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ORIGINAL ARTICLE

Hydrodynamic shear removal of the nuisance stalk-forming diatom *Didymosphenia geminata*

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Abstract

The removal of benthic algae during periods of high flow is critical in maintaining the biodiversity of stream ecosystems. Here we determine a shear removal function for the nuisance, stalk-forming benthic diatom Didymosphenia geminata *by using samples collected from Rocky Mountain streams subjected to increasing bed shear stress in a laboratory flow chamber experiment. A linear shear removal function was observed to apply over the range of the shear stress obtained in the flow chamber. The overall removal of biomass was low. Less than 25% of the biomass was removed at a shear stress similar to that which would result in widespread bed disturbance in the stream. These results support the hypothesis that physical abrasion during periods of bed disturbance, rather than simply elevated shear stress, is the primary control on the removal of benthic algae such as* D. geminata *that are well adapted to the high-shear environments of mountain streams. The results also indicate that the shear removal function generally decreases with increasing biomass and mat thickness, the potential consequence of a positive feedback with near-bed hydrodynamics as the mats develop in the streams. The shear removal function was also influenced by the health and condition of the mats. Greater biomass removal was observed for mats in poorer condition. These mats had higher sediment content and were collected at the end of the growing season and from sites at lower elevations.*

Introduction

[1] Among the many biotic and abiotic factors that affect the growth dynamics of benthic algae, variations in flow are particularly significant in streams (Biggs and Close 1989). Periodic flood events are important in maintaining the diversity of stream ecosystems because floods remove benthic algae allowing space for new and different species to grow (Townsend 1989). Benthic mats with different algal communities have different levels of resistance to disturbance due to both intrinsic and conditioning variations (Biggs and Thomsen 1995).

[2] The three primary mechanisms for the removal of benthic algae are shear removal due to increased drag resistance, abrasion due to suspended particles, and physical scouring resulting from disturbance of the substrate (Biggs and Stokseth 1996). The removal of benthic algae during flood events is not uniform across the streambed because of spatial variations in the hydraulic properties driving the

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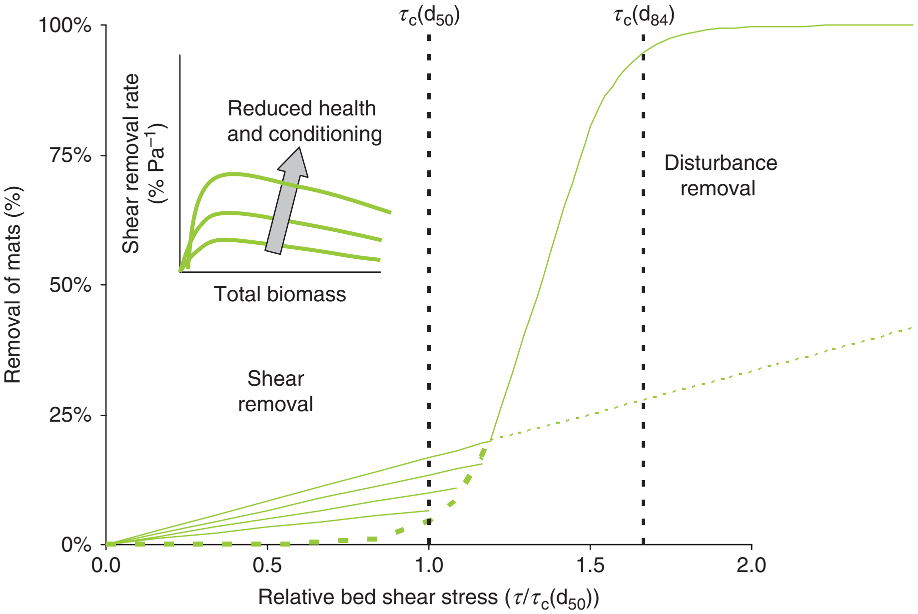

Fig. 1 Conceptual model for the relative magnitudes of bed shear stress and disturbance removal of benthic algal mats adapted to growing in high-gradient, high-shear stress streams such as those produced by *D. geminata*. The expected proportion of mat removal is a function of the applied bed shear stress (τ) relative to the critical shear stress for disturbance of the median bed particle size ($\tau_c(d_{50})$). The inset shows the expected relationship between the total biomass and the shear removal rate below the critical threshold for disturbance and how this is likely influenced by mat health and condition. The different lines in the shear removal zone show how the shear removal function could vary as a function of mat thickness or mat condition as demonstrated by the insert. The solid lines represent the dominant removal function and the dashed lines represent the less dominant removal.

removal process, primarily increased bed shear stress, and the potential for bed disturbance (Segura et al. 2011). Variations in the resistance of different algal species also contributes to nonuniform removal (Peterson and Stevenson 1992). The result is patchiness in the distribution of benthic algal communities that supports stream diversity and the functioning of stream ecosystems (Lake 2000).

[3] Benthic algae are thought to be well adapted to the dynamics of their natural "conditioning" environment (Biggs and Stokseth 1996). Specifically, shear removal experiments conducted in a laboratory flow chamber for a range of different types of benthic algae (Biggs and Thomsen 1995) have shown that variations in the shear resistance of benthic algae are due both to "inherent" properties of different species (i.e., physical properties such as shape, size, texture, tensile strength, and attachment strength) and ecophysiological properties for different communities of the same species (i.e., factors relating to the community and its environment such as age, occurrence of secondary structure, and acclimation to a given shear stress and/or resource conditions). For example, adaptation to the high-turbulence and high-shear environments of swift flowing, high-gradient streams is indicated by the low-stature and low-surface-to-volume ratios of algal species in benthic mats from mountain streams. These characteristics reduce the potential for removal during periods of elevated shear stress (Biggs et al. 1998).

[4] A diatom species that challenges this conceptual model is the lotic, stalk-forming diatom *Didymosphenia geminata* (Lyngbye) A. Schmidt (Larned et al. 2007). The preferred habitat for *D. geminata* is swift-flowing mountain streams characterized by low stream water nutrient concentrations, high-light availability, and stable substrates (Kilroy et al. 2005; Spaulding and Elwell 2007; Rost et al. 2011); this is particularly true downstream of dams and reservoirs (Kirkwood et al. 2009). Despite the highly dynamic flow regime and the high-shear rates characteristic of these preferred habitats, *D. geminata* is capable of producing very thick benthic algal mats in a short period of time (Spaulding and Elwell 2007). These extensive benthic algal mats reduce the aesthetic qualities of a stream and can affect local economies dependent on recreation and tourism (Branson 2006). They also affect foodweb structure and potentially the functioning of stream ecosystems (Kilroy et al. 2009; Gillis and Chalifour 2010).

