

Herbivory, current velocity and algal regrowth: how does periphyton grow when the grazers have gone?

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SUMMARY

1. An experiment conducted in streamside channels was used to document the regrowth of grazed periphyton. Our objective was to determine the relative importance of current velocity, grazing duration, and grazer type in shaping the trajectory of algal and periphytic regrowth.
2. The grazing mayflies *Baetis bicaudatus* and *Epeorus longimanus* were used alone and in combination to create three grazing treatments at slow, medium and fast current (2–5, 15–20 and 30–40 cm s⁻¹, respectively). Duration treatments consisted of 2, 4, 6, 8, 10 days of grazing. Chlorophyll *a* and ash-free dry mass (AFDM) accumulation on grazed tiles was measured (as periphytic AFDM and chlorophyll *a*, respectively) at 2, 4, 6, 8 and 10 days following the removal of grazers.
3. Chlorophyll *a* and AFDM was best predicted by interactions between current velocity, grazing duration and regrowth time.
4. The two grazer species did not differ in their effect on Chlorophyll *a* and AFDM during the period of periphytic regrowth that followed grazing.
5. Longer grazing duration reduced periphytic biomass, but also accelerated algal regrowth, and this growth enhancement was more pronounced at slower current velocities.
6. Data from this study suggest that herbivory can have important historical effects on periphytic accrual.

Keywords: stream herbivory, current velocity, periphytic removal, *Baetis*, *Epeorus*, historical grazing effects

Introduction

Studies of stream herbivory generally focus on the way in which grazers remove periphyton, not on how it grows back after grazing has occurred (but see DeNicola *et al.*, 1990; Tuchman & Stevenson, 1991). Little is known about what happens to stream periphyton between grazing events, or even how frequent those events are. Patch visitation frequencies in natural streams have been proposed to vary with patch biomass, community composition and renewal rates (Hart, 1981; Kohler, 1983, 1984; Wiley & Kohler, 1984; Hart, Kohler & Carlton, 1991), but actual

durations between grazing events are largely unknown. Nevertheless, it is improbable that grazing pressure is regular and continuous across the entire streambed and visitation times likely vary from minutes to hours to days.

Several factors might influence post-grazing periphytic development in streams. First, current velocity can regulate the levels of subsidy and stress experienced by periphytic communities by simultaneously regulating nutrient uptake rates and shear forces (Biggs, Goring & Nikora, 1998). These antagonistic processes serve as determinants of periphytic architecture and the kinds of algal cells that can successfully colonise and become established on grazed surfaces (e.g. Poff *et al.*, 1990; Stevenson, 1990; Biggs & Hickey, 1994). Secondly, grazing duration influences the extent of periphyton removal and character-

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istics of the mat as it begins to regrow. Although fewer algal cells will remain with increased grazing duration, these cells may have a higher growth potential due to reduced competition for limiting nutrients and less over-story shading (McCormick, 1994). Thirdly, the species of herbivore foraging on a mat may influence post-grazing recovery. Many lotic grazers possess distinctive mouthpart structures and exhibit specialised foraging behaviours (Hill & Knight, 1988; Arens, 1989; Wellnitz & Ward, 1998, 2000), and different modes of foraging can result in dissimilar patterns of periphytic removal. Consequently, different herbivores may impart different 'legacies' in terms of how their grazing affects subsequent regrowth and community succession. The effects of species-specific herbivory on periphytic removal have been well documented in both artificial (e.g. Lamberti *et al.*, 1987; Steinman *et al.*, 1987) and natural (e.g. Hill & Knight, 1988; Feminella & Resh, 1991) streams; however, we are aware of no study that has quantified the effect of specific grazers on periphytic regrowth.

In the present study, we examined the influence of *Baetis* and *Epeorus*, two common, but morphologically distinct mayfly herbivores, on the 2–10 days regrowth of grazed periphyton grown under different current velocities. We define 'regrowth' to mean periphytic and algal biomass accumulation occurring after grazing has ceased. In addition to controlling grazer type and current velocity, grazing duration was manipulated. The objectives of this study were to (1) determine the relative importance of current velocity, grazing duration, and grazer type in regulating periphytic regrowth; and (2) assess if the two grazers, either singly or in combination, influence the rate and amount of periphytic regrowth that occurs. We hypothesised that *Epeorus* grazing would promote more periphyton regrowth when compared with *Baetis* because heptageniid mouthparts are thought to be more effective in removing periphytic overstory layers (Wellnitz & Ward, 1998), and this can lead to enhanced algal productivity (Steinman, 1996).

