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**Environmental constraints on *Didymosphenia geminata* occurrence and bloom formation
in Canadian Rocky Mountain lotic systems**

by

Leland J. Jackson^{1*}, Lisa Corbett^{1,2} and Garry Scrimgeour^{3,4}

1. Ecology and Evolutionary Biology Research Cluster, Department of Biological Sciences,
University of Calgary, Calgary, Alberta, Canada

2. Program Development and Implementation, Glenbow Ranch Provincial Park Foundation,
Cochrane, Alberta, Canada and Program Leader at Weaselhead Preservation Society,
Calgary, Alberta, Canada.

3. Protected Areas Establishment and Conservation, Office of the Chief Ecosystem Scientist,
Parks Canada, Calgary, Alberta, Canada.

4. Adjunct Professor, Department of Biological Sciences, University of Alberta, Edmonton,
Alberta, Canada T6G2E9

*Correspondence: LJ Jackson, Department of Biological Sciences, University of Calgary, 2500
University Drive NW, Calgary, Alberta, Canada T2N 1N4

E-mail: ljackson@ucalgary.ca

Abstract

The first documented bloom of *Didymosphenia geminata* in Alberta occurred in 2003 and subsequent field investigations revealed that *D. geminata* was present in the periphyton of a number of lotic systems, yet did not always form blooms. We sampled 76 sites in Canadian Rocky Mountain National Parks, chosen to provide ranges in exposure to *D. geminata* propagules and environmental conditions thought to affect *D. geminata* growth and bloom formation. Generalized Linear Models were then used to determine environmental constraints on habitat suitability and requirements for blooming and non-blooming populations across the landscape. *D. geminata* was detected at 88% of sites and of those, 34% had blooms, defined as visible mats of *D. geminata* stalks. *D. geminata* cell abundance was significantly negatively related to stream velocity, stream order and TP concentration, yet there was no significant relationship between *D. geminata* blooms and any of environmental variables measured. There was a significant negative relationship between ash free dry mass (AFDM) and temperature when cells were present but blooms absent, and a positive relationship between temperature and stalk abundance when blooms were present. Total phosphorus, flow velocity and temperature were significant environmental correlates of cell abundance, but we detected no thresholds related to *D. geminata* blooms. The widespread occurrence of *D. geminata* over 1000s of km² and close proximity of sites with and without blooms suggests that local, rather than regional factors drive bloom development.

Keywords: algae, algal stalk, diatom, *Didymosphenia geminata*, invasive species, nuisance bloom, oligotrophic stream, periphyton.

Introduction

Aquatic system eutrophication typically results from excessive inputs of nitrogen and/or phosphorus (Nixon 1995; Schindler 1977; Biggs 2000; Dodds et al. 2002; Sunda et al. 2006). Enhanced growth of algae can degrade water quality and change ecosystem structure-function relationships. Algal blooms can produce toxins or accumulate biomass that alters food web dynamics (Nielsen et al. 1990; Johansson and Graneli 1999a; Gobler et al. 2002). Large algal blooms may alter habitat and trophic structure by depleting oxygen as algae decay (Grindley et al. 1964; Cho 1979; Mahoney and Steimle 1979), reducing food and space for co-occurring organisms, destroying habitat and shading out submerged vegetation (Onuf 1994; 1996).

Blooms of *Didymosphenia geminata* (Lyngbye) Schmidt on Scandinavian river bottoms were reported a century ago (Lindstrom and Skulberg 2008) and have expanded globally over the last decade. The first reports of blooms in Western Canada occurred in 1989 on Vancouver Island (Sherbot and Bothwell 1993) and recently blooms have been identified in Rapid Creek, South Dakota (Shearer and Erickson, 2006; Larson and Carreiro 2008), the Bow River, Alberta (Kirkwood 2007; Bowman 2008), the Yukon River, Yukon (Barracough 1995 cited in Bothwell et al. 2009) the Kootenai River, Montana (Holderman and Hardy 2004), and Quebec (Simard and Simoneau 2008), which led to the hypothesis of a rapid expansion of *D. geminata* to streams throughout North America, potentially on anglers' felt soled waders (Bothwell et al. 2009). However, as more data have been collected it appears more likely that *D. geminata* blooms are driven by low phosphorus and other possible environmental drivers. *D. geminata's* first record in the Kootenay area of British Columbia is from 1866, yet blooms in the Alberta portion of the

Rocky Mountains were not noticed until the 1990s, with the spatial extent of blooms expanding since then (Kirkwood et al. 2007; Bowman 2008).