[5] A recent general conceptual model for the growth dynamics of *D. geminata* (Cullis et al. 2012) is

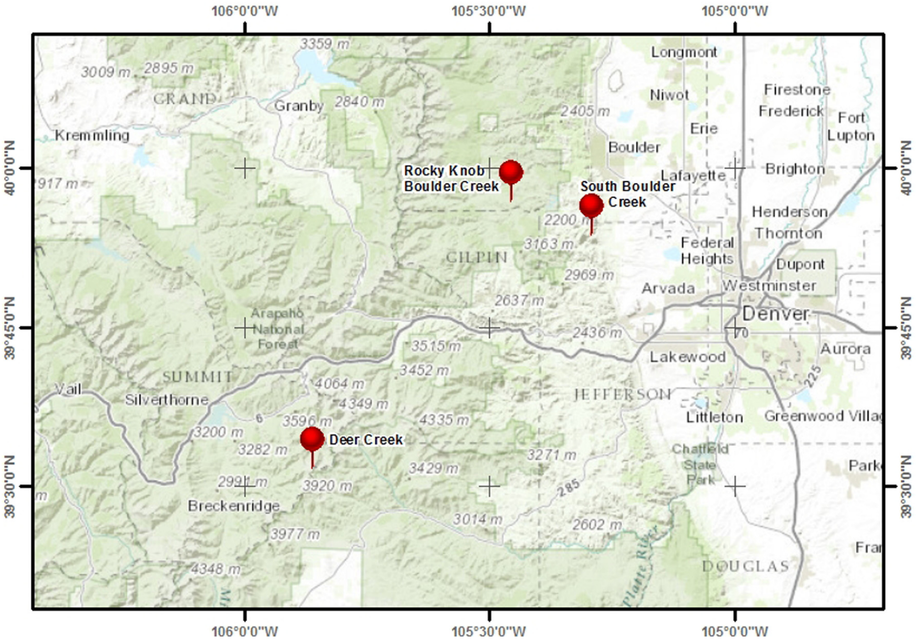

Fig. 2 Map of Colorado showing the locations from which samples were taken for the shear removal experiments indicated by red markers.

premised upon two main hypotheses for the removal of benthic algal mats (Fig. 1). The first is that *D. geminata* is well adapted to growing in high-shear environments, and, therefore, removal due to elevated shear stress alone is limited. Effective removal of mats thus requires flood events sufficiently large to result in widespread physical bed disturbance. This hypothesis is based on the field observations of Miller et al. (2009) and Cullis et al. (2012) as well as the observation that *D. geminata* is more persistent in areas with reduced occurrence of high-flow events, such as the regulated conditions downstream of dams and reservoirs (Kirkwood et al. 2009). The second hypothesis is that the removal rate due to elevated shear stress is influenced by the total amount of algal biomass and the condition of the mats. Thicker mats are predicted to be less susceptible to removal due to increasing shear stress because of positive feedback on the near-bed hydrodynamics. This positive feedback was observed in laboratory studies when using *D. geminata* samples taken from a stream in New Zealand where the presence of the algal mats reduced the turbulence intensity above the mats and thereby reduced the potential for shear removal during periods of high flow (Larned et al. 2011). In addition, healthier, better-conditioned mats are predicted to have lower shear removal relative to senescent mats in poorer condition.

[6] The flow chamber studies by Larned et al. (2011) did not, however, determine the relationship between increasing shear stress and the removal of *D. geminata.* Such information would be useful in designing artificial flood releases, or flushing flows, as proposed mitigation measures for nuisance *D. geminata* blooms, particularly downstream of dams (Kilroy 2010). A critical question that needs to be answered is how large do these flushing flows need to be to be effective in mitigating future blooms? If, as is hypothesized here, *D. geminata* is well adapted to high-shear environments, then increased flow that elevate the bed shear stress will not be effective at removing nuisance blooms unless they are large enough to produce widespread physical disturbance of the substrate that results in the mechanical scouring of the algal mats. This has implications for reservoir management and the trade-off between competing demands for water, particularly in cases where the maintenance of stream ecosystems is important to the local economy.

[7] Here we present the results of laboratory flow chamber experiments that quantify a hydrodynamic shear removal function for *D. geminata* using mat samples taken from three streams in the Rocky Mountains (Colorado, USA). We examine the hypothesis that increasing fluid shear stresses will lead to the removal of *D. geminata*; as opposed to the possibility that effective removal requires flows sufficiently high to cause widespread bed disturbance and physical scoring of the mats.

Table 1 Location and elevation of sampling locations as well as stream water chemistry parameters (average ± standard deviation) for locations from which samples were taken. TDN = total dissolved nitrogen, TDP = total dissolved phosphorus, and DOC = dissolved organic carbon.

Stream reach	Location	Elevation (m)	Temp. (°C)	pH	TDN (mg L^{-1})	TDP (μg L^{-1})	DOC (mg L^{-1})
Rocky Knob (RK), Middle Boulder Creek[1]	39°58′57″ N 105°26′45″ W	2340	11.42 ± 2.65	7.78 ± 0.33	0.19 ± 0.05	4.15 ± 2.65	2.99 ± 0.68
South Boulder Creek (SBC)[2]	39°55′51″ N 105°17′28″ W	1843	6.98 ± 3.86	7.92 ± 0.38	0.36 ± 0.12	7.60 ± 7.43	3.20 ± 1.04
Deer Creek (DC)[3]	39°33′49″ N 105°51′38″ W	3222	8.5				

[1] Biweekly samples taken during the spring and summer from May 2008 to October 2010.

[2] Monthly grab samples taken by Denver Water from January 2008 to October 2010.

[3] Individual grab sample taken on date algal samples were collected from Deer Creek: 10 September 2011.