Methods

The grazers

Epeorus longimanus (Eaton) (Heptageniidae) and *Baetis bicaudatus* (Dodds) (Baetidae) are abundant grazers in

the upper Colorado River during July and August (T. Wellnitz, unpublished data). These two species inhabit overlapping ranges of current in the stream, but differ in morphology and behaviour (Merritt & Cummins, 1996). *Baetis* prefers near-bed current velocities of $<50 \text{ cm s}^{-1}$, whereas *Epeorus* prefers current $>50 \text{ cm s}^{-1}$ (T. Wellnitz, personal observation). *Epeorus* has a clinging mode of existence, possesses a dorsal-ventrally compressed body, and uses sweeping motions of its labial palps to dislodge attached periphyton. *Baetis*, by comparison, is an active swimmer and uses its mouthparts to scrape and gouge periphyton from substrates (Arens, 1989). Whereas *Epeorus* gleans wide swaths of periphyton from substrata with each feeding motion, *Baetis* takes smaller and deeper 'bites'.

Stream grazer survey

To characterise the streambed current velocities inhabited by *Baetis* and *Epeorus* in the upper Colorado River, between 25 July and 10 August 2000, we surveyed the streambed and measured current velocity within 1 cm of 40 individual larvae (c. 0.5–1.0 cm in size) for each species. Sampling points were selected from a streambed riffle by using a 'random walk' technique. Starting from the approximate centre of the riffle, pairs of random numbers were used to determine the distance and direction of each sampling point. If the walk brought the sampler to shore, random number pairs were generated until sampling points were returned to the stream. Once a point was selected, the nearest *Baetis* and *Epeorus* individual to that point was located, and near-bed current velocity was measured with a Schiltknecht current meter (Zürich, Switzerland) which has a temporal resolution of 1 s and a spatial resolution of 10 mm.

Experimental apparatus

Experiments were conducted in an array of 96 small, flow-through, circular streamside channels situated on the bank of the upper Colorado River and described previously in Poff, Wellnitz & Monroe (2003). These channels were constructed from two cylinders of PVC pipe mounted concentrically on a PVC base to create a 210 cm^2 raceway area (Fig. 1). Stream water for the channels was pumped directly from the upper Colorado River into an elevated, 378 L

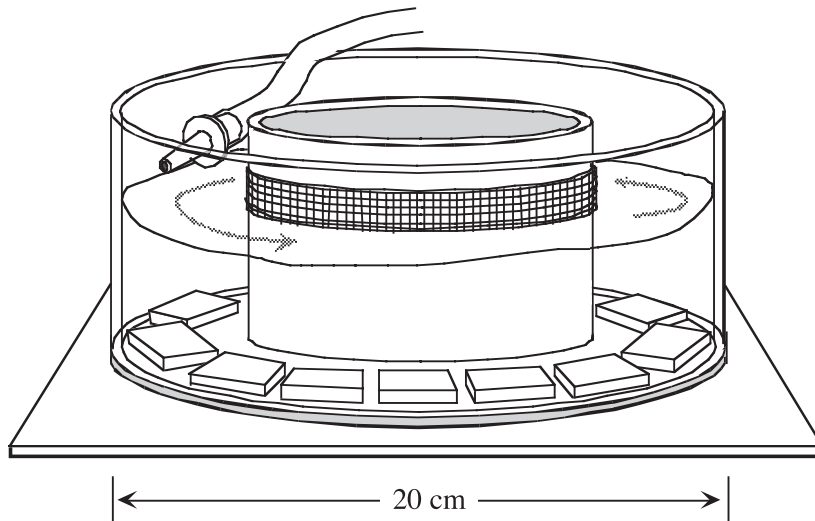


Fig. 1 Design of flow-through circular channels showing water jet, ceramic tiles, drain and scale.

holding tank that drained into to the channel array. Stream water entering the array was directed through a 6 cm diameter PVC pipe fitted with brass spigots along its length. Each spigot was connected to a 40 cm length of Tygon tubing that fed into a plastic jet that projected into the raceway at an acute angle to create flow. Velocities within the channels were maintained within three ranges: 'slow' ($2\text{--}5\text{ cm s}^{-1}$), 'medium' ($15\text{--}20\text{ cm s}^{-1}$), and 'fast' ($30\text{--}40\text{ cm s}^{-1}$). Adjusting individual spigots controlled current, and velocity was measured with the Schiltknecht current meter at 12 points spaced equidistantly along the channel's raceway. Water exchange rates in the experimental channels were rapid, *c.* $1.0\text{--}1.5\text{ L min}^{-1}$, and measured temperatures in the channel differed only $\pm 1\text{ }^{\circ}\text{C}$ from the stream.

