

# The influence of channel bed disturbance on algal biomass in a Colorado mountain stream

Catalina Segura,<sup>1\*</sup> James H. McCutchan,<sup>2</sup> William M. Lewis Jr<sup>2</sup> and John Pitlick<sup>1</sup>

<sup>1</sup> Department of Geography, University of Colorado, Boulder, CO, USA

<sup>2</sup> Center for Limnology, Cooperative Institute for Research in Environmental Sciences, University of Colorado, Boulder, CO, USA

## ABSTRACT

The effects of channel bed disturbance on benthic chlorophyll *a* accrual were examined in three reaches of the Williams Fork River, CO, USA. A field calibrated multidimensional hydraulic model was used for estimation of shear-stress distributions. Sediment grain size was used to determine the critical shear stress for bed movement. Disturbance at a given location is defined as the percentage of time during the growing season that the bed sediment is in motion. This metric was compared with periphyton biomass accrual. Growth control factors including temperature, grazing intensity, nutrient concentrations, and irradiance also were measured. Disturbance mapping showed that the common concept of bed disturbance as a byproduct of high-flow events is overly simplistic. In the Williams Fork, bed movement occurs constantly over certain portions of the bed, even at low flows. There is a continuum of bed movement, expressed as percentage of the bed in motion, extending from low to high flows. Periphyton biomass accumulated exponentially in all study reaches but accumulation rates were inversely proportional to local disturbance. Periphyton biomass increased by approximately three orders of magnitude across the three reaches, but failed to reach a plateau. A combination of moderate grazing rates, low-nutrient concentrations, moderately impaired solar irradiance, and, most importantly, low temperatures explains the failure of periphyton biomass to reach a plateau. This study shows that the control of periphyton biomass may be explained in streams by bed disturbance over the growing season plus the separate, superimposed on influence of population growth rate control factors. Copyright © 2010 John Wiley & Sons, Ltd.

KEY WORDS attached algae; bed disturbance; shear stress; flow modelling; stream sediments

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## INTRODUCTION

Substrate stability in streams and rivers may affect biomass, metabolism, and community composition of periphyton and macroinvertebrates. Most of the studies of bed stability have been based on reach-scale metrics involving estimated critical flow for bed movement or movement of marked (painted) rocks or fixed markers (chains). Many of the studies confirm that movement of large portions of the bed suppresses periphyton biomass (Cobb *et al.*, 1992; Death and Winterbourn, 1995; Townsend *et al.*, 1997; Biggs *et al.*, 1999). Fewer studies have documented spatial variation in bed disturbance within a stream reach as related to periphyton or other organisms (Biggs and Stokseth, 1996). Matthaai *et al.* (2003) found that local disturbance history within a reach had long-term effects on the distribution of invertebrates and algal biomass. Cronin *et al.* (2007), who modelled disturbance based on shear-stress distribution over a stream reach, showed that exceedance of shear-stress thresholds corresponding to bed movement was strongly related to suppression of chlorophyll *a* (chl *a*).

Heterogeneity of disturbance may explain heterogeneous recovery of periphyton, but recovery from disturbance also may reflect other kinds of influences on periphyton growth rate, such as temperature, grazing, substrate irradiance, or nutrient concentrations. Biotic controls may become increasingly important for periphyton as the duration of substrate stability increases because recovery of invertebrate grazers and losses from autogenic sloughing and herbivory develop progressively following disturbance (Fisher *et al.*, 1982; Biggs and Close, 1989; Power, 1992).

The purpose of this study was to use quantitative information on the spatial distribution of shear stress over stream reaches to predict periphyton biomass accumulation in three reaches of a Colorado mountain stream. Shear-stress maps were developed from a field calibrated model that incorporates information on channel geometry and stream discharge. Shear-stress maps, in conjunction with information on the distribution of particle sizes in the stream channel, supported the production of bed disturbance maps for each stream reach on all dates spanning most of the growing season for 3 years. Thus, as proposed by Resh *et al.* (1988), disturbance was quantified on a physical basis rather than by biological indices.

For a given location in a stream reach, disturbance is defined here as percentage time during the growing

\*Correspondence to: Catalina Segura, Department of Forestry, North Carolina State University, 3120 Jordan Hall, Box 8008, Raleigh, NC 27695-8008, USA. E-mail: csegura@ncsu.edu

season that the bed is in motion. Thus, each location (point) in the stream bed has a uniquely determined disturbance metric in a given growing season. Bed disturbance is used here as an independent variable in studying periphyton biomass accrual, but it is considered along with information on other independent variables: temperature, nutrient concentrations, irradiance, and abundance of benthic invertebrate grazers.

### STUDY SITE AND METHODS

This study was conducted on three reaches of the Williams Fork River (Figure 1), a snowmelt-dominated stream (Figure 2) that drains mostly forested areas near the Continental Divide near Parshall, Colorado. The study reaches are relatively straight and are near US Geological Service (USGS) gaging stations.

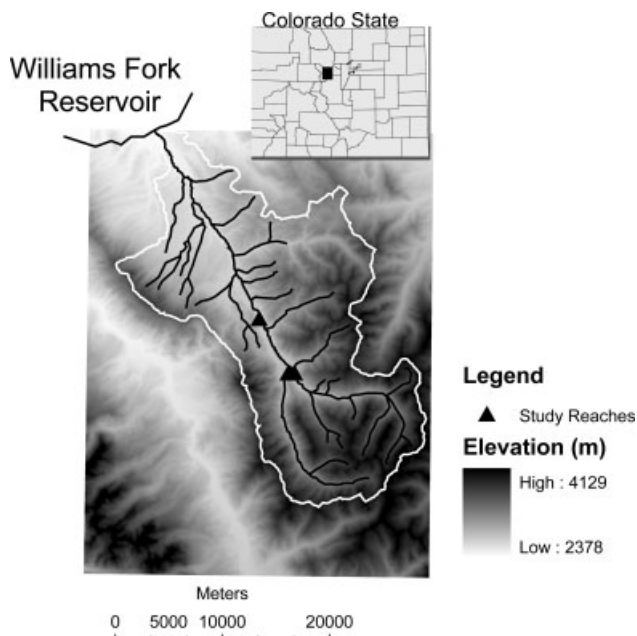


Figure 1. Location of the Williams Fork drainage basin in Colorado.