We also investigate the role of increasing biomass and mat condition on the removal of *D. geminata*.

Methods

Site Description and Sample Collection Conditions

[8] To evaluate the response of *D. geminata* to the high-shear environments of its natural habitat, the shear removal tests were done using mat samples collected where *D. geminata* was growing naturally in the stream (e.g., Larned et al. 2011). A total of 10 shear removal tests were performed using rocks with varying coverage of *D. geminata*, which were taken from study sites on Middle Boulder Creek, South Boulder Creek, and Deer Creek (Fig. 2). All three sites are typical of the mountain streams in Colorado and the preferred habitat for *D. geminata* with generally cool, clear water and low stream water nutrient concentrations (Table 1).

[9] Previous studies of *D. geminata* in Boulder Creek (Miller et al. 2009) showed no significant difference in abundance due to variations in stream water chemistry between the Middle and South Boulder Creek. No previous studies of *D. geminata* have been conducted in Deer Creek, but conditions appear to be favorable for growth and consistently thick algal mats, and high levels of abundance have been observed over a number of years (McKnight, personal observations).

[10] Samples for the first test (RK1) were taken from the Rocky Knob site on Middle Boulder Creek in May 2010. The stream reach is ∼20 m wide, and the samples were collected in the deepest part of the stream which was ∼20 cm deep during low-flow conditions. Coverage by *D. geminata* at the time of sampling was close to 100% of the streambed. The average mat thickness was greater than 1 cm, and numerous characteristic "streamers" of stalk material were evident on the stream bed. Flow on the day of sampling was low (Table 2).

[11] Soon after the RK1 experiment was conducted Boulder Creek experienced high flows due to the early onset of spring runoff (Fig. 3). These flows were also higher than the average annual peak flow and

Table 2 Sampling dates, average flow conditions, average dimensions of rocks (length × width × height) used for each shear removal test, and the average representative stream bed area. Flow in Deer Creek was estimated based on the ratio of the measured discharge and the recorded flow at a stream gauge downstream of the confluence with the Snake River on the day on which the samples were collected.

Location	Test	Date	Flow on date of sample (m^3 s^{-1})	Max flow for calendar year (m^3 s^{-1})	Average dimensions for rocks in tests (mm)	Representative area of streambed (cm^2)
Rocky Knob (Boulder Creek)	RK1	19 May 2010	0.04	15.08	105 × 84 × 53	421
	RK2	10 May 2011	0.39	20.42	105 × 90 × 57	448
	RK3	10 May 2011	0.39	20.42	108 × 88 × 50	452
	RK4	23 May 2011	0.28	20.42	108 × 82 × 53	426
	RK5	23 May 2011	0.28	20.42	100 × 77 × 53	374
Eldorado Canyon (S Boulder Creek)	SBC1	9 Nov 2010	0.38	13.39	101 × 71 × 46	402
	SBC2	9 Nov 2010	0.38	13.39	88 × 64 × 37	319
	SBC3	9 Nov 2010	0.38	13.39	84 × 63 × 44	420
Deer Creek	DC1	10 Sep 2011	0.11	1.50	107 × 78 × 43	415
	DC2	10 Sep 2011	0.11	1.50	100 × 83 × 50	203

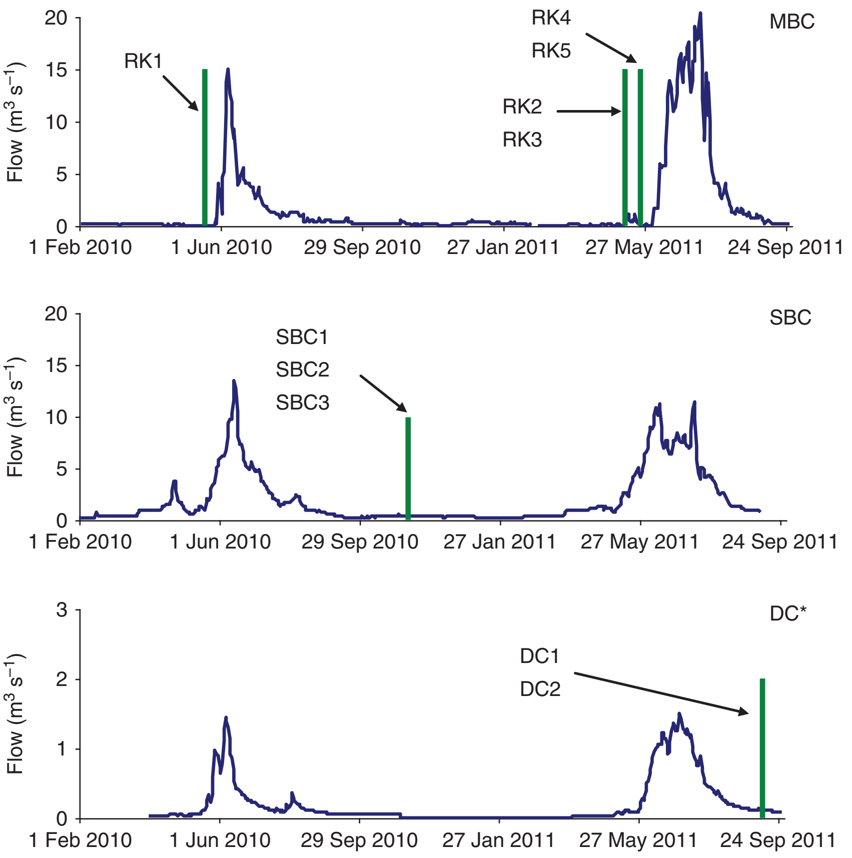

Fig. 3 Annual hydrographs for Boulder Creek (A), South Boulder Creek (B), and Deer Creek (C). Green bars indicate the date on which samples were collected. *Flow in Deer Creek was estimated based on the ratio of the measured discharge and the recorded flow at a stream gauge downstream of the confluence with the Snake River on the day samples were collected.

effectively removed *D. geminata* colonies from all sites along Boulder Creek. By May 2011, *D. geminata* mats had reappeared, and four additional tests (RK2–RK5) were run using samples taken from the same location as the RK1 test. The low flow on these sampling dates was much higher than the RK1 test, but still occurred prior to the start of the annual spring runoff. The abundance of *D. geminata* during these tests, however, was much lower compared with the previous year, with ~50% coverage by smaller colonies with average mat thickness of <1 cm. This was due to the limited recovery after the high flows observed during the spring peak in the previous year, described above.