Mitigation of many algal blooms involves nutrient input reductions. The frequency of dividing *D. geminata* cells shows a positive relationship with dissolved phosphorus (Bothwell et al. 2014), yet the amount of stalk material produced increases as dissolved phosphorus decreases (Kirkwood et al. 2007; Bothwell and Spaulding 2008; Kilroy and Bothwell 2011). *D. geminata* typically blooms in streams with low to undetectable phosphorus (Lindstrom and Skulberg 2008; Kirkwood et al. 2009; Bothwell and Kilroy 2011) and ironically, *D. geminata* blooms are indicative of pristine water quality (Sherbot and Bothwell 1993; Jonsson et al. 2000; Kirkwood et al. 2007). *D. geminata* blooms in streams with low water velocity (Kilroy et al. 2005d; Larned et al. 2006; Kirkwood et al. 2007; Tomas et al. 2010), regulated flows (Kirkwood et al. 2009), and very cold water (Blanco and Ector 2002; Kirkwood et al. 2007; Lindstrom and Skulberg 2008). In contrast to stalk production, cell presence has been linked to low base flow (Kumar et al. 2009) and maximum cell growth to high water velocity (Miller et al. 2009; Cullis et al. 2012).

D. geminata blooms are largely mucopolysaccharide stalk created during growth; large blooms can completely homogenize streambeds (Larned et al. 2006; Spaulding and Elwell 2007). The stalk is composed of long-lasting polysaccharides with apparently little nutritional value for many benthic invertebrates (Larned et al. 2006; Larned et al. 2007; Spaulding and Elwell 2007). Following invasion by *D. geminata*, changes in benthic invertebrate community composition from dominance by Ephemeroptera, Plecoptera and Trichoptera to Diptera (Chironomidae, Ceratopogonidae and Chaoboridae) have been found (Gillis and Chalifour 2010; James et al. 2010; Rost and Fritsen 2014). Alterations to benthic invertebrate community composition and

sediment homogenization may affect the long-term growth and survival of fish populations (Larned et al. 2006).

The goal of this research was to measure stream characteristics at 76 sites within Canadian Rocky Mountain National Parks to identify relationships between site characteristics and *D. geminata* cell abundance and bloom formation as a function of regional and local variables. Our goal was to identify constraints on *D. geminata* distribution and abundance, and whether or not environmental thresholds exist that distinguish blooming and non-blooming sites. If thresholds are identified, such information could potentially be used to identify additional rivers and streams at risk for *D. geminata* invasion or bloom development.

Methods

Study sites

The Canadian Rocky Mountain areas we sampled have geology dominated by shale, sandstone, limestone and quartzite sedimentary material that formed a little less than ca. 0.5 billion years ago under ancient oceans. The areas of the Rocky Mountains we sampled were formed and above water by ca. 75 million years ago.

Periphyton samples were collected during August and September, 2009, at 76 sites on first to fifth order streams within National Parks of the Rocky Mountains of Alberta and British Columbia (Figure 1). Streams are circumneutral to slightly alkaline pH, moderate to high slope and typically clear in late summer (water turbidity < 20 NTU). Concentrations of total phosphorus (TP) and total nitrogen (TN) are typically very low (TP <2 to 10 µg/L; TN <50 to 200 µg/L). Streams are typically ice covered during November to April and open otherwise.

Larger streams support rainbow trout (*Oncorhynchus mykiss*), bull trout (*Salvelinus confluentus*) and mountain whitefish (*Prosopium williamsoni*) populations, which provide angling opportunities. The sites experience a range of tourist and recreational activities, including angling, and we chose sites to provide a range of stream order, stream type, substrate type, area use, public access, algal community composition and nutrient concentrations following identification by Parks Canada staff who are familiar with park usage and geography.

At each site, 13 environmental variables thought to potentially explain variation in the occurrence and abundance of *D. geminata* were measured (Table 1). Variables were chosen to represent variation at regional and local scales (Table 1).