Algal colonisation and quantification

Before running the experiment, algae were grown for 30 days, under the three velocity regimes described above, in 12 flow-through channels constructed from PVC rain gutters ($300 \times 10 \times 8\text{ cm}$) paved with small (6.45 cm^2) ceramic tiles. Tiles were colonised with algal propagules from pumped stream water and grown in the absence of grazers and other macroinvertebrates. Consequently, periphytic assemblages were shaped primarily by current velocity until the grazing phase of our experiment began.

At the end of the 30 days, four tiles were sampled from each colonisation channel by removing periphyton with a razor blade and toothbrush, and rinsing it

into a beaker with a wash bottle. These samples were brought up to a constant volume, homogenised, and divided into two sub-samples. The first sub-sample was drawn onto a glass fibre filter (Gelman A/E, Pall Corp. East Hills, NY, U.S.A.) and used to determine ash-free dry mass (AFDM) by taking the difference between dried (at $60\text{ }^{\circ}\text{C}$ for 24 h) and ashed ($480\text{ }^{\circ}\text{C}$ for 2 h) weights. The remaining sub-sample was preserved in 2% formalin and used to determine algal taxonomic composition.

Taxonomic composition was based on a semi-quantitative determination of relative abundance according to each taxon's contribution to sample biovolume. This method is based on the Braun-Blaquet approach widely used in terrestrial vegetation analysis and permits a robust assessment of the main contributors to community biomass (Kershaw, 1973; Biggs & Kilroy, 2000). Relative algal taxon abundance was determined using a four-step scoring system that ranked algae on the basis of their percent contribution to community volume. The ranks were as follows: dominant, $>60\%$; abundant, $60\text{--}30\%$; common, $<30\text{--}5\%$; and rare, $<5\%$. Rankings were done by visually estimating the percentage abundance of the four to six most common taxa within nine fields from each sub-sample. Estimates were made at $125\times$ magnification; identifications of small taxa were checked at higher power ($450\text{--}725\times$).

Experimental procedure

Following the colonisation period, 15 tiles and their associated periphytic assemblages were transferred

from the colonisation channels to the circular, experimental channels having the matching current regime. This gave three sets of 32 circular channels with the appropriate, velocity-grown periphyton for each current velocity treatment. One of four grazer treatments was applied to each set of 32 channels: *Epeorus* alone (10 channels), *Baetis* alone (10 channels), *Epeorus* and *Baetis* in combination (10 channels), and ungrazed controls (two channels). Each grazer treatment was randomly assigned one of five grazing duration treatments: 2, 4, 6, 8 or 10 days. Each current \times grazer \times duration treatment had two replicates (e.g. $3 \times 3 \times 5 \times 2 = 90$), and there were two grazer-free controls for each current velocity treatment ($3 \times 2 = 6$).

We set *Baetis* and *Epeorus* densities for the experimental channels using natural, streambed densities. These densities were determined by collecting 10 large cobbles with a D-frame kick net. Each cobble was carried to shore, placed in an enamel pan, and macro-invertebrates were removed from cobble surfaces and from inside the net. *Baetis* and *Epeorus* individuals were preserved in 5% formalin in the field, and then separated and counted in the laboratory. Sampled cobble surface areas were estimated by wrapping the sampled cobble surface with aluminium foil and trimming off the excess material. The foil was air-dried, weighed and a mass/area relationship was used to determine the sampled cobble area (Steinman & Lamberti, 1996). From this information, we calculated the number of individuals of each species, alone or in combination, needed per channel to equal the mean, ambient streambed density of both grazer species on the streambed. Final densities in channels were *Epeorus* alone, 8; *Baetis* alone, 10; *Epeorus* and *Baetis* in combination, 4 and 5 individuals, respectively.

On 1 July 2001, grazer treatments were applied to the experimental channels. The channels were checked daily to count and replace any mayflies that had escaped or died. When the grazing duration treatment for a channel had ended, the mayflies were removed with forceps (*Epeorus*) or a wide-bore plastic pipette (*Baetis*). On the day grazers were removed, two tiles were sampled. Thereafter, two tiles were sampled every second day for 10 days to monitor algal regrowth following grazing. The longest experimental treatment ran a total of 20 days (10 days grazed; 10 days to recover). Controls were sampled throughout the experiment (20 days), and conse-

quently were sampled more frequently than any grazing treatments; thus, to assure there would be sufficient tiles to last until the experiment's last day, only one tile was sampled per sampling date. After a tile was sampled, it was wrapped in aluminium foil, labelled, and immediately frozen on dry ice for later analysis of chlorophyll *a* and AFDM using standard methods (American Public Health Association, 1992).