### Modelling

Spatial distribution of shear stress over the channel bed at each of the three study reaches was modelled for four flows ranging between 0.3 and 1 bankfull ( $Q_{bf}$ ) by use of a multidimensional model, Multi-Dimensional Surface Water Modeling system (MD-SWMS) (USGS; Nelson *et al.*, 2003). The input data for the model include detailed topographic measurements collected in early June of 2004 (13–18 cross-sections one bankfull width apart at each of the three reaches), discharge, water surface elevation at the margins of the reach, and roughness length or drag coefficient (Lisle *et al.*, 2000). The model calculates boundary shear stress ( $\tau$ ) in the downstream ( $x$ ) and cross-stream ( $y$ ) directions based on average vertical downstream and cross-stream velocities ( $u$  and  $v$ , respectively), water density ( $\rho$ ) and drag coefficient ( $C_d$ ):

$$\tau_x = \rho C_d u \sqrt{(u^2 + v^2)} \quad (1)$$

$$\tau_y = \rho C_d v \sqrt{(u^2 + v^2)} \quad (2)$$

The distance between the model grid nodes was <1 m. The model was calibrated by the adjustment of roughness and the lateral eddy viscosity; the goal of this calibration procedure was to obtain the best agreement between observed and predicted water surface elevation and vertically averaged velocity surveyed during the four flows modelled on each margin of the channel and along several cross-sections. The model was calibrated for all flows using both variable and constant roughness (i.e. using constant or spatially variable grain size distribution in the channel bed). In agreement with the results of Lisle *et al.* (2000), no significant difference ( $p > 0.05$ ) was found between the two cases for both water surface elevation and velocity, indicating that the variability in the bed grain size distribution does not significantly influence the estimates of shear stress and velocity. In addition, a comparison between the distribution of the median grain size,  $D_{50}$ , and the distribution of shear stress at different flows indicated that the variability in  $D_{50}$  is smaller than the variability of the shear stress.

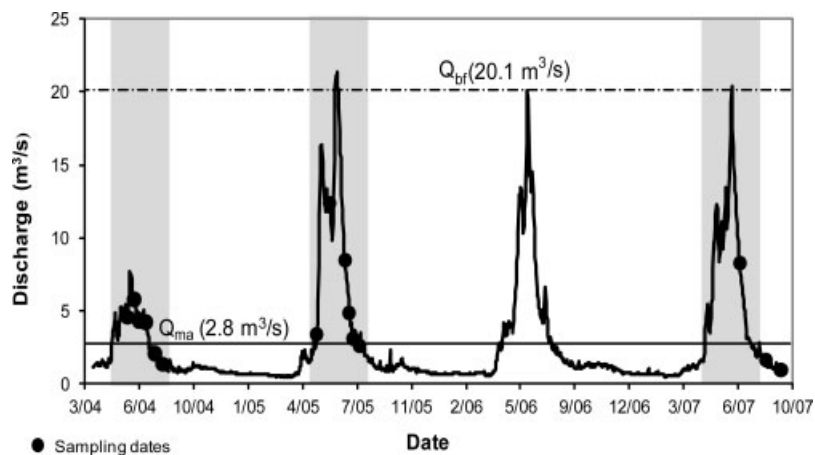


Figure 2. Daily discharge of the Williams Fork near Reach 3 (USGS gage no. 09036000).  $Q_{bf}$  is the bankfull flow and  $Q_{ma}$  is the mean annual flow. Dots show the sampling dates (no sampling in 2006); shading shows the sampling period over which the disturbance metric was calculated.

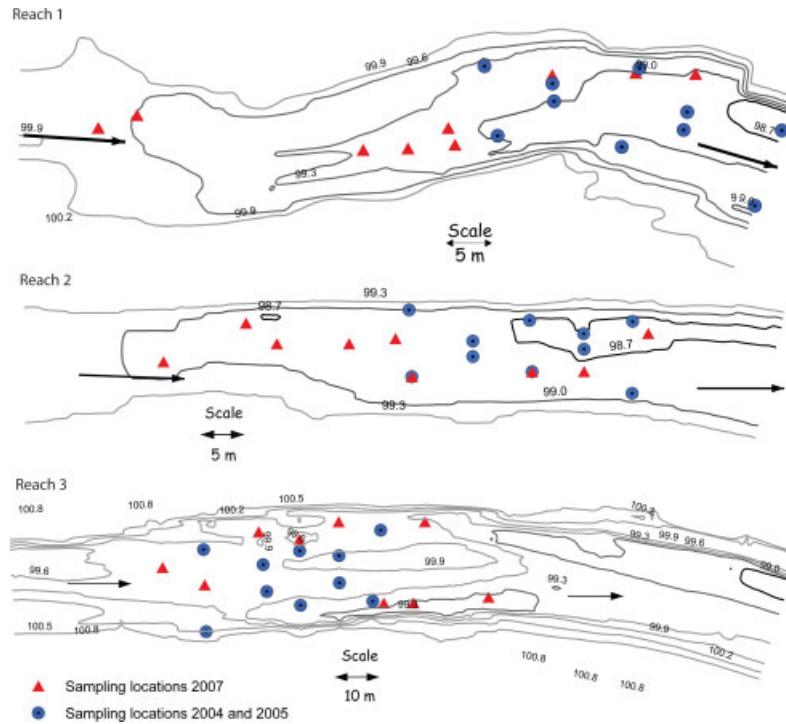


Figure 3. Location of periphyton sampling points in 2004, 2005, and 2007. Contour lines show 30 cm intervals with respect to an arbitrary datum of 100 m.

The coefficient of variation of the shear stress in all runs is above 47%, whereas the coefficient of variation of the  $D_{50}$  varied between 11 and 38% (Segura, 2008). Therefore, the simpler solution of constant roughness was chosen and a uniform grain size distribution per reach was assumed.

