

Current-mediated periphytic structure modifies grazer interactions and algal removal

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Abstract By shaping the architecture and taxonomic composition of periphyton, stream current may create periphytic mats on which some grazers can feed and forage more effectively than others. Current-mediated periphytic structure also has the potential to foster positive interactions among grazers if one grazer's foraging facilitates another's access to algal food. To examine the extent to which these indirect effects of current influenced periphytic removal and grazer interactions, we conducted a mesocosm experiment with two common grazers, the caddisfly (Trichoptera) *Glossosoma verdoni* and the mayfly (Ephemeroptera) *Drunella grandis*. Periphyton was allowed to colonize ungrazed tiles for 30 d and assume its natural growth form under three ranges of near-bed current, "slow" ($1\text{--}5\text{ cm s}^{-1}$), "medium" ($15\text{--}20\text{ cm s}^{-1}$), and "fast" ($30\text{--}40\text{ cm s}^{-1}$). Tiles were then exposed to the two grazer species at five densities. A streambed survey

quantified *Glossosoma* and *Drunella* distributions in relation to near-bed current and periphytic structure (i.e., diatom films vs. filamentous mats) in the Colorado River. After 22 days of grazing, periphytic removal by *Glossosoma* was influenced by near-bed current and attendant periphytic structure. In slow current, where senescent *Ulothrix* filaments were abundant, increased *Glossosoma* density was correlated with an increase in periphyton biomass. Larvae became entangled and immobilized by the diffuse and senescent *Ulothrix* mat that characterized slow velocity, and *Glossosoma* mortality and weight loss was greatest in this treatment. By contrast, *Drunella* reduced periphyton across all density and current treatments. *Drunella* density correlated with increased *Glossosoma* survivorship and weight gain in slow current. The driving mechanism for this facilitation appeared to be removal of entangling overstory filaments by *Drunella*. The streambed survey showed that *Glossosoma* were negatively associated with filamentous mats, lending support to the hypothesis that clearing action by *Drunella* in the slow current/senescent *Ulothrix* treatment facilitated *Glossosoma* growth and survival. Our study helps underscore the importance of evaluating species interactions over ranges of abiotic conditions and consumer pressure to understand the patterns and processes shaping benthic communities.

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Introduction

Moving water defines stream ecosystems, and water flowing over the streambed creates patches of fast and slow near-bed current that have diverse effects on benthic organisms and their functional contributions to ecosystem processes (Hart and Finelli 1999; Syrovatka et al. 2009; Lancaster and Downes 2010). Resource acquisition by benthic species is often flow dependent, and current velocity can influence nutrient uptake by periphyton (Larned et al. 2004; Reid et al. 2006), interactions among macroinvertebrates (Meissner et al. 2009; Hoover and Richardson 2010), and algal removal by benthic grazers (Opsahl et al. 2003; Katano et al. 2005; Merten et al. 2010). Near-bed current may directly or indirectly shape each of these processes. A grazer's ability to remove benthic algae, for example, depends not only on its ability to operate under the shear imposed by current (direct effect), but also on the type of algal food found within that current (indirect effect) (Wellnitz and Poff 2006; Darcy-Hall and Hall 2008). Some algae are known to be more resistant to grazing than others (Rosemond and Brawley 1996; Wellnitz and Rader 2003), and it follows that if the near-bed current favors grazer-resistant forms, algal removal will be affected.

Near-bed current may also indirectly influence algal removal by mediating interactions among grazers. Species' performances can vary across gradients of near-bed current (Poff et al. 2003), and flow across streambeds has the potential to change the strength and outcomes of grazer interactions. Grazers having high profile cases or shells, for instance, are vulnerable to dislodgment in fast current, and this could make them inferior competitors on surfaces exposed to high flow (Holomuzki and Biggs 2000; Lancaster et al. 2006). Near-bed current may set the stage for positive interactions by promoting the growth of periphyton that allows grazers with different traits to have complementary function (Hertonsson et al. 2008; Lee et al. 2011), for example, by establishing conditions in which two grazer species are more effective at removing periphytic algae than either is alone (Wilson et al. 1999).