Statistical analysis

To examine differences in periphytic AFDM between the current velocity treatments at the end of the 30 days algal colonisation period – and before beginning the grazing phase of the experiment – we used an ANOVA. The data were log-transformed, to meet assumptions of normality and homogeneity of variance, and homogeneity of variance assumptions were checked using Bartlett's test.

We used backwards, stepwise multiple regression to examine how grazing history affected periphytic regrowth. In this type of regression analysis, independent variables are removed one at a time until all the remaining terms are statistically significant. We analysed the independent and interactive effects of grazer type, current velocity, duration of grazing, and time of regrowth, on periphytic chlorophyll *a* and AFDM. The analysis began with a full model and specified 0.10 as the 'P-to-enter', and 0.05 as the 'P-to-remove' (Sokal & Rohlf, 1995). The unique contribution of each factor for predicting measures of periphytic biomass was examined using standardised partial regression coefficients (Zar, 1996). The data for this analysis were square root-transformed to meet assumptions of normality before analysis.

Results

Stream grazer survey

The stream grazer survey measured near-bed current for 86 *Epeorus* and 59 *Baetis* individuals. The data show *Epeorus* widely distributed at near-bed current velocities ranging between 10 and 100 cm s⁻¹, whereas *Baetis* was rarely encountered above 50 cm s⁻¹ (Fig. 2). *Epeorus* was not seen at velocities <10 cm s⁻¹ and preferred fast current ranging from 60 to 70 cm s⁻¹; *Baetis* showed preference for a range of current between 5 and 45 cm s⁻¹.

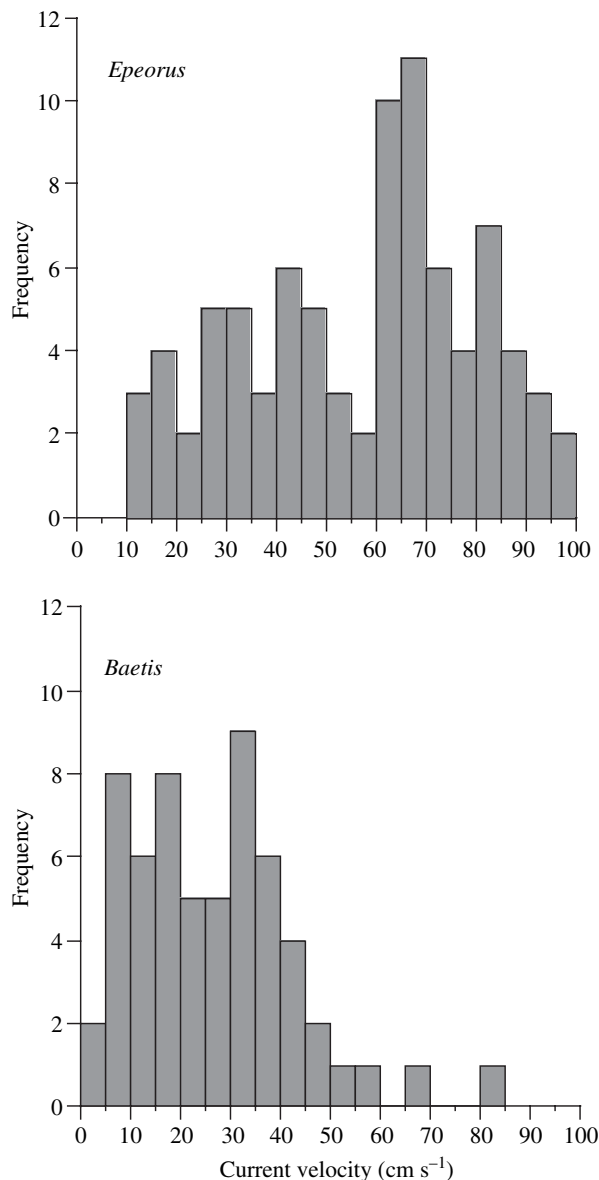


Fig. 2 Histograms showing the distribution of *Epeorus* and *Baetis* in relation to near-bed current velocity on the upper Colorado River streambed.

Effects of current on periphyton during colonisation

Current velocity influenced the physical structure and taxonomic composition of periphytic mats. Periphytic AFDM differed among current velocity treatments such that medium > slow = fast (ANOVA, $F_{2,6} = 49.4$, $P < 0.001$; Tukeys multiple comparisons, $P < 0.01$). Although periphyton grown at slow and fast current velocity did not differ in AFDM levels, the mats grown under each of the three current

velocity treatments were architecturally and taxonomically distinct and exhibited the following characteristics:

At slow current velocity, living and senescent chlorophyte filaments entrapped detritus and created a 'fluffy', brown periphytic overstory layer. Chlorophyte filaments were comprised of *Ulothrix* spp. (Dominant) and *Mougeotia* sp. (Abundant), and the remaining cells were mostly *Scenedesmus* spp., and *Oedogonium* spp. (Chlorophyta) and diatoms (each ranked as Common).

