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Redundancy among three herbivorous insects across an experimental current velocity gradient

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Abstract We conducted streamside experiments to determine if the ability of herbivorous insects to remove algal periphyton varies with local current velocity. We used two mayfly species (*Baetis bicaudatus* and *Drunella grandis*) and one caddisfly species (*Glossosoma verdoni*), which differ from one another in body morphology and mobility. Periphyton was grown for 30 days on ceramic tiles in constant velocity to create similar initial forage conditions for grazers. Tiles were transferred to three velocity regimes characteristic of the natural streambed: slow (3–5 cm s⁻¹), medium (15–20 cm s⁻¹) and fast (32–41 cm s⁻¹). Four grazer treatments (*Baetis*, *Drunella*, and *Glossosoma* alone, and all species combined) were repeated for each velocity treatment to isolate the effect of local current on grazer ability to crop periphyton. Grazers differed in their abilities to remove periphyton across current treatments. *Glossosoma* removed significantly ($P < 0.05$) more periphyton at fast versus either slow or medium velocities; *Baetis* showed a similar (but non-significant) trend; and, *Drunella* always removed about 75% of periphyton, irrespective of current. At fast current, periphyton removal was equivalent among the species. At medium current, *Drunella* removed significantly more than both *Baetis* and *Glossosoma*, whereas at slow current, *Drunella* removed more than *Baetis*, which removed more than *Glossosoma*. Periphyton removal under the combined three-grazer treatment was similar qualitatively to the combined effects of individual grazers. More periphyton tended to be removed as current increased, with the fast versus slow contrast showing marginal significance ($P = 0.10$). Under all current regimes, the quantity of periphyton removed did not differ from the null model expectation of simple additive effects

among individual grazers (i.e., no facilitation or inhibition). These experiments show that for some species, herbivory varies with current, which suggests that the herbivore “function” of cropping periphyton may vary with the environmental context of local current. Under some local velocities, however, different herbivore species “function” similarly and are potentially redundant with respect to periphytic removal. In naturally heterogeneous streams characterized by sharp gradients in local current velocity, we expect current-dependent species interactions to be common and at least partially contribute to intra-guild co-existence of species.

Keywords Context-dependency · Current velocity · Functional redundancy · Herbivory · Heterogeneity

Introduction

Ecologists have long appreciated that physical environmental conditions can influence the performance of species and thus regulate many ecological processes and patterns (e.g., Connell 1961; Dayton 1971; Menge and Olson 1990; Dunson and Travis 1991; Bertness and Callaway 1996; Power et al. 1996; Reser and Bernardo 1998; Hart and Finelli 1999). Because heterogeneity in environmental conditions is characteristic of most natural ecosystems, this recognition has numerous implications for understanding process-pattern relationships, such as herbivory and energy flow (Huntly 1991), coexistence and local diversity (Menge and Sutherland 1987; Werner and McPeck 1994), resource regulation by keystone species (Menge et al. 1994; Power et al. 1996), top-down versus bottom-up structuring of ecosystems (Hunter and Price 1992; Leonard et al. 1998), and species functional redundancy and ecosystem performance (Johnson et al. 1996; Huston 1997). A more careful examination of the frequency and magnitude of “context-dependency” in heterogeneous ecosystems is needed to help ecologists formulate valid generalizations of the importance of species interactions in structuring ecolog-

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ical communities or regulating community processes within and among ecosystems (Power et al. 1996).

Stream ecosystems are characterized by a high degree of spatial and temporal variability in many environmental factors (Allan 1995). Among these, current velocity is a physical factor that directly influences the performances of both producer and consumer species, and it has the clear potential to regulate the outcomes of species interactions (see review by Hart and Finelli 1999). A growing number of lotic studies illustrate that the strength and outcome of biotic interactions and processes can depend on current velocity conditions, e.g., interspecific competition (Fausch and White 1981), predation (Peckarsky et al. 1990; Hansen et al. 1991; Hart and Merz 1998), grazing ability (Hart 1992; Power 1992; Poff and Ward 1995), and sediment removal (Flecker 1997).

Stream herbivory typically occurs on sunlit streambeds, where topographic variation interacts with flowing water to create great spatial heterogeneity in nearbed flows (e.g., Poff and Ward 1992; Hart et al. 1996). Current imposes strong, direct energetic and ecological constraints on both algae and herbivores. For example, algal production, species composition, and physiognomy vary along current gradients (Stevenson 1996). For invertebrates, respiratory stress is related to local flow (Wiley and Kohler 1980) and individual foraging behavior and grazer density can reflect local current (e.g., Poff and Ward 1992). Grazers strongly regulate algal communities and production (see Feminella and Hawkins 1995;


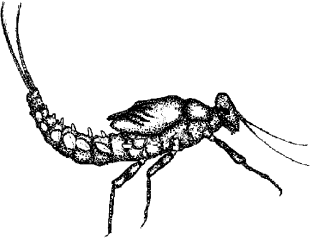

Steinman 1996), yet the extent to which this effect *depends* on current is poorly understood (Stevenson 1996), in large part because current has rarely been incorporated as an experimental variable in studies on stream herbivory (Feminella and Hawkins 1995).