Physico-chemical Attributes

Anthropogenic activity was evaluated as site use and angling pressure by Parks Canada Agency staff familiar with each park. Site use was scaled one to five (one rarely used; five highly frequented). Angling pressure was scored as frequent, occasional or rare. Mean water velocity was calculated at 60% water depth using a velocity meter (Global Water Flow Probe (FP111)). Water temperature (± 0.1 °C) was measured using a glass thermometer. Five stream widths and depths were taken randomly at each site. Dissolved oxygen was measured with a YSI Professional Plus dissolved oxygen meter. Triplicate water samples were taken at each site in acid-washed, double-distilled water rinsed 1L Nalgene bottles. Bottles were completely filled and stored on ice, prior to being sent to the Environment Canada Pacific and Yukon Laboratory for Environmental Testing, in North Vancouver, British Columbia, for total phosphorus (TP) and total nitrogen (TN) analyses. Soluble reactive phosphorus, total dissolved phosphorus and NO_2^- were not measured as their concentrations are typically below detection limits in these systems.

At each site, three cobbles (0.05 - 0.1 m) were chosen randomly within 0.5 - 2.5 m from shore and 0.2-0.7 m water depth. Three 14.3 cm² circles were traced on each cobble following a PVC template and the algal material within the traced circle was mechanically dislodged from the cobble with a combination of scalpels, tweezers and toothbrushes. The material from one circle was placed in a 125 mL borosilicate bottle with some distilled water and Lugol's acid-iodine fixative and stored in the dark. For enumeration, the entire sample was resuspended in 100 mL of water, then 10 mL sub-samples were poured into setting chambers for *D. geminata* cell identification and enumeration using a Leica DM IRB inverted microscope (Leica Microsystems, Wetzlar, Germany). Cells were counted at 100x magnification and identified by multiple (2-5) stigmata positioned radially and symmetrically about one side of the central nodule and the conspicuous size of 60-150 µm length.

The material from the second circle was wrapped in aluminum foil, kept on ice during transport to the lab, then stored at - 20 °C until chlorophyll *a* was extracted and quantified. Samples were extracted into methanol and processed following Thompson et al. (1999), without correction for phaeopigments. Chlorophyll *a* was analyzed with a Spectromax Gemini XS dual-scanning microplate spectrofluorometer (Molecular Devices, Sunnyvale, California USA) at an excitation wavelength of 440 nm and emission wavelength of 665 nm.

The material from the third circle was collected in a small plastic bottle and used for ash-free dry mass (AFDM) determination. We use AFDM as a surrogate for the organic stalk content of *D. geminata* sampled to distinguish this mass from the total dry mass, which would also include Si from *D. geminata* frustules and any trapped inorganic particles. All AFDM samples were processed according to Biggs and Kilroy (2000).

Statistical Analyses

Descriptive statistics were calculated with Microsoft Excel (2011). Statistical analyses were conducted using R (V2.8.1) (R development core team, 2008). Maps were traced by hand from 1:250,000 topographic maps produced by the Canadian Centre for Mapping (Natural Resources Canada). Any chemical concentrations that were undetectable were removed from analyses. All hypothesis tests used a critical $\alpha = 0.05$.

Spatial autocorrelation was assessed using a Mantel test. Generalized Linear Models (GLM) and analyses of covariance (ANCOVA) were used to quantify relationships between occurrence and abundance of *D. geminata* and selected environmental variables (Table 2) in two ways. First, models of *D. geminata* occurrence or abundance and environmental variables from the 76 sites were derived. Second, data from the 76 sites were used to identify relationships between *D. geminata* bloom versus non-bloom sites and their corresponding environmental matrices.

Generalized Linear Models (GLMs)

The 13-predictor variables were reduced to seven after correlations identified multicollinearity between some variables. Seven predictor variables were then used to test 10 *a priori* models that represented multiple combinations of variables (Table 2). Environmental variables were either measured during stream surveys (i.e. water velocity, water temperature, TP and TN) or derived from queries of geographic information system (GIS) databases (latitude, stream access and stream order). Elevation, stream depth and stream width were all correlated to stream order ($\rho = -0.34$, $p = 0.0063$; $\rho = 0.63$, $p < 0.001$; and, $\rho = 0.73$, $p < 0.001$, respectively). Site access and angling pressure ($\rho = 0.59$, $p = 1.93 \times 10^{-8}$), dissolved oxygen and

temperature ($r = -0.44$, $p < 0.001$) and latitude and stream type ($\rho = 0.26$, $p = 0.025$) were also correlated. As a result, the final predictor variables were stream order, temperature, site access and latitude, TP, TN and stream type.

