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THE INFLUENCE OF *DIDYMOSPHENIA GEMINATA* ON FISHERIES RESOURCES IN RAPID CREEK, SOUTH DAKOTA – AN EIGHT YEAR HISTORY

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ABSTRACT – The aquatic nuisance diatom *Didymosphenia geminata* was established in Rapid Creek in the Black Hills of South Dakota in 2002. Shortly thereafter, large declines (>50%) of the naturalized brown trout *Salmo trutta* population were observed. We evaluated the influence of water resources and *D. geminata* on (1) declines in brown trout biomass, (2) changes in food resources, and (3) diet of brown trout in Black Hills streams. Drought conditions were largely responsible for trout declines in Black Hills streams. However, comparison of brown trout size-structure between the pre-*D. geminata* and post-*D. geminata* periods revealed that juvenile brown trout abundance increased while adult abundance decreased in Rapid Creek. Changes in food resources in *D. geminata*-impacted areas were thought to favor juvenile brown trout and negatively impact adults. In the presence of *D. geminata*, macroinvertebrate abundance was composed of fewer, larger taxa and higher numbers of smaller taxa (i.e., chironomids). Brown trout in Rapid Creek consumed fewer ephemeropterans and a high amount of dipterans. Nonetheless, diet analysis showed that brown trout in Rapid Creek consumed as much or more prey than trout from two other streams unaffected by *D. geminata*. Moreover, relative weight of brown trout from Rapid Creek was high (>100), implying that food availability was not limiting. These findings imply that *D. geminata* did not negatively impact feeding and condition of brown trout in Rapid Creek, although mechanisms affecting size-structure in Rapid Creek remain unknown.

INTRODUCTION

The spread and establishment of *Didymosphenia geminata* has prompted much concern in North America and New Zealand (Branson 2006; Kilroy 2004; Spaulding and Elwell 2007). It is capable of producing large masses of extracellular stalks that can cover up to 100% of the stream bottom in areas of high infestation, which can make *D. geminata* populations a nuisance in stream ecosystems. Recent research on invertebrate communities has shown that invertebrate composition tends to shift from larger taxa (i.e., Ephemeroptera, Plecoptera, Trichoptera [EPT]) to smaller taxa such as Diptera in areas impacted by *D. geminata* (Gillis and Chalifour 2009; Kilroy et al. 2009; James et al. 2010b). Total invertebrate abundance tends to increase in areas where *D. geminata* is present (Gillis and Chalifour 2009;Kilroy et al. 2009). *D. geminata* was first documented in the Black Hills of South Dakota in 2002 and became established concurrent with drought conditions (2000-2008). Shortly after the appearance of *D. geminata* in Rapid Creek, large biomass declines (>50%) of the naturalized brown trout *Salmo trutta* population in Rapid Creek were observed. It was unclear if drought conditions or the presence of *D. geminata* were responsible for brown trout biomass declines. Here, we evaluate the influence of water resources and *D. geminata* on (1) declines in brown trout biomass, (2) alteration of food resources, and (3) diet of brown trout in Black Hills streams.

METHODS

The various components of our research were conducted within four stream reaches in South Dakota's Black Hills: Spearfish Creek, an unregulated stream that flows through Spearfish Canyon (*D. geminata* absent), upper Rapid Creek (tailwater reach below Pactola Reservoir; *D. geminata* present), lower Rapid Creek (in Rapid City below Canyon Lake; *D. geminata* absent), and Castle Creek (tailwater reach below Deerfield Reservoir; *D. geminata* absent; Figure 1). For a detailed description of the Rapid and Spearfish Creek study reaches, see James et al. (2010a, b).

We estimated *D. geminata* biovolume (when stream flows permitted) once per month from March through September (high April discharge prohibited field sampling) in each study section from 2007-2009 using an approach modified from Hayes et al. (2006) and Kilroy et al. (2006). For each of one hundred randomly selected rocks from a standard riffle at each sampling site, percent coverage of *D. geminata* was visually estimated and the thickness of the *D. geminata* mat was measured (mm). Thickness was assigned a score from 0 to 5 based on the following: 0; 1 (< 1 mm thick); 2, (1-5 mm); 3, (6-15 mm); 4 (16-30 mm); 5, (> 30 mm). The percent coverage of *D. geminata* was multiplied by the thickness score to provide a *D. geminata* biovolume index (DBI), which ranged from 0 to 500.

