Didymosphenia geminata in two Alberta headwater rivers: an emerging invasive species that challenges conventional views on algal bloom development

Andrea E. Kirkwood, Troina Shea, Leland J. Jackson, and Edward McCauley

Abstract: The diatom *Didymosphenia geminata* (Bacillariophyceae) has garnered increased attention as a nuisance and invasive species in freshwater systems. Historically described as rare yet cosmopolitan, a suspected new variant of *D. geminata* has the capacity to inundate kilometres of river bottom during a bloom. Unlike most other bloom-forming algae, *D. geminata* proliferates under high water quality (i.e., low turbidity and low nutrient) conditions. To inform management strategies, the environmental factors and conditions that promote bloom events must be ascertained. Our study of the Bow and Red Deer rivers in southern Alberta, Canada, provides supporting evidence that the mean flow regime is associated with bloom development, based on a significant negative relationship detected between *D. geminata* biomass and mean discharge (r^2 = 0.30). While flow regulation by dams can create the stable flow environment preferred by *D. geminata*, our results indicate that flow regime (rather than just proximity to dam outflows) is the likely mechanism, in addition to other environmental factors, such as water clarity, temperature, pH, conductivity, and total phosphorus. We discuss the formidable challenges to *D. geminata* management, particularly along unregulated river reaches, yet also recognize the unique research opportunities that this organism poses for the growing field of invasion biology.

Résumé : La diatomée *Didymosphenia geminata* (Bacillariophyceae) attire de plus en plus l'attention comme espèce nocive et envahissante dans les systèmes d'eau douce. Décrite dans le passé comme rare, bien que cosmopolite, *D. geminata* semble présenter une nouvelle forme capable de couvrir des kilomètres de lit de rivière durant un épisode d'efflorescence. Contrairement à la plupart des autres algues qui connaissent des proliférations, *D. geminata* foisonne dans des conditions de qualité d'eau de crue (c'est-à-dire de faible turbidité et de concentrations basses de nutriments). Afin d'obtenir les assises nécessaires pour les stratégies de gestion, il est essentiel de déterminer les facteurs et les conditions du milieu qui favorisent les épisodes de prolifération. Notre étude faite dans les rivières Bow et Red Deer dans le sud de l'Alberta, Canada, fournit des indications que le régime moyen du débit est relié au développement des efflorescences, puisqu'elle révèle l'existence d'une relation négative significative entre la biomasse de *D. geminata* et le débit moyen (r^2 = 0,30). Bien que le contrôle du débit par les barrages puisse créer l'environnement de débit stable préféré par *D. geminata*, nos résultats indiquent que le régime de débit (plutôt que la seule proximité des émissaires des barrages) constitue vraisemblablement le mécanisme important, en plus des autres facteurs du milieu, tels que la clarté de l'eau, la température, le pH, la conductivité et le phosphore total. Nous discutons des défis considérables que génère la gestion de *D. geminata*, particulièrement dans les sections de rivière à débit non contrôlé, tout en reconnaissant aussi les occasions de recherche que cet organisme fournit dans le domaine en expansion de la biologie des invasions.

[Traduit par la Rédaction]

Introduction

Didymosphenia geminata (Lyngbye) M. Schmidt, 1899 has historically been described as a cosmopolitan, but rare, lotic diatom normally found in moderately flowing, cool to cold-water montane and boreal forest streams and rivers in Europe and North America (Schmidt 1899; Hustedt 1930; Patrick and Reimer 1975). Over the last decade, *D. geminata* has emerged as a nuisance, bloom-forming species in the northern hemisphere and, most recently, New Zealand (Kilroy 2004). The first reports of *D. geminata* blooms in North America were documented by Sherbot and Bothwell (1993) on Vancouver Island. Unlike filamentous cyanobacteria and chlorophytes that form blooms under eutrophic

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conditions, *D. geminata* blooms are not associated with elevated nutrient levels or poor water quality (Sherbot and Bothwell 1993; Kilroy et al. 2005*a*). Bothwell et al. (2006) explored the possibility that *D. geminata* blooms may be a symptom of environmental change, but also hypothesized that blooms are a characteristic of a new genetic variant.