At medium current, long filaments of *Ulothrix* (Dominant) created thick, waving mats of bright green algae that bore epiphytic diatoms (Common, e.g. *Achnanthes* and *Cocconeis* spp.).

At fast current velocity periphyton was predominantly diatoms (Dominant), consisting primarily of *Fragillaria* spp., *Navicula* spp., and *Melosira varians*. *Ulothrix* (Common) was encountered as discrete tufts of short filaments, and *Chlorococcum* was also Common. Filamentous cyanophytes (Rare, e.g. *Lyngbya* spp.) made up the remainder of algae in the mat, which was compact, tightly attached, and yellow-brown in colour.

Maintenance of experimental conditions

Individual herbivore losses during the grazing phase of the experiment were low. Across treatments only 10% (45) and 5% (18) of *Baetis* and *Epeorus* individuals, respectively, escaped, emerged or died. Current velocities stayed within ± 2 cm s⁻¹ of the established current ranges throughout the study.

Experimental results

Grazer Type (variables are capitalized in text to distinguish them) had no significant effect on periphytic development following grazing. *Baetis* and *Epeorus* could not be differentiated in terms of their effects on either chlorophyll *a* or AFDM.

Chlorophyll *a* concentrations on tiles were influenced by the variables Current Velocity, Grazing Duration and Regrowth following grazing (Table 1). Current Velocity had a significant effect on chlorophyll *a* such that algal biomass increased with current speed. This effect can be seen by looking at the data from the non-grazed controls (Fig. 3); after 20 days algal chlorophyll *a* at medium and fast velocity was

Table 1 Results from backward stepwise regression on periphytic chlorophyll *a* (upper section) and AFDM (lower section) removed from tiles

Variable	Partial correlation coefficient	Partial r^2	P -level
Chlorophyll			
Current \times regrowth	0.306	0.63	<0.0001
Regrowth \times grazing duration	0.358	0.72	<0.0001
Current \times regrowth \times grazing duration	-0.127	0.83	<0.0001
AFDM			
Grazing duration	0.313	0.67	<0.0001
Current \times regrowth	0.462	0.26	<0.0001
Current \times grazing duration	-0.340	0.62	<0.0001

A full model was tested in each case, but only significant variables and interactions are shown. 'Current' is current velocity, 'regrowth' is the days of algal growth after grazing ceased, 'grazing duration' is the days duration that grazing occurred. Results for final regression model for chlorophyll *a* were: adjusted $R^2 = 0.60$, $F_{3,426} = 209.43$, $P < 0.0001$. For periphytic AFDM the final regression model results were: adjusted $R^2 = 0.21$, $F_{3,429} = 39.32$, $P < 0.0001$.

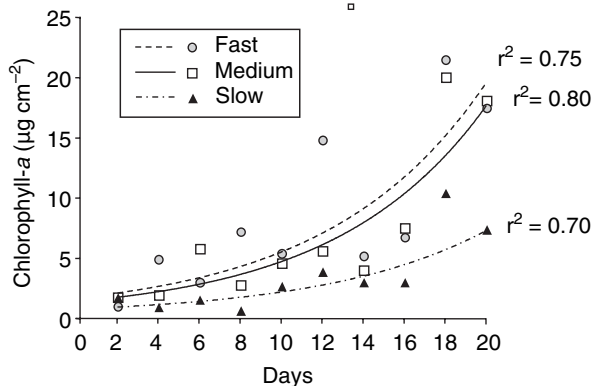


Fig. 3 The effect of current velocity and time on chlorophyll *a* collected from tiles in control channels. Data points represent individual tiles sampled every 2 days throughout the grazing and non-grazing phases of the 20 day experiment. Exponential curves have been fitted to each data set and the r^2 value for each line is shown at the right end of the curve.

approximately twice that seen in the slow current velocity treatment.

The effect of current was modified by the grazing history. There was a negative relationship between chlorophyll *a* and the Grazing Duration \times Current Velocity term, indicating less periphytic accrual at faster velocity as grazing duration increased (Table 1). This relationship can be seen by comparing chlorophyll *a* accumulation after 10 days grazing duration

under the slow and fast current velocity treatments (Fig. 4); note that slow current velocity produced more chlorophyll *a* at 10 days than did fast.