In a previous study, Poff et al. (2003) demonstrated that near-bed current could directly regulate the ability of three insect grazer species to remove periphyton and showed that the species' proficiency differed across a gradient of near-bed current. However, that

study held periphytic mat structure constant to avoid the confounding influence of mat morphology on grazer performance. By not allowing periphyton to respond either to current or the longer-term grazing effects, this previous work presented an incomplete picture of current-mediated algal-grazer dynamics in streams. The present study builds on Poff et al. (2003) by examining how grazing is influenced by current through its effects of periphytic structure.

We used two of the grazers examined in Poff et al. (2003), the caddisfly *Glossosoma verdoni* (Ross) and the mayfly *Drunella grandis* (Eaton). We predicted that current-mediated effects on periphytic structure would influence both periphytic removal and the outcome of grazer–grazer interactions. Algal physiology, species composition, and mat architecture may all be shaped by stream current (Passy 2001; Wellnitz and Poff 2006; Larson and Passy 2012), and each of these attributes may potentially affect a grazer's ability to forage, feed, and remove periphyton (Poff and Ward 1992; Villanueva et al. 2004; Hoffman et al. 2006). Other work in this system (Wellnitz and Poff 2006) showed that near-bed current $<30 \text{ cm s}^{-1}$ typically produces periphytic mats dominated by the filamentous chlorophyte *Ulothrix*. Filamentous algae are generally difficult for grazers to remove (Dudley 1992); therefore, we hypothesized that *Glossosoma* and *Drunella*—which differ in size, mobility, and mouthpart morphology—would be more effective in removing filamentous algae in combination than either was alone. This functional complementarity would facilitate growth, leading to increased weight gain when the two species foraged together in slow current. We did not expect to see such facilitation in higher velocity conditions where easily grazed diatoms tend to dominate.

Methods

Study area and organisms

Our study was conducted in streamside mesocosms in October 2000 and on the streambed of the upper Colorado River in October 2002. This site is located at 2400 m elevation (a.s.l.) and 7 km downstream of Lake Granby, a hypolimnetic-release reservoir in Grand County, Colorado, USA. The upper Colorado River at this location is wide (10–15 m) and shallow

(≤ 0.50 m) and has an open riparian canopy. The streambed is comprised of large cobbles (15–25 cm diameter) underlain by sand and gravel. Discharge during the study period ranged from $0.75\text{--}0.80\text{ m}^3\text{ s}^{-1}$, and near-bed current within 10 mm of the streambed ranged from $0\text{--}90\text{ cm s}^{-1}$.

Periphytic algae at our study site can be broadly characterized as comprised of either filamentous chlorophytes and cyanobacteria or diatom films. Filamentous periphyton consisted of thick (5–10 mm) mats of filamentous algae, whereas diatomaceous periphyton was a thin, adherent film. Diatomaceous mats characterized regions of the streambed with fast current ($>30\text{ cm s}^{-1}$), whereas filamentous mats were common at slower velocities (Poff and Ward 1992).

Drunella grandis and *Glossosoma verdoni* were among the predominant grazers in the upper Colorado during the study period. Both exhibit a clinging mode of existence, do not swim, and rarely enter drift (Merritt and Cummins 1996). *Glossosoma* are smaller than *Drunella* (mean \pm SE; $2.89 \pm 0.08\text{ mg}$ vs. $0.38 \pm 0.02\text{ mg}$; $n = 60$), build and occupy cases of sand (particle size 0.5–1.0 mm), and were more abundant at our study site. The (mean \pm SE) streambed density for *Glossosoma* in October 2000 was 350 ± 140 individuals m^{-2} versus 17 ± 6 individuals m^{-2} for *Drunella*.

Streamside channels

A streamside channel experiment examined periphytic removal and interactions between *Glossosoma* and *Drunella* across a gradient of near-bed current. Periphyton was allowed to assume its ungrazed growth form under three ranges of near-bed current, which we designated as: “slow” ($1\text{--}5\text{ cm s}^{-1}$), “medium” ($15\text{--}20\text{ cm s}^{-1}$), and “fast” ($30\text{--}40\text{ cm s}^{-1}$). The experiment was conducted in 90 circular channels described in Wellnitz and Poff (2006). Plastic (PVC) channels were constructed of two concentric cylinders glued to a flat base to create a 3.8-cm-wide circular raceway having a 10 cm depth. Stream water was pumped from the Colorado River into a header tank mounted 4 m above the channel array. Incoming stream water was passed through a nylon sock (1 mm mesh) to filter out macroinvertebrates and large particles. Water from the tank was gravity-fed to channels through a network of PVC pipes that ended in

short lengths of Tygon™ tubing (40 cm \times 1 cm diameter) attached to adjustable valves. Current velocity was set by adjusting the flow of water through plastic jets angled into the channels, and adjustments to valves were made as necessary to maintain velocity ranges. Channel current velocity was monitored daily using a MiniWater20 Micro current velocity probe (Schiltknecht Messtechnik AG, Zürich), which has a spatial resolution of 10 mm.