GLMs were conducted on binary (*D. geminata* present or absent and *D. geminata* blooming or non-blooming) and continuous (*D. geminata* abundance and AFDM) data and environmental variables. Binomial, negative binomial and Gaussian error structures were evaluated for best fit. AFDM was $\log(x+1)$ transformed to reduce variance and over dispersion.

Akaike's Information Criterion corrected for small sample sizes (AICc) was used to select the most parsimonious model (Burnham and Anderson 1998; Anderson et al. 2000). Each model was evaluated by the difference in AICc values from the most parsimonious model (Δ_i), which was weighted against other models. The top three models were selected but only models that had a $\Delta_i < 10$ were considered statistically meaningful (Anderson et al. 2001). For all models with variables that had Akaike's weights ≥ 0.01 , model averaged estimates of coefficients and associated p -values were calculated to assess the variables' relative contributions to the variance observed in *D. geminata* growth.

Because the GLMs indicated different responses of *D. geminata* cells and blooms to the environmental variables, additional analyses were conducted to consider interactions between sites where *D. geminata* bloomed and where *D. geminata* cells were present but did not bloom. This analysis was conducted to evaluate relationships between environmental variables identified as significant and their respective *D. geminata* bloom status.

Results

Of the 76 sites sampled within the Alberta and British Columbian Rocky Mountain National Parks, *D. geminata* was detected at 67 (88%) sites, and of those 67 sites with *D. geminata* cells, 23 (34%) had *D. geminata* blooms (Figure 1). Blooms occurred along the Bow River from the Bow Lake outflow and into the Banff town site. However within the Banff town site, there were two sites with no blooms and one site where *D. geminata* was not detected (Figure 1). In Waterton Lakes National Park there were two streams within the same tributary that had differences in *D. geminata* abundance. There was no evidence of *D. geminata* blooms along the heavily visited Red Rock Creek, but in a remote site along the Blakiston Creek a large *D. geminata* bloom was observed (Figure 1).

Mantel tests revealed no spatial autocorrelation regarding where *D. geminata* cells were present or absent ($p = 0.37$), where *D. geminata* blooms occurred ($p = 0.11$), or the amount of AFDM ($p = 0.30$). However, there was spatial autocorrelation to *D. geminata* cell abundance ($p = 0.011$).

D. geminata cell presence and abundance

The most parsimonious model (Table 3) for *D. geminata* presence/absence included stream order, water velocity, water temperature and TP. Although this model best fit the data, the relationship was not statistically significant. *D. geminata* was found in streams that ranged in order from one to five, water velocities that ranged from 0.11 - 1.36 m/s, temperatures that ranged from 2.25 - 12.54 °C and TP concentrations that ranged from < 2.0 - 42 µg/L.

Model averaging was only conducted on the presence or absence of *D. geminata* cells model set as other model sets lacked appropriate Akaike's weights. The following ranking of the

contribution of the main variables resulted for *D. geminata* presence/absence: latitude (coefficient = -0.004, $p = 0.004$) > TN (coefficient = 0.109, $p = 0.009$) > velocity (coefficient = 0.48, $p = 0.074$) > TP (coefficient = 11.97, $p = 0.088$) > temperature (coefficient = 0.0149, $p = 0.396$).

We found an effect of local variables on *D. geminata* cell abundance at a site (Table 3). The most parsimonious model, based on AICc scores, revealed that *D. geminata* cell abundance was significantly, negatively related to stream velocity, stream order and TP concentration (Table 3). The abundance of *D. geminata* cells was highest in stream orders 2 and 3, and lowest in stream orders 5 and 6 (Figure 2). Higher *D. geminata* cell abundances were also found in low water velocities and at low TP concentrations.

***D. geminata* blooms and AFDM abundance**

The most parsimonious model, based on AICc scores, included stream order, water velocity, water temperature and TP (Table 3). Although this model best fit the data, there was no significant relationship between the presence or absence of *D. geminata* blooms and any measured environmental variables. *D. geminata* blooms were observed across a range of stream orders (2 to 5), water velocities (0.17 m/s to 0.76 m/s), temperatures (3.7 °C to 12.03 °C) and TP concentrations (< 2 µg/L to 8 µg/L).