Understanding how herbivory varies as a function of spatial heterogeneity may inform ecologists about the extent to which species within a guild perform the same ecological function. The notion of functional redundancy has received much recent attention (e.g., Walker 1992; Johnson et al. 1996; Huston 1997; Wellnitz and Poff 2001), but it has not been rigorously examined for many systems, including streams. If guild members perform the same functional role (e.g., efficiency in regulating primary production or producer biomass), then they could be considered as being substitutable for one another (e.g., Frost et al. 1995; Covich 1996). For herbivorous stream insects, substitutability or redundancy could be inferred if different species are equivalent in their ability to remove algae. However, such redundancy might be condition specific if, for example, the relative abilities of individual grazer species to regulate algae changed across an environmental gradient (Wellnitz and Poff 2001). The degree of redundancy among co-existing stream herbivores across gradients of current velocity gradient is unknown.

In this study, we tested hypotheses related to abilities of co-existing herbivore insects to regulate periphytic biomass across a range of current velocities typical of

Table 1 Characteristics of the three grazer species used in this study. Illustrations of the grazers are not to scale, but are presented to show the distinct morphology of each species. The *Biomass* column shows the mean (and range of) size of the grazers. *Mode of movement* indicates each grazer's relative speed, and primary means, of movement across the streambed. *Mode of feeding*

indicates the mouth or body parts known (for *Glossosoma* and *Baetis*; see Arens 1989) or observed (for *Drunella*) to remove periphyton from substrates. *Current range* shows the mean (and range of) velocity and the number of observations made for each grazer in the upper Colorado River

Grazers	Biomass (mg indiv. ⁻¹)	Mode of movement	Mode of feeding	Current range (cm s ⁻¹)
	1.02 (0.57–1.29)	Slow crawler, non-drifter	Scraping (mandibles)	26 (2–67), n=44
	1.00 (0.61–1.21)	Fast crawler and swimmer, frequent drifter	Shearing (mandibles + maxilla)	29 (2–74), n=20
	1.90 (1.81–1.92)	Slow crawler, infrequent drifter	Scraping + shearing (maxilla + mandibles + leg movements)	26 (4–64), n=17

their natural habitats. Specifically, we asked three questions: (1) Does the ability of a grazer species to reduce periphyton biomass vary with current velocity? (2) Do different species respond similarly in their ability to remove biomass as current velocity changes? (3) When multiple grazer species forage together, is their interactive removal effect on algae greater or less than the sum of their individual removal effects and does this change with current velocity? We used three widespread and abundant insect species that differ in several attributes important to foraging efficacy across a current velocity gradient: body morphology, mobility, body size, and foraging mode (see Materials and methods, Table 1). To isolate the effect of current, we experimentally grew algae under one velocity before transfer to the three target velocities for short-term exposure to individual and combined grazer species.

Materials and methods

Grazer species

The three grazer species used in this study co-exist in the upper Colorado River and overlap in terms of the local velocity conditions where they are found (see Table 1). These species constitute >65% of the benthic grazer biomass in the stream in the late fall (T.A. Wellnitz, unpublished data), but differ substantially in their morphologies and behaviors (Table 1; also see Merritt and Cummins 1996). *Baetis bicaudatus* has a fusiform body shape and is a strong swimmer, traits that allow it to move easily between resource patches in fast-flowing water (Kohler 1992). *Drunella grandis* is a large, slow-crawling mayfly adapted for clinging and resisting displacement in fast flows. *Glossosoma verdoni* is a caddisfly that builds a tortoise-shaped case composed of large sand grains. It crawls slowly over substrates, and its bulky and high profile case probably reduces its maneuverability as local current increases (cf. Poff and Ward 1992).

Experimental design

The foraging experiments were conducted over a 3-day period in October 2000 in streamside channels along the banks of the upper Colorado River. These channels permitted control of current velocity and grazer composition and abundance, so that periphyton (live algae, microbes, and detritus) responses could be unambiguously interpreted in terms of treatment variables. For the 30 days prior to the experiment, algae colonized small, square ceramic tiles (6.45 cm²) that paved the bottoms of three linear streamside channels that matched streambed light intensities (validated with a LI-COR PAR quantum sensor). Stream water was pumped into an elevated holding tank that drained via gravity to the channels. Tank water was well mixed and had a residence time of <5 min, which maintained water temperatures within 1°C of ambient stream temperatures. Bulk flow through each channel was adjusted to create a relatively narrow range of current across all tiles, as determined from average velocities taken at ten points. Current speed was measured on tile surfaces with a 10-mm diameter Schiltknecht velocity probe, by taking a 6-s reading. Depth ranged between 2 and 3 cm across the channels.

To create similar initial periphytic conditions for the grazing experiments, all tiles were colonized at a common, intermediate velocity (17–19 cm s⁻¹) and occasional, small grazers (baetids, chironomids) that immigrated into the channels were removed with forceps. Further, developing periphyton mats were lightly brushed with a soft bristle brush every few days to create homogeneous mats among individual tiles; this process also served to prevent

periphyton biomass from becoming very large in the ungrazed growth channels.