Macroscopic biomass growing on submerged substrates mainly consists of >90% extracellular polymeric material produced by the diatom. The polysaccharide stalks terminate in adhesive pads, which attach to substrates such as cobble-sized rocks, boulders, and woody debris. Cells propagate stalk material from the pad, and stalks bifurcate with each cell division (Gretz et al. 2006). We have observed that stalk material can persist on substrates beyond the life cycle of the cells that produce it, which may explain in part why nuisance levels occur. Scouring events usually remove the stalk material from substrates, and the sloughed material that accumulates on riverbanks is commonly mistaken as toilet paper by the public.

In 2004, *D. geminata* was reported as a new invasive species in New Zealand (Kilroy 2004), indicating that it was emerging as a global invasive species. A group of international scientists recently highlighted how little is known of the basic ecology of *D. geminata*, despite the enormous implications blooms could have to ecosystem function and particularly fisheries (Spaulding and Elwell 2007).

Here we present research that compares the distribution, occurrence, and bloom development of *D. geminata* in two headwater rivers in Alberta, Canada, with contrasting flow regimes. Although there have previously been no documented reports of *D. geminata* in Alberta rivers, there are historical reports of *Gomphonema geminatum* (a synonomous taxon) along the western slopes of the Canadian Rockies in the 1860s (Lord 1866). The occurrence of nuisance blooms was first noticed anecdotally in the late 1990s in the upper Bow River in Banff National Park (M. Bowman, Ontario Ministry of the Environment, Dorset Environmental Sciences Centre, 1026 Belwood Acres Road, P.O. Box 39, Dorset, ON P0A 1H0, Canada, personal communication). By 2002, anglers and provincial scientists noticed blooms on lower reaches of the Bow River near Calgary, and the Oldman River below the Oldman Dam (M. Bryski, Alberta Environment, Water Management Operations, 200–5th Avenue South, Lethbridge, AB T1J 4L1, Canada, personal communication). In 2004, we initiated a large-scale periphyton study in the Red Deer and Bow rivers to investigate natural and anthropogenically driven transitions in Alberta rivers. The periphyton sample collection and associated environmental data accrued from this broad study offered an opportunity for us to document the spatial and temporal variation in *D. geminata* distribution and abundance in these rivers. Also, the notable differences in flow regulation between the Red Deer and the Bow rivers make them ideal systems to assess the role of flow regime in *D. geminata* bloom development.

Materials and methods

Study location

The Bow and Red Deer rivers are adjacent sub-basins of the South Saskatchewan River Basin (SSRB) in southern Alberta, Canada (Fig. 1). The Bow River sub-basin is 26 240 km^2, whereas the Red Deer River sub-basin is 47 831 km^2. The SSRB is located in the transition between the Rocky Mountains of western Alberta and the eastern Great Plains. Source water for these rivers originates along the eastern slopes of the Rocky Mountains and is a mixture (depending on the time of year) of rain water, glacial and snowmelt water, and groundwater. Though the Bow and Red Deer rivers share similar edaphic and land-use characteristics, they differ with respect to urban footprints, sewage–agricultural inputs, and flow regulation–diversion by dams and hydroelectric utilities. The Bow River has five dams and one substantial weir that regulates and stabilizes flows, while the Red Deer River has one dam (Fig. 1).

