

The influence of light, stream gradient, and iron on *Didymosphenia geminata* bloom development in the Black Hills, South Dakota

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Received: 30 May 2013 / Revised: 29 July 2013 / Accepted: 3 August 2013 / Published online: 17 August 2013
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Abstract The aquatic nuisance species *Didymosphenia geminata* was first documented in Rapid Creek of South Dakota's Black Hills during 2002. Since then, blooms have occurred primarily in a 39-km section of Rapid Creek while blooms were rarely observed in other Black Hills streams. In this study, we evaluated factors related to the presence and development of visible colonies of *D. geminata* in four streams of the Black Hills. At the watershed scale, stream gradient was negatively associated with the occurrence of *D. geminata* whereas stream width was positively related to *D. geminata* presence. At the stream scale, *D. geminata* coverage was inversely related to canopy coverage and iron concentration. At the local scale, shading by bridges virtually eliminated growth of *D.*

geminata colonies under bridges. At all three scales, proxy measures of light such as stream width, canopy coverage, and bridge shading revealed that light availability was an important factor influencing the presence and coverage of *D. geminata* colonies. In general, streams that had relatively wide stream reaches (mean = 9.9 m), shallow gradients (mean = 0.22%), and little canopy cover (mean = 13%) were associated with *D. geminata* blooms. In addition, iron concentrations in streams with *D. geminata* colonies were lower than in streams without blooms.

Keywords *Didymosphenia geminata* · Aquatic nuisance species · Light availability · Iron

Handling editor: Luigi Naselli-Flores

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Introduction

Didymosphenia geminata ([Lyngbye] Schmidt) was first reported from North America during the mid-1800s (Blanco & Ector, 2009), but in recent years interest in this diatom has increased due to observations of *D. geminata* blooms worldwide (Whitton et al., 2009). Blooms occur when *D. geminata* cells form a large quantity of elongated stalks that constitute the bulk of biomass in *D. geminata* colonies (Domozych et al., 2010). *D. geminata* stalks are composed primarily of sulfated polysaccharides and protein (Gretz, 2008) and can persist for up to two months

following peak production even if the cells are removed from the stalks (Spaulding & Elwell, 2007). As a result, conspicuous growths of the diatom and its reputation as an aquatic nuisance species have led to increased concerns about the effect of *D. geminata* in stream ecosystems.

The reported instances of *D. geminata* blooms have expanded appreciably since the late 1980s (Whitton et al., 2009). After large *D. geminata* blooms were observed on Vancouver Island, British Columbia, Canada (Sherbot & Bothwell, 1993), blooms were reported from other parts of Canada (Kirkwood et al., 2007), Europe (Kawecka & Sanecki, 2003), New Zealand (Kilroy et al., 2005), and South America (Segura, 2011). In the United States, *D. geminata* blooms have been documented in Arkansas, California, Colorado, Idaho, Minnesota, Montana, South Dakota, Utah, Virginia, Washington, and Wyoming (Spaulding & Elwell, 2007). While many of these blooms occurred in what was considered the native range of *D. geminata*, some reports have classified the diatom as an introduced species (see review by Whitton et al., 2009). In either case, the relatively recent appearance of *D. geminata* blooms worldwide has generated much concern among ecologists and prompted new questions aimed at identifying factors that influence the presence or absence of the diatom, and perhaps more importantly, conditions that allow for the diatom to bloom (Bothwell et al., 2012).

Much current research has focused on factors that influence the presence and magnitude of *D. geminata* blooms. Flow regime (Kirkwood et al., 2007), phosphorus concentration (Ellwood & Whitton, 2007; Kirkwood et al., 2009; Whitton et al., 2009; Bothwell & Kilroy, 2011), light availability (Kirkwood et al., 2009; Whitton et al., 2009; Bothwell & Kilroy, 2011), water chemistry, underlying geology (Rost et al., 2011), or combinations of these factors (Kumar et al., 2009) have been shown to influence the presence of *D. geminata*. Thus, physical habitat, water quality, and nutrient availability all have the potential to influence whether or not *D. geminata* will bloom when present in a stream.

In South Dakota's Black Hills, *D. geminata* blooms were first reported from Rapid Creek in 2002. Since then, *D. geminata* blooms have occurred primarily in a section of Rapid Creek (~39 km) from below the dam at Pactola Reservoir downstream to Rapid City, South

Dakota. In this study, we explored physical and chemical factors associated with the presence and development of visible colonies of *D. geminata* in the Black Hills because blooms of the diatom have been associated with biotic changes to stream ecosystems (Gillis & Chalifour, 2009; Kilroy et al., 2009; James et al., 2010). The objectives of this study were threefold: (1) to determine factors associated with the presence or absence of *D. geminata* colonies at the watershed scale; (2) to explore factors influencing *D. geminata* coverage at the stream scale; and, (3) to examine the influence of light availability on *D. geminata* coverage at the macro-habitat scale.