After the 30-day colonization, tiles were transferred to circular channels for the 3-day grazing experiment. These channels, based on the design of Peckarsky et al. (1994), were constructed from two cylinders of PVC pipe mounted concentrically on a PVC base to create a 210-cm² raceway area. Water drained through a 1-mm mesh screen near the top of the smaller, internal cylinder and then out through a hole in the bottom PVC plate. The screens were brushed twice daily to remove algae and detritus. A piece of nylon stocking was fitted over the drain to quantify any invertebrate emigration from each channel.

The 93 channels used were divided into three current velocity treatments to span a range of velocities inhabited by the grazer species: “slow” (3–5 cm s⁻¹), “medium” (15–20 cm s⁻¹), and “fast” (32–41 cm s⁻¹). Stream water feeding two jets on opposite sides of each circular channel (from the gravity-fed plumbing system) were adjusted to create the desired within-channel current regime, which was quantified by measuring flow within 10 mm of the bottom at 14 points. The bottom was paved with 15 algae-colonized tiles, haphazardly selected from the colonization channels. Water temperatures in the grazing channels remained within 1°C of those measured in the river.

Five grazing treatments were employed for each current regime: independent foraging by *Baetis* (five replicates), *Drunella* (eight replicates), and *Glossosoma* (eight replicates), a three-way combination of all grazers (four replicates), and an ungrazed control (six replicates). These replicated grazer treatments were repeated for each of the three current velocities.

We held grazer biomass constant for each of the four grazing treatments, in order to assess mass-specific grazing effects of the different species. Holding grazer biomass constant allowed us to standardize grazer effects across species and assess their functional redundancy in terms of periphyton removal. We estimated mean ambient streambed biomass for these three grazers combined by separately collecting eight stones from a range of current velocities on the streambed. Stone surface area (upper surface) was estimated using the aluminum foil method (see Steinman and Lamberti 1996). All individuals from each of the three species were preserved in 5% formalin in the field, and then divided in the laboratory into two size classes (large individuals and “others”). Ten individuals in each size class were randomly selected and dried for 24 h to determine the average dry mass of individuals in each size class. From this information, we determined the number of large individuals for each species needed to equal total ambient, combined biomass for the three grazer species and across all size classes.

Estimates of ambient total grazer biomass for the eight stones ranged from 0.007 to 4.19 mg cm⁻² (mean=0.019). The size ranges of individuals for the three species are given in Table 1. At the beginning of the grazer experiment, large individuals of each of the three species were collected live from the stream, and sorted by size class on the stream bank. We selected individuals from the large size class for each species and distributed them to the channels according to the biomass estimates described above (see Table 1). Keeping biomass constant among the four grazer treatments required the following numbers of large individuals to be used in each: *Baetis* alone (18 individuals), *Glossosoma* alone (18 individuals), *Drunella* alone (10 individuals), *Baetis* + *Glossosoma* + *Drunella* (6, 6, and 3 individuals, respectively). None of the individuals used were close to either emergence (mayflies) or pupation (*Glossosoma*).

No immigration was observed into our channels; however, some emigration of *Baetis* and *Glossosoma* (which abandoned cases) did occur. Escapees were captured in the emigration trap and replaced daily with newly captured individuals from the stream. Similarly, dead individuals or case-free *Glossosoma* observed during daily inspections were immediately replaced. Average replacement proportions were 10% for *Baetis* (8% for slow, 6% for medium, and 16% for fast currents), 4% for *Glossosoma* (7% for slow, 2% for medium, and 3% for fast currents), and <1% for *Drunella*.

Tiles were grazed for 3 days to minimize divergence of initially-similar periphytic communities placed in different current regimes. Six tiles from each channel were collectively preserved in 5% formalin to determine periphytic ash-free dry mass (AFDM) using standard methods (APHA 1992). Initial periphytic biomass on foraging tiles was compared to final biomass for ungrazed control tiles to assess whether periphyton diverged during the 3-day exposure to different current velocity conditions.

We used two-way ANOVA to analyze the effects of current velocity and grazer treatment on periphytic AFDM. We calculated grazer effect size as $(\text{ungrazed control AFDM at day 3} - \text{grazed AFDM at day 3}) / (\text{ungrazed control AFDM at day 3})$, where the ungrazed AFDM was calculated from the mean of the ungrazed replicates for that current regime. Because periphytic biomass increased similarly among ungrazed current velocity treatments during the 3-day experiment (see below), we assumed that differences between grazed and ungrazed periphyton mats reflect grazer treatments alone. Percentage data were arcsine-transformed to meet assumptions of homogeneity of variance and normality, as determined by Bartlett's and Shapiro-Wilks tests, respectively. Multiple comparisons were made using Tukey's test (Zar 1984).