Following calibration, the root mean square of the difference between observed and predicted values was 0.021–0.050 m for water surface elevation and 0.11–0.28 m s<sup>-1</sup> for vertically averaged velocity (Segura, 2008).

The critical shear stress for bed motion,  $\tau_c$ , was calculated from the Shields equation:

$$\tau_c^* = \frac{\tau_c}{(\rho_s - \rho)gD_{50}} \quad (3)$$

where  $\tau_c^*$  is the critical Shields stress for motion,  $\rho_s$  and  $\rho$  are the densities of sediment and water,  $g$  is the gravitational acceleration, and  $D_{50}$  is the median grain size in the channel bed.  $\tau_c^*$  was calculated from channel slope with the equation of Mueller *et al.* (2005):

$$\tau_c^* = 2.18S + 0.021 \quad (4)$$

where  $S$  is the channel slope and  $\tau_c^*$  was 0.029–0.055.

Shear stress was determined for all model nodes on each of the calibration dates over all three reaches. Shear stress for flows on dates that were not modelled was estimated for each node by linear interpolation of shear stress for modelled discharges. Daily shear stress values on each channel node were compared with the critical shear stress for bed motion to compute the disturbance metric.

### Sampling

Periphyton samples were collected biweekly in 2004, 2005, and 2007 from late May or early June into the first half of August (Figure 2). In 2004 and 2005, one set of samples also was collected prior to runoff. No sampling was done in 2006.

Periphyton samples were collected from gravel and cobble ranging from 0.9 to 3.6  $D_{50}$ . On each sampling date, periphyton was collected from the upper surface of two to four rocks at each of 10 sampling locations per reach; five locations were randomly selected near the channel edge and five were randomly selected near the channel thalweg (Figure 3). In 2007, unlike 2004 and 2005, points of contrasting bed disturbance were identified *a priori* for sampling (Figure 3). Samples were stored cold and dark for transport to the laboratory.

Water temperature was recorded continuously in 2004 and 2005, as was PAR irradiance above the canopy (June–August). The fraction of above-canopy irradiance reaching the stream surface was estimated by hemispherical photography and image analysis (Gap Light Analyzer Burnaby, Canada and Millbrook, USA). Water samples were collected monthly (July–September) for analysis of soluble reactive phosphorus (SRP), total dissolved phosphorus (TDP), ammonium (NH<sub>4</sub><sup>+</sup>-N), and nitrate (NO<sub>3</sub><sup>-</sup>-N). Benthic macroinvertebrates were sampled twice in 2004 (July 23 and August 4) and 2005 (May 20 and July 7). On each sampling date, five samples were collected from points near the locations where periphyton was collected with a modified Surber sampler (225 mm mesh; 0.143 or 0.25 m<sup>2</sup>) to a depth of approximately 20 cm into the stream substrate and were preserved with 70% ethanol.

Table I. Characteristics of the three study reaches (standard error is shown for some variables).

Characteristic	Reach 1	Reach 2	Reach 3
Coordinates	39°47'36", 103°58'11"W	39°47'49 · 9"N, 106°01'32 · 3"W	39°50'38"N, 103°56'2"W
Drainage area (km <sup>2</sup> )	71	91	231
Slope	0.0155	0.0049	0.0039
Elevation (m)	2730	2730	2660
Bankfull flow (m <sup>3</sup> /s)	7.0	10.5	20.1
2004-peak flow (m <sup>3</sup> /s)	3.6	2.8	7.7
2005-peak flow (m <sup>3</sup> /s)	6.8	9.1	21.4
2007-peak flow (m <sup>3</sup> /s)	6.0	8.8	20.4
Mean flow (m <sup>3</sup> /s)	0.93	1.1	2.8
Flow record (years)	40	40	72
<i>D</i> <sub>50</sub> (mm)	71 ± 7.4	61 ± 2	40 ± 1.1
Mean water temperature 2004 (°C)	8.4 ± 0.2	9.5 ± 0.3	9.8 ± 0.2
Mean water temperature 2005 (°C)	7.6 ± 0.3	8.3 ± 0.4	9.0 ± 0.3
Canopy cover (%)	50 ± 3	16 ± 2	7 ± 2

### Analysis

Abundance of benthic chl *a* was determined by spectrophotometry after sonication and hot ethanol extraction (Marker *et al.*, 1980; Nusch, 1980). SRP was measured by an acid–molybdate method (Murphy and Riley, 1962) and TDP was measured by the same method following oxidation (Valderrama, 1981; Lagler and Hendrix, 1982). NH<sup>+</sup><sub>4</sub>-N was measured by a modified Solarzano method (Grashoff, 1976) and NO<sup>-</sup><sub>3</sub>-N was measured by ion chromatography.

Daily net primary production (NPP) was estimated from daily measurements of water temperature and chl *a* according to the equation of Morin *et al.* (1999). Daily abundances of chl *a* were obtained from linear interpolation of the measured chl *a*.

Secondary production of herbivorous benthic insects (scrapers and gathering collectors) was estimated for each of the three reaches in 2004 and for Reach 1 in 2005. Macroinvertebrates from each sample were sorted under 6–50× magnification. Most Ephemeroptera and Coleoptera were identified to genus or species; other taxa were identified to the lowest practical taxonomic level with keys of Ward and Kondratieff (1992).

For invertebrate taxa that could be followed over time as distinct cohorts, production was estimated by the increment–summation method; production of the other taxa was estimated by the instantaneous growth rate method (Gillespie and Benke, 1979) from mean individual dry mass and temperature according to an equation developed for North Saint Vrain Creek, Colorado, by McCutchan and Lewis (2002). Assimilation efficiency (AE; ratio of assimilation to ingestion) and net production efficiency (NPE; ratio of growth to assimilation) were assigned average values for invertebrates feeding on diatoms (NPE = 53 ± 7% and AE = 44 ± 5%; Benke and Wallace, 1980; Huryn, 1996). Periphyton is dominated by diatoms in the Snake River (Vavilova and Lewis, 1999), which is near and similar to the Williams Fork. AE and NPE were used to estimate the consumption of periphyton biomass by herbivores. The estimates of

both NPP and periphyton consumption rates involve substantial uncertainties; they are used here only to give an approximation of the effect of grazing on algal biomass accrual.