Materials and methods

Study area

Our study area included four streams from three watersheds in South Dakota's Black Hills (Fig. 1). Streams included Castle Creek, Rapid Creek, Spearfish Creek, and Whitewood Creek. Castle Creek, located in the upper Rapid Creek watershed, begins as a headwater stream in the central Black Hills and flows into Rapid Creek. Blooms of *D. geminata* have been reported from a single reach (~500 m) in Castle Creek, but blooms of the diatom are sparsely distributed and infrequently observed. Mean annual discharge from Castle Creek was $0.34 \text{ m}^3 \text{ s}^{-1}$. Rapid Creek is the largest of the four streams with a mean annual discharge of $1.47 \text{ m}^3 \text{ s}^{-1}$ (USGS, 2008). *D. geminata* was first reported from Rapid Creek in 2002 and blooms are particularly notable in the tailrace area below Pactola Reservoir. Further downstream (~39 km) near Canyon Lake in Rapid City, *D. geminata* is present, but sparsely distributed. Spearfish Creek, located in the northern Black Hills, is an unregulated stream that flows through Spearfish Canyon and drains approximately 360 km^2 (USGS, 2008). Mean annual discharge of Spearfish Creek near Spearfish, SD averages $1.6 \text{ m}^3 \text{ s}^{-1}$ (USGS, 2008). *D. geminata* blooms have not been reported from Spearfish Creek. Whitewood Creek is another unregulated, headwater stream located in the northern Black Hills maintained through springs and precipitation and drains approximately 201 km^2 (USGS, 2008). Mean annual discharge in Whitewood Creek averages $0.82 \text{ m}^3 \text{ s}^{-1}$ (USGS, 2008). Like Spearfish Creek, *D.*

geminata blooms have not been reported from White-wood Creek.

Stream surveys

Physical habitat surveys were conducted during the week of 14 July, 2008 by sampling ten 100-m reaches

in each of the four study streams using a point-sampling protocol (Gorman & Karr, 1978). Physical habitat parameters measured at each site included stream width (m), water depth (m), water velocity (m s^{-1} ; Marsh-McBirney Flo-Mate model 2000; HACH, Loveland, CO, USA), gradient (m elevation difference/100 m stream; reported as %), substrate