Chlorophyll *a* also was related to the time of periphyton regrowth following grazing. The positive interaction term for Grazing Duration \times Regrowth indicates that, regardless of current velocity or grazer type, the longer the mat was grazed the greater the algal accumulation following grazing (Table 1). This relationship is most clearly seen in Fig. 5, which shows that algal mats grazed for longer duration generate much greater levels of chlorophyll *a* than mats grazed for shorter periods. The general pattern shown in Fig. 5 occurred for each of the three current velocities, despite the distinct taxonomic characteristics initially exhibited by the periphyton.

Periphytic AFDM was also influenced by the three variables that affected chlorophyll *a*, but in different combinations. Grazing Duration was the only variable that independently affected AFDM, such that longer grazing duration resulting in more periphytic AFDM, irrespective of regrowth time or current velocity (Table 1). The two significant interaction terms affecting AFDM involved current. Periphytic AFDM showed a negative relationship to the Grazing Duration \times Current Velocity interaction term, suggesting (as before with chlorophyll *a*) that grazing duration was associated with greater periphytic accrual at slower velocities. By contrast, the relationship of AFDM to the Regrowth \times Current Velocity interaction was positive, indicating more periphyton accumulated at faster velocity if allowed longer periods of regrowth.

Plotting the relationship of either chlorophyll *a* or AFDM against grazing duration and regrowth and fitting a quadratic response surface to these data produced similar plots; however, the quadratic surface fit to chlorophyll *a* was considerably better than for AFDM, and for this reason, only chlorophyll *a* is plotted in Fig. 5. R^2 -values were 0.60 and 0.21 for chlorophyll *a* and AFDM, respectively (cf. Table 1).

Discussion

We found that current velocity and duration of past herbivory had a considerable effect on periphytic accumulation. Whether measured as chlorophyll *a* or periphytic AFDM, the longer that periphyton was grazed, the more periphytic biomass accrued over time after grazing, and this effect was most