### RESULTS

The 2004 peak flows at the three gaging stations are the first, second, and fourth lowest on record; peak flows in 2005 and 2007 were near bankfull discharge (Table I and Figure 2). Multiple pebble counts (Wolman, 1954) involving 2500–4750 particles at each reach indicated that the bed material is dominated by gravel and cobble with median grain sizes (*D*<sub>50</sub>) between 40 and 71 mm (Table I).

Water temperature was low at all reaches and varied only slightly among reaches (Table I). PAR below the canopy was nearly uniform across sampling locations at each site. Canopy cover was highest at Reach 1 (Tukey Kramer HSD, *p* < 0.050; Table I), but is not statistically different at Reaches 2 and 3 (Tukey Kramer HSD, *p* = 0.052). Below the canopy, PAR remained below 200 μmol m<sup>-2</sup> s<sup>-1</sup> at least 85% of daylight hours at all reaches. PAR was between 200 and 400 μmol m<sup>-2</sup> s<sup>-1</sup> (optimal range for photosynthesis; Hill, 1996) 2, 15, and 9% of daylight hours at Reaches 1, 2, and 3 and >400 μmol m<sup>-2</sup> s<sup>-1</sup> 3% of daylight hours at all reaches.

Concentrations of phosphorus and nitrogen were low but detectable in the Williams Fork (Table II) except for NO<sup>-</sup><sub>3</sub>-N in Reach 2, which became undetectable (<1 μg l<sup>-1</sup>) in August and September. The concentrations were sufficient to support growth of periphyton (Borchardt, 1996), but not indicative of enriched conditions.

Bed disturbance (Figures 4–6) differed across the three study reaches, across years, and within each reach. Percentage of days with bed disturbance was low at individual points near the channel edge and high along the thalweg at all three reaches. In 2004, over 80% of the bed was entirely undisturbed within all reaches (Figure 4). In

Table II. Nutrient concentration during the summers of 2004, 2005, and 2007 at study Reaches 1, 2, and 3.

Date	SRP ( $\mu\text{g l}^{-1}$ )			TDP ( $\mu\text{g l}^{-1}$ )			NH <sup>+</sup> <sub>4</sub> -N ( $\mu\text{g l}^{-1}$ )			NO <sup>-</sup> <sub>3</sub> -N ( $\mu\text{g l}^{-1}$ )		
	Reach 1	Reach 2	Reach 3	Reach 1	Reach 2	Reach 3	Reach 1	Reach 2	Reach 3	Reach 1	Reach 2	Reach 3
4 April 2004	0.4	0.9	0.7	1.5	2.1	2.0	5.1	5.9	4.4	50	10	24
6 July 2004	0.3	0.6	0.6	1.8	1.6	2.0	5.1	5.4	4.6	52	43	47
4 August 2004	1.3	1.9	1.3	2.6	4.6	2.8	5.3	4.6	6.0	44	0	28
11 May 2005	1.3	0.6	0.9	2.1	3.4	3.4	11	9.3	9.5	232	150	163
7 July 2005	2.2	0.9	1.0	3.8	2.5	1.8	8.8	3.3	5.2	74	75	73
22 July 2005	1.0	1.3	1.3	2.0	3.1	3.1	9.2	8.2	8.4	59	14	41
4 August 2005	1.2	2.1	1.3	5.3	9.5	7.4	4.6	5.7	5.0	75	9	25
2 July 2007	2.0	0.2	1.3	3.1	2.1	2.0	5.1	1.1	0.6	80	70	67
19 August 2007	1.3	1.8	1.3	2.0	3.8	3.4	5.1	6.2	5.6	42	0	35
15 September 2007	1.6	3.3	3.6	1.6	6.2	6.9	3.4	3.7	4.1	32	0	29

2005 and 2007, undisturbed bed extended over 50, 84, and 34% of the bed at Reaches 1, 2, and 3.

Abundances of periphyton were low prior to runoff (May–June) as is typical for subalpine streams in Colorado (McCutchan and Lewis, 2002; Table III). Abundance of chl *a* increased exponentially over time in both 2004 and 2005 (Table IV) and did not reach a plateau within the sampling period (Figure 7). Initial and final chl *a* were higher in 2005 than in 2004 in Reaches 1, 2, and 3 (Table III), but the rate of accrual was significantly higher in 2004 than in 2005.

In 2007, when sampling locations of contrasting disturbance were chosen *a priori*, chl *a* usually was lowest where disturbance was high (Figure 8). Disturbance was only weakly related to chl *a* in Reach 2, most likely because contrasts in disturbance were small.

The three reaches showed high diversity and moderate abundance of benthic invertebrates, with strong dominance by insect larvae (Table V). Grazing losses, as estimated from NPP and herbivore food consumption, range from low to moderate (Table III). There is no evidence that grazing had a strong suppressive effect on the periphyton community.

In overview, periphyton accrual across the study reaches and across years corresponds inversely to mean percentage bed disturbance over the growing season in years of either low- or high-peak flows. In addition, the within-reach accrual of periphyton was not uniform; locations with higher disturbance showed slower accrual than locations with lower disturbance. Thus, the rate of periphyton accumulation during the growing season shows a quantitative relationship to channel bed disturbance over the growing season.

## DISCUSSION AND CONCLUSIONS

This study shows that a shear-stress model, when calibrated across a range of flows in a stream reach and coupled with measurements of sediment grain size, can produce maps of stream bed disturbance on a daily basis over an extended interval for use in studying ecological effects of bed disturbance. Application of this method to the Williams Fork River of Colorado shows that the common concept of bed disturbance as a byproduct of high-flow events is misleadingly simplistic. In the Williams Fork, and likely in most streams that have gravel or sand sediments, bed movement occurs constantly over certain portions of the bed, even at low flows. Thus, bed disturbance varies on a spatial continuum across the full range of flows. The proportion of the bed that is disturbed increases with flow until the entire bed is in motion.