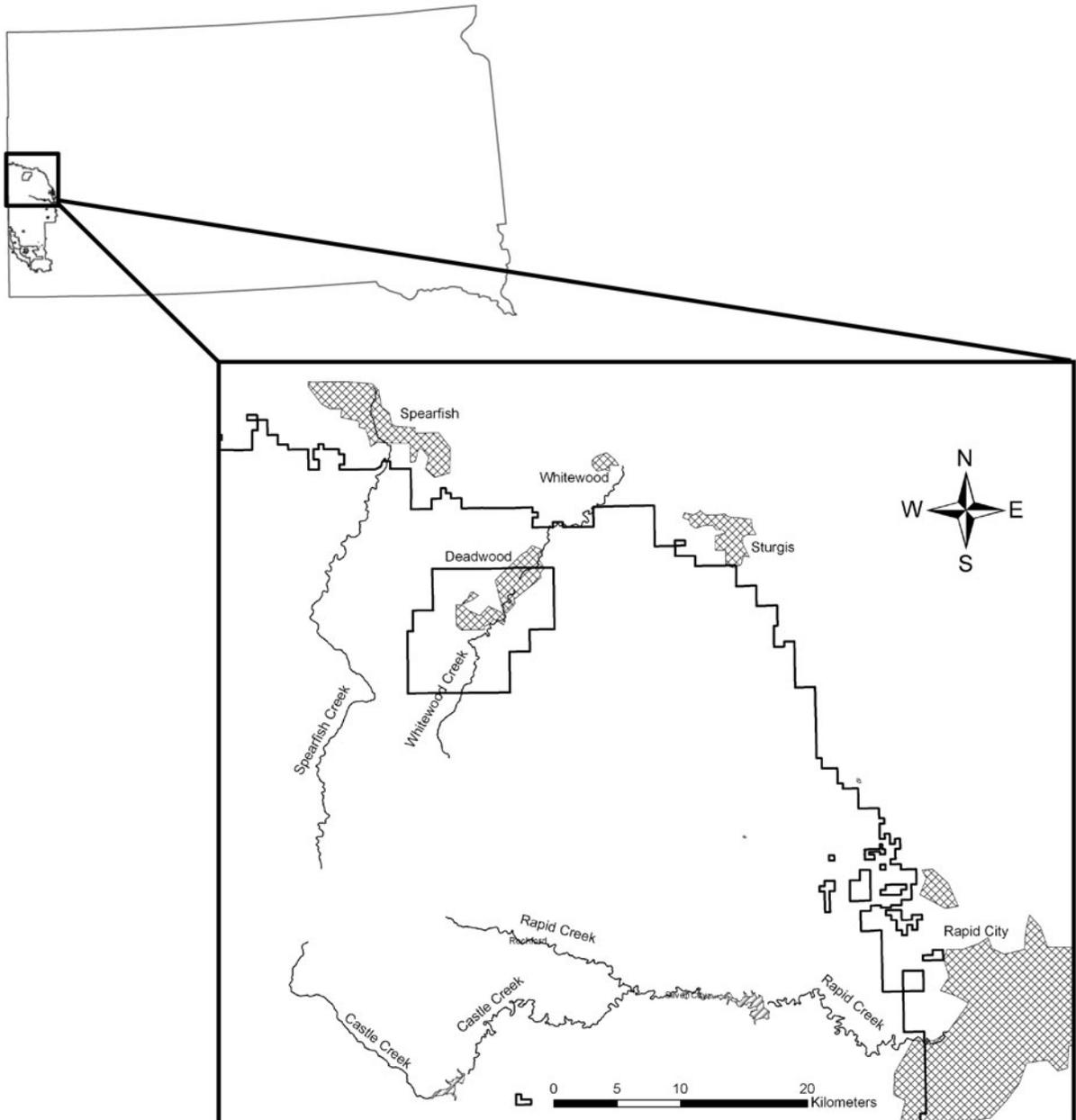


Fig. 1 Map of Castle, Rapid, Spearfish, and Whitewood Creek study streams in the Black Hills, South Dakota. The *outline* within South Dakota depicts the boundary of the Black Hills. Areas within the *inset* marked with *cross-hatches* indicate city boundaries

composition (Wentworth scale), and canopy cover (%). For each stream reach, four transects oriented perpendicular to the stream channel were randomly selected for sampling. At each transect, water depth, water velocity, and substrate composition were recorded at four equidistant points across the stream channel (Gorman & Karr, 1978). Percent canopy cover was estimated once per transect from the center of the stream channel using a spherical densiometer (Lemmon, 1956, 1957). Stream width was measured as the distance of wetted area. Stream gradient was estimated by measuring relative height differences of the upstream and downstream water surface at each stream reach using an engineering surveyor's tripod, level, and rod. Substrate composition was summarized as the proportion of the substrate greater than 64 mm (cobble). Measures of stream width ($n = 4$), water depth ($n = 16$), water velocity ($n = 16$), and canopy cover ($n = 4$) were each averaged to obtain a single value per reach.

Water temperature ($^{\circ}\text{C}$) and pH were measured using a HACH HQ40d multi-parameter meter (HACH, Loveland, Colorado, USA). Water turbidity (NTU) was measured using a HACH 2100Q Turbidimeter. A 1-l water sample was collected from each reach, placed on ice, and frozen until analysis. Sub-samples from each one-liter sample were analyzed for total Kjeldahl nitrogen (TKN; $\mu\text{g l}^{-1}$), silica concentration (mg l^{-1}), and total dissolved iron (Fe) (mg l^{-1}) according to APHA (2002). Total phosphorus (TP; $\mu\text{g l}^{-1}$) was analyzed using methods outlined in Wetzel & Likens (1991).

To quantify *D. geminata* at each sampling reach, an index of *D. geminata* coverage (IDC) was estimated using an approach similar to Kilroy et al. (2005). One hundred rocks were randomly selected from each reach while moving in a zig-zag pattern upstream; without looking into the stream, an observer reached into the stream and lifted the first rock they contacted. We then visually estimated the percent areal coverage of *D. geminata* on each rock and measured the thickness of the *D. geminata* mat to the nearest mm. Thickness was assigned a score from 0 to 5 based on the following: 0; 1, (<1 mm); 2, (1–5 mm); 3, (6–15 mm); 4, (16–30 mm); and 5, (>30 mm). The percent coverage of *D. geminata* was multiplied by the thickness score to provide the IDC, which ranged from 0 to 500. Kilroy et al. (2005) showed that the IDC was

significantly related to *D. geminata* ash-free dry mass and provided a quantitative measure of *D. geminata* coverage.