Periphyton for the experiment was grown on small, square ceramic tiles (6.54 cm^2). The tiles were colonized in nine linear channels (three for each current regime) constructed of plastic rain gutter (8 \times 6 \times 200 cm) with Colorado River water running through them. Following a colonization period of 30 days, the tiles were transferred into circular channels having equivalent velocity ranges. Fifteen tiles were transferred to each channel providing 0.098 m^2 of periphyton on which grazers could feed.

The experiment employed a $5 \times 5 \times 3$ factorial design: five densities of *Glossosoma* by five densities of *Drunella* by three current velocities (slow, medium, and fast). Grazer densities in channels were based on mean streambed densities and were determined by counting individuals on the natural streambed using an underwater viewer ($n = 20$ samples). Channel densities for both grazers were 0, 0.5, 1, 2, and 3 times ambient streambed densities. Initial grazer numbers were 0, 9, 17, 34, and 69 individuals per channel for *Glossosoma* and 0, 1, 2, 5, and 7 individuals per channel for *Drunella*. Grazer treatments were applied to channels so that all density combinations were represented (75 channels). In addition, *Drunella* treatments having just one individual (i.e., the 0.5 ambient density treatment) were replicated once (in case of *Drunella* mortality), giving 90 channels in total.

The channel experiment ran for 22 d from October 7 to 28, 2000. A subsample of 50 *Glossosoma* and 18 *Drunella* were dried and weighed on day 0 to obtain initial mass of *Drunella* and *Glossosoma*. The experiment ended when ice began to form on drain screens, at which point grazers were collected and tiles were sampled for periphyton. Eight tiles were selected randomly from each channel; of these, four were frozen on dry ice for determination of chlorophyll-*a* (cold acetone extraction), and four were preserved in 5 % formalin for determination of ash-free dry mass

(AFDM) of periphyton (American Public Health Association 1992). *Glossosoma* and *Drunella* were collected from each channel and preserved in 5 % formalin for later drying and weighing to determine treatment effects on grazer weight gain.

Streambed survey

A streambed survey was conducted during October 2002 to quantify *Glossosoma* and *Drunella* distributions on the streambed in relation to near-bed current and periphytic abundance (quantified as chlorophyll-*a*). Sampling points were selected from a streambed riffle by using a “random walk” technique (Wellnitz et al. 2001). Once a point was selected, the nearest visible *Drunella* or *Glossosoma* individual to that point was located. Once found, the grazer’s position was referenced to topographic features of the cobble and the grazer was removed. Near-bed current (i.e., within 10 mm of cobble surface) was then measured by placing the Schiltknecht current velocity probe directly on the cobble surface at the location the grazer had occupied. After recording the near-bed velocity, the cobble was lifted from the streambed and periphyton was sampled using the method from Poff and Ward (1992). A metal tube (30 × 10 mm diameter) fitted with a rubber gasket to maintain a watertight seal was held to the cobble surface where the grazer had been, and stream water was pipetted into the tube. The periphyton enclosed by the tube was dislodged using a 5-mm-diameter nylon brush fitted to a battery-operated Dremel™ rotary tool, and the resulting slurry was removed with the pipette. This process was repeated three times. The slurry was then filtered through an AE glass fiber filter (47 mm), frozen on dry ice, and later analyzed in the laboratory for chlorophyll-*a* using the cold acetone extraction method.

Statistical analysis

Channel experiment response variables were analyzed using the General Linear Model module in JMP (version 8) statistical software (SAS Institute Inc.). Model effect terms were *Drunella* and *Glossosoma* densities, the three current velocity treatments, and interactions among these factors. Models were run on the following response variables: *Drunella* and *Glossosoma* mortality, periphytic AFDM and chlorophyll-*a*, and *Drunella* and *Glossosoma* weight gain.