There was an effect of local variables on the amount of AFDM present at a site (Table 3). The most parsimonious model, based on AICc scores, revealed that the amount of AFDM was significantly, positively related to temperature, and slightly negatively related to water velocity (Table 3).

Relationship between *D. geminata* bloom sites and non-bloom sites

Variables that had a significant relationship with *D. geminata* growth in the previous subset of models were analyzed to identify differences between bloom sites and sites with *D. geminata* cells and no blooms. There was a significant negative relationship between log TP (($\mu\text{g/L}$)+1) and log *D. geminata* cells ((cells/cm^2)+1) ($Z_{3,31} = -3.407, p < 0.001$) in bloom and non-bloom sites (Figure 3). *D. geminata* did not bloom if TP > 8 $\mu\text{g TP/L}$, whereas *D. geminata* cells in non-bloom sites occurred if TP $\geq 47 \mu\text{g TP/L}$. Unfortunately, TP was below analytical detection (2 $\mu\text{g TP/L}$) at 27 sites and these cases were excluded from analyses. We chose to exclude such data, rather than use the analytical detection limit or 0.5 of the detection limit, to maintain a conservative statistical approach. The message wouldn't change and indeed, increased TP corresponded to lower *D. geminata* cell abundance wherever *D. geminata* occurred.

Blooms were present in streams with velocities that ranged from 0.162 - 0.712 m/s (average velocity 0.46 m/s), while non-bloom sites ranged from 0.08 - 1.23 m/s (average velocity 0.52 m/s). There was a significant negative relationship between *D. geminata* abundance and stream velocity ($Z_{3,66} = -3.081, p = 0.0021$), but this relationship did not significantly differ between bloom sites and non-bloom sites.

Stream temperature at all sites ranged from 2.4 - 15.2 °C. There was a significant positive relationship between AFDM and temperature at those sites with blooms present (Figure 4A - $T_{3,64} = -2.05, p = 0.044$); however, the AFDM-temperature relationship was negative at those sites where *D. geminata* was present but did not bloom ($T_{3,64} = 2.204, p = 0.031$) (Figure 4B). Here we note that our characterization of 'non-blooming' refers to no stalks being present.

Discussion

The presence of *D. geminata* cells at 67 of 76 sites, yet blooms at only 23 of these sites, indicates that *D. geminata* is widely distributed throughout the area sampled, but blooms at only a subset of sites. This observation is consistent with at least two possible hypotheses. First, there may be patchily distributed specific environmental conditions, such as low phosphorus (Bothwell and Kilroy 2011; Bothwell et al. 2014), relatively stable flows (Kawecka and Sanecki 2003; Noga 2003; Kirkwood et al. 2007; Bowman 2008) or a combination of these and other conditions that lead to bloom development at sites within the larger landscape. Second, there may be multiple strains of *D. geminata*, one or more of which is responsible for the blooms we first discovered in 2003 (Kirkwood et al. 2007) in southern Alberta, and a strain that does not bloom. We have not seen evidence that conclusively rejects a multiple strain hypothesis; however, growing evidence that draws on observations of spatial and temporal characteristics of blooms suggests that very low phosphorus is key to bloom formation (Taylor and Bothwell 2014) and bloom formation can be induced by dissolved phosphorus near or below analytical detection (Kilroy and Bothwell 2012; 2014). The occurrence of blooming and non-blooming populations in the same rivers, sometimes at adjacent sites, also suggests that blooms are driven by local, rather than regional factors, which is consistent with other findings (Bothwell et al. 2014).

When relations were explored between bloom and non-bloom sites and measured environmental variables a difference between temperature and AFDM was found. The fact that AFDM increases with temperature in bloom sites is consistent with temperature-dependent rates of metabolism to grow the stalk since most AFDM at these sites is *D. geminata* stalk. The very slightly negative relationship at non-bloom sites suggests that the periphyton community is not

temperature controlled. Our measure of AFDM includes other diatoms, yet cursory examination of the stalks via microscopy indicates that most organic material is *D. geminata* stalks.