Factors associated with the presence or absence of *D. geminata* blooms

To explore factors associated with *D. geminata* bloom occurrence, we used logistic regression analysis and coded each stream reach based on the presence (value = 1) or absence (value = 0) of visible *D. geminata* colonies. Prior to analysis, we compared habitat and water quality variables between reaches with or without *D. geminata* using a Mann–Whitney *U* test ($\alpha < 0.05$; Rich et al., 2003). Canopy cover and substrate composition (e.g., proportion data) were not normally distributed so were arcsine \sqrt{p} transformed prior to analysis. Variables were excluded from further analysis if no difference was detected between reaches with or without *D. geminata*. For variables that differed significantly between reaches with or without *D. geminata*, a Spearman's rank correlation analysis and variance inflation factor (VIF) test were used to explore collinearity (Kutner et al., 2004). Non-collinear variables (i.e., $\text{VIF} < 3$; Cody & Smith, 2006) were then used as input in a forward-selection, logistic regression analysis with the presence or absence of *D. geminata* as the response variable. The Hosmer–Lemeshow goodness-of-fit test ($P > 0.10$) was used to assess model fit (Hosmer & Lemeshow, 1989).

We evaluated the relative importance of individual model parameters by calculating odds ratios as $e^{\hat{\beta}i}$ where $\hat{\beta}i$ is the parameter coefficient for variable *i* estimated from logistic regression analysis. As calculated, the odds ratios are based on a single-unit change that may not reflect the magnitude of difference between stream reaches (Rich et al., 2003). To make these units more biologically meaningful (i.e., smaller or larger), we multiplied $\hat{\beta}i$ by a scaling factor (*C*) to obtain a scaled, odds ratio ($e^{\hat{\beta}i \cdot C}$). The scaling factor (*C*) was derived by calculating the median value of each variable for reaches where *D. geminata* was present or absent, and then taking the difference between these values (Rich et al., 2003). We then calculated 95% confidence intervals ($e^{C \cdot \hat{\beta}i \pm z_{0.975} \cdot C \cdot SE(\hat{\beta}i)}$) where $z_{0.975} = 1.96$, for the scaled odds ratio to evaluate the significance of values at the

lower (positive parameter) and upper (negative parameter) bounds (Rich et al., 2003).

Factors associated with *D. geminata* coverage (IDC)

To evaluate factors associated with *D. geminata* coverage (IDC), we analyzed habitat and water quality information collected from 13 reaches sampled in Rapid Creek during July 2008 ($n = 8$) or 2009 ($n = 5$) by stepwise, multiple regression analysis. A Spearman's rank correlation analysis and VIF test were conducted to detect non-collinearity of variables prior to model development (Kutner et al., 2004). Non-collinear variables were included as independent parameters in the regression analysis ($\alpha < 0.05$) with IDC as the response variable. Canopy cover and substrate composition (proportion) data were arcsine \sqrt{p} transformed prior to analysis due to non-normality.

Influence of stream shading on *D. geminata* coverage (IDC)

To examine the influence of stream shading on *D. geminata* coverage (IDC) in Rapid Creek, we relied upon existing girder bridges that spanned the stream and provided permanent shading cover. Unlike culvert-style bridges, girder bridges are supported by vertical abutments located outside of the stream margins and thus have minimal effects on substrate composition under the bridge. We selected four girder bridges in sections of Rapid Creek where visible *D. geminata* colonies were present. The dimensions of each bridge were similar (length = 9.5–11.9 m; width = 8.0–8.3 m; distance from water surface = 1.2–3.0 m) as were stream width (9–10 m wide) and water depth (<0.5 m) near each bridge.

We assigned three treatments at each bridge defined as: (1) upstream (within 10 m of the vertical plane of the upstream edge of the bridge), downstream (within 10 m of the vertical plane of the downstream edge of the bridge), or underneath (the area directly beneath and within the vertical planes of the outside bridge edges). Substrate composition was estimated in each treatment by randomly selecting 50 point samples from the stream bottom and assigning the substrate to a size category based on the Wentworth scale. *D.*

geminata coverage (IDC) was estimated from each treatment as previously described from 50 randomly selected rocks. Due to the close proximity of treatments (i.e., within 30 m), water quality and nutrient assessments were not conducted and were assumed to be similar at each bridge.