[12] Three tests (SBC1, SBC2, and SBC3) were conducted in November 2010 by using samples taken from the Eldorado Canyon site on neighboring South Boulder Creek. *D. geminata* mats at this site had recovered following the high spring runoff of that year, and coverage was similar to the May 2011 Rocky Knob samples. Because this sample was taken at the end of the summer there was the potential for greater accrual of suspended sediments and the mats appeared to be less cohesive, suggesting a reduction in their health due to reduced light availability and potential senescence. The stream channel was ~12 m wide with samples taken from a shallow section of the channel, which was 2–3 cm deep during the low flow period during sample collection. No *D. geminata* mats were observed in deeper waters of the channel, although they had been more widespread in the previous spring.

[13] Two final tests (DC1 and DC2) were conducted using samples collected from Deer Creek in September 2011 at a site 10 m downstream of a beaver dam. These samples consisted of very thick (>1 cm) and apparently healthy *D. geminata* mats (Fig. 4), but only covering 50%–75% of the substrate.

Shear Removal Experiments

[14] For each shear removal test, between six and eight rocks were removed from the stream and placed on a plastic tray measuring 20 cm × 25 cm and transported to a laboratory at the University of Colorado. A small amount of water was added to keep the samples damp, but the mats were not covered so as to limit the disturbance during transport.

[15] The experimental flow chamber was 5 m long and 60 cm wide and fitted with a temporary test section (2.20 m long and 25 cm wide and inclined at a slope of 2.5%; Fig. 5) to increase the applied shear stress. The bed

Fig. 4 Photograph facing downstream in the flow chamber with rocks covered in thick healthy mats of *D. geminata* taken from the Deer Creek site during the September 2011 shear removal tests (DC1). Note the ADV and the plankton net in the background used to collect any material removed due to the increasing applied bed shear stress.

of the flow chamber was lined with medium-sized river cobbles (median diameter, $d_{50} = 60$ mm) to maintain a rough turbulent boundary layer characteristic of the conditions occurring in a natural stream. The sample tray was placed two-thirds of the way down the test section and a plankton net (Fieldmaster, Wildco, USA) with a mesh size of 80 µm was attached at the end of the test section to catch the dislodged sediment and particulate organic material. The plankton net was fitted with a removable 125-mL sample bottle. After each test run the net was removed, and the trapped material was transferred to a 250-mL brown high-density polyethylene bottle.

[16] Similar shear removal experiments by Francoeur and Biggs (2006) showed that the majority of benthic algae is removed in the first 5–10 min of elevated shear stress and appears to reach an asymptote after 30 min, with minimal additional removal at longer durations unless the applied shear stress is further increased. Based on these observations the pumps were run for a total of 30 min at a given flow for each test.

[17] The material caught in the net during each period was removed and analyzed for inorganic sediment concentrations, ash-free dry mass (AFDM), *D. geminata* cell densities, and chlorophyll *a* (chl *a*). The net was replaced, and the pumps were run for another 30 min at a higher flow. In total, four periods of increasing flow and associated bed shear stress were used. At the end of the last period at the highest flow the remaining material on the sample rocks was physically removed using a scalpel and tooth brush and analyzed as described below.

Total Biomass and Sediment Content of the Algal Mats

[18] The material caught in the net during each run was diluted to a total volume of 300 mL with dionized water. The samples were agitated and split into duplicates with two aliquots of 50 mL each being filtered onto a 0.7-µm glass fiber filter (Whatman PLC, UK) and two aliquots of 100 mL each being placed in a preweighed 150-mL aluminum dish. The filters were frozen for later analysis of chl *a* with buffered acetone extraction and spectral absorption (Wetzel and Likens 2000) by using a spectrophotometer (Orion Genysis 20, Thermo Orion Scientific, USA). The samples in the aluminum dishes were dried at 60 °C for 24 h, weighed, combusted at 450 °C for 4 h, and weighed for a final time to determine the total biomass measured as AFDM.

[19] After recording the final ashed weight, the samples were placed into 50-mL centrifuge tubes and cleaned using 10–20 mL of 30% hydrogen peroxide to remove any remaining organic material from the silica frustules, which facilitates the counting of *D. geminata* cells. The sample was diluted to 50 mL and between 1 and 5 mL of sample was put into an Uterhmöhl settling chamber. The number of *D. geminata* cells in each chamber were counted for a total of 50 fields (magnified 200 times using a Nikon TS100 inverted microscope), which were used to estimate the total number of cells in each sample.

[20] The initial sediment and biomass concentrations for each sample were determined as the sum of all the material removed during the tests and the residual material remaining on the samples after completion of the tests. The initial sediment and biomass concentrations were used to normalize the shear removal function to enable comparisons among samples.

[21] To account for variations in the number and size of rocks sampled, the total biomass either removed during the experiments or remaining after the completion of the experiment was normalized by the

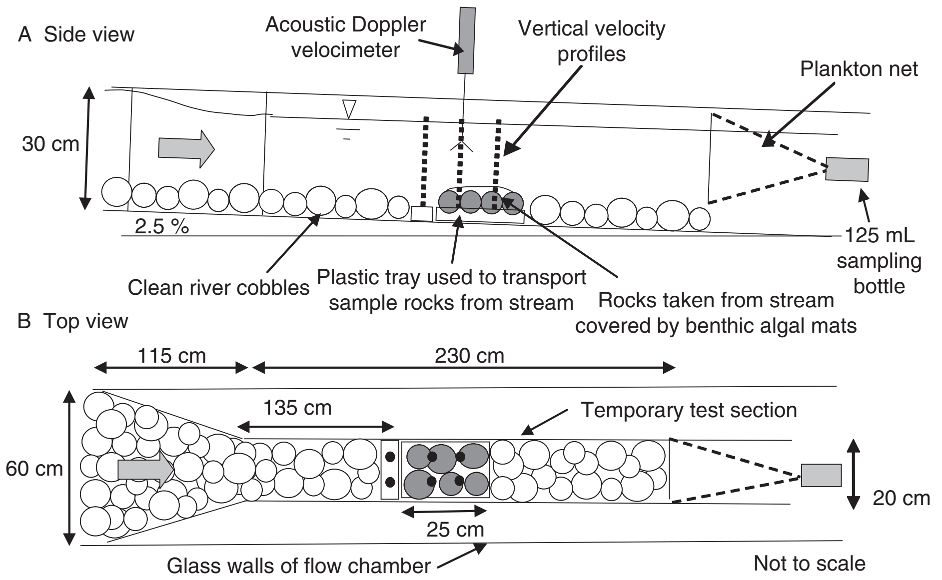

Fig. 5 Experimental setup for shear removal tests (not to scale) in side view (A) and top view (B). Gray arrow indicates flow direction.