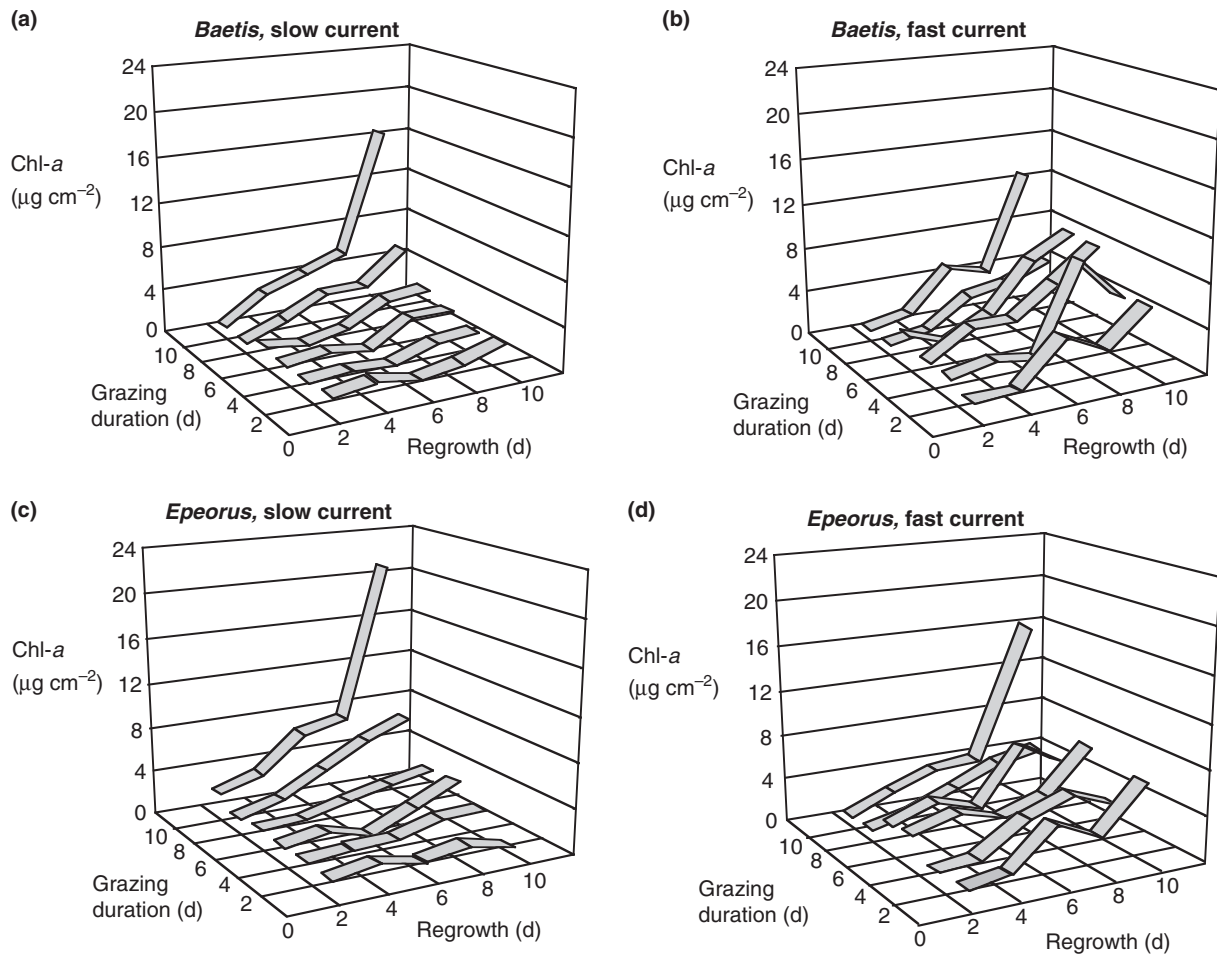


Fig. 4 The effect of current velocity, grazing duration, and regrowth following grazing on chlorophyll *a* taken from tiles grazed by *Baetis* (a, b) and *Epeorus* (c, d) at 'slow' ($2\text{--}5\text{ cm s}^{-1}$) and 'fast' ($30\text{--}40\text{ cm s}^{-1}$) current. Only slow and fast current velocity data are presented to show contrast; data for medium current were similar to fast.

pronounced at slower velocities (i.e. there was a significant current \times grazer duration interaction). As single factors, current velocity and grazing duration had a positive effect on the accumulation of chlorophyll *a* and periphytic AFDM, respectively. This meant that faster current increased algal growth regardless of grazing regime, whereas the length of time a mat was grazed helped predict the total amount of periphyton produced.

Overall, chlorophyll *a* showed a better relationship to experimental variables than did periphytic AFDM, and this may have resulted from the former being a better measurement of algal biomass than the latter. Whereas chlorophyll *a* measures only living algal biomass, AFDM does not distinguish between living and dead algal cells, nor does this metric differentiate among other types of organic matter present in

samples. Consequently, periphytic AFDM is a coarser measure of periphyton and this may explain why the overall adjusted R^2 -value for the AFDM data was poorer than that of chlorophyll *a* (cf. 0.21 versus 0.60).

Although current velocity, grazing duration and regrowth period were each important factors for determining final periphytic standing crop, either singly or through interactions with other factors, herbivore type *per se* had no enduring influence. The absence of any lasting herbivore-specific effect was quite interesting. A sizeable literature has documented the various effects that different herbivore taxa have on periphytic architecture and community structure (see reviews by Feminella & Hawkins, 1995, and Steinman, 1996). There are instances where grazers have caused changes in the prevailing algal growth form (Tuchman & Stevenson, 1991; Rosemond

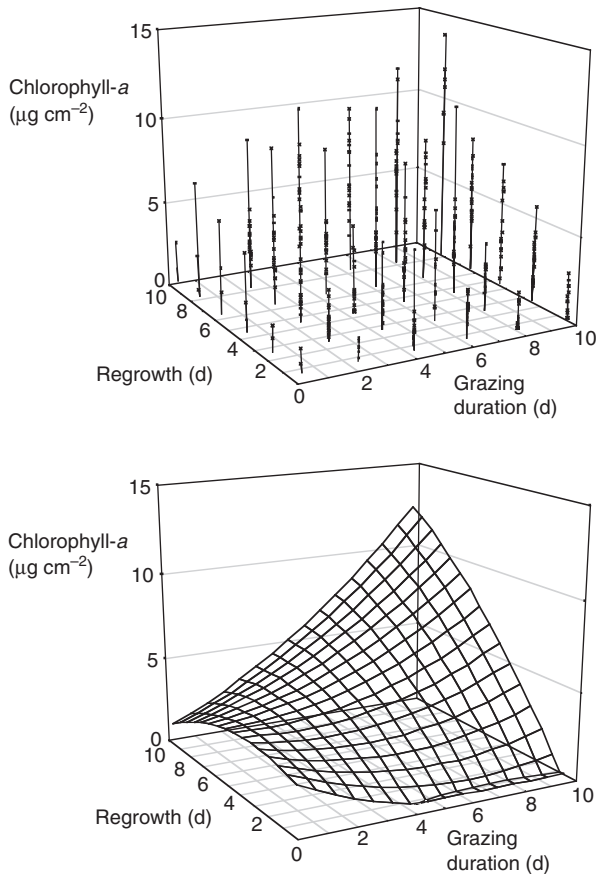


Fig. 5 Plot of chlorophyll *a* against the duration of grazing and periphytic regrowth following grazing (top). In the lower figure, a quadratic-surface is fitted to the 448 data points. These graphs show the combined data from the two grazer and three current velocity treatments.