***D. geminata* cell presence and abundance**

Our data indicate that most Alberta and British Columbia streams sampled support *D. geminata* because it was found at 88% of sites sampled. Our sampling process used 3 x 14.3 cm² circular templates at each site to collect the periphyton matrix. Thus, if *D. geminata* is relatively rare at some sites, we may not have detected it although it might be present - a finding that has likely contributed to the idea that *D. geminata*'s range has apparently expanded as the historic range is poorly described. Models indicate that latitude and TN are important correlates of *D. geminata* presence/absence. Historically, *D. geminata* was found at northern latitudes yet recently its range has expanded (Spaulding and Elwell 2007; Blanco and Ector 2009). *D. geminata* was historically found in low TN streams (Kirkwood et al. 2007; Schweiger et al. 2011) and can be limited by nitrogen availability (Larned et al. 2006), which is supported by our data.

The significant negative relationship between *D. geminata* abundance and stream order is consistent with Kilroy and Unwin (2011), who found that the New Zealand systems invaded by *D. geminata* were strongly related to stream order. However, while they found most streams invaded were stream order > 3 and the occurrence of blooms increased with higher stream order, we found that more cells occurred in lower stream orders. In New Zealand, *D. geminata* is considered an invasive species. Low order streams may be visited less frequently and experience fewer potential propagules than larger streams, and low order streams would require time for the

diatom to move upstream from larger systems (Kilroy and Unwin, 2011). In the systems we sampled, *D. geminata* may be native and cells may persist better in lower order streams and passively flow to higher order streams.

The most parsimonious GLM indicated that lower water velocities and lower TP concentrations were associated with higher *D. geminata* abundances, consistent with Kilroy et al. (2005), Larned et al. (2006), Kirkwood et al. (2007) and Tomas et al. (2010), and who have correlated *D. geminata* abundance with lower, stabilized flows. The negative relationship between *D. geminata* cell abundance and TP concentration is also consistent with previous studies that found *D. geminata* in oligotrophic systems (Bowman et al. 2007; Kirkwood et al. 2009). Kilroy and Bothwell (2012) demonstrated that ambient dissolved reactive phosphorus concentrations trigger a switch in *D. geminata* colony growth such that below 2 µg/L cell division slows and stalk growth commences, which is a challenge for all field surveys since this puts the dissolved phosphorus threshold at the analytical detection limits. Others, (e.g., Lindstrom and Skulberg 2008; Khan-Bureau et al. 2014) have found a somewhat higher threshold for DP than those reported by Kilroy and Bothwell (2012). Thus at high TP, *D. geminata* can exist, does not appear to form blooms and cell density is negatively related to temperature while at low phosphorus cell division slows and stalks form, perhaps to acquire phosphorus from an alternate source, and stalk production is positively related to temperature. The stalk formation - P relationship is consistent with P being used to reduce *D. geminata* blooms (James et al. 2015). Finally, *D. geminata* stalks can contain alkaline phosphatase (Elwood and Whitton 2007), which presumably allows some use of organic P as a P substrate.

***D. geminata* bloom presence and AFDM abundance**

The most parsimonious GLM indicated that regional (order) and local (water velocity, water temperature and TP) variables were related to *D. geminata* bloom occurrence. However, none of these variables were identified as significant effects.

The most parsimonious GLM revealed that stream order, water velocity, water temperature and TP are related to the AFDM measured at a site. However stream order and TP do not have a significant effect on the AFDM. There was a statistically significantly negative relationship between water temperature and AFDM and a slight negative relationship between AFDM and stream velocity.

AFDM was inversely related to stream velocity and we found no *D. geminata* blooms at velocities above 0.8 m/s at the time of sampling. Flow velocity (Kilroy et al. 2005; Larned et al. 2006; Kirkwood et al. 2007; Tomas et al. 2010) and flow stability (Kirkwood et al. 2009) have been correlated with *D. geminata* blooms.

We found that AFDM was significantly, inversely related to water temperature across all sites. However, we also found a negative relationship between AFDM and temperature where no *D. geminata* blooms were observed and a significant positive relationship between AFDM and temperature where *D. geminata* bloomed, up to a maximum temperature of 14°C. Sundareshwar et al. (2011) suggested that when *D. geminata* mats form, a positive feedback is established because stalk material can absorb Fe and P, which can facilitate further cell growth. Because we sampled streams in late summer at low flow, temperatures measured were at, or close to, annual maxima. Thus, there might be a temperature threshold around 14°C in these systems or temperature may be correlated to an environmental driver we did not measure. Kilroy et al. (2006) noted that blooms appeared to be restricted to locations where the lowest winter air