We examined water resources from 2000 to 2007. Since 2000, annual precipitation in the Black Hills region has generally been below average, leading to an extended drought period that lasted until fall 2008. To characterize periods of relatively higher and lower water availability from 2000-2007, we evaluated mean monthly stream discharge and mean monthly summer (June-August) stream temperature from two time periods, early-drought (2000-2002) and late-drought (2005-2007) using a paired t-test ($\alpha \leq 0.05$) to verify that mean monthly discharge was indeed lower during the late-drought than the early-drought period (see James et al. 2010a).

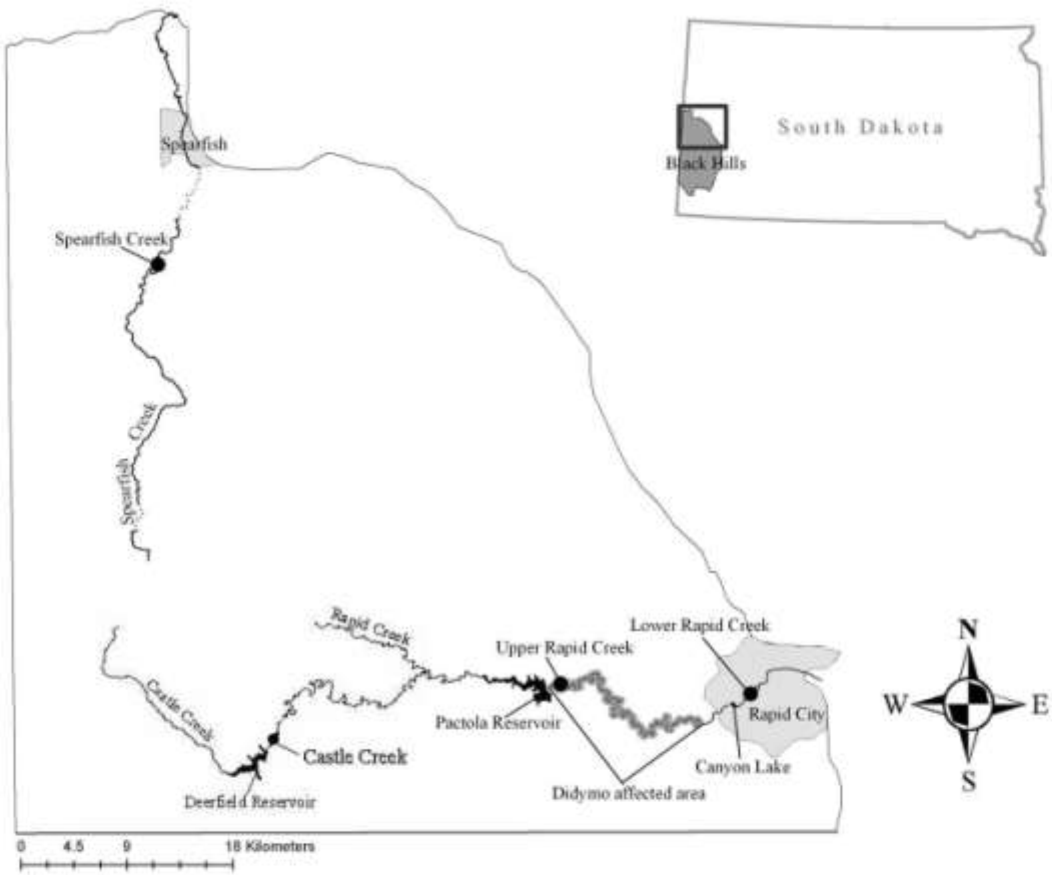

Figure 1. Locations of the Spearfish Creek, lower Rapid Creek, upper Rapid Creek, and Castle Creek study reaches in the Black Hills, South Dakota. The current *D. geminata* distribution in Rapid Creek is indicated by dark shading.