estimated total exposed surface area of the sampled rocks. This was calculated based on the assumption that each rock had a roughly elliptical shape with the exposed surface area related to the measured semimajor (a_i) and semiminor (b_i) axis given in Eq. (1),

$$\text{Area} = \sum_{i=1}^{n} a_i b_i \pi. \tag{1}$$

Determining the Average Bed Shear Stress for the Flow Chamber Studies

[22] The average bed shear stress over the sample was determined for each flow based on the bed shear stress estimated from six velocity profiles taken in a grid pattern over the sample tray. An acoustic Doppler velocimeter (ADV; MicroADV, Sontek, USA) was used to make between four and eleven discrete velocity measurements (2 min at 50 Hz) to determine the velocity profile starting from ~1 cm above the rocks. The presence of suspended material meant that the average signal-to-noise ratio could be maintained above 20 dB without the need for artificial seeding. The shear velocity (u_*) at each location was calculated by fitting Eq. 2 to the logarithmic portion of the velocity profile,

$$u_z = \frac{u_*}{\kappa} \ln\left(\frac{z}{z_0}\right), \tag{2}$$

where u_z is the time-averaged velocity at elevation z above the bed, z_0 is the roughness height, and κ is the von Kármán's constant (0.41). The bed shear stress (τ_0) was calculated as

$$\tau_0 = \rho u_*^2, \tag{3}$$

where ρ is the density of water (1000 kg m^{-3}). The average bed shear stress over the whole sample for each flow was determined from the average of the estimated bed shear stress values for each of the six velocity profiles.

Shear Removal Function

[23] The total amount of material removed during each period was added to the material removed during previous periods to determine the cumulative amount of biomass and sediment removed from each sample. The amount of material removed from the sample was divided by the estimated total initial biomass to determine the cumulative percentage of material removed. This was compared with the estimated τ_0 during each period of the increasing flow to determine the final shear removal function for each sample. The shear removal function for each sample was given by the slope of the line and is presented in terms of the percentage of the initial biomass measured in terms of AFDM, chl *a*, cells, and the percentage of the initial sediment content removed with a unit increase in applied shear stress.

[24] To place the results of the shear removal experiments in the context of the average bed shear stress to which the samples would be exposed to in the field, the spatial distribution of the average bed shear stress at the Rocky Knob site was modeled using the U.S. Geological Survey Fastmech two-dimensional flow model (Nelson et al. 2003). The model was used to determine the average bed shear stress due to the peak annual flows in 2009 and 2010 at the location from

Table 3 Hydraulic properties for different flow used in shear removal experiments. The average bed shear stress was calculated from measurements of six velocity profiles over the sampling test area. The Froude No is based on $U/(gD)^{1/2}$, where U is the average velocity, g the acceleration due to gravity and D the depth. The Renolds No. is given by Ud_h/ν, where d_h is the hydraulic diameter of the chamber, and ν is the kinematic viscosity.

Pump setting	Flow (L s^{-1})	Average velocity (cm s^{-1})	Average depth (m)	Froude no.	Reynolds no.	Shear stress from velocity profiles (N m^{-2})
15 Hz	11	31	0.12	0.33	1.4×10^5	12 (± 6)
30 Hz	30	57	0.18	0.50	3.1×10^5	25 (± 11)
45 Hz	50	87	0.24	0.52	4.6×10^5	59 (± 38)
60 Hz	61	94	0.28	0.53	5.4×10^5	83 (± 35)

which the samples were taken for the shear removal experiments; it showed good comparison between observed and model water surface elevations (Cullis 2011). The average bed particle size distribution at the sampling location was determined using a random sampling approach (Wolman 1954). The critical shear stress for the initiation of disturbance of the median bed particle size was determined using an equation for the critical nondimensional Shields stress as a function of the average channel slope (Mueller et al. 2005).

Results

[25] The initial benthic algal biomass, *D. geminata* cell density, and sediment content of the mats varied considerably among the different tests due to the different sampling locations, the different flow regimes, and the different times of the year when the tests were conducted (Table 4). The greatest amount of algal biomass was observed for the RK1 test measured as both AFDM ($t_8 = 5.67, p = 0.001$) and chl *a* ($t_8 = 26.2, p < 0.001$). This is consistent with the observation in the field of much greater coverage and the presence of characteristic streamers of *D. geminata* mat material. The *D. geminata* cell density for the RK1 test was, however, similar to the Deer Creek samples, which were the healthiest looking mat ($t_2 = 0.99, p = 0.391$).

[26] The lowest biomass was observed during the May 2011 samples at the Rocky Knob site (RK2–RK5), which were as a group significantly lower than the DC samples and the SBC samples both in terms of AFDM ($t_5 = 5.60, p = 0.011$) and cell density ($t_5 = 8.66, p = 0.003$). The average cell density for the DC samples was significantly higher than the SBC samples ($t_3 = 3.87, p = 0.031$), but not in terms of AFDM ($t_3 = 1.06, p = 0.366$). Due to the greater variation in the results, however, there was no significant difference between the groups of samples for chl *a*. The South Boulder Creek samples had the highest sediment content in the mat, which was expected as these samples were collected at the end of the summer ($t_8 = 5.77, p = 0.01$).

Table 4 Initial sediment and biomass aerial densities for each test and the percentage removed up to the maximum applied shear stress. The SBC1 samples were dropped prior to placing in the flume, resulting in a much higher overall percentage of the biomass removal than for the other tests.

