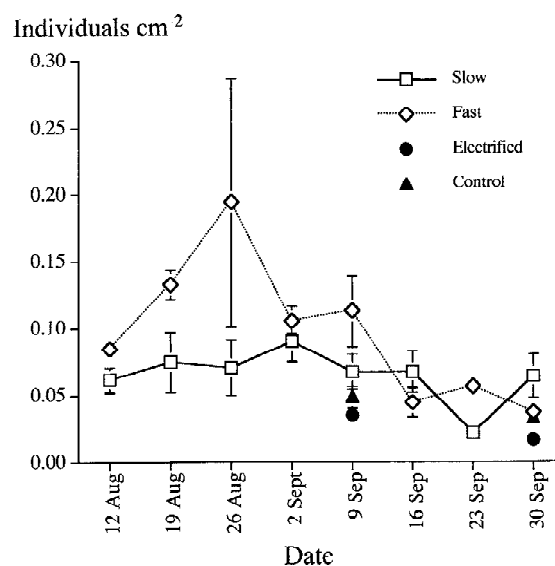


Figure 4. Mean (\pm SE) grazer densities on streambed cobbles (fast and slow current) and experimental tiles (electrified and control averaged across current) during August and September 2000. Error bars are not apparent for tile data because these values were very small.

1987), thus, it is probable that if this same study were conducted at a different time of the year the results could be different from those reported here.

The high variance in chlorophyll *a* (see Fig. 3) was due to the sampling design. The periphytic sampling protocol was designed *a priori* to sample points randomly across the surface of the tile. A pilot study prior to the main experiment yielded fewer invertebrates on electrified tile surfaces than controls after 48 h. Although we knew the electric field did not extend uniformly across the tile (Reynolds, 1996), our observations lead us to assume that the exclusionary effect would. Three weeks into the experiment, however, it became apparent that the electrical field was not equally effective across the entire tile surface. In addition, it was observed that *Lepidostoma* sp. caddisflies and chironomids exhibited high tolerance to the electric field because neither taxon showed reduced densities on electrified tiles. The selectivity of electricity on invertebrates has been noted in other studies (Brown et al., 2000; Taylor et al., 2001) and Brown et al. (2000) found similar results to our own with regard to case-bearing Trichoptera and chironomid species. Nevertheless, our data confirmed our initial observations that electricity reduced most grazers, notably the abundant and mobile baetid mayflies, from the entire tile surface. The fact that current velocity-mediated

effects on herbivory were significant for whole tiles, despite the variance in the chlorophyll *a* data, suggests that our results are robust.

The possibility exists that the pattern of algal accumulation observed under natural and reduced grazing levels was an artifact of the substrate employed in the experiment. Several studies have pointed to the importance of substrate texture and roughness on algal colonization, composition and persistence (Tuchman & Stevenson, 1980; DeNicola & McIntire, 1990; Dudley & D'Antonio, 1991; Downes et al., 2000). However, even if the pattern on tiles *were* an artifact of the experimental substrates, our results show that grazer effects on benthic algal accrual were plainly and visibly altered by current velocity.

Recent theory has proposed that the ecological roles of species may change along environmental gradients, and consequently their functional contribution to ecosystem processes may be determined by their position along gradient axes (Walker et al., 1999; Cardinale et al., 2000; Wellnitz & Poff, 2001). If functional roles can change across natural gradients, it is reasonable to assume interaction strengths may also change. In fact, there is a growing literature demonstrating the importance of environmental gradients for mediating competitive and facultative interactions (see Bertness & Callaway, 1994). Since flowing water is a pervasive gradient and ubiquitous feature of streams, knowing how current influences species interactions is critical for understanding how stream communities function.

Acknowledgements

We thank the Tillotson and Mirr families for generously allowing access to the study site, Travis Allen and Jeremy Monroe for their assistance with collecting and processing samples, Julian Olden for help with the logistics and construction of the exclusion experiment, and David Pepin for advice during sample analyses. Jim zumBrunnen helped with statistics and Dick Dufford identified algae, and our manuscript greatly benefited from helpful comments by Barry Biggs and two anonymous reviewers. This study was supported by funding from the Research Experience for Undergraduates Program (to R.W.O.) and National Science Foundation grants DEB-98-06504 awarded to N.L.P. and DEB-00-75352 awarded to N.L.P. and T.W.

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