Sampling regime

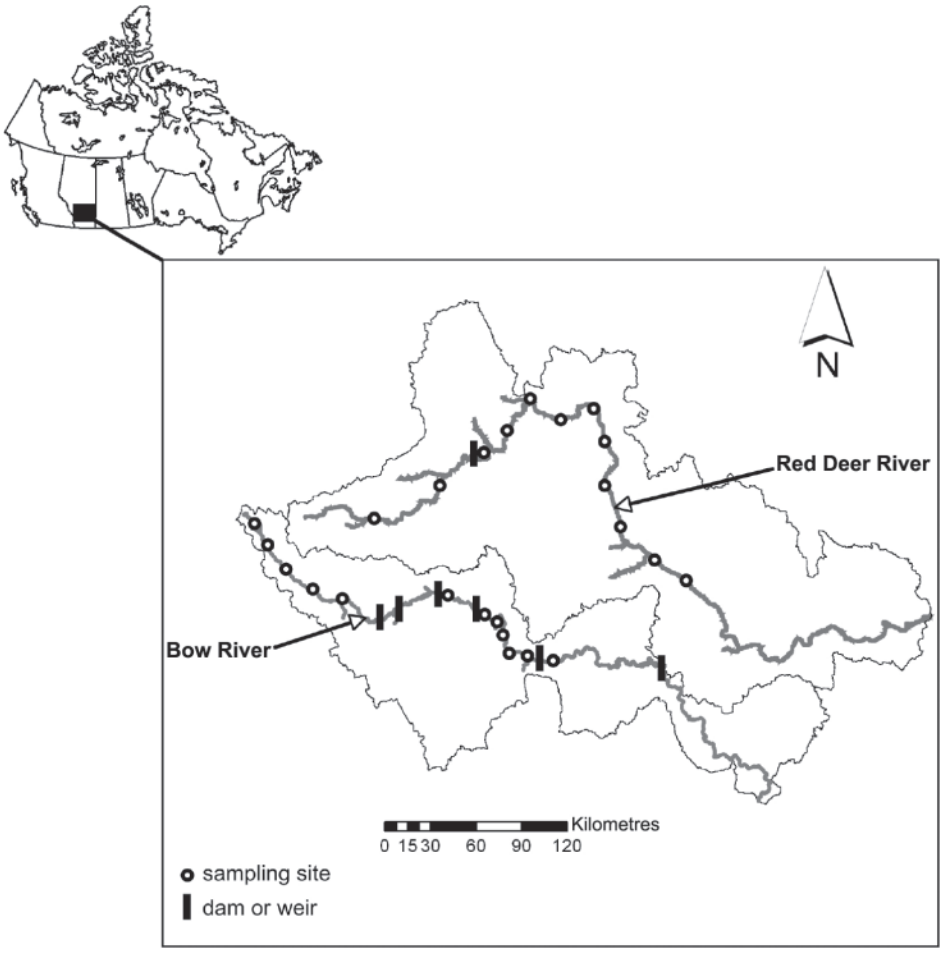
In 2004, 12 sites in the Red Deer River that spanned a 432 km reach from the headwaters were sampled 17–19 August and 1–7 October (Fig. 1). The Bow River was sampled 13–15 October at eight sites covering a 125 km reach, starting approximately 150 km from the headwaters. In 2005, sampling frequency was increased to include spring (20 March – 20 June), summer (21 June – 22 September), and fall (23 September – 20 December) periods. The Red Deer River was sampled 3–5 May, 19–21 July, and 27–28 September at all 12 sites. The Bow River was sampled 10–12 May, 26–28 July, and 4–6 October at the eight sites from 2004, plus an additional four sites from the upper reach (Fig. 1).

Water sampling and analyses

Temperature, pH, conductivity, and dissolved oxygen measurements were taken with a Hydrolab Minisonde Multiprobe (Hydrolab Corp., Houston, Texas, USA) near the rocks collected for periphyton scrapes (usually 2–3 m from the bank, depending on water depth and velocity). Flow velocity was measured at substrate level using a Marsh-McBirney flow meter (Marsh-McBirney Corp., Frederick, Maryland, USA). A Li-COR spherical light meter (model SPQA 2052, Li-COR Biosciences, Lincoln, Nebraska, USA) was used to measure light at the surface and substrate levels to calculate light extinction coefficients at each site. Water turbidity was measured on-site with an Orbeco-Hellige turbidimeter (model 966, Orbeco-Hellige Corp., Farmingdale, New York, USA). Three replicate 1 L water samples were taken at each site in Nalgene bottles that were acid-washed and rinsed with double-distilled water. The samples were then stored on ice and transported to the lab within hours of collection. Within 24 h of collection, water samples were processed for total suspended solids (TSS) and total phosphorus (TP) employing standard protocols (American Water Works Association 1995).