Multi-species grazing

Because natural periphyton communities typically experience grazing from multiple herbivores, we wished to evaluate whether multiple grazers foraging together had a different effect on periphyton removal compared to individual grazer species across a current velocity gradient. As a null model for the combined effects of "multiple predator effects" (sensu Sih et al. 1998), we used a multiplicative risk model developed by Soluk and Collins (1988) (see also Soluk 1993; Sih et al. 1998). The prediction of this model is that the combined effect of multiple grazers is simply the summation of individual grazer effects and their linear interactions; deviation from this expectation indicates higher order (nonlinear) grazer interactions such as facilitation or interference (Sih et al. 1998). The model, for each current velocity treatment, is written as

$$P_{abc} = P_A + P_B + P_C - P_AP_B - P_AP_C - P_BP_C - P_AP_BP_C$$

where P is the proportion of periphyton removed by individual or combined grazers ($A = \text{Drunella}$, $B = \text{Baetis}$, and $C = \text{Glossosoma}$).

Because we kept biomass constant across all treatments, we applied a mathematical correction factor to account for the fact that the densities of the combined grazer treatment were not equivalent to the sum of the individual grazer treatments combined. The coefficients for the individual grazer terms reflect the biomass adjustments required due to the difference in number of individuals used in the single species versus combined species trials (i.e., $a = 3/10$ for *Drunella*, $b = 6/18$ for *Baetis* and $c = 6/18$ for *Glossosoma*). Thus, the "corrected" multiplicative risk model is written as

$$P_{ABC} = aP_A + bP_B + cP_C - abP_AP_B - acP_AP_C - bcP_BP_C - abcP_AP_BP_C$$

Use of a correction factor makes the assumption of no density dependence in the per capita grazing rate for individual grazers. We cannot directly evaluate the validity of this assumption; however, there are distinct advantages to our approach. First, using higher densities (i.e., 10 *Drunella* + 18 *Baetis* + 18 *Glossosoma*) would confound density with grazer treatment, a common problem in assessing multiple predator effects (see Sih et al. 1998). Second, because we ran the experiment for 3 days, using 46 individuals in the small mesocosms could have resulted in significant resource depletion and thus an effective reduction in potential per capita consumption, thereby masking grazer interaction effects. Third, our initial motivation for maintaining constant biomass across the individual and combined grazer treatments was to allow for a direct evaluation of functional redundancy, which would have been greatly complicated by confounding density with grazer treatment.

The observed three-species grazing effect (P_{ABC}) was calculated for the four replicates (as described above for the individual grazer

terms). The two-way and three-way interaction terms were estimated as products of the observed individual grazer effects. For each model and for each of the three current velocity treatments, a t -test (on arcsine-transformed data) was used to determine whether the expected proportion of periphyton consumed (null model prediction) differed from the observed three-species grazing effect (P_{ABC}). A significant difference would result in rejection of the null model and indicate deviation from simply additive grazer effects (e.g., facilitation, interference). Because our replication was low ($n = 4$) for each current treatment, we followed Sih et al.'s (1998) advice and calculated statistical power ($1 - \beta$) using an internet-based power calculator at <http://calculators.stat.ucla.edu/powercalc/>.

Results

Initial periphytic biomass on foraging tiles (i.e., after 30 days of colonization) was $0.215 \pm 0.02 \text{ mg cm}^{-2}$ (mean \pm SE, $n = 12$). After 3d of additional growth in the ungrazed controls, AFDM increased 4 to 5-fold, but with no significant differences attributed to current alone ($F_{2, 83} = 1.81$, $P = 0.17$, Fig. 1). Because periphytic biomass did not diverge after transfer to new current regimes, differences among grazing treatments can be attributed directly to current velocity and not to differences in resources.

Grazers significantly reduced AFDM across all current treatments (Fig. 1). The overall mean effect of grazing (averaged across grazing treatments) was highly significant ($F_{1, 83} = 86.84$, $P < 0.0001$), and there were differences among current treatments, as indicated by a significant grazer \times current interaction ($F_{2, 83} = 3.28$, $P = 0.04$), with the greatest reduction occurring in fast velocity (Tukey's $P = 0.045$).

AFDM removal also varied depending on specific grazer treatment and current velocity. The main effect of grazer treatment was highly significant ($F_{3, 62} = 30.21$, $P < 0.0001$), as was current treatment ($F_{2, 62} = 23.91$, $P < 0.0001$) and their interaction ($F_{6, 62} = 3.94$, $P = 0.002$). Among the different grazing treatments (Fig. 2A), *Drunella* removed more periphyton than *Baetis* or *Glossosoma* (Tukey's, $P < 0.001$ for both comparisons),

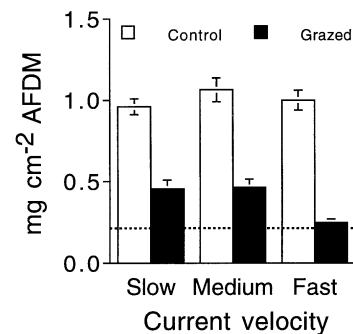


Fig. 1 Periphyton response after 3 days of either no grazing (controls, $n = 4$ per treatment) or to all grazers ($n = 4-8$ per treatment, see text) for each of three current velocity treatments. Error bars are \pm SE for untransformed data. Dashed line represents initial periphytic ash free dry mass at onset of 3-day foraging trials