Effects were examined in a scale-invariant fashion by using the “Scaled Estimates” command in JMP, which gives coefficients corresponding to factors scaled to have a mean of zero and a range of two. Assumptions of normality and homoscedasticity were checked and confirmed using residual analysis and Bartlett’s test, respectively. A one-way ANOVA with post hoc Tukey’s HSD tests compared periphyton grown under the three current velocity regimes at the start and end of the experiment.

Streambed survey data were analyzed with a median test to determine whether *Glossosoma* and *Drunella* distributions differed across the range of near-bed current, and a *t* test was used to examine their occurrence on filamentous versus diatomaceous periphyton. These analyses were also performed using JMP.

Results

Current velocity markedly influenced the physical structure of periphyton. Following the 30-d colonization period, periphytic AFDM on tiles differed among current velocity treatments such that medium >>slow = fast (ANOVA, $F_{2, 6} = 49.4$, $p < 0.001$). Although slow and fast current had similar biomass, algal composition and mat structure in these treatments were very different. At slow velocity, senescent *Ulothrix* dominated the assemblage and created a diffuse, brown, filamentous mat. In contrast, fast-velocity periphyton was composed almost entirely of diatoms, creating golden-brown films. Medium-velocity mats were dominated by living *Ulothrix* filaments that gave the periphyton a bright green color.

Grazer mortality for the 21-d experiment was 22 % for *Drunella* and 43 % for *Glossosoma*. *Drunella* mortality did not correlate with any treatment variable (ANOVA, $F_{11, 45} = 1.79$, $p = 0.09$), whereas *Glossosoma* mortality did (Table 1). *Glossosoma* mortality declined with increasing *Drunella* density, but increased as intraspecific density rose. *Glossosoma* mortality was also greater in medium and slow current (where filamentous mats predominated) than in fast velocity.

Algal chlorophyll-*a* and periphytic AFDM responded to grazer density and near-bed current velocity (Table 2). Increasing densities of each grazer correlated with reduced chlorophyll-*a*, and *Drunella* density was associated with decreased periphytic

AFDM. Chlorophyll-*a* and AFDM were greatest in the medium-velocity treatment where living *Ulothrix* filaments were abundant. By contrast, chlorophyll-*a* values were lowest in slow velocity where senescent algal filaments were common, and AFDM was lowest in fast velocity where diatomaceous films predominated.

Near-bed current and attendant periphytic structure modified *Glossosoma* effects on periphytic AFDM (Table 1, Fig. 1). Under slow current, in which diffuse mats of senescent *Ulothrix* filaments were abundant, increasing *Glossosoma* density was correlated with an increase in AFDM. We observed that these diffuse mats did not support the weight of *Glossosoma* cases, and individuals frequently dropped down within the mat matrix where they had difficulty moving or became immobilized. Under medium and fast current, by contrast, increased *Glossosoma* density correlated

with a decrease in periphytic AFDM (Fig. 1), and the larvae were able to stay on top of the periphyton that formed under these velocities.

Drunella effects were invariant across treatments and appeared unaffected by periphytic structure (Table 2); higher densities of this grazer always correlated with a decrease in periphytic AFDM. However, there was a three-way, *Drunella* x *Glossosoma* x current interaction indicating that the two grazers in combination removed less periphytic AFDM in the fast current/diatomaceous periphyton treatment as their densities increased (Table 1), suggesting that grazer–grazer interference occurred (Table 2).

The weight of *Glossosoma* larvae changed in response to treatment variables ($F_{11, 54} = 5.23$, $p < 0.0001$), whereas the weight of *Drunella* nymphs did not ($F_{11, 54} = 0.87$, $p = 0.57$). There was strong evidence for treatment-mediated grazer facilitation and competition (Table 3). In particular, larval *Glossosoma* showed substantial weight gains with increased *Drunella* density in slow current/senescent *Ulothrix* treatment; in contrast, *Glossosoma* weight decreased with increasing intraspecific density (Fig. 2) at slow velocity.

Observations made during the experiment indicated *Drunella* frequently occurred within mats of filamentous periphyton whereas *Glossosoma* did not. In instances where *Glossosoma* occupied the filamentous mats that characterized slow current, their cases sometimes became entangled. *Drunella* movement, by contrast, appeared unaffected by mat structure and was observed dislodging periphyton fragments as it foraged in filamentous mats.