Next, we analyzed brown trout biomass and size structure in our study reaches. Brown trout were sampled by multiple-pass depletion backpack electrofishing surveys in the fall (late-August through September) in 2000-2002 and 2005-2007 at standardized locations from Rapid and Spearfish creeks. Population and biomass estimates were calculated for each year sampled in each stream. Brown trout in this study were assigned to one of two size categories. Fish ≤ 199 mm TL were considered juveniles and fish ≥ 200 mm TL were considered adults. Relative weight was calculated by dividing the weight of each brown trout by its length-specific standard weight (Anderson and Neumann 1996). We used a repeated measures analysis of variance (RMANOVA) to test for differences in mean juvenile and adult biomass between early- and late-drought time periods (PROC MIXED, SAS 9.1). Similarly, we used a RMANOVA to compare size structure (i.e., ratio of juvenile to adults) of brown trout between the early- and late-drought time periods in each stream reach (α ≤ 0.05) (Neumann and Allen 2007; see James et al. 2010a).

To examine the abundance and composition of macroinvertebrates in Rapid Creek, we selected four sites to sample – two in areas with high relative abundance of *D. geminata* and two with low relative abundance. At each of the four sites, benthic invertebrates were collected using a D-frame dip net, a Surber sampler, and drift nets. Invertebrate sampling was conducted in September and October 2006. Invertebrates were identified to Order. We tested for differences among the four sites using multivariate analysis of variance (MANOVA; SAS 9.1 SAS Institute 2007). We also calculated the proportion of EPT for each sampling gear at each site. Similarly, the proportion of dipterans was calculated. We tested for differences among sites for EPT and Diptera using analysis of variance (see James et al. 2010b).

Finally, we sampled diets of brown trout from Spearfish, Rapid, and Castle creeks using gastric lavage monthly from June through August 2008 - 2009. From each sampling occurrence we collected up to 10 brown trout in three size categories (100-199, 200-299, and >300 mm TL). Stomach contents were preserved in ethanol, enumerated, identified to Order, and weighed (dry weighting) to quantify biomass. We compared gut contents of brown trout among streams using mean percent composition by weight (MWi; Chipps and Garvey 2007) of the most common invertebrate orders using analysis of variance (ANOVA; data were $\arcsin\sqrt{p}$ transformed prior to analysis). Alpha was set at ≤ 0.05 and a Bonferroni correction was used; a Tukey test was used to evaluate differences among streams. We also calculated a gut fullness index by dividing the weight of the prey in the stomach by the weight of the fish and used analysis of covariance (ANCOVA) with length as a covariate (α ≤ 0.05). Finally, we conducted a weight-at-length (condition) analysis (using ANCOVA with fish length as a covariate to control for effects of differing size ranges; data were log transformed prior to analysis; α ≤ 0.05; Pope and Kruse 2007).

RESULTS

The Spearfish and Rapid creeks study sections had significantly lower mean monthly discharges during the late-drought compared to the early-drought (Spearfish Creek, $t_{11} = 4.42$, $P = 0.001$; lower Rapid Creek, $t_{11} = 6.24$, $P < 0.0001$; upper Rapid Creek, $t_{11} = 4.02$, $P = 0.002$; Table 1). In contrast to stream discharge, mean summer stream temperature did not differ significantly between the early- and late-drought time periods in each study reach (Spearfish Creek, $t_2 = 0.86$, $P = 0.48$; lower Rapid Creek, $t_2 = 0.21$, $P = 0.85$; upper Rapid Creek, $t_2 = 0.03$, $P = 0.97$; Table 1; see James et al. 2010a).

Mean *D. geminata* biovolume in upper Rapid Creek was variable from March to September during 2007-2009 (Figure 2). April values were not obtained due to high stream discharge. Mean DBI was 57.6 (SE = 6.8), and mean substrate coverage percentage was 24.2 (SE = 3.0). Visible *D. geminata* was absent from the Castle and Spearfish creeks.