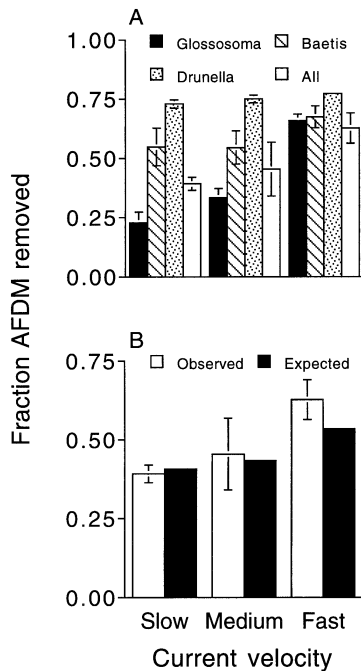


Fig. 2 Fraction of periphyton removed (\pm SE for arcsin-transformed fractional data) **A** over a 3-day period in response to grazer treatment and current velocity, and **B** by combined three-grazer treatment (same as in **A**) compared to that expected under the multiplicative risk model (see text). Error bars not shown in **A** are too small to depict

whereas *Baetis* removed more than *Glossosoma* (Tukey's, $P < 0.001$). Among the velocity treatments (Fig. 2A), more AFDM was removed at fast (Tukey's, $P < 0.0001$) than at either medium or slow velocity, which were equivalent to each other.

The interaction between grazing and current revealed that individual grazer species responded differently to current (Fig. 2A). *Glossosoma* removed more AFDM at fast velocity (Tukey's, $P < 0.001$) than at either slow or medium, which were not significantly different from each other. Neither *Baetis* nor *Drunella* showed a significant difference in AFDM reduction across current treatments, although *Baetis* (with a replication of only $n=5$) exhibited a trend for more reduction in fast velocity (Fig. 2A). As velocity increased, all grazer species converged toward high AFDM reduction. At slow velocity, *Glossosoma* removed less than either *Baetis* (Tukey's, $P=0.02$) or *Drunella* (Tukey's, $P < 0.001$); at medium velocity, *Glossosoma* and *Baetis* removed less than *Drunella* (Tukey's, $P=0.03$); and at fast velocity, all species were equivalent in AFDM reduction.

For the multi-grazer treatment there was a trend of greatest reduction in AFDM occurring at faster velocities; however, this was not significant at the $\alpha=0.05$ level (e.g. Tukey's $P=0.097$ for slow vs fast comparison; Fig. 2A). No differences were found in periphyton removed by all 3 grazers compared to either *Baetis* or *Glossosoma* alone ($P > 0.50$); however, all grazers combined removed less in

periphyton in slow ($P < 0.001$) and medium ($P=0.003$) but not fast ($P > 0.30$) flows.

The observed proportion of periphytic AFDM removed was not significantly different from that expected under the multiplicative risk model, as shown in Fig. 2B. Thus, there was no direct evidence for non-additive grazer interactions under any current velocity regime. However, statistical power to detect a real deviation from the null expectation was low for all current treatments, ranging from $<10\%$ for both slow and medium velocities to about 40% for fast velocity (where mean effect size was larger).

Discussion

Context-dependent herbivory

Previous experimental studies on stream herbivory have largely ignored the issue of how herbivory may vary across important environmental gradients such as current velocity (see review in Feminella and Hawkins 1995). Only a handful of studies have used current as an experimental variable, and these have focused on only one grazer species (Vaughn 1986; DeNicola and McIntire 1991; Welton et al. 1991; Hart 1992; Power 1992; Poff and Ward 1992, 1995). Similarly, a few studies have examined variation in herbivory across other environmental gradients such as light intensity, which directly affects algae, but not herbivores (but see Bothwell et al. 1994). Only rarely have these studies focused on more than one species (Wellnitz and Ward 1998, 2000). Thus, to our knowledge, this is the first study to experimentally demonstrate the effects of multiple grazers (both independently and interactively) on periphytic communities across a critical environmental gradient in streams, current velocity.

The differences among individual grazer species in effectiveness at removing periphyton across a velocity gradient most likely reflect an interaction between grazer species traits and conditions prevailing in the different current treatments. A mechanistic explanation for our results is difficult, however, because of the general paucity in the literature of studies examining how aquatic insect performance changes as a function of local current conditions.

Drunella consistently removed relatively large quantities of periphyton, irrespective of current. This robust clinger species (sensu Merritt and Cummins 1996) is adept at crawling slowly in a wide range of velocities without being displaced (J.B. Monroe, personal observation). It is also capable of dislodging attached algae non-consumptively as it moves across the substrate (T.A. Wellnitz, unpublished data), which may help explain its relatively large effect on periphytic removal.