Table 1 Treatment variable effects on *Glossosoma* mortality in experimental channels after 22 d. Grazer numbers are based on channel densities at the end of the experiment. Current was a categorical variable comprised of slow, medium, or fast near-bed velocity ranges (Whole model fit: ANOVA, $F_{11, 72} = 8.42$, $p < 0.0001$, $R^2 = 0.56$)

Variables	DF	F-ratio	p value
Current	2	10.31	0.0001*
<i>Drunella</i>	1	4.65	0.0344*
<i>Glossosoma</i>	1	63.47	<0.0001*
<i>Drunella</i> x current	2	0.35	0.7088
<i>Glossosoma</i> x current	2	6.13	0.0035*
<i>Glossosoma</i> x <i>drunella</i>	1	0.24	0.6282
<i>Glossosoma</i> x <i>drunella</i> x current	2	0.29	0.7485

Table 2 Treatment variable effects on algal chlorophyll-*a* ($F_{11, 69} = 7.80$, $p < 0.0001$, $R^2 = 0.76$) and periphytic AFDM ($F_{11, 69} = 8.68$, $p < 0.0001$, $R^2 = 0.58$) collected from channel tiles after 22 d

Variables	DF	Chlorophyll		AFDM	
		F-ratio	p value	F-ratio	p value
Current	2	26.54	<0.0001*	8.88	0.0004*
<i>Drunella</i>	1	48.49	<0.0001*	26.02	<0.0001*
<i>Glossosoma</i>	1	13.41	0.0005*	1.83	0.1806
<i>Drunella</i> x current	2	1.13	0.3296	1.76	0.1789
<i>Glossosoma</i> x current	2	1.29	0.2823	8.06	0.0007*
<i>Glossosoma</i> x <i>drunella</i>	1	0.02	0.9017	3.04	0.0857
<i>Glossosoma</i> x <i>drunella</i> x current	2	1.42	0.2488	3.83	0.0264*

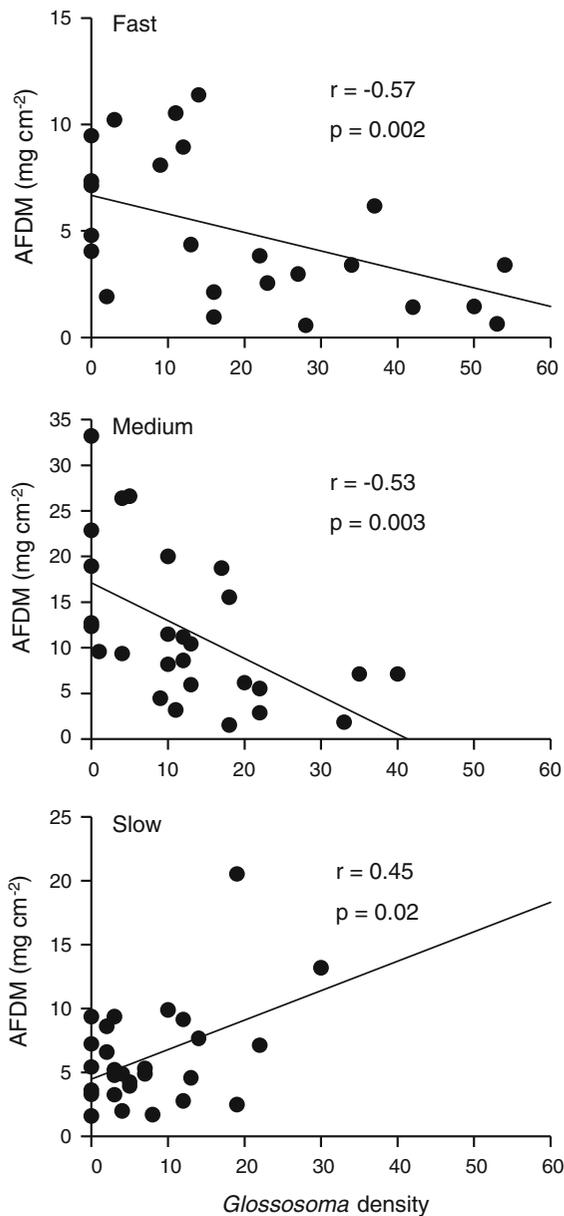


Fig. 1 Response of periphytic ash-free dry mass (AFDM) to *Glossosoma* density under three near-bed current velocity treatments. Each data point represents the periphytic AFDM collected from four tiles from each experimental channel after 22 d