We compared substrate composition (% >64 mm) between treatments using a χ^2 test. Variation in *D. geminata* coverage (IDC values) among treatments was analyzed using one-way analysis of variance (ANOVA; $\alpha < 0.05$; Tukey post hoc test). All statistical analyses were completed using SAS 9.2 (SAS Institute Inc., Cary, NC).

Results

Factors associated with the presence or absence of *D. geminata* blooms

Didymosphenia geminata colonies were present at six of the 39 stream reaches (~15%) sampled in 2008. We were unable to collect data from one site in Rapid Creek above Pactola Reservoir due to high water conditions. The Mann–Whitney *U* test revealed that water temperature, pH, total Fe, water depth, water velocity, canopy cover, and substrate composition did not differ between sites with or without visible *D. geminata* colonies, so these variables were excluded from further analysis. Turbidity, Si, TKN, TP, and stream gradient were significantly lower at sites with *D. geminata*. In contrast, mean stream width was significantly greater at sites with *D. geminata* (Table 1). Since collinearity among variables was low (VIF < 3), we included habitat and water quality parameters listed above as variables in the logistic regression analysis. The global model included stream gradient and stream width as significant predictor variables and provided a reasonable fit to the data (Hosmer and Lemeshow goodness-of-fit test, $\chi^2 = 3.28$, $P = 0.91$, $df = 8$; Table 2). The odds ratio for stream gradient was significant, as shown by a confidence interval that did not include the value one (Table 2). Based on the scaled odds ratios, a 0.8% increase in stream gradient would be associated with about a 39% (1/0.72) decrease in the odds of *D. geminata* occurrence. For stream width, the confidence interval for the scaled odds ratio included the value one. However, the confidence interval (e.g.,

Table 1 Parameter means and ranges at sites with ($n = 6$) or without ($n = 33$) *D. geminata* colonies in the Black Hills, South Dakota

Parameter	<i>D. geminata</i> absent		<i>D. geminata</i> present	
	Mean (SE)	Range	Mean (SE)	Range
Canopy cover (%)	21 (3)	0–70	13 (4)	4–29
Depth (m)	0.31 (0.01)	0.14–0.53	0.33 (0.03)	0.21–0.42
Gradient ^a	0.95 (0.08)	0.27–1.90	0.22 (0.08)	0.02–0.51
Iron, Fe (mg l ⁻¹)	0.32 (0.08)	0.03–1.90	0.11 (0.02)	0.07–0.21
N, TKN (μg l ⁻¹) ^a	310.4 (22.3)	130.1–648.2	198.8 (21.3)	138.0–276.3
P, total (μg l ⁻¹) ^a	31.1 (7.8)	0.9–170.3	5.2 (4.2)	0.9–26.5
pH	8.6 (0.03)	8.2–9.1	8.5 (0.03)	8.5–8.7
Silica, Si (mg l ⁻¹) ^a	4.6 (0.13)	1.90–5.70	4.0 (0.1)	3.45–4.22
Substrate (% >cobble)	56 (5)	0–100	41 (5)	19–56
Temperature (°C)	15.1 (0.8)	7.0–19.9	11.3 (1.23)	8.8–16.5
Turbidity (NTU) ^a	2.9 (0.2)	1.2–5.6	1.1 (0.1)	0.6–1.6
Velocity (m s ⁻¹)	0.49 (0.03)	0.04–0.83	0.37 (0.03)	0.26–0.48
Width (m) ^a	7.11 (0.51)	2.43–15.80	9.95 (0.52)	8.20–11.35

Standard errors (SE) are indicated in parenthesis. Data were collected in July 2008

^a Significant difference between parameters in sites with and without *D. geminata* colonies (Mann–Whitney *U*; $\alpha \leq 0.05$)

Table 2 Logistic regression parameters for predicting the presence of *D. geminata* in the Black Hills, South Dakota

Variable	df	Parameter estimate	Standard error	Scaling factor (<i>C</i>)	Scaled odds ratio	95% CI for scaled odds ratio	$P > \chi^2$
Intercept	1	-3.45	3.13				0.27
Stream gradient (%)	1	-7.56	3.66	0.8	0.0023	(0.0000076, 0.727)	0.03
Stream width (m)	1	0.61	0.34	3.0	6.23	(0.84, 45.60)	0.07

Scaled odds ratios were calculated using a scaling factor (*C*) determined from median differences between sites with or without *D. geminata* (see text for details)

CI confidence interval

odds ratios) for stream width was appreciably skewed to the right implying that the association between stream width and *D. geminata* occurrence could be biologically important (Hosmer & Lemeshow, 1989; Rich et al., 2003). Using the derived scaling factor, a 3-m increase in stream width would be associated with at least a 20% increase (1/0.84) in the predicted odds of occurrence for *D. geminata*.