Mean biomass for adult brown trout in all three stream sections was significantly lower in the late-drought than the early-drought (Spearfish Creek, $P = 0.02$; lower Rapid Creek, $P = 0.01$; upper Rapid Creek, $P = 0.01$; Table 1). For juvenile brown trout in lower Rapid Creek, mean biomass was significantly lower during the late-drought time period ($P = 0.01$; Table 1). In Spearfish Creek, juvenile biomass was not significantly different between time periods ($P = 0.14$). Juvenile biomass in upper Rapid Creek was also not significantly different ($P = 0.08$; Table 1), but in contrast to the other two study reaches, juvenile brown trout biomass increased in upper Rapid Creek (see James et al. 2010a).

Table 1. Mean summer (June – August) stream temperature (^oC), mean annual monthly discharge ($m^3 \cdot s^{-1}$), and mean biomass (kg/ha) of brown trout in Spearfish Creek, upper Rapid Creek, and lower Rapid Creek during early- (2000-2002) and late-drought (2005-2007) time periods in the Black Hills, South Dakota. Values in parentheses represent 1 S.E. Adapted from James et al. (2010a).

	Temperature		**Discharge**		**Adult Biomass**		**Juvenile Biomass**	
Stream	Early	Late	Early	Late	Early	Late	Early	Late
Spearfish	12.4 (0.5)	11.5 (0.5)	1.95 (0.08)	1.50 (0.14)	238 (24)	69 (29)	43 (7)	23 (8)
Upper Rapid	9.8 (1.2)	9.8 (0.6)	1.41 (0.15)	0.84 (0.17)	159 (17)	32 (17)	14 (18)	73 (18)
Lower Rapid	19.2 (0.8)	19.3 (0.2)	2.01 (0.19)	0.94 (0.11)	272 (27)	91 (27)	136 (13)	45 (13)

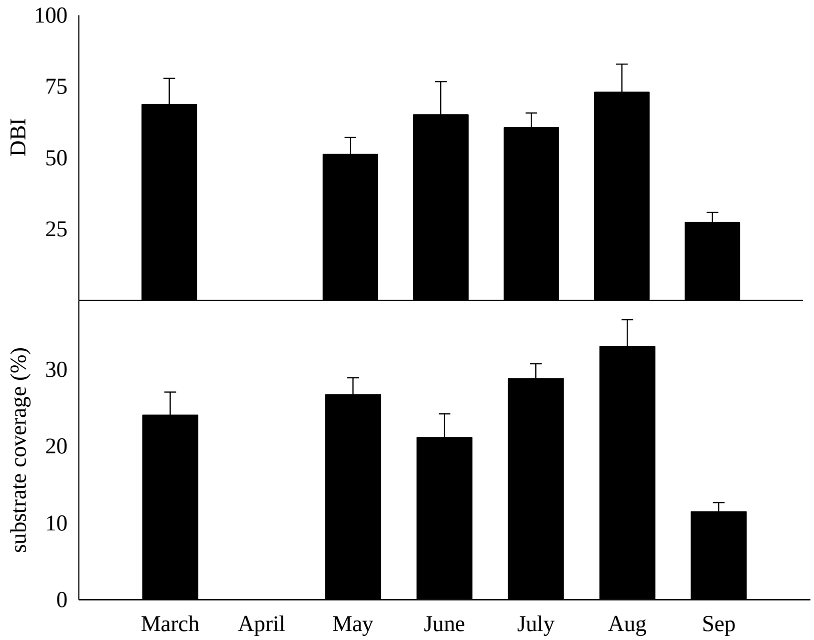

Figure 2. Three-year monthly mean *D. geminata* biovolume index (DBI) and percent substrate coverage in Rapid Creek from March through September 2007-2009. Bars represent 1 SE. No data were available for April.

Representatives were collected from several orders of insects, but because EPT and Diptera represented 72 to 94% of the insects collected at each site, we focused our analysis on those four orders. Invertebrate abundance varied significantly among locations for each of the gear types used (MANOVA: dip nets, $F_{12, 35} = 2.05$, $P = 0.04$; Surber, $F_{12, 13} = 4.32$, $P = 0.006$; drift nets, $F_{12, 34} = 4.25$, $P = 0.004$). For each gear type used, Diptera abundance varied significantly among locations and was generally higher at locations with *D. geminata*. The proportion of EPT varied among locations and was generally higher at sampling locations without *D. geminata*. In contrast, the percentage of Diptera was higher at sites with *D. geminata* as indexed by Surber samples ($F_{3, 17} = 14.2$, $P < 0.0001$) and drift nets ($F_{3, 8} = 14.46$, $P = 0.0014$; see James et al. 2010b).