The streambed survey showed that *Drunella* and *Glossosoma* co-occurred on the Colorado River streambed within similar ranges of near-bed current. Both grazers were most frequently found at velocities $<20 \text{ cm s}^{-1}$ (Fig. 3), and their distribution across current did not differ (median test, $X^2 = 1.75$,

Table 3 Treatment variable effects on *Glossosoma* weight gain in channels after 22 d (Whole model fit: ANOVA, $F_{11, 72} = 8.42$, $p < 0.0001$, $R^2 = 0.56$)

Variables	DF	F-ratio	p value
Current	2	9.18	0.0004*
<i>Drunella</i>	1	0.74	0.3923
<i>Glossosoma</i>	1	8.73	0.0046*
<i>Drunella</i> x current	2	7.58	0.0013*
<i>Glossosoma</i> x current	2	6.31	0.0035*
<i>Glossosoma</i> x <i>drunella</i>	1	13.79	0.0005*
<i>Glossosoma</i> x <i>drunella</i> x current	2	2.15	0.1268

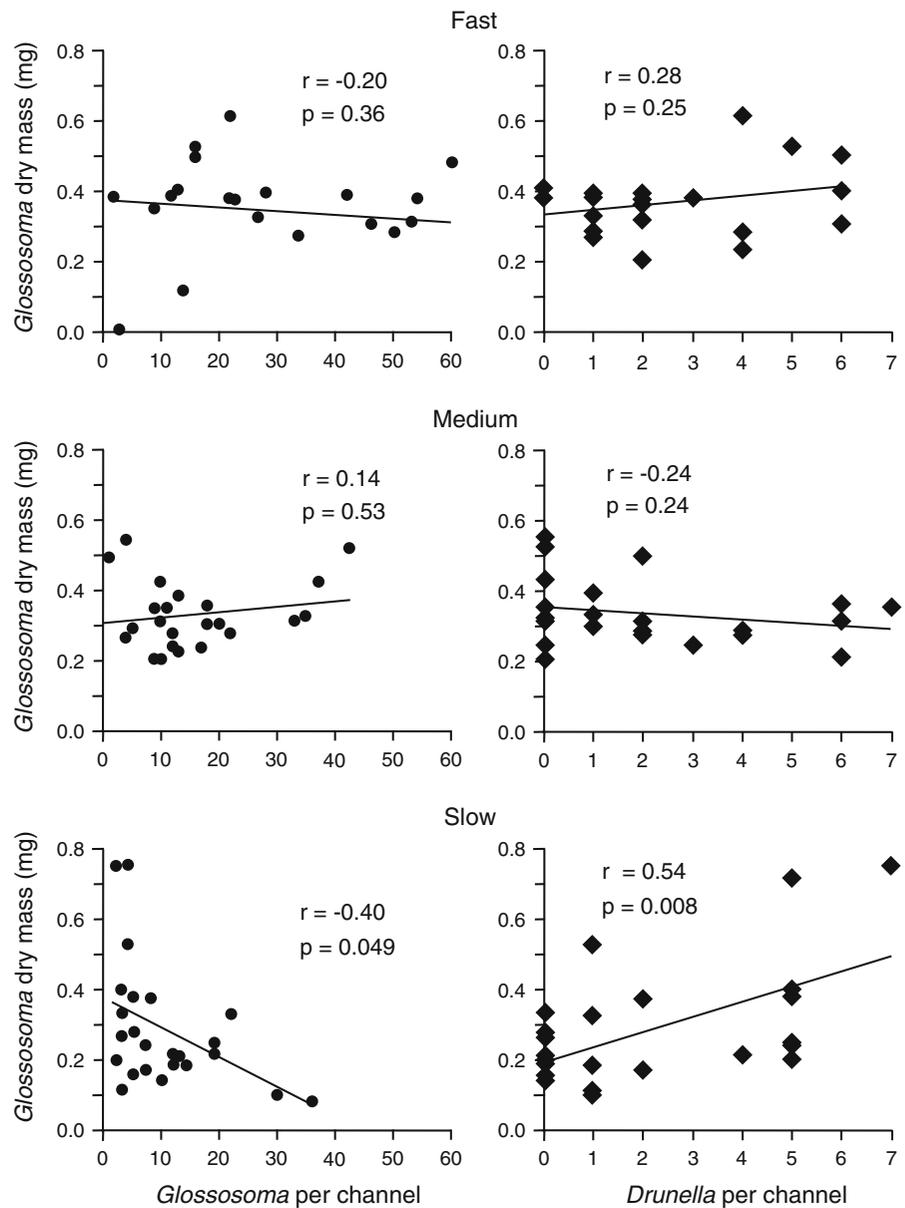
$p = 0.42$). Their occurrence on filamentous and diatomaceous periphyton, however, was different. *Glossosoma* larvae were typically found on diatom films, whereas *Drunella* nearly always occurred in thick patches of filamentous algae. This difference was reflected in the amount of chlorophyll-*a* collected from *Drunella* vs. *Glossosoma* locations, which was 6 × greater in *Drunella* locations (mean ± SE, 5.75 ± 1.21 vs. 0.98 ± 0.72 ; $t = 2.08$, $p = 0.001$).