Factors associated with *D. geminata* coverage (IDC)

Thirteen stream reaches were sampled in Rapid Creek in July 2008 ($n = 8$) or 2009 ($n = 5$). On eleven occasions (85%), visible colonies of *D. geminata* were

present (IDC range = 10–111). Collinearity of habitat variables ($n = 13$) was low with VIF's <1.7; thus all variables were entered into the stepwise multiple regression model. Variables retained in the regression model included canopy coverage and Fe concentration, and together these two variables explained 70% of the variation in IDC ($F_{1,11} = 13.17$; $P = 0.0012$; $R^2 = 0.70$). *D. geminata* coverage (IDC) was inversely related to both canopy coverage and Fe concentration (Fig. 2), where IDC was predicted as,

$$\text{IDC} = 153.9 - 182.4 \cdot (\arcsine \sqrt{\text{proportion [canopy cover]}}) - 272.1 \cdot (\text{Fe concentration}).$$

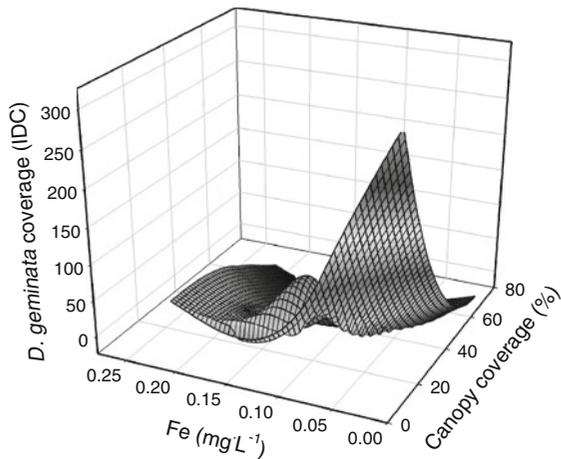


Fig. 2 Surface plot curve showing relationship of iron concentration and canopy cover to *D. geminata* coverage (IDC) in Rapid Creek, South Dakota

Influence of stream shading on *D. geminata* coverage (IDC)

Substrate composition measured at the four bridge locations was similar among upstream, downstream, and underneath treatments ($\chi^2 = 0.56$, $P = 0.75$). Coverage estimates (IDC) for *D. geminata* were similar for upstream and downstream treatments, ranging from 32.6 to 94.5 and 38.8 to 115, respectively. IDC values measured underneath of bridges, however, only ranged from 0.8 to 10, and on average were significantly lower than that measured for

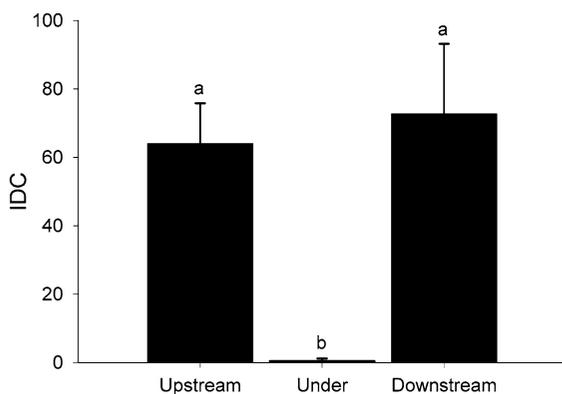


Fig. 3 Mean index of *D. geminata* coverage (IDC) at downstream, underneath, or upstream locations of girder bridge structures ($n = 4$) in Rapid Creek, South Dakota. Error bars represent one SE. Values with the same letter are not significantly different (Tukey's multiple comparison test; $P > 0.05$)

upstream or downstream locations (one-way analysis of variance; $F_{2,11} = 8.31$, $P = 0.009$; Fig. 3).