temperatures were below 5°C. *D. geminata* is characterized as a cold water species (Kirkwood et al. 2007; Lindstrom and Skulberg 2008; Blanco and Ector 2009) although it can persist in water up to 23°C and rarely is in its vegetative state above 18°C (Lindstrom and Skulberg 2008). Recent reports of blooms appearing in warmer water (Spaulding and Elwell 2007; Kumar et al. 2009) might indicate that there may be more susceptible rivers and continued *D. geminata* range expansion, possibly because *D. geminata* can alter its phenotype when exposed to different temperatures. Despite remaining uncertainty regarding a possible genetic basis for temperature adaptation or plasticity of one original strain, we have shown that *D. geminata* was widespread throughout the seven Canadian National Parks we sampled, that drivers of blooms vary over relatively small spatial scales, and that blooms are associated with very low to undetectable total phosphorous concentrations.

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List of Tables

Table 1. Environmental variables used to predict the occurrence and abundance of *D. geminata* at 76 sites within Alberta and British Columbia Rocky Mountain National Parks sampled during summer, 2009.

Variable	Abbreviation	Units	Range
<i>Regional Variables</i>			
Elevation	Elev	m	576 - 2449
Latitude*	Lat	°	-118.45 - -113.68
Stream Order*	Order	dimensionless	1-6
Stream Type	Type	dimensionless	fast / slow riffle, fast/slow run, pool or cascade
<i>Local Variables</i>			
Water Velocity*	Velocity	m/s	0.08-1.23
Total Nitrogen*	TN	mg/L	0.01 (min. detection) - 0.26
Total Phosphorus*	TP	mg/L	0.002 (min. detection) – 0.047
Water Temperature*	Temp	°C	2.25 - 18.2
Dissolved Oxygen	DO	mg/L	0.75 – 14.19
Stream Depth	Depth	m	0.046 - 1.46
Stream Width	Depth	m	0.56-121.33
Angling Pressure	Fish	dimensionless	rare, occasional, frequent
Site Access*	Access	dimensionless	highway, paved road, gravel road, marked trail or unmarked trail.

Note: ‘*’ indicates variables that were used in model selection. All others were correlated to a combination of these variables and were dropped from these analyses to avoid co-linearity.

Table 2. Summary of *a priori* candidate models used to evaluate relationships between the occurrence of *D. geminata* cells and blooms and environmental variables, including metrics of anthropogenic activity in the Canadian Rocky Mountains. K is the number of independent variables.

Model	Variables	K
<i>Regional Variables</i>		
1	Lat + Order + Access	3
2	Lat + Order	2
<i>Local Variables</i>		
3	Velocity + TP + TN + Temp	4
4	TP + TN	2
5	Velocity + Temp	2
6	Velocity + TP	2
<i>Regional + Local Variables</i>		
7	Access + Velocity + TP	3
8	Lat + Velocity + TP	3
9	Lat + Velocity + TP + TN	4
10	Order + Velocity + Temp + TP	4

Table 3. A summary of the three most parsimonious General Linear Models for presence or absence of *D. geminata* cells and blooms and the three most parsimonious General Linear Models for *D. geminata* cells and amount of AFDM. Model numbers refer to the models outlined in Table 2.

Model	Variable	Coefficient	SE	AIC _c	Δ _i	w _i
Presence or Absence of <i>D. geminata</i> cells						
10	Intercept	-1.66	2.37	35.94	0	0.92
	Order	0.49	0.45			
	Velocity	2.053	1.91			
	Temperature	0.032	0.20			
	TP	54.60	65.03			
6	Intercept	1.041	0.90	41.36	5.42	0.061
	Velocity	0.96	1.43			
	TP	22.25	63.70			
3	Intercept	-0.23	1.74	43.52	7.59	0.021
	Velocity	1.31	1.60			
	TP	11.36	72.15			
	TN	6.98	10.35			
	Temperature	0.066	0.18			
Abundance of <i>D. geminata</i> cells (cells/cm ²)						
10	Intercept	15.85***	1.80	354.99	0	1.00
	Order	-1.71***	0.32			
	Velocity	-2.14*	0.98			
	Temperature	0.081	0.13			
3	TP	-273.96***	41.47	496.09	141.10	2.29x10 ⁻³¹
	Intercept	12.48***	1.53			
	Velocity	-3.31**	1.08			
	TP	-170.98***	44.88			
	TN	-11.58	7.37			
	Temperature	0.014	0.15			
6	Intercept	11.14***	0.72	547.88	192.89	1.30x10 ⁻⁴²
	Velocity	-2.27	0.97			
	TP	-202.93***	40.69			