Interestingly, *Baetis* efficacy also did not differ significantly among velocity treatments. This highly mobile mayfly is able to actively enter the water column and swim to find new food patches (Kohler 1992; Palmer 1995), thus its foraging ability might not be constrained

across the range of currents used in this experiment. However, we do note that *Baetis* removed 15% more periphyton biomass in the fast versus slow or medium current treatments (Fig. 2A), albeit this difference was not significant, due to low replication and high variance. Speculatively, *Baetis* may be less efficient at foraging in slower velocities, where it must rely on more active swimming as opposed to passive drifting to find algal patches (J.B. Monroe, personal observation).

Glossosoma exhibited a strong response to current, showing a consistent increase in foraging efficacy with increasing velocity. This intriguing result was not expected. Previous work in this system has shown that glossosomatids are constrained in their movement rates and directions by faster flows (Poff and Ward 1992). This, combined with the presumed drag on the high-profile *Glossosoma* mineral case, led us to expect that AFDM reduction by this species would *decline* as current increased. One possibility is that at slow velocities individuals were physiologically stressed by low dissolved oxygen, as has been shown elsewhere for other glossosomatid species (Kovalak 1976). However, in the cool upper Colorado River, river water is nearly always completely saturated with oxygen (N.L. Poff, unpublished data). Further, *Glossosoma* individuals did not abandon their cases in high numbers at slow (7%) versus medium (2%) or fast (3%) velocities in our experiment, suggesting “suitable” respiratory conditions.

An alternative hypothesis for our finding is that similar periphytic mats under high velocity may simply have been more amenable to foraging. Our periphytic mats were similar in biomass across velocity treatments (see Fig. 1) and, based on previous experience with experimentally-grown algal mats in this system (e.g., Poff et al. 1990; Poff and Ward 1995; T.A. Wellnitz, unpublished data), we expect they consisted of a mix of chlorophytic and diatom filaments that would likely lay flat under the force of moving water. We have observed *Glossosoma* to experience difficulty in dragging its bulky case over more upright algal mats as it forages; therefore, movement and foraging by this grazer may have been facilitated at higher flows, as a function of current impingement on mat uprightness.

Finally, because *Glossosoma* does occur in the stream at velocities greater than what we tested experimentally (see Table 1), we may not have created fast enough flow conditions to induce a decline in *Glossosoma* foraging ability. The same would be equally true for *Baetis* and even *Drunella*.

When foraging together, the three grazers showed, at best, only suggestive evidence for non-additive foraging, and only for the fast velocity, where the deviation of the observed foraging effect from the multiplicative risk model prediction was greatest (Fig. 2B). The size of the deviation was, however, small and our low replication ($n=4$) limited statistical power to detect a real difference ($1-\beta=ca. 40\%$). A sample size of at least $n=7$ would be needed to detect a real difference at $\alpha=0.05$ and 95% power. Beyond this, one of the assumptions of the

multiplicative risk model is that prey are not replaced during bouts of predation (Soluk and Collins 1988; Sih et al. 1998). However, in algal-grazer systems, algae can replenish themselves through growth and immigration, as seen in Fig. 1 for the ungrazed controls. Masking of depletion rates by algal renewal may make it difficult to test the multiplicative risk model for algal-grazer systems, much as high flux rates of mobile prey may mask predator effects in cage experiments (cf. Cooper et al. 1990).

Functional redundancy among herbivorous insects?

One of the more important implications of context dependency relates to the issue of functional redundancy among species in the same nominal guild (e.g., “herbivores”). The question of whether species are substitutable for one another, or whether they perform the same “function” is one of great interest among ecologists (e.g., Lawton and Brown 1994; Frost et al. 1995; Covich 1996; Johnson et al. 1996; Huston 1997), but it has received little experimental attention in streams (but see Cardinale et al. 2002). If function is defined in terms of ability to regulate periphytic biomass, then our experiments provide some evidence that herbivore function can vary with current velocity. Because different species vary in their abilities to regulate periphytic biomass across the velocity gradient, the degree of “redundancy” among species depends on the environmental context, as evidenced in this experiment by all 3 species being similarly efficient (*Drunella* = *Baetis* = *Glossosoma*) at high velocity but not at medium (*Drunella* > *Baetis* = *Glossosoma*) or at slow (*Drunella* = *Baetis* > *Glossosoma*) (Fig. 2A). If grazer effects on periphytic biomass shift along a current gradient, then functional redundancy may itself be context-dependent, and references to “redundancy” may require specification of the particular environmental conditions (see Wellnitz and Poff 2001).