	Estimated initial aerial densities on samples				Percentage removed during tests			
Test	AFDM (mg cm^{-2})	Chl *a* (µg cm^{-2})	Cell density (cells cm^{-2})	Sediment (mg cm^{-2})	AFDM	Chl *a*	Cell density	Sediment
RK1	7.06	12.70	3935	41.77	18%	9%	15%	No data
RK2	2.16	2.44	1179	3.41	35%	16%	10%	25%
RK3	2.74	3.45	1881	4.73	16%	19%	12%	13%
RK4	3.43	2.78	1038	10.05	22%	21%	26%	11%
RK5	3.06	6.46	1149	8.13	17%	16%	24%	12%
SBC1	4.05	4.52	2277	25.78	48%*	48%*	60%*	56%*
SBC2	5.05	7.39	2195	17.83	27%	16%	63%	27%
SBC3	2.92	3.17	1511	24.12	28%	21%	28%	14%
DC1	6.41	2.81	3911	9.51	11%	11%	3%	11%
DC2	4.85	5.38	3219	15.22	14%	19%	7%	9%

[27] The total amount of benthic biomass removed during the shear removal tests was low in all cases except for SBC1, which was unintentionally dropped on placing the samples in the flow chamber (Table 4). This resulted in the physical scoring of some of the mats and resulted in a much higher removal of the benthic biomass at the initial flow and hence overall. For the other samples, 21% ± 8% (mean ± standard deviation) of the total initial AFDM, 16% ± 4% of the chl *a*, 21% ± 18% of the *D. geminata* cells, and 15% ± 7% of the trapped inorganic sediment was removed.

[28] The average bed shear stress (τ_0) for each flow estimated from the measured velocity profiles is given in Table 3. The variability in measured τ_0 across the sample was expected given the rough nature of the bed and the relatively shallow flow depths (Stone and Hotchkiss 2007). The Froude and Reynolds numbers determined indicate that the conditions in the flow chamber were subcritical and turbulent, respectively (Table 3).

[29] The cumulative removal function for sediment, AFDM, chl *a*, and *D. geminata* cell density were well described by a linear function for all samples with increasing τ (R^2 values given in Table 5). An example of the results for the second set of samples from the Rocky Knob site (RK2–RK4) is given in Fig. 6. In all cases and for all metrics the slope of the removal function was found to be low, ranging from 0.05% to 0.35% of the initial biomass removed with each unit (N m^{-2}) of increasing bed shear stress (Table 5). The slopes of the shear removal function were all significantly different from zero (R^2 values given in Table 5); for AFDM, $R^2 = 0.91 – 0.99$, $t_2 = 5.80 – 16.3$, $p = < 0.001–0.011$) and the slopes for the South Boulder Creek samples were statistically similar to each other and to the RK1 sample, but different from the May 2011 Rocky Knob samples (RK2–RK4). The slope of the shear removal function for the Deer Creek samples, which appeared to be the healthiest of the sampled *D. geminata* mats, was significantly lower than for both the South Boulder Creek and Rocky Knob samples.

[30] The relationship between the normalized slope of the shear removal function and the initial sediment and biomass densities for each test (Fig. 7) suggest that the shear removal rate was generally lower for more abundant or thicker mats than for thinner mats consisting of less total biomass. This correlation was strongest for the most healthy, productive biomass indicated by chl *a* ($r = –0.654$, $t_8 = –2.431$, $p = 0.041$). These observations were, however, based on a limited sample set and influenced by the single RK1 test. Additional tests, particularly with high levels of biomass, are required to confirm the relationship between increasing biomass and a reduction in the amount of biomass removed due to elevated shear stress alone.

Table 5 Shear removal rates calculated in terms of the absolute amount removed and the percentage of initial sediment or biomass concentrations removed per unit of increasing average bed shear stress (N m^{-2}). Values are derived from the slope of the linear regression ± standard error of the slope. The goodness of fit is indicated by the R^2 values given in parentheses. For all tests $n = 4$ data points.

	Slope of the removal function in absolute terms per N m^{-2}				Removal as a % of initial amount per N m^{-2}			
Test	AFDM (mg cm^{-2})	Chl *a* (µg cm^{-2})	Cells (cells cm^{-2})	Sediment (mg cm^{-2})	AFDM (%)	Chl *a* (%)	Cells (%)	Sediment (%)
RK1	0.010 ± 0.0013 (0.97)	0.006 ± 0.0012 (0.93)	3.763 ± 0.762 (0.92)	No Data	0.14	0.05	0.10	No Data
RK2	0.006 ± 0.0010 (0.95)	0.004 ± 0.0007 (0.93)	1.294 ± 0.455 (0.80)	0.009 ± 0.0018 (0.99)	0.30	0.15	0.11	0.26
RK3	0.004 ± 0.0005 (0.96)	0.006 ± 0.0005 (0.99)	1.744 ± 0.395 (0.91)	0.005 ± 0.0010 (0.92)	0.13	0.18	0.09	0.11
RK4	0.006 ± 0.0011 (0.95)	0.005 ± 0.0008 (0.95)	2.543 ± 0.095 (0.99)	0.011 ± 0.0014 (0.93)	0.18	0.19	0.25	0.11
RK5	0.005 ± 0.0008 (0.94)	0.010 ± 0.0013 (0.97)	2.666 ± 0.383 (0.96)	0.009 ± 0.0018 (0.97)	0.15	0.16	0.23	0.12
SBC1	0.011 ± 0.0011 (0.99)	0.011 ± 0.0026 (0.94)	5.916 ± 0.142 (0.99)	0.096 ±0.0022 (0.99)	0.28	0.23	0.26	0.37
SBC2	0.013 ± 0.0021 (0.99)	0.010 ± 0.0026 (0.88)	11.810 ± 2.038 (0.94)	0.042 ± 0.0101 (0.89)	0.25	0.13	0.54	0.24
SBC3	0.010 ± 0.0006 (0.99)	0.007 ±0.0008 (0.98)	5.408 ±0.528 (0.98)	0.045 ± 0.0054 (0.97)	0.35	0.22	0.36	0.19
DC1	0.003 ± 0.0005 (0.91)	0.003 ± 0.0005 (0.94)	0.740 ± 0.184 (0.89)	0.005 ± 0.0016 (0.84)	0.05	0.10	0.02	0.05
DC2	0.006 ± 0.0017 (0.96)	0.009 ± 0.0017 (0.94)	1.608 ± 0.231 (0.96)	0.012 ± 0.0015 (0.84	0.1	0.17	0.05	0.08
Mean	0.007	0.007	3.748	0.026	0.20	0.17	0.21	0.17
Std. dev.	0.003	0.003	3.513	0.030	0.10	0.04	0.17	0.10