Discussion

Our experiment demonstrated that near-bed current velocity and attendant periphytic structure could affect periphytic removal by grazers. We also showed that periphytic structure could create conditions that appeared to foster positive interactions between grazers. The three regimes of near-bed current produced distinct periphytic mats to which *Glossosoma* and *Drunella* responded to and affected differently. In particular, *Glossosoma* was less capable than *Drunella* at removing the senescent, filamentous periphyton that grew in slow current. Our data suggest that *Glossosoma* foraging was facilitated by *Drunella*'s removal of periphyton because *Glossosoma* gained weight and survived better as the density of this mayfly increased. We conclude it was the structure of the periphytic mat rather than the direct effects of near-bed current that established the conditions for this grazer facilitation.

Filamentous *Ulothrix* was abundant in both medium and slow current velocity treatments, but living *Ulothrix* filaments were abundant in medium current whereas dead or dying filaments dominated slow

Fig. 2 Response of *Glossosoma* dry mass to increasing density of *Glossosoma* and of *Drunella* under three near-bed current treatments. Each data point represents the mean dry mass of all *Glossosoma* individuals collected from each channel after 22 d



current. This difference was apparent in the mat's color (bright green vs. brown), density, and relative chlorophyll-*a* content (high vs. low). Filamentous mats growing in medium near-bed current were dense and substantial enough to support *Glossosoma* as they foraged; those in slow current did not always support the weight of larval cases. As a consequence, *Glossosoma* larvae frequently had to negotiate their way through the mat instead of foraging across its surface, a phenomenon that may have accounted for the high mortality *Glossosoma* showed in this treatment.

Foraging within the mat structure may also help explain the caddisfly's positive influence on periphytic accrual in slow current. The increase in periphyton may have been due to nutrient enrichment from fecal pellets deposited within the mat, the decomposition of *Glossosoma* larvae that were trapped there, or enhanced nutrient exchange resulting from bioturbation as larvae struggled through the mat (Geddes and Trexler 2003; Liess and Haglund 2007; Rober et al. 2011). Whatever the mechanism, nutrients were likely more limiting in slow current because chlorophyll-