Implications for stream ecology

An issue confronting any experimental study is the question of how applicable the results are to a real community (Resetarits and Bernardo 1998). Our experiments were performed in simpler environments than those found in the natural stream to gain specific understanding of how local current regulates herbivory. By showing that grazer species ability to crop algae can vary with current, we provide an empirical foundation on which to base further questions and hypotheses in more complex systems (see Peckarsky 1998). Streams are very heterogeneous systems, yet the significance of this heterogeneity for a wide variety of process-pattern relationships is only poorly understood (Palmer and Poff 1997; Cooper et al. 1998). One oft-cited consequence of habitat heterogeneity is that it promotes species coexistence by providing a wide range of resources and conditions, and precludes dominance by only a few

species. There is growing evidence that a variety of species interactions in streams are dependent on current velocity context (see review by Hart and Finelli 1999). Other environmental gradients may also provide important sources of context-dependency in streams (e.g., light – see DeNicola and McIntire 1991; Wellnitz et al. 1996; Wellnitz and Ward 1998, 2000). Given the high heterogeneity of stream systems, we suspect that context-dependent interactions are common in these systems, but without directed experimentation, they are likely to go undetected (Power et al. 1996). Gaining a better understanding of the ecological organization in streams will require more explicit experimental incorporation of current velocity, a ubiquitous and defining physical variable in streams.

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References

- Allan JD (1995) Stream ecology: structure and function of running waters. Chapman and Hall, London
- APHA (American Public Health Association) (1992) Standard methods for the examination of water and wastewater, 18th edn. Washington, DC.
- Arens W (1989) Comparative functional morphology of the mouthparts of stream animals feeding on epilithic algae. Arch Hydrobiol [Suppl] 83:253–354
- Bertness MD, Callaway R (1996) Positive interactions in communities. Trends Ecol Evol 9:191–193
- Bothwell ML, Sherbot DMJ, Pollock CM (1994) Ecosystem response to solar ultraviolet-B radiation: influence of trophic-level interactions. Science 265:97–100
- Cardinale BJ, Palmer MA, Collins SL (2002) Species diversity enhances ecosystem functioning via interspecific facilitation. Nature 415:426–429
- Connell JH (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology 42:710–723
- Cooper S, Walde S, Peckarsky B. (1990) Prey exchange rates and the impact of predators on prey populations in streams. Ecology 71:1503–1514
- Cooper SD, Diehl S, Kratz K, Sarnelle O (1998) Implications of scale for patterns and processes in stream ecology. Aust J Ecol 23:27–40
- Covich AP (1996) Stream biodiversity and ecosystem processes. Bull N Am Benthol Soc 13:294–303
- Dayton PK (1971) Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol Monogr 41:351–389
- DeNicola DM, McIntire CD (1991) Effects of hydraulic refuge and irradiance on grazer-periphyton interactions in laboratory streams. J North. Am Benthol Soc 10:251–262
- Dunson WA, Travis J (1991) The role of abiotic factors in community organization. Am Nat 138:1067–1091
- Fausch KD, White RJ (1981) Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. Can J Fish Aquat Sci 38:1220–1227
- Feminella JW, Hawkins CP (1995) Interactions between stream herbivores and periphyton: a quantitative analysis of past experiments. J North Am Benthol Soc 14:465–509
- Flecker AS (1997) Habitat modification by tropical fishes: environmental heterogeneity and the variability of interaction strength. J North Am Benthol Soc 16:286–295
- Frost TM, Carpenter SR, Ives AR, Kratz TK (1995) Species compensation and complementarity in ecosystem function. In: Jones CG, Lawton JH (eds.) Linking species & ecosystems. Chapman and Hall, New York, pp 224–239
- Hansen RA, Hart DD, Merz RA (1991) Flow mediates predator-prey interactions between triclad flatworms and larval black flies. Oikos 60:187–196
- Hart DD (1992) Community organization in streams: the importance of species interactions, physical factors, and chance. Oecologia 91:220–228
- Hart DD, Finelli CM (1999) Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms. Annu Rev Ecol Syst 30:363–395
- Hart DD, Merz RA (1998) Predator prey interactions in a benthic stream community: a field test of flow-mediated refuges. Oecologia 114:263–273
- Hart DD, Clark BD, Jasentuliyana A (1996) Fine-scale field measurement of benthic flow environments inhabited by stream invertebrates. Limnol Oceanogr 41:297–308
- Hunter MD, Price PW (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73:724–732
- Huntly NJ (1991) Herbivores and the dynamics of communities and ecosystems. Annu Rev Ecol Syst 22:477–504
- Huston MA (1997) Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. Oecologia 110:449–460
- Johnson KH, Vogt KA, Clark HJ, Schmitz OJ, Vogt DJ (1996) Biodiversity and the productivity and stability of ecosystems. Trends Ecol Evol 11: 372–377
- Kohler SL (1992) Competition and the structure of a benthic stream community. Ecol Monogr 62:165–188
- Kovalak WP (1976) Seasonal and diel changes in the positioning of *Glossosoma nigrior* Banks (Trichoptera: Glossosomatidae) on artificial substrates. Can J Zool 54:1585–1594
- Lawton JH, Brown VK (1994) Redundancy in ecosystems. In: Schulze ED, Mooney HA (eds.) Biodiversity and ecosystem function. Springer, Berlin Heidelberg New York, pp 255–270
- Leonard GH, Levine JM, Schmidt PR, Bertness MD (1998) Flow driven variation in intertidal community structure in a Maine estuary. Ecology 79:1395–1411
- Menge BA, Olson AM (1990) Role of scale and environmental factors in regulation of community structure. Trends Ecol Evol 5:52–57
- Menge BA, Sutherland JP (1987) Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. Am Nat 130:730–757
- Menge BA, Berlow EL, Blanchette CA, Navarrete SA, Yamada SB (1994) The keystone species concept: variation in interaction strength in a rocky intertidal habitat. Ecol Monogr 64:249–286
- Merritt RW, Cummins KW (eds) (1996) An introduction to the aquatic insects of North America, 3rd edn. Kendall/Hunt, Dubuque, Iowa
- Palmer MA, Poff NL (1997) The influence of environmental heterogeneity on patterns and processes in streams. J North Am Benthol Soc 16:169–173
- Palmer TM (1995) The influence of spatial heterogeneity on the behavior and growth of two herbivorous stream insects. Oecologia 104:476–486
- Peckarsky BL (1998) The dual role of experiments in complex and dynamic natural systems. In: Resetarits WJ Jr, Bernardo J (eds)