Presence or Absence of <i>D. geminata</i> blooms						
10	Intercept	3.47	2.68	31.36	0	1.00
	Order	-0.60	0.44			
	Velocity	-0.85	1.93			
	Temperature	0.14	0.21			
	TP	-416.38	267.37			
3	Intercept	0.42	1.63	47.36	16.00	0.00034
	Velocity	0.19	1.30			
	TP	-113.78	143.93			
	TN	-8.60	9.18			
	Temperature	0.030	0.16			
6	Intercept	0.23	0.91	47.66	16.30	0.00029
	Velocity	-0.048	1.11			
	TP	-164.74	163.026			
Amount of log(AFDM (mg/cm ²)+1)						
10	Intercept	4.64***	0.79	61.90	0	1.00
	Order	-0.24	0.14			
	Velocity	-0.78 ~	0.41			
	Temp	-0.14*	0.058			
	TP	-18.91	16.21			
3	Intercept	3.60***	0.60	84.037	22.14	1.56x10 ⁻⁵
	Velocity	-0.83 ~	0.41			
	TP	-7.21	16.59			
	TN	1.14	2.84			
	Temperature	-0.13	0.58*			
6	Intercept	2.51***	0.32	100.78	38.89	3.60x10 ⁻⁹
	Velocity	-0.53	0.43			
	TP	-0.91	17.3			

Note: * indicate significant deviations from the null model. ‘~’ is a p-value of <0.1, ‘**’ is a p-value of <0.05, ‘***’ is a p-value of <0.01 and ‘****’ is a p-value of <0.0001. Δ_i is the change in AIC_c scores from the lowest AIC_c score and w_i are the AIC_c weights.

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Figure 1. Location of 76 sites within the Canadian Rocky mountains sampled during summer,

2009, to determine distribution and abundance of *D. geminata*. Black circles indicate

blooms, hatched circles indicate that cells were present but blooms were absent, and open

circles indicate that no cells were detected. Glacier National Park is in British Columbia and

part of the Banff-Yoho-Kootany map. Note the change of scale between Waterton Lakes

(bottom left), Jasper (top right) and the remaining National Parks. Arrows indicate the

direction of water flow. All maps are oriented in the same direction. Some tributaries have

been omitted for clarity.

Figure 2. Mean *D. geminata* cell abundance (Number/cm²) in 1st to 6th order rivers in Alberta and

British Columbia Rocky Mountain National Park streams at all sites, sampled during

summer, 2009. Error bars represent 95% confidence intervals.

Figure 3. Relationship between mean density of *D. geminata* cells (Number/cm²) and mean

concentration of total phosphorus (µg/L). Solid circles (A) indicate sites with *D. geminata*

blooms and open squares (B) indicate sites with *D. geminata* cells present but no blooms.

Figure 4. Relationship between ash-free dry mass (mg/cm²) and temperature (°C) for 76 sites

sampled during summer, 2009, in Alberta and British Columbia Rocky Mountain National

Parks. Solid circles (A) indicate sites with *D. geminata* blooms and open squares (B)

indicate sites with *D. geminata* cells present, but no blooms. Lines represent the best fit from

linear regressions with the test statistics presented in the text.

Jackson, Corbett & Scrimgeour, Figure 1

Jackson, Corbett & Scrimgeour, Figure 2

Jackson, Corbett & Scrimgeour, Figure 3

Jackson, Corbett & Scrimgeour, Figure 4

Biosketches

Leland Jackson is a professor in the Department of Biological Sciences at University of Calgary. His research focuses on relationships ecosystem structure and function and contaminant impacts on aquatic food webs.

Lisa Corbett is involved with program development and implementation with the Glenbow Ranch Provincial Park Foundation and the Weaselhead Park Preservation Society.

Garry Scrimgeour is a senior scientist with Parks Canada Agency. His work focuses on environmental assessments, restoration and monitoring of surface waters in National Parks.

Author Contributions: LJ and GS conceived of the initial idea. GS coordinated access to National Park sites, arranged nutrient analyses and acquired funding. LJ and LC wrote the manuscript. LC helped collect samples, conducted laboratory analyses for cell density, chlorophyll and AFDM and conducted statistical analyses.