In this study, as in other studies (Biggs and Stokseth, 1996; Cronin *et al.*, 2007), movement of the bed at a given location correlates with suppression of periphyton biomass accumulation at that location. The mapping of shear stress and identification of the threshold for bed movement produce a mechanistic understanding of periphyton biomass suppression at the reach scale. Thus, the

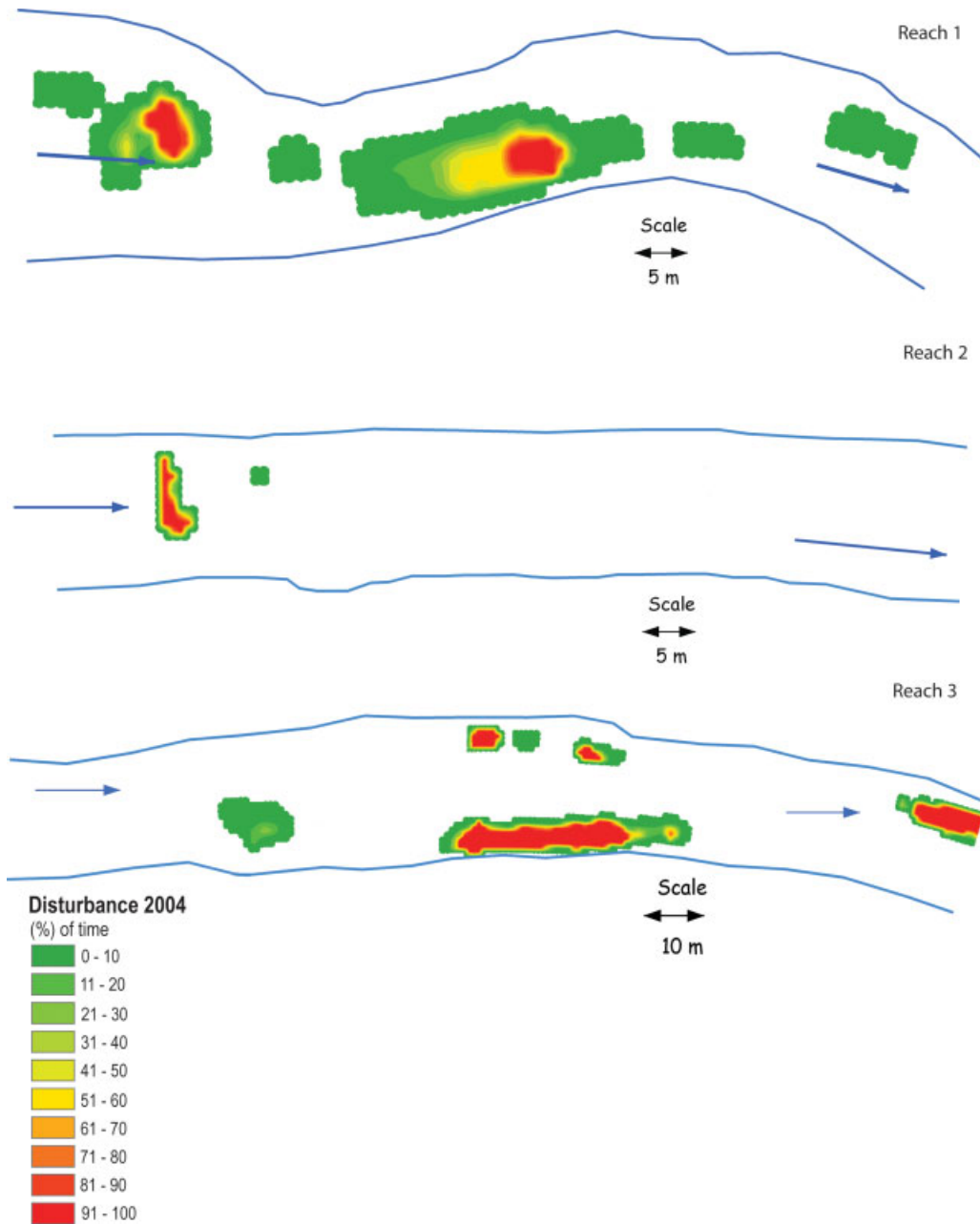


Figure 4. Channel bed disturbance maps for the three study reaches in 2004, shown as percentage of days between May 1 and August 8.

Table III. Chlorophyll *a* in  $\text{mg m}^{-2}$  on the first (pre-runoff) and last sampling dates and calculated NPP (June through August), and production of grazers  $\text{g dry mass m}^{-2} \text{ year}^{-1}$  (estimated for 2004 Reaches 1–3 between July 23 and August 6 and 2005 Reach 1 between May 20 and July 7 only), as well as percentage of NPP lost to grazing ( ).

Reach	2004				2005			
	chl <i>a</i> , June	chl <i>a</i> , August	NPP	Grazing (%)	chl <i>a</i> , May	chl <i>a</i> , August	NPP	Grazing (%)
1	0.93	28	6.85	1.23 (46)	4.77	42	10.5	3.9 (7)
2	1.89	94	13.8	0.6 (9)	2.7	46	18.8	NA
3	0.63	12	3.95	0.2 (12)	1.42	23	1.8	NA

reach-averaged periphyton biomass accumulation corresponds to the mean percentage bed movement over time in a given reach. The modelling of shear stress using both constant and variable roughness indicated that the variability in grain size is small and produces no differences

in the calculation of shear stress and velocity. Therefore, in mountainous gravel and cobble bed streams with relatively homogenous grain size distributions disturbance can be calculated based solely on the spatial variation of shear stress and a mean grain size distribution. These