- Experimental ecology: issues and perspectives, Oxford University Press, New York, pp 311–324
- Peckarsky BL, Horn SC, Stutzner B (1990) Stonefly predation along a hydraulic gradient: a field test of the harsh-benign hypothesis. *Freshw Biol* 24:181–191
- Peckarsky BL, Cowan CA, Anderson CR (1994). Consequences and plasticity of the specialized predatory behavior of stream-dwelling stonefly larvae. *Ecology* 75:166–181
- Poff NL, Ward JV (1992) Heterogeneous currents and algal resources mediate *in situ* foraging activity of a mobile stream grazer. *Oikos* 65:465–478
- Poff NL, Ward JV (1995) Herbivory under different flow regimes: a field experiment and test of a model with a benthic stream insect. *Oikos* 71:179–188
- Poff NL, Voelz NJ, Ward JV, Lee RE (1990) Algal colonization under four experimentally-controlled current regimes in a high mountain stream. *J North Am Benthol Soc* 9:303–318
- Power ME (1992) Habitat heterogeneity and the functional significance of fish in river food webs. *Ecology* 73: 1675–1688
- Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla UC, Lubchenco J, Paine RT (1996) Challenges in the quest for keystones. *BioScience* 46:609–620
- Reseratis WJ Jr, Bernardo J (eds) (1998) *Experimental ecology: issues and perspectives*. Oxford University Press, New York
- Sih A, G Englund, D Wooster (1998) Emergent impacts of multiple predators on prey. *Trends Ecol Evol* 13: 350–355
- Soluk DA (1993) Multiple predator effect: predicting combined functional response of stream fish and invertebrate predators. *Ecology* 74: 219–225
- Soluk DA, Collins NC (1988) Synergistic interactions between fish and stoneflies: facilitation and interference among stream predators. *Oikos* 52: 94–100
- Steinman AD (1996) Effects of grazers on freshwater benthic algae. In: Stevenson JR, Bothwell ML, Lowe RL (eds) *Algal ecology: freshwater benthic ecosystems*. Academic Press, New York, pp 341–374
- Steinman AD, Lamberti GA (1996) Biomass and pigments of benthic algae. In: Hauer FR and GA Lamberti, (eds.) *Methods in stream ecology*. Academic Press, San Diego, Calif. pp 295–313
- Stevenson RJ (1996) The stimulation and drag of current. In: Stevenson JR, Bothwell ML, Lowe RL (eds.) *Algal ecology: freshwater benthic ecosystems*. Academic Press, New York, pp 321–340
- Vaughn CC (1986) The role of periphyton abundance and quality in the microdistribution of a stream grazer, *Helicopsyche borealis* (Trichoptera: Helicopsychidae). *Freshw Biol* 16:485–493
- Walker, BH (1992) Biological diversity and ecological redundancy. *Conserv Biol* 6:18–23
- Wellnitz TA, Poff NL (2001) Functional redundancy in heterogeneous environments: implications for conservation. *Ecol Lett* 4:177–179
- Wellnitz TA, Ward JV (1998) Does light intensity modify the effect mayfly grazers have on periphyton? *Freshw Biol* 39:135–159
- Wellnitz TA, Ward JV (2000) Herbivory and irradiance shape periphytic architecture in a Swiss alpine stream. *Limnol Oceanogr* 45:64–75
- Wellnitz TA, Rader R, Ward JV (1996) Light and a grazing mayfly shape periphyton in a Rocky Mountain stream. *J North Am Benthol Soc* 15:496–507
- Welton JS, Ladle M, Bass JAB, Clarke RT (1991) Grazing of epilithic chironomid larvae at 2 different water velocities in recirculating streams. *Arch Hydrobiol* 121:405–418
- Werner EE, McPeck MA (1994) Direct and indirect effects of predators on two anuran species along an environmental gradient. *Ecology* 75:1368–1382
- Wiley MJ, Kohler SL (1980) Positioning changes of mayfly nymphs due to behavioral regulation of oxygen consumption. *Can J Zool* 58:618–622
- Zar JH (1984) *Biostatistical analysis*. Prentice Hall, Englewood Cliffs, N.J.