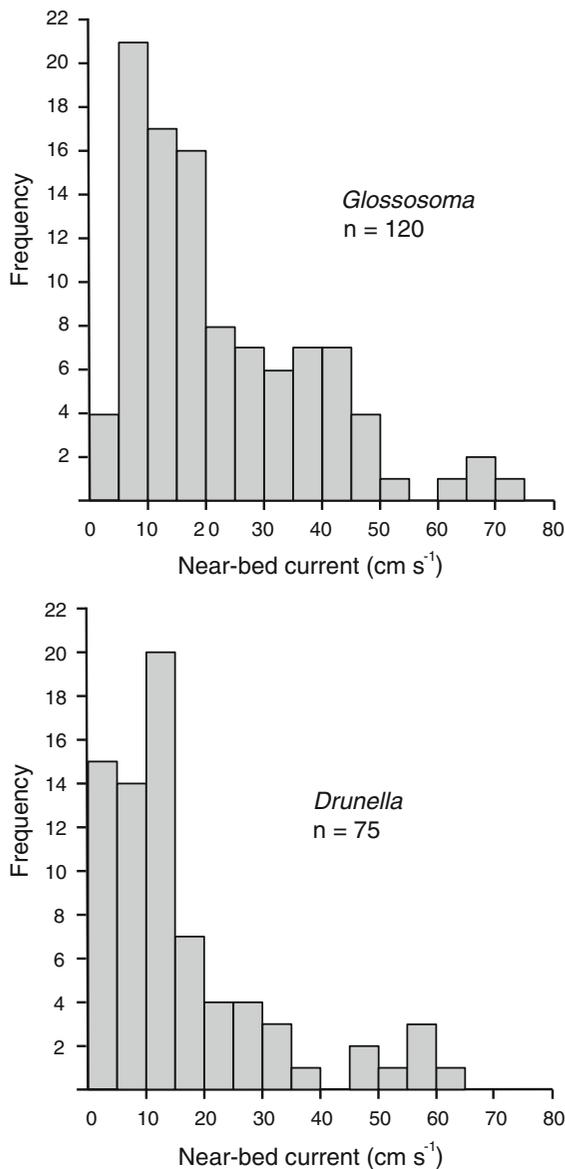


Fig. 3 The distribution of *Drunella* and *Glossosoma* individuals found on the streambed of the upper Colorado River in relation to near-bed current velocity

a content was lower relative to medium current and mass transfer and turbulent mixing generally decrease as water velocity slows (Dodds and Biggs 2002; Hondzo and Wang 2002).

The morphological and functional traits of *Drunella* are very different from those of *Glossosoma* (Dahl and Peckarsky 2002; McNeely et al. 2007). *Drunella* nymphs are larger and have no case, and their longer legs may allow them to crawl over filamentous mats

with less difficulty compared to *Glossosoma*. *Drunella* also dislodged periphyton in a manner that *Glossosoma* did not. We observed *Drunella* individuals “bulldozing,” or detaching mat fragments, with their forelegs and heads as they foraged over and through filamentous mats. Non-consumptive removal by benthic grazers can be an important source of periphytic loss (Scrimgeour et al. 1991; Merten et al. 2010), and we hypothesize that by clearing filamentous mats and opening up space, *Drunella* allowed *Glossosoma* to more effectively forage and grow.

Our survey of the upper Colorado River showed that *Drunella* and *Glossosoma* were abundant on cobbles having velocities $<20 \text{ cm s}^{-1}$, which approximated our slow and medium experimental regimes. Within this range, streambed periphyton presented a mosaic of filamentous algal tuffs interspersed with patches of diatom films. *Drunella* primarily occupied the filamentous tuffs, whereas *Glossosoma* were more abundant on films (T. Wellnitz, pers. obs.). The mats of vigorous green *Ulothrix* that characterized our medium-velocity treatment were less common on the natural streambed, and filamentous mats generally contained more detritus. This may indicate that the relatively “clean” *Ulothrix* mats in our medium-velocity treatment were experimental artifacts. However, vigorous *Ulothrix* filaments may also represent a high-value food resource that is rapidly consumed by grazers. Alternatively, other grazers in the system may have changed the appearance of filamentous mats. Chironomids, for example, are abundant in the Colorado River (Monroe et al. 2005) and could have altered filamentous mat architecture by their case construction and feeding activities (Power 1991; Botts 1993; Wellnitz and Ward 1998). Regardless of these differences, the distribution patterns of *Drunella* and *Glossosoma* on the Colorado River streambed were consistent with our experimental results and suggest that *Glossosoma* avoids filamentous mats in preference to diatomaceous films.

Our study has demonstrated that context-dependent facilitation between benthic grazers can be mediated by periphytic structure. Context dependency is a well-documented phenomenon in streams (e.g., Vaughn et al. 2007; Murdock et al. 2011), and consumer facilitation is known to occur for a variety of benthic organisms (Cardinale et al. 2002; Katano et al. 2007; Colon-Gaud et al. 2010); however, these phenomena are seldom examined together. Positive interactions in

lotic systems are often overlooked (Holomuzki et al. 2010) and may be more common than is generally appreciated (Bruno et al. 2003; Halpern et al. 2007); however, they are rarely examined across environmental gradients. Our study helps underscore the importance of evaluating facilitative and mutualistic interactions over ranges of abiotic conditions and consumer pressure to better understand patterns and processes in benthic communities.

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