We analyzed the gut contents of 316 brown trout collected from Castle, Spearfish and Rapid creeks from June through August in 2008 and 2009. Prey items (n = 20,615) representing 19 Orders were used in the analyses. The most common prey items encountered in stomach samples were from the Orders Ephemeroptera, Plecoptera, Trichoptera, Diptera, and Amphipoda. All other prey items were combined and referred to as other. We observed significant differences in mean percentage composition by weight (MWi) throughout the study period (Table 2). The Ephemeroptera, Diptera, Amphipoda, and other Orders had significant differences in the summer time period (Table 2). Analysis of gut fullness (g prey/g of predator) revealed that brown trout from Rapid and Castle creeks had more prey biomass in their stomach compared with brown trout from Spearfish Creek ($F_{3, 306} = 4.18$, $P = 0.0161$; Figure 3). The interaction term ($F_{5, 304} = 1.76$; $P = 0.1733$) indicated that fish had similar trends in gut fullness relative to length in all three study streams. Relative weights of brown trout were highest in Rapid Creek, followed by brown trout in Castle and Spearfish creeks ($F_{3, 315} = 20.58$; $P < 0.0001$). The interaction term (F 2, 313 = 0.70; $P = 0.4990$) indicated that fish from each stream had similar trends in weight relative to length. Relative weights were generally higher in Rapid Creek compared to the other two study sections (Figure 3).

Table 2. Mean percent composition by dry weight (MWi; g) and standard error of gut contents from brown trout in Rapid, Castle, and Spearfish creeks, South Dakota. Results of ANOVA analyses. The summer period represents pooled data from June to August 2008-2009. Values with the same letters are not significantly different (*P* > 0.0083).

		Stream							
	Time	Castle		Rapid		Spearfish			
Order	Period	MWi	SE	MWi	SE	MWi	SE	F	P
Ephemeroptera	summer	0.443 [a]	0.03	0.263 [b]	0.04	0.546 [a]	0.06	11.35	< 0.0001
Plecoptera	summer	0.055	0.01	0.049	0.01	0.033	0.01	0.54	0.5862
Trichoptera	summer	0.406	0.03	0.300	0.03	0.326	0.05	2.80	0.0624
Diptera	summer	0.238 [a]	0.02	0.461 [b]	0.05	0.448 [b]	0.04	13.55	< 0.0001
Amphipoda	summer	0.450 [a]	0.04	0.490 [a]	0.05	0.035 [b]	0.02	24.13	< 0.0001
Other	summer	0.234 [a]	0.03	0.160 [a]	0.03	0.394 [b]	0.06	9.78	< 0.0001