Daily river discharge for 2004 and 2005 was obtained from Environment Canada's Hydat Database (www.wsc.ec.gc.ca/hydat/H2O/). Data were not available for all sites in our study, thus only a subset of four sites on each river were used in statistical analyses that included discharge. Mean discharge was calculated by averaging daily discharge for the 30 days preceding sample collection. We believe this to be the best reflection of the average discharge experienced by periphyton, as it reflects an inferred timescale required

Fig. 1. Map of the Red Deer River (51.66°N, 115.29°W to 51.48°N, 112.72°W) and Bow River (51.66°N, 116.48°W to 50.83°N, 113.42°W) sub-basins in Alberta, Canada, showing the locations of sampling sites and dams–weirs on each river.



for *D. geminata* to recolonize and grow to bloom levels. This was based on the number of days that passed between a large-scale scouring event (i.e., flood and subsequent spate in late June 2005) and the emergence of a bloom in the upper Bow River in late July 2005.

Periphyton collection and analyses

Epilithic periphyton were collected from five randomly chosen, cobble-sized rocks (20–40 cm in diameter) at each site (usually 2–3 m from the bank) at a water depth greater than 30 cm, but less than 100 cm. Two circles were demarcated with a 14.5 cm^2 polyvinyl chloride (PVC) template on each rock: one for chlorophyll *a* (Chl *a*) and ash-free dry mass (AFDM) and one for *D. geminata* enumeration. Periphyton was mechanically dislodged with a combination of dissecting tools and a toothbrush until the rock surface was devoid of visible biomass. Removed material was transferred to 50 mL polyethylene snap-cap cups and stored on ice in the field.

At each site, periphyton collected for taxonomic assessment was pooled in a 100 mL borosilicate bottle and preserved with Lugol's acid–iodine fixative. Within 24 h, refrigerated biomass was equally divided and processed for Chl *a* and AFDM. Chl *a* was extracted into methanol following Thompson et al. (1999), and the values reported here were not corrected for phaoephytin content. AFDM was processed following Biggs and Kilroy (2000). Chl *a* was measured spectrofluorometrically (excitation = 440 nm) with a Spectromax Gemini XS dual-scanning microplate spectrofluorometer (Molecular Devices, Sunnyvale, California, USA). Lugol's preserved samples were diluted 1- to 100-fold prior to taxonomic identification and enumeration. A Leica DM IRB inverted microscope (Leica Microsystems, Wetzlar, Germany) was used to count cells along two transects (= 40 fields) per sample at 200× magnification. Although *D. geminata* is large (60–125 µm) and conspicuous, care was taken to ensure that all cells identified as *D. geminata* had the diacritical feature of 2–5 stigmata.

Statistical analyses

Repeated-measures analysis of variance (ANOVA) was used to compare the seasonal means ($n = 3$) of environmental variables measured in the Bow and Red Deer rivers in 2005 (Table 1). To normalize the effect of distance from headwaters on environmental variables, this analysis only included a subset of six matched sampling sites from each river based on their approximately equal (i.e., <10 km difference) distance from headwaters. The total distance for each river included in the analysis was a contiguous reach of 216 km. Preliminary analyses using repeated-measures ANOVA detected a number of statistical differences in environmental variables between sites with and without *D. geminata*. Since all of these statisti-

Table 1. Summary statistics for repeated-measures analysis of variance (ANOVA) comparing the seasonal means of environmental variables measured in the Bow and Red Deer rivers in 2005 from matched-distance sites within a 216 km contiguous reach.

Variable	*n*	Bow River mean	Red Deer River mean	Sum of squares	*F* ratio	*p*
Mean discharge ($m^3 \cdot s^{-1}$)	24	87.09 (23)	82.72 (17)	114.98	0.03	0.87
Discharge (CV)	24	24.54 (4)	46.05 (6)	2 774.79	8.78	**<0.01**
Turbidity (NTU)	31	2.76 (0.3)	10.50 (2.3)	320.84	34.60	**<0.01**
TSS ($g \cdot L^{-1}$)	36	5.05 (1)	9.35 (2)	165.84	4.58	**0.04**
Dissolved oxygen ($mg \cdot L^{-1}$)	36	13.31 (0.6)	11.97 (0.5)	16.61	3.27	0.08
Temperature (°C)	36	10.48 (1)	11.09 (1)	0.67	0.14	0.71
Conductivity ($\mu S \cdot cm^{-1}$)	36	267.92 (15)	293.51 (7)	6 170.24	2.72	0.11
pH	36	8.59 (0.03)	8.61 (0.04)	0	0.28	0.60
Light extinction coefficient	34	0.02 (0.003)	0.02 (0.002)	0	0.02	0.89
Flow ($m \cdot s^{-1}$)	36	0.42 (0.05)	0.40 (0.04)	0.01	0.23	0.64
TP ($\mu g \cdot L^{-1}$)	25	16.91 (6)	26.56 (3)	469.24	2.41	0.13
AFDM ($\mu g \cdot cm^{-2}$)	36	3.2 (0.001)	7.7 (0.002)	0.18	4.07	**0.05**
Total Chl *a* ($\mu g \cdot cm^{-2}$)	36	101.50 (28)	44.73 (13)	29 008.78	3.52	0.07
Didymosphenia geminata ($cells \cdot cm^{-2}$)	36	214.83 (115)	38.25 (23)	280 622.10	2.08	0.16