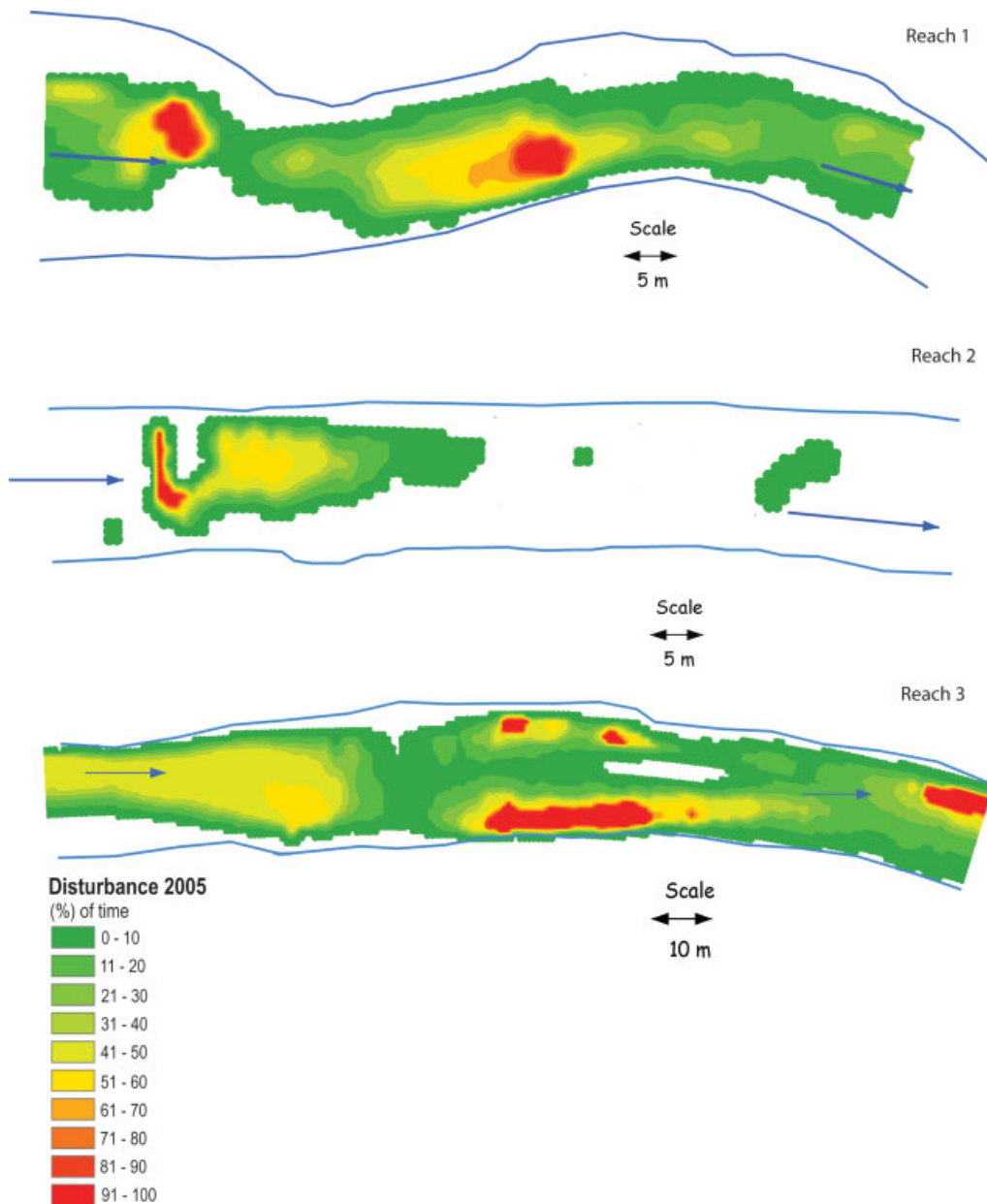


Figure 5. Channel bed disturbance maps for the three study sites in 2005, shown as percentage of days between May 1 and August 8.

Table IV. Summary of statistics for the regression between chlorophyll *a* and time since the peak flow.

Site (year)	<i>a</i>	<i>b</i>	Doubling time (days)	SE <sub>r</sub>	<i>r</i> <sup>2</sup>	<i>p</i>
1 (2004)	-0.138	0.469 (0.059)	12 (3)	0.76	0.81	0.014
2 (2004)	0.703 (0.499)	0.499 (0.061)	11 (3)	0.81	0.80	0.015
3 (2004)	-0.588	0.447 (0.050)	14 (4)	0.72	0.77	0.021
1 (2005)	1.656 (0.294)	0.294 (0.027)	26 (6)	0.42	0.81	0.014
2 (2005)	1.598 (0.268)	0.268 (0.036)	19 (3)	0.38	0.91	0.003
3 (2005)	0.716 (0.385)	0.385 (0.039)	18 (4)	0.55	0.86	0.023

*a* and *b* are the parameters of the linear relation,  $\log(\text{mean chl } a) = a + bx$ ; values shown in parentheses are SEs, SE<sub>r</sub> is the standard error of the regression; *r*<sup>2</sup> is the coefficient of determination; and *p* is the probability.

results are not applicable to systems with channel beds covered with smaller grain sizes as found for a small river of the Virginia Piedmont (Tett *et al.*, 1978).

Exponential periphyton biomass accumulation in the Williams Fork at the reach scale follows the spring flood

despite the constant presence of some bed movement after the flood because substantial amounts of substrate remain completely undisturbed or infrequently disturbed during the growing season. Even so, periphyton biomass does not reach a plateau at the reach scale. In some rivers,