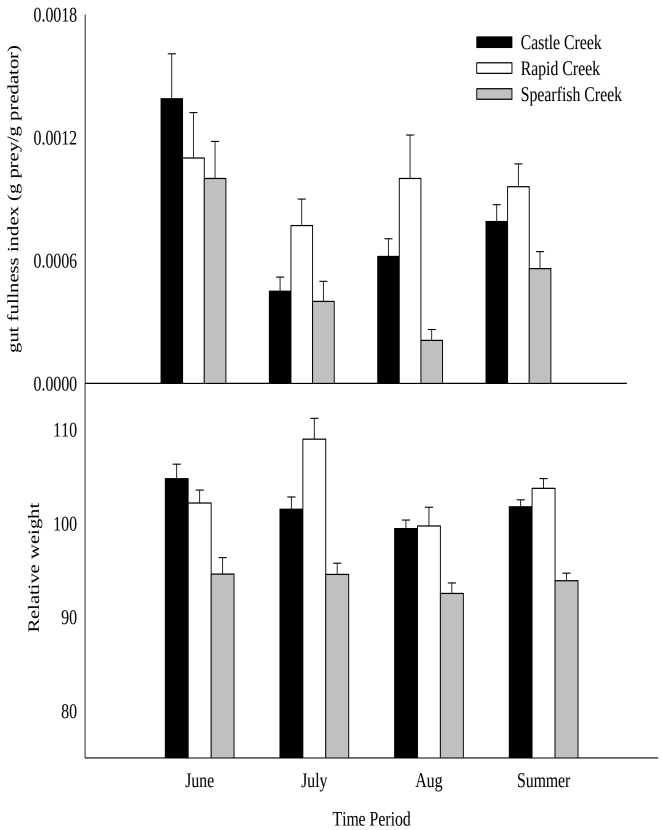

Figure 3. Mean gut fullness index (g prey / g predator) and mean relative weight of brown trout from Castle, Rapid, and Spearfish creeks, South Dakota. The summer period represents pooled data from June-August 2008-2009. Bars represent SE.

Discussion

Since the establishment of *D. geminata* in Rapid Creek, the naturalized brown trout population has experienced a large (> 50%) biomass decline. Initially, declines in biomass were attributed to *D. geminata* due to an incomplete understanding of the diatom and its interactions with fish. We determined that drought conditions were largely responsible for overall trout biomass decreases, regardless of the presence of *D. geminata* (James et al. 2010a). However, comparison of brown trout size-structure between the early-drought (pre-*D. geminata*) and late-drought (post-*D. geminata*) periods revealed that juvenile brown trout abundance increased while adult abundance decreased in Rapid Creek (James et al. 2010a). Reasons for these size-structure differences were unknown, but changes in food resources in *D. geminata*-impacted Rapid Creek were suspected.

Changes in invertebrate abundance and composition have been documented in recent studies. Invertebrate composition tends to shift from larger taxa (i.e., EPT) to smaller taxa such as Diptera in areas impacted by *D. geminata*, while total invertebrate abundance also generally increases (Larson 2007; Gillis and Chalifour 2009; Kilroy et al. 2009; James et al. 2010b). A higher abundance of dipterans and lower percentage of EPT taxa were present in *D. geminata*-impacted areas of Rapid Creek compared with non-impacted areas (James et al. 2010b). An increase in numbers of smaller invertebrate Diptera taxa (e.g., Chironomidae) and a decrease in number of larger, energy-rich EPT taxa could explain increased numbers of juvenile brown trout in Rapid Creek (i.e., increased size-specific food abundance). Food resources for juvenile brown trout were abundant while these same food resources could be limiting for adult brown trout growth and survival.

Examination of brown trout gut contents from upper Rapid, Castle, and Spearfish creeks, showed a lower composition of ephemeropterans in brown trout from Rapid Creek (*D. geminata* present; Table 2). Composition of plecopterans and trichopterans was not different in Rapid Creek compared with Castle and Spearfish creeks (*D. geminata* absent). Brown trout in Rapid Creek consumed a high composition of dipterans as well (Table 2). These findings were consistent for both juvenile and adult brown trout, which supported our hypothesis that changes in invertebrate composition may have influenced decreases in adult biomass. However, after analysis of gut fullness index, we observed that brown trout from Rapid Creek consumed more prey overall than brown trout in Castle or Spearfish creeks (Figure 3). Moreover, relative weight of brown trout from Rapid Creek was generally high (>100), implying that food availability was not limiting. Although brown trout in *D. geminata* affected Rapid Creek consumed fewer ephemeropterans and a high amount of lower energy-density prey items (i.e., dipterans) compared to the non-impacted streams, the brown trout also consumed a high amount of energy-rich Amphipods. Despite differences in prey consumption among *D. geminata* affected and unaffected streams, brown trout in Rapid Creek (*D. geminata* affected) were able to consume enough prey such that food resources, although altered, were not limiting.

Our findings imply that despite changes in invertebrate composition, *D. geminata* (at relatively low levels; approximately 25% substrate coverage, < 5mm thick) did not negatively impact gut fullness or condition of brown trout in Rapid Creek. Further research is necessary to determine if *D. geminata* negatively affects trout prey consumption in higher levels of *D. geminata* coverage and biovolume. Furthermore, more research is necessary to determine the mechanisms affecting size-structure differences in Rapid Creek.

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