Note: Statistically significant *p* values ($p \leq 0.05$) are in bold; standard errors are in parentheses. CV, coefficient of variation; NTU, nephelometric turbidity units; TSS, total suspended solids; TP, total phosphorus; AFDM, ash-free dry mass; Chl *a*, chlorophyll *a*.

cally significant ($p < 0.05$) environmental variables covaried with distance from headwaters, an analysis of covariance (ANCOVA) was performed using distance from headwaters as an interaction effect variable in the model test, with *D. geminata* presence or absence as the categorical independent variable. To account for possible serial correlation of environmental variables with time in season, only seasonal means ($n = 3$) were used (Table 2). Logistic regression analyses were performed using the seasonal means ($n = 3$) of environmental variables to detect statistically significant predictive relationships with *D. geminata* presence or absence. Prior to performing a logistic multiple regression (whole model test) with statistically significant parameters from the individual model tests, all covariables were removed from the analysis (Table 3). Least-squares linear regression analyses were performed with natural log-transformed *D. geminata* cell densities (with zero-counts removed) as a function of each environmental parameter measured. The only statistically significant predictor variable detected was mean discharge. Cell densities of five other diatom taxa from both rivers were regressed against mean discharge for comparison with *D. geminata* (Table 4). All statistical analyses were performed using the statistical software package SAS JMP (SAS Institute Inc., Cary, North Carolina, USA).

Results and discussion

Four of 14 environmental parameters significantly differed between rivers during our sampling period (Table 1). In particular, water clarity (represented by TSS and turbidity) and the coefficient of variation (CV) in discharge differed, even though site distances from the river source were comparable. We found *D. geminata* in both rivers in 2004 and 2005 during all sampling periods, but there were markedly higher cell densities in the Bow River (Fig. 2). Maximum cell densities of *D. geminata* were five times higher in the Bow River, and an extensive bloom (i.e., rocks completely covered) occurred in the upper reach of the river during summer 2005. Two years of sampling revealed coarse spatial distribution and abundance patterns (Fig. 2). In both years, *D. geminata* was detected on the Bow River within the city limits of Calgary. Bloom-level densities occurred on the Bow River in the summer of 2005 at our third sampling site, 64 km downstream of the headwaters within the boundaries of Banff National Park. The Banff townsite (89 km downstream of headwaters) had detectable levels of *D. geminata* in the fall only. In the Red Deer River, *D. geminata* was never detected upstream of Dickson Dam (Fig. 1). The highest cell densities in both years reported for the Red Deer River were consistently at the Dickson Dam site, which is 182 km downstream of the headwaters. The City of Red Deer site had detectable levels of *D. geminata* only in the summer of 2004.

When comparing the environmental characteristics of sites with and without *D. geminata* (Table 2), it is apparent that lower mean values of mean discharge, turbidity, temperature, conductivity, pH, and TP were all associated with the presence of *D. geminata*. Furthermore, logistic regression analyses identified the noncovarying parameters of temperature, turbidity, and flow as statistically significant predictor variables in *D. geminata* presence or absence. A multiple logistic regression model incorporating these variables explained 45% of the variation in *D. geminata* presence or absence. Though all environmental parameters were tested as model predictors, least-squares linear regression analyses detected only mean discharge as having a statistically significant negative relationship with *D. geminata* biomass (Table 4). In contrast, comparable regression models applying biomass data from other diatoms in these rivers all had positive slopes (Table 4), albeit none were statistically significant.