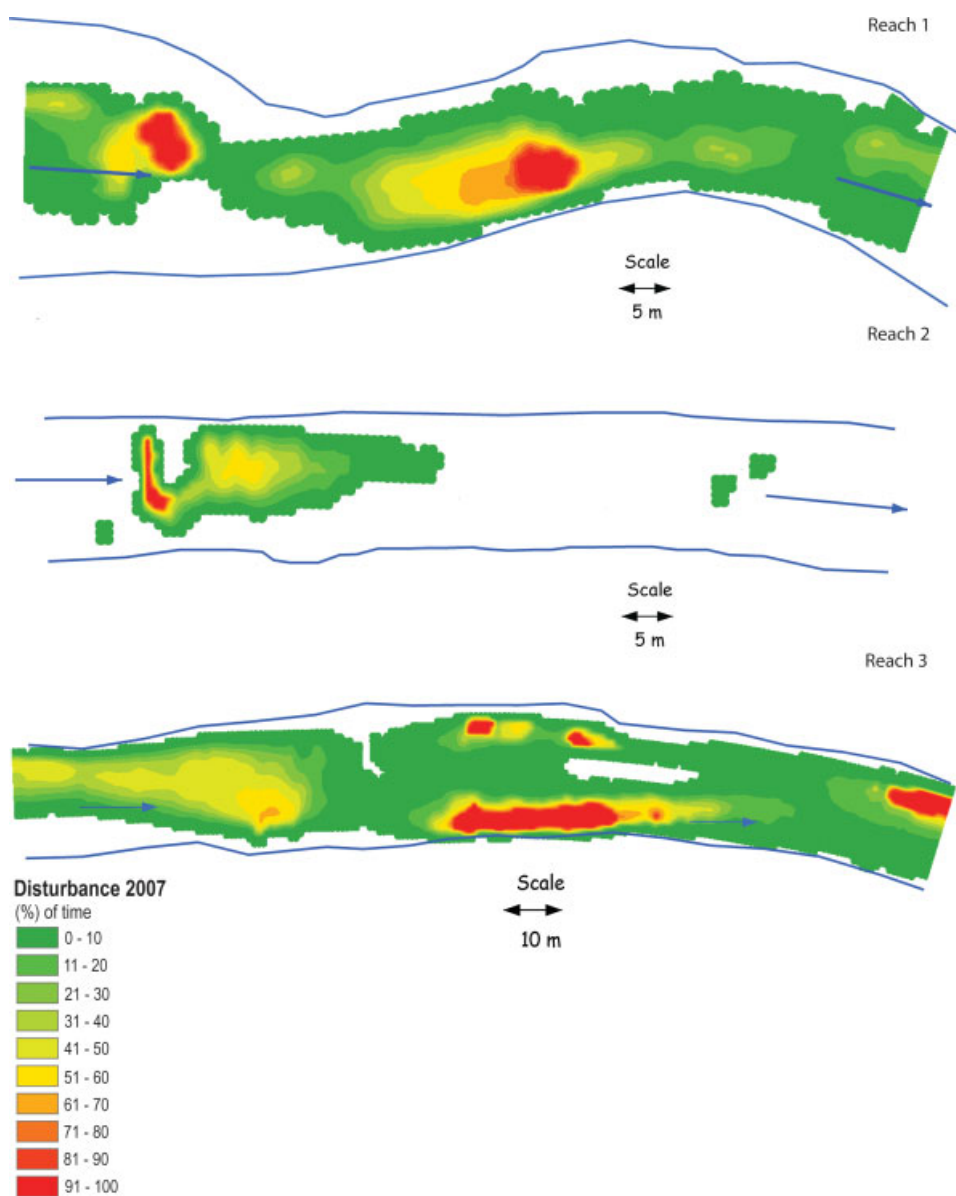


Figure 6. Channel bed disturbance maps for the three study sites in 2007, shown as percentage of days between May 1 and August 8.

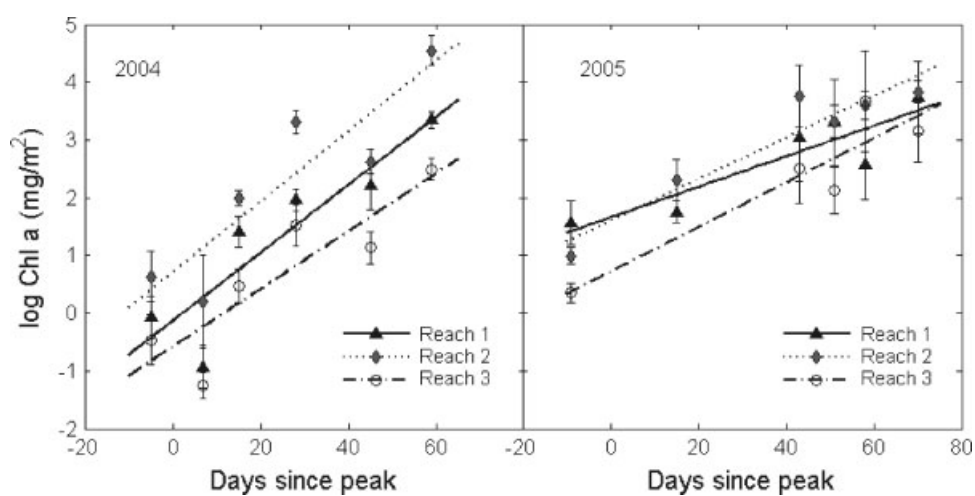


Figure 7. Trends in chl *a* abundance for 2004 and 2005.