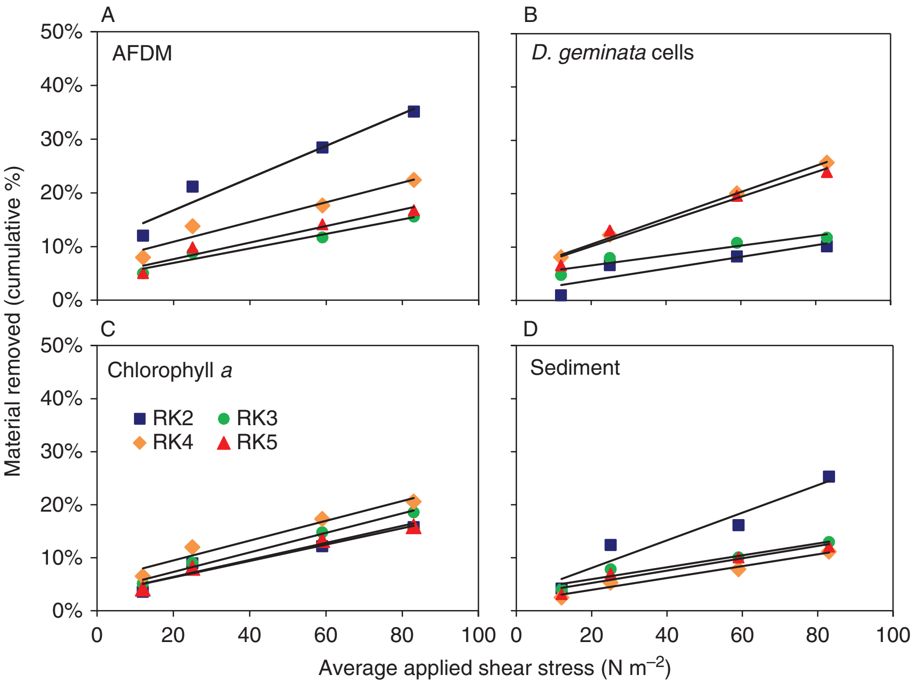

Fig. 6 Examples of the results of the shear removal tests in terms of the cumulative removal function for AFDM (A), *D. geminata* cell density (B), chl *a* (C), and total inorganic sediment (D) for the four samples taken from the Rocky Knob site in May 2011.

Discussion

[31] The results from this study show that the removal of *D. geminata* due to elevated shear stress (τ_0) is low compared with other benthic algal species. Extrapolation of the results shows that in all cases removal of 50% of the initial biomass requires $\tau_0 > 90$ N m^{-2}. For comparison Biggs and Thomsen (1995) determined that the shear stress required for the removal of 50% of algal biomass for the filamentous diatom communities of *Melosira varians/Gomphonema parvulum* and *Spirogyra* sp./*Gomphoneis herculeana/Ulothrix zonata* was ~3.6 N m^{-2} and 10.0 N m^{-2}, respectively. They also found the shear removal rate for the nonfilamentous communities *Fragilaria construens/Cymbella minuta/Archmanthes minutissima* and *Fragilaria vaucheriae/Cymbella minuta* to be approximately linear with removal of 50% of biomass requiring a τ of 50.6 N m^{-2} and $>$ 90 N m^{-2}, respectively. In this respect, *D. geminata* appears to be more similar to low-growing, tightly adhering, nonfilamentous algal species than filamentous diatom species that produce similar levels of total benthic algal biomass as *D. geminata*.

[32] The observed relationship between the removal rate due to elevated τ_0 and the total organic biomass (Fig 7), particularly for chl *a*, is similar to that anticipated in the conceptual model (Fig. 1); that is, it reduces with increasing initial biomass or mat thickness. This conceptual model results from a consideration of the potential interaction between increasing biomass and the near-bed hydrodynamics as observed by Larned et al. (2011). Initially increasing biomass results in an increasing shear removal function as the thickness of the algal mat increases and projects out into areas beyond the viscous sublayer on the substrate surface. At some point, however, the increasing algal mat starts to influence the near-bed hydrodynamics, resulting in reduced turbulence intensities. Thereafter increasing mat thickness produces a reduction in the shear removal rate as seen in the results for this study.

[33] The negative correlation between the AFDM removal function and the total initial biomass observed in this study (Fig. 7) was, however, only significant at the 90% confidence interval level, while the negative trend in the removal function for *D. geminata* cell density was only significant at the 80% confidence interval level. The results from this study are, therefore, not conclusive with respect to these parameters and further investigations of this potential phenomenon are required. However, consideration of the calculated shear removal functions (Table 5) shows a difference in the removal function for AFDM and cell density for the South Boulder Creek samples compared with the Rocky Knob and Deer Creek samples. This is potentially due to variations in the health and condition of the mats. The South Boulder Creek samples were taken late in the season