While others have concluded that the general hydraulic preference of *D. geminata* includes relatively low, stable flows (Kilroy 2004; Spaulding and Elwell 2007), Kilroy et al. (2005*b*) showed *D. geminata* abundance (using a visual biovolume index) to be quite variable over a range of flow velocities ($m \cdot s^{-1}$). We also found a high degree of variation in *D. geminata* presence or absence relative to flow velocity and did not detect a statistically significant relationship between flow and biomass (data not shown). However, our results do show a statistically inferred preference for lower discharge velocities ($m^3 \cdot s^{-1}$) and less variation in discharge

Table 2. Summary statistics for analysis of covariance (ANCOVA; using distance from headwaters as the interaction effect covariable) comparing the seasonal means of environmental variables at sites in both rivers where *Didymosphenia geminata* was detected (+Didymo) and not detected (–Didymo) in 2005.

Variable	*n*	+Didymo mean	–Didymo mean	Sum of squares	*F* ratio	*p*
Mean discharge ($m^3 \cdot s^{-1}$)	12	53.39 (15)	103.14 (12)	28 437.51	9.12	**0.005**
Discharge (CV)	12	27.12 (8)	38.57 (6)	1 255.86	1.52	0.28
Turbidity (NTU)	36	2.21 (2)	10.26 (2)	1 278.52	8.87	**<0.001**
Temperature (°C)	36	9.36 (0.9)	11.94 (0.7)	214.0	9.0	**0.002**
Conductivity ($\mu S \cdot cm^{-1}$)	36	238.23 (12)	269.96 (8)	39 989.81	13.59	**<0.001**
pH	36	8.62 (0.03)	8.63 (0.02)	0.12	3.43	**0.02**
TP ($\mu g \cdot L^{-1}$)	28	18.66 (4)	24.99 (2)	3 932.09	11.06	**<0.001**

Note: Statistically significant *p* values ($p \leq 0.05$) are in bold; standard errors are in parentheses.

Table 3. Summary statistics for logistic multiple-regression (whole-model test) assessment of environmental parameters with no covariation as model predictors of *Didymosphenia geminata* occurrence in the Bow and Red Deer rivers.

	df	χ^2	$p > \chi^2$	r^2
Whole model test	3	20.00	<0.01	0.45
Individual parameter test				
Temperature (°C)	1	4.31	0.04	0.08
Turbidity (NTU)	1	15.61	<0.01	0.34
Flow ($m \cdot s^{-1}$)	1	4.18	0.04	0.09

Note: The individual parameter tests of the independent variables used in the model are also presented. The goodness of model fit statistic ($p > \chi^2$) denotes statistical significance where $p \leq 0.05$.

(Tables 2 and 3). These results coincide with the higher *D. geminata* abundance found in the Bow River, which is partly due to the higher degree of flow regulation on the Bow River compared with the Red Deer River (Fig. 1). At Dickson Dam, where flow is regulated on the Red Deer River, we consistently found the highest *D. geminata* abundance (Fig. 2).

Though our results show a consistent link between dam proximity and *D. geminata* occurrence, the overarching mechanism is likely flow levels and stability, given that we documented a bloom along an unregulated reach of the upper Bow River in July 2005 (Fig. 2). This site had low discharge CV and low mean discharge among years, which contributed to the significant negative relationship found between *D. geminata* biomass and mean discharge (Table 4). Interestingly, other diatom taxa common to these rivers regressed positively with mean discharge (Table 4), though the data tested were not statistically significant. However, the biological inference from these data suggests that low, stable flows may offer a competitively advantageous environment for *D. geminata* over other algal taxa.

Flow is not the only factor that regulates *D. geminata* occurrence and bloom development. We found significant differences in water temperature, turbidity, pH, conductivity, and TP at sites with and without *D. geminata* (Table 2). These environmental parameters can describe algal growth tolerances and, when combined, determine growth rates (Stevenson et al. 1996). Flow velocity affects periphyton communities by affecting boundary layers and nutrient diffusion and the cell's ability to remain attached given velocity-driven shear stress (Stevenson 1996). Velocity gradients can structure periphyton communities, with long filamentous growth forms typically more prevalent at slower velocities (Biggs et al. 1998). Our data show that *D. geminata* can tolerate and grow in variable flow regimes typical of montane rivers, but the development of blooms likely requires both lower mean discharge and variation in discharge.