Discussion

Stream shading has an important influence on solar insolation that in turn can affect stream biota (Li et al., 1994; Zoellick, 2004). In a New Zealand study for example, Towns (1981) found that periphyton biomass under experimentally shaded stream reaches was significantly lower than that in un-shaded portions. The importance of stream shading on *D. geminata* blooms has received little attention, but likely influences the blooming behavior of this periphyton species. Light availability is known to influence periphyton abundance and based primarily on anecdotal observations, and is generally considered to favor *D. geminata* blooms (Whitton et al., 2009). In the South Saskatchewan River for example, *D. geminata* blooms were typically observed below dams where the authors postulated that bloom formations were partly attributable to increased water clarity (Kirkwood et al., 2009) as water of higher clarity attenuates less light and thus allows more light to reach the substrate (Hill, 1996) where *D. geminata* is located. Although not directly measured in our study, light availability appeared to have an important influence on the presence and coverage of *D. geminata* in the Black Hills. A number of variables identified in our study could be considered proxies of light availability. Canopy cover, for example, was a significant variable in our model and was inversely related to *D. geminata* coverage in Rapid Creek (Fig. 4). Similarly, wider stream reaches are often associated with increased light availability owing to the reduced shading effects from riparian vegetation (Hill, 1996). Stream width was an important factor in determining *D. geminata* colony occurrence in Black Hills streams and was positively associated with the presence of blooms. Finally, permanent shading structures, such as those associated with bridges, provided a fortuitous opportunity to explore shading effects, where *D. geminata* colonies were virtually absent under bridges, despite being present immediately up- and downstream of shaded areas.

Because light is essential to autotrophic periphyton, it is reasonable to surmise that factors influencing light availability play an important role in *D. geminata*

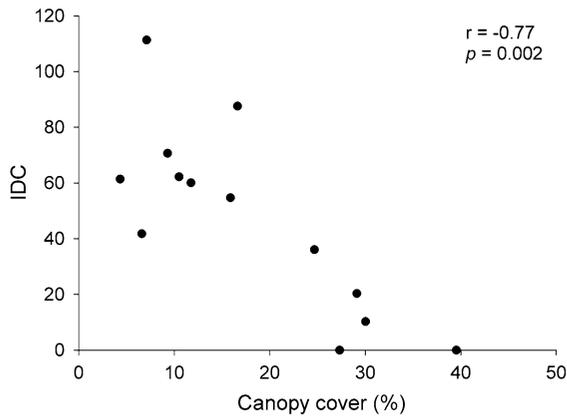


Fig. 4 Relationship between canopy cover (%) and *D. geminata* coverage (IDC) in Rapid Creek, South Dakota. Pearson's correlation coefficient and significance value are given

blooms. In a study that examined environmental control of *D. geminata* stalk length, Kilroy & Bothwell (2011) found that when *D. geminata* was nutrient limited, cell division rates decreased and stalk length increased, especially as light level increased. Longer stalk lengths were thought to be a result of “photosynthetic overflow” under nutrient-limited conditions (Kilroy & Bothwell, 2011) where production of extracellular polymeric substances (i.e., *D. geminata* stalks) is thought to release surplus fixed carbon that photosynthetic cells are incapable of storing (Smith & Underwood, 2000; Staats et al., 2000).

In our study, Fe concentration was negatively related to *D. geminata* coverage. Recently, Bothwell et al. (2012) argued that *D. geminata* blooms were not favored in waters with high Fe concentrations and showed that blooms most often occur in Fe-poor rivers. It is well known that sorption of Fe and other metals on periphyton exopolysaccharide can remove Fe from surrounding waters (Lawrence et al., 1998). Indeed, extracellular accumulation of metals by periphytic mats can be affected by light availability (Gray & Hill, 1995) and periphyton biomass (Hill et al., 2000; Letovsky et al., 2012). Given evidence that elevated Fe does not initiate or sustain *D. geminata* blooms (Bothwell et al., 2012), *D. geminata* (IDC) might reduce Fe concentration in surrounding water via sorption by exopolysaccharide (Letovsky et al., 2012). Lower Fe levels during blooms compared to values prior to bloom commencement were reported from one river on Vancouver Island (Bothwell et al., 2012) and agree with our observations of lower Fe

concentrations associated with greater amounts of *D. geminata* coverage.

Stream gradient was associated with the presence of *D. geminata* blooms in the Black Hills (Fig. 5). It has been hypothesized that stream bed disturbance owing to flood events could be one mechanism controlling the establishment and growth of *D. geminata* colonies (Spaulding & Elwell, 2007; Cullis et al., 2012). Stream reaches with steeper gradients likely experience increased water velocities during flood events and thus an increased propensity for bed scouring. In a comparison of three sites in Boulder Creek, CO, one site with a relatively low gradient (located between two sites with a high gradient) had larger *D. geminata* coverage (Miller et al., 2009), consistent with our observations. Furthermore, measurements of bed movement showed that substrate changes in reaches with steeper gradients had a negative influence on *D. geminata* coverage (Miller et al., 2009).