& Brawley, 1996) or altered the dominant alga within an assemblage (Hill & Knight, 1988; Wellnitz & Ward, 1998). In the present study, we reasoned that if these changes occurred, they would translate into different rates of periphytic regrowth. That periphyton growth trajectories differed little suggests the two grazers differed little in their effect on mat structure. Or more precisely, within the 2–40 cm s⁻¹ range of current velocity tested in the present study, *Epeorus longimanus* and *Baetis bicaudatus* were functionally ‘redundant’ (sensu Wellnitz & Poff, 2001) in terms of their short-term influence on periphyton accrual.

As for the effect of current velocity itself on periphyton, while strongly influencing initial structural characteristics and the rate of accrual over time, current did not alter the trajectory of algal biomass accumulation following grazing. This similar response to grazing history suggests that grazing may have had

a ‘homogenising’ effect on community structure at the spatial and temporal scales of resolution examined in this study (but see Kawata, Hayashi & Hara, 2001). There is evidence in the literature that this occurs, in particular with regard to periphyton physiognomy. In his review of 43 studies examining the effects of grazers on periphyton, Steinman (1996) found that all but six reported a decline in the percentage of overstory growth forms in response to grazing.

We hypothesise that a time-dependent reduction of periphytic overstory layers explains why grazing duration, and duration of regrowth following grazing, were important predictors of chlorophyll *a*. Each day of grazing would successively remove more overstory layers, with the consequence that the remaining algal cells would experience less shading, have more direct access to water column nutrients, fewer competitors for limiting factors, and likely, divide and grow more rapidly (Lamberti *et al.*, 1989; McCormick & Stevenson, 1989, 1991; Wellnitz & Ward, 1998). Eventually, after several days of grazing, only a thin film of highly productive algal cells would remain and these would show faster rates of growth and greater rates of chlorophyll *a* accumulation.

Another explanation, one that is complementary to the first, is that faecal matter deposited by grazers could accumulate and increase available nitrogen in the periphyton and enhance algal growth (McCormick & Stevenson, 1989; McCormick, 1990; Gresens, 1995). The longer a grazer fed, the more benthic algae would be removed, and naturally, the more faecal matter would be deposited. As a consequence, the thin film of cells that remained after an extended period of grazing would experience a nutrient-enhanced environment during subsequent regrowth.

These mechanisms of overstory removal and nutrient enhancement have been invoked before to explain how grazing may enhance algal production (e.g. see Steinman, 1996), but it is clear from our data that *past* grazing may also increase algal biomass. Increased biomass accumulation can result from enhanced productivity (but see Berman-Frank & Dubinsky, 1999); however, in the considerable literature on the subject (see reviews by Feminella & Hawkins, 1995; Steinman, 1996), algal biomass is seldom reported to increase in response to grazing. A plausible reason for this is that these reviews deal with algae growth in the presence of grazers, whereas our study analysed the algal regrowth in the absence of grazers.

Grazing of benthic stream periphyton is often assumed to be continuous rather than a discrete process. If viewed from a large enough spatial and temporal scale, this assumption may be valid; however, from an algal cell's perspective stream herbivory is not a stream-wide phenomenon. Rather, the act of herbivory occurs on a 'bite by bite' basis, and the period of time since an algal patch was last grazed has significance for the algal assemblage, as well as the next grazer that encounters it. Data from this study indicate that grazing duration and the period of regrowth determine the amount of algae in a patch and the rate at which it accumulates. These two variables also serve to establish food availability – and perhaps food quality – for grazers that visit and feed on a patch (Wilson *et al.*, 1999; Wilson & Richards, 2000), and this in turn may regulate grazer movement and foraging across the streambed (Kohler, 1984; Poff & Ward, 1992; Palmer, 1995). Although this study was conducted at a small scale, grazing and algal patch dynamics are important determinants of benthic heterogeneity (Sarnelle, Kratz & Cooper, 1993; Sommer, 2000; Kawata *et al.*, 2001) and influence whole-stream processes, such as primary production. To better understand the role herbivory plays in structuring the benthic habitat, as well as influencing stream ecosystem functioning, we suggest that the time-dependent effects of grazing and algal responses be more thoroughly explored.

Acknowledgments

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