The results from our study reaffirm that *D. geminata* occurs and forms blooms under oligotrophic conditions. Its preference for clear water implies that it either tolerates or prefers high incident light, which is common for many diatoms (DeNicola and Hoagland 1992). Diatoms are sensitive to nutrients and are frequently used as bioindicators of water quality (Kutka and Richards 1996; Lavoie et al. 2006). Kawecka and Sanecki (2003) reported the occurrence of *D. geminata* under mesotrophic conditions in Poland, but blooms only occurred immediately downstream of reservoirs. Although their study documented the occurrence of *D. geminata* under mesotrophic conditions, most reports to date indicate that *D. geminata* typically forms nuisance blooms in oligotrophic environments.

The enigma of oligotrophic blooms is not unknown in freshwater systems, but it certainly is rare. Filamentous green algae such as *Mougeotia* sp. and *Zygogonium* sp. bloom as metaphyton in the littoral zones of oligotrophic lakes (Turner et al. 1995). Watson et al. (2001) documented an algal bloom in an oligotrophic reservoir, but related high densities of mixotrophic algae to the relatively high concentrations of bacteria and dissolved organic carbon. In these examples, blooms only occurred in stable water columns (summer and winter stratification, respectively). To our knowledge, *D. geminata* is the only documented example of a periphytic alga that blooms in oligotrophic conditions. Interestingly, it also appears to require a stable flow regime to generate bloom densities. However, a question remains as to how *D. geminata* can bloom when external phosphorus is apparently at growth-limiting concentrations. One potential mechanism may involve highly efficient internal cycling of nutrients within the bloom matrix (Wetzel 1993). Compared with pelagic systems, this would seem to be a challenge in lotic environments, yet potentially possible in thick, dense *D. geminata* mats. We also observed *D. geminata* mats to be effective particle traps, which may be an important source of labile nutrients. Further research on nutrient acquisition and requirements should help improve our understanding of *D. geminata* bloom dynamics.

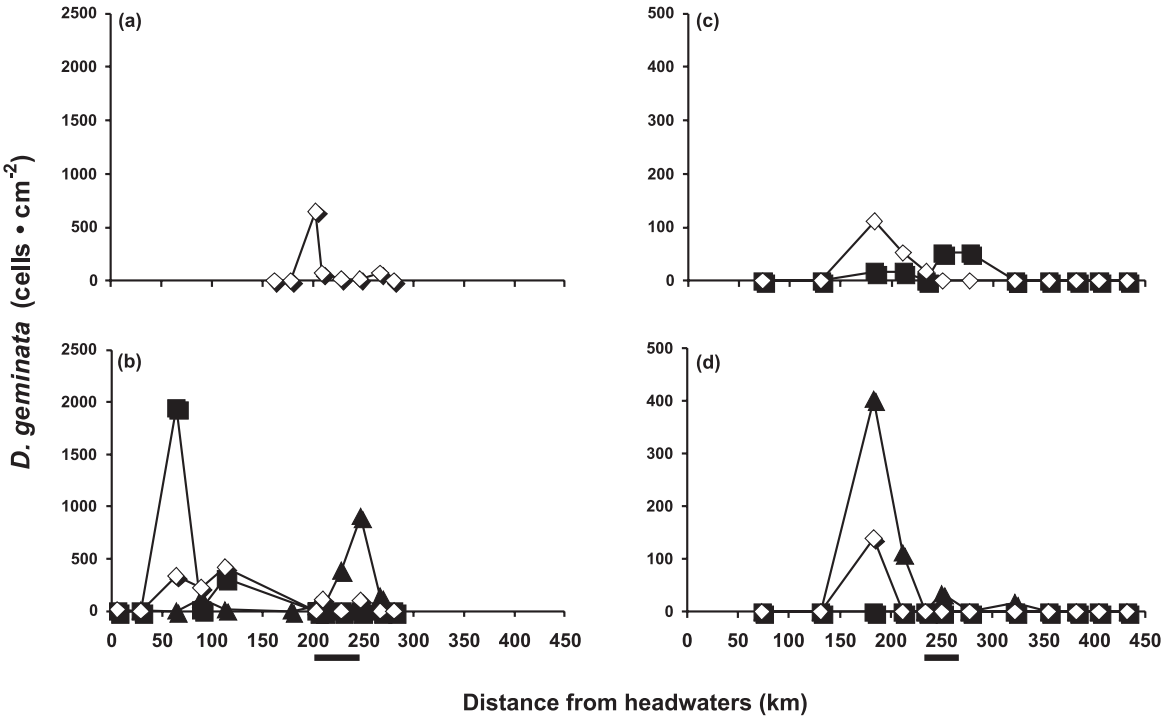
Considering our regression model of *D. geminata* biomass and mean discharge only explained 30% of the variation in biomass, other environmental constraints must be important