It appears that *D. geminata* is less likely to establish colonies when the potential for scour, associated with steeper gradients, is greater. Flood events have been shown to influence *D. geminata* blooms (Kilroy et al., 2005), although the effects of stream gradient could be mediated in locations below dams where stable, regulated flows might reduce bed movement and enhance colonization by *D. geminata* (Kirkwood et al., 2007, 2009). In the Black Hills, *D. geminata* blooms were predominant in a lower gradient (mean = 0.22%) section of Rapid Creek, where flows

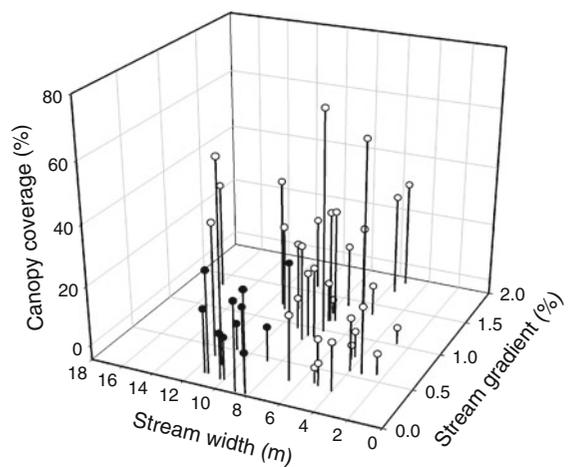


Fig. 5 Canopy coverage, stream width, and stream gradient for Black Hills stream sites with (black circles) or without (open circles) visible *D. geminata* colonies

are generally stable owing to regulated releases below Pactola Reservoir. In Castle, Spearfish, and White-wood creeks, where blooms were absent, mean stream gradients were greater at 0.48, 1.10, and 1.34%, respectively.

While factors such as light availability, stream gradient, or low phosphorus concentration (Kilroy & Bothwell, 2012) have been associated with the development of *D. geminata* blooms at local scales, factors such as these have not yet been able to fully address the recent phenomenon of blooms worldwide. Although not specifically examined in our study, a potential link between light availability and *D. geminata* blooms could be related to global changes in ultraviolet radiation (UVR). Since 1979, particularly between the latitudes of 40 and 50°, UVR reaching the Earth's surface has increased in both the northern and southern hemispheres (Caldwell et al., 1980; Herman, 2010) and evidence that diatoms are sensitive to UVR was reported in a few, older studies. Abundance of stalked diatoms (*Cymbella* and *Gomphonopsis* spp.) exposed to UVR was 2–4 times greater than that in communities shielded from UVR (Bothwell et al., 1993). Similarly, mucopolysaccharide tube-dwelling diatoms were present only at UVR-enhanced study sites in a Colorado stream (Rader & Belish, 1997). Perhaps not coincidentally, *D. geminata* seems to be concentrated between 40 and 50° latitude (north and south; e.g., Rocky Mountains, USA; south island, New Zealand, and Chile; Spaulding & Elwell, 2007; Segura, 2011) where UVR increases have been largest (Herman, 2010). This hypothesis has not been addressed in the published literature, but given the importance of light availability and potential links to UVR, experimental research is needed to better understand the role of UVR on *D. geminata* blooms.

Implications

Because light availability influences the blooming behavior of *D. geminata*, one pragmatic option for reducing the severity of blooms may include shading. For example, in some canal systems that transport water for hydropower, agriculture, or human consumption, managers regularly implement removal of *D. geminata* colonies by physically scraping it from concrete surfaces of the canal (Spaulding & Elwell, 2007). One way to mitigate nuisance growths of *D. geminata* colonies could be to limit incident light by

using shading structures. Irrigators that use instream water pumps could reduce *D. geminata* colonization by placing shading covers over pumps to prevent fouling. Similarly, in natural systems such as streams, establishing riparian vegetation to enhance shading effects could prevent or limit blooms while simultaneously providing cover and cooler water for fish (i.e., salmonids; Fausch & White, 1981; Zoellick, 2004). Future efforts aimed at quantifying mechanisms controlling *D. geminata* blooms and pragmatic approaches for reducing bloom formation would contribute to a better understanding of the ecology and management of the species.

Acknowledgments We thank personnel from the South Dakota Department of Game, Fish and Parks, and South Dakota State University for laboratory and field assistance during this study. J. Stafford provided assistance with statistical analyses. Funding for this project was provided by Federal Aid in Sport Fish Restoration (Project F-15-R 1514) administered by the South Dakota Department of Game, Fish and Parks. Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Fish and Wildlife Service or the U.S. Government.

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