INFLUENCE OF CHANNEL BED DISTURBANCE ON ALGAL BIOMASS

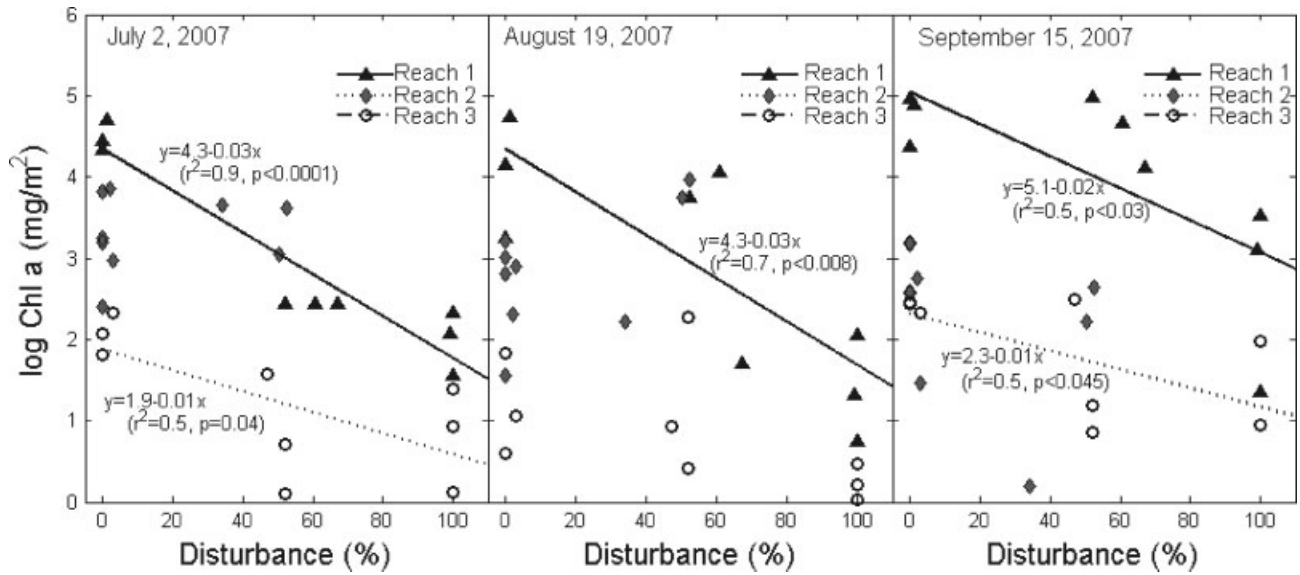


Figure 8. Chl *a* versus bed disturbance between May and August on the three sampling dates in 2007. Each panel shows the chl *a* abundance at the nine sampling locations for each study site versus the local disturbance. A line is plotted where a significant linear correlation between disturbance and chl *a* is found in the data ( $p < 0.05$ ).

Table V. Benthic community of the three sampling reaches.

Class/family	Genus or species	Mean biomass, g DM m <sup>-2</sup>		
		Reach 1	Reach 2	Reach 3
<b>Insecta</b>				
<b>Coleoptera</b>				
Dytiscidae		NA	NA	NA
Elmidae	<i>Zaitzevia parvula</i>	0.0219	0.0229	0.0071
Elmidae	<i>Heterlimnius corpulentus</i>	0.0182	0.0525	0.0059
<b>Diptera</b>				
Ceratopogonidae		NA	NA	NA
Chironomidae		0.0227	0.0586	0.0114
Simuliidae		NA	NA	NA
<b>Ephemeroptera</b>				
Baetidae		0.0343	0.0038	0.0066
Ephemerellidae	<i>Drunella doddsi</i>	0.0413	0.0010	0.0218
Ephemerellidae	<i>Drunella grandis</i>	0.0060	0.0243	0.0008
Ephemerellidae	<i>Ephemeralla</i>	0.0194	0.0302	0.0252
Heptageniidae	<i>Epeorus</i>	0.1663	0.0055	0.9250
Heptageniidae	<i>Rhithrogena</i>	0.0506	0.0000	0.3029
Heptageniidae	<i>Cinygmula</i>	0.0592	0.0074	0.0058
Siphonuridae		0.0033	0.0400	0.0235
<b>Plecoptera</b>				
Leuctridae		NA	NA	NA
Nemouridae		NA	NA	NA
Chloroperlidae		NA	NA	NA
Perlodidae		NA	NA	NA
<b>Trichoptera</b>				
Brachycentridae		0.0030	0.0228	0.1370
Hydropsychidae		NA	NA	NA
Rhyacophilidae		NA	NA	NA
Glossosomatidae		NA	NA	NA
<b>Arachnida</b>				
<b>Acari</b>				
Hydracarina		NA	NA	NA
Mollusca		NA	NA	NA
Oligochaeta		NA	NA	NA

Estimates of mean biomass (g DM m<sup>-2</sup>) are given for herbivore taxa (i.e. scrapers and gathering collectors); biomass was not estimated for other taxa (NA).

periphyton biomass reaches a plateau within the growing season, or may reach a plateau at multiple times separated by major disturbances (spates).

This study, when taken in contrast with studies that show a plateau of biomass accumulation during the growing season (Cronin *et al.*, 2007), supports a concept of dual control for periphyton biomass in streams, similar to the disturbance—resource supply—grazer concept described by Biggs (1996). Disturbance sets back the average biomass accumulation per unit area for a stream reach. Rate of increase in biomass where disturbance is not occurring, however, is dictated by a second set of factors (growth rate control factors) that also constrain net accumulation rates for periphyton. In the Williams Fork, low concentrations of potentially limiting nutrients, moderate grazing associated with benthic macroinvertebrates, moderate impairment of photosynthesis by tree canopy shading and, most importantly, consistently low temperature, together suppress the biomass accumulation that can occur at the reach scale even when most of the bed is stable. On the contrary, a river such as the plains zone of South Platte, which has abundant nutrients, full solar exposure, high mean temperatures, and very weak macroinvertebrate populations due to the mobility of substrate, builds periphyton biomass much more quickly, thus reaching a plateau that is sustained until a flow occurs that is capable of disturbing most of the bed.

It seems likely that streams will populate an intersection of the two sets of controlling factors (disturbance factors and growth rate control factors) that encompass all possible combinations, within which the Williams Fork may be near one extreme and the plains zone South Platte River near another (Figure 9). If so, the quantification of bed disturbance in terms of percentage movement per unit time, when taken in context with the growth rate control factors for stable portions of the bed, may offer a way of organizing information on periphyton growth control in streams.

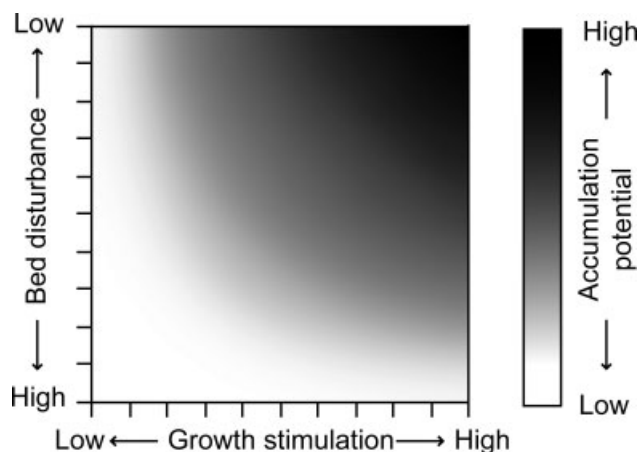


Figure 9. Conceptual diagram illustrating the simultaneous control of periphyton accumulation by disturbance and growth rate control factors. Accumulation potential is a function of both growth control factors and bed disturbance.

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