Table 4. Comparison of least-squares linear regressions of diatom species biomass (cells·cm^{-2}) as a function of mean discharge (m^3·s^{-1}) in the Bow and Red Deer rivers.

Diatom taxon	*n*	Slope	Intercept	r^2	*p*
Didymosphenia geminata	15	–0.03	5.89	0.30	**0.03**
Gomphonema sp.	8	0.02	6.82	0.45	0.07
Navicula sp.	7	0.01	7.0	0.49	0.08
Cymbella sp.	9	0.02	6.82	0.16	0.29
Achnanthidium sp.	12	0.009	9.42	0.16	0.20
Synedra sp.	10	0.002	8.79	0.005	0.84

Note: Biomass values were natural log-transformed to normalize residuals. The *p* value is the probability that the slope is significantly different from zero at $\alpha = 0.05$. Significance is denoted in bold where $p \leq 0.05$.

Fig. 2. Distribution of *Didymosphenia geminata* abundance along the sampling reaches of the Bow River in 2004 (*a*) and 2005 (*b*) and the Red Deer River in 2004 (*c*) and 2005 (*d*). Seasonal data are presented as follows: spring (solid triangles), summer (solid squares), and fall (open diamonds). See Materials and methods for exact sampling dates. The bars below the *x* axes represent the location and city limit boundaries of the City of Calgary (Bow River) and the City of Red Deer (Red Deer River). Note that the Bow River *y* axis scale is five times greater than that of the Red Deer River.



to bloom development. For example, bed load and stability have been shown to influence periphyton establishment, abundance, and taxonomic richness (Biggs and Smith 2002). Our study sites were along reaches with cobble-dominated riverbeds, yet there were qualitative differences in bed features, such as braided vs. nonbraided main stems. Braided rivers are fundamentally less stable than nonbraided rivers of similar size and discharge, which should be important to the development of *D. geminata* blooms.

While many factors are likely important to bloom development, the relationship between *D. geminata* abundance and mean discharge suggests that flow regulation is a potential mitigation candidate to control and (or) prevent blooms. We would expect an increased frequency of high volume discharges from dams to impede the development of blooms near spillways. However, many dams serve a dual purpose of water storage and hydroelectric power generation, and it may prove to be very difficult to compel dam operators to voluntarily discharge large volumes of water. An even greater challenge remains for those unregulated river reaches that experience *D. geminata* outbreaks from year to year. Mitigation measures would be difficult to implement in these situations, particularly in areas that have strict watershed management (e.g., national parks). Ironically, it is these protected areas that may be greatly impacted if it is determined that *D. geminata* blooms negatively affect other trophic levels by impacting ecosystem structure and function.

Despite the growing concern regarding impacts to ecosystem services, the current global spread of *D. geminata* does pose a unique opportunity to address fundamental questions in invasion biology. For example, the *D. geminata* invasion and spread model could integrate aspects of ecological invasion dynamics with aspects of pandemic models. As a microorganism, *D. geminata* may have more in common with

global diseases than classic higher organism invaders. Given that a genetic alteration may have been responsible for the emergence of a nuisance-variant of *D. geminata* and the important role of humans as vectors, global pandemic models may prove quite useful in our understanding of *D. geminata* invasion events.

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