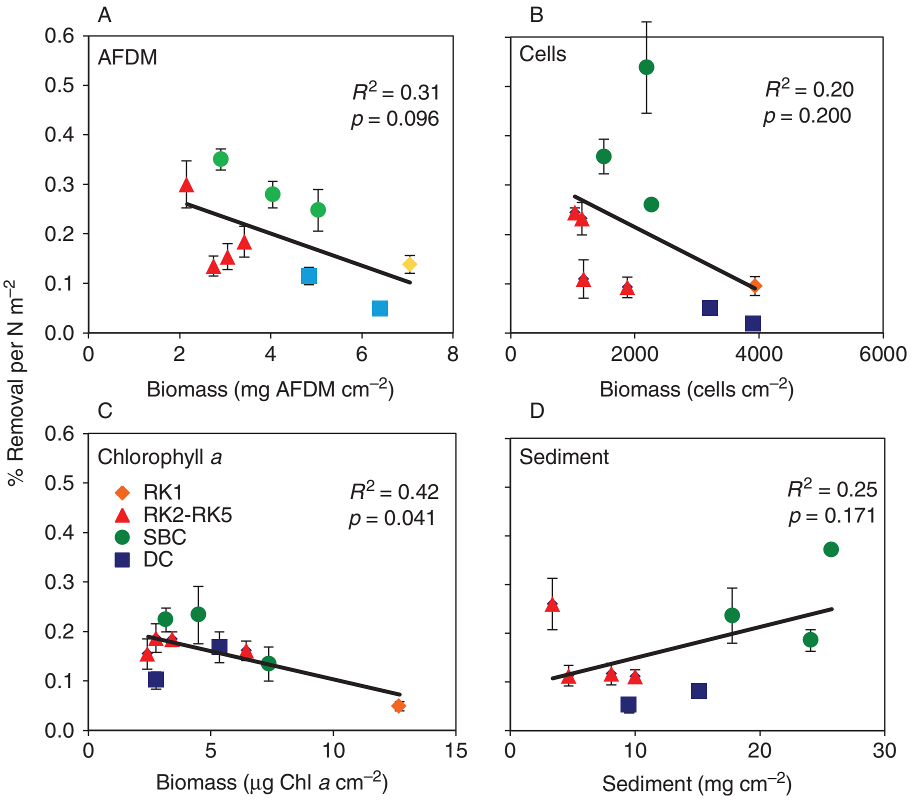

Fig. 7 Removal of AFDM (A), *D. geminata* cells (B), chl *a* (C), and inorganic sediment (D) per N m^{-2} increase in applied shear stress determined for the different removal experiments using samples from the Rocky Knob (RK), South Boulder Creek (SBC), and Deer Creek (DC) study sites. Error bars indicate the standard deviation for the shear removal rate calculated for individual experiments.

and following a year of high flow. Qualitatively, the *D. geminata* colonies observed at the South Boulder Creek did not appear to be as healthy or as well conditioned as the samples collected from the Rocky Knob site and even less so than the samples collected at the Deer Creek site. The poorer mat condition at the South Boulder Creek site might explain the higher shear removal function for AFDM and cell density.

[34] The interpretation of the results that the difference in the shear removal function for the South Boulder Creek samples is due to poorer, less well-conditioned mats is supported by the results for the cell density removal rates for the South Boulder Creek samples. These were much higher than for both the Rocky Knob and Deer Creek samples (Fig. 7). Although the cell density measurement does not distinguish between live and dead cells, dead cells may have been more easily removed from the benthic mat than live cells, suggesting a greater proportion of senescent or dead cells. In addition, the higher levels of trapped sediment in the mat for the South Boulder Creek samples may also result in poor mat condition as the individual cells become smothered by the sediment in the mat.

[35] The spring runoff peak flow that occurred in 2010 after the initial Rocky Knob samples (RK1) were collected resulted in the near-complete removal of *D. geminata* from Boulder Creek. In contrast, the maximum peak flow in 2009 resulted in only limited removal of *D. geminata* (Cullis 2011). The main difference was that the peak flow in 2010 was much higher than in 2009 and resulted in widespread physical disturbance of the substrate. The maximum peak was 15.1 m^3 s^{-1}, and the average bed shear stress was estimated to be ~110 N m^{-2} in 2010 compared with 10.8 m^3 s^{-1} and 87 N m^{-2}, respectively, at the Rocky Knob site. This is equivalent to the maximum τ_0 achieved in the flow chamber and the average annual maximum peak flow in Boulder Creek.

[36] The estimated critical shear stress for the disturbance of the median bed particle size ($\tau_c(d_{50})$) and the particle size for which 84% of bed particles are finer ($\tau_c(d_{84})$) at the sampling location in the Rocky Knob site were estimated to be 60 N m^{-2} and 103 N m^{-2}, respectively (Cullis 2011). Hence the peak flow in 2010 should have resulted in widespread physical bed disturbance being greater than $\tau_c(d_{84})$. In contrast, the peak flow in 2009 would only have resulted in limited physical bed disturbance, being between $\tau_c(d_{50})$ and $\tau_c(d_{84})$. These predictions are consistent with the results of the

shear removal experiments where $<25\%$ of the benthic algal biomass was removed up to τ_0 equivalent to those estimated at the sampling locations during the peak flow of 2009. As the peak flow in 2009 was equivalent to the average annual maximum flow, these observations also support the hypothesis that benthic algae such as *D. geminata* are well adapted to the normal variable high-shear conditions of mountain streams.

Significance to Aquatic Environments

[37] The results of this study show that the removal of *D. geminata* due to increases in bed shear stress (force per unit area normal to the bottom caused by the velocity gradient) is relatively low. The relationship appears linear but physical disturbance of the substrate is required for effective removal of this nuisance alga. *D. geminata* appears to be well adapted to survival in the high-shear environments of mountain streams. Physical–biological coupling between the benthic mats and the near-bed hydrodynamics may result in a further reduction in the removal of benthic algae with increase in mat thickness and better mat condition. Further investigations are, however, required to confirm these observations due to the limited sample size in this study and the difficulties of relying on material sampled in situ in the natural environment.

[38] There are also implications for the understanding of the dynamics of stream ecosystems in high-gradient streams. Benthic algal mats growing in swift-flowing streams are well adapted to these high-shear environments and removal due to elevated shear stress is limited. These observations are important in the context of climate change and river management, as future changes in the flow regime may affect the sustainability of benthic algal communities and the continuum of stream ecosystems.

[39] In particular, the use of artificial flood releases has been proposed as a management option for the mitigation of future nuisance blooms of species such as *D. geminata*. The observations from this study support the hypothesis that effective removal of benthic algae such as *D. geminata* requires flows that result in widespread physical bed disturbance and mechanical scouring of the mats. The implication of this is that flood flows, either natural or artificial as part of a management plan, that are less than or equal to the average annual maximum flow will not result in significant removal of this nuisance species. These releases would, therefore, be inefficient for the purpose of controlling nuisance blooms of benthic algae and a waste of water. In this case a single large flood release may be far more effective than a number of smaller flood releases. This type of information is vital for the management of reservoirs where there is a struggle to balance competing demands for water and the maintenance of diverse and sustainable stream ecosystems in a changing environment.

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