

Influence of Drought Conditions on Brown Trout Biomass and Size Structure in the Black Hills, South Dakota

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Abstract.—We evaluated the influence of drought conditions on the biomass of brown trout *Salmo trutta* in Spearfish Creek, upper Rapid Creek, and lower Rapid Creek in the Black Hills of western South Dakota. Stream discharge, mean summer water temperature, the biomass of juvenile and adult brown trout, and brown trout size structure were compared between two time periods: early (2000–2002) and late drought (2005–2007). Mean summer water temperatures were similar between the early- and late-drought periods in Spearfish Creek (12.4°C versus 11.5°C), lower Rapid Creek (19.2°C versus 19.3°C), and upper Rapid Creek (9.8°C in both periods). In contrast, mean annual discharge differed significantly between the two time periods in Spearfish Creek (1.95 versus 1.50 m³/s), lower Rapid Creek (2.01 versus 0.94 m³/s), and upper Rapid Creek (1.41 versus 0.84 m³/s). The mean biomass of adult brown trout in all three stream sections was significantly higher in the early-drought than in the late-drought period (238 versus 69 kg/ha in Spearfish Creek, 272 versus 91 kg/ha in lower Rapid Creek, and 159 versus 32 kg/ha in upper Rapid Creek). The biomass of juvenile brown trout was similar (43 versus 23 kg/ha) in Spearfish Creek in the two periods, declined from 136 to 45 kg/ha in lower Rapid Creek, and increased from 14 to 73 kg/ha in upper Rapid Creek. Size structure did not differ between the early- and late-drought periods in lower Rapid and Spearfish creeks, but it did in upper Rapid Creek. In addition to drought conditions, factors such as angler harvest, fish movements, and the nuisance algal species *Didymosphenia geminata* are discussed as possible contributors to the observed changes in brown trout biomass and size structure in Black Hills streams.

Habitat availability has an important influence on the production of brown trout *Salmo trutta* in montane streams (Bowlby and Roff 1986; Jager et al. 1999; Stoneman and Jones 2000; Lobón-Cerviá 2007). Although changes in stream habitat are often linked to anthropogenic effects (Chapman and Knudsen 1980), they can also occur as a result of environmental variation. Drought conditions, for example, can lead to reduced habitat volume and increased stream temperatures that negatively affect trout production. During drought periods (e.g., low-discharge conditions), the amount of pool habitat can limit the carrying capacity for adult fish (Elliot 1987; Hakala and Hartman 2004). Elliot (2000) found that temperature increased and oxygen decreased as pool size decreased during drought conditions. Additionally, brown trout were

absent from pools during drought years but present in the same pools during nondrought years (Elliot 2000).

The survival of brown trout can be affected by drought conditions. In two English streams, survival decreased during summer droughts, much more so for age-2 fish than for age-1 fish (Elliot 1987). The density of adult brook trout *Salvelinus fontinalis* in northern Appalachian streams declined 60% during a severe drought in 1999, while that of age-1 brook trout declined 67% (Hakala and Hartman 2004). Hakala and Hartman (2004) also found that habitat availability and quality were significantly lower during the drought.

In the Black Hills of western South Dakota, drought conditions have had an appreciable influence on water resources from 2000 to 2007 (USGS 2008). During this period, water discharge was reduced in many streams that support naturalized brown trout populations. During the latter part of the drought, annual census surveys revealed appreciable (>50%) declines in the biomass of adult brown trout (>20 cm total length [TL]) in Rapid Creek, causing concern for anglers and

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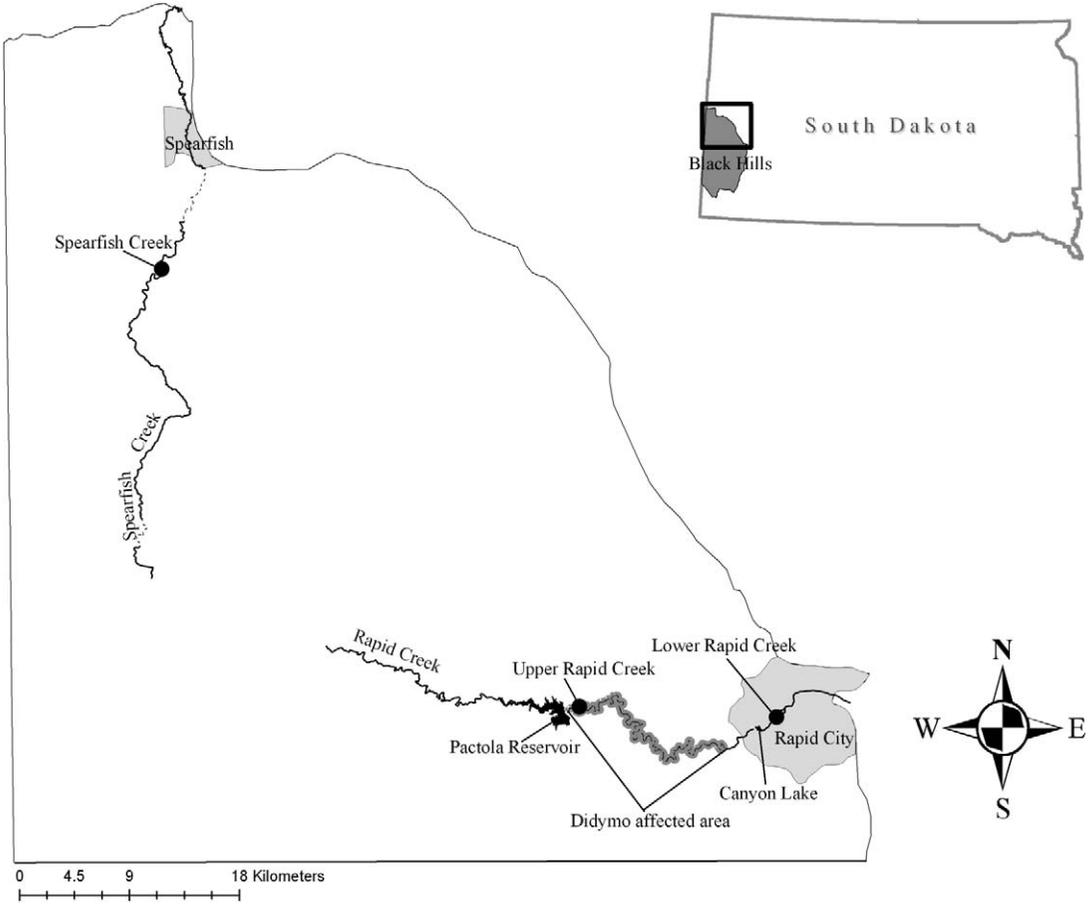


FIGURE 1.—Locations of the Spearfish Creek, lower Rapid Creek, and upper Rapid Creek study reaches in the Black Hills.

biologists. Furthermore, a section of Rapid Creek has received extra attention from anglers and biologists because *Didymosphenia geminata*, a nuisance diatom species, became established concurrent with drought conditions in 2002.

In this study, we evaluate the temporal patterns in stream discharge and mean summer water temperature over a period of 8 years at two drought-affected streams in the Black Hills. We then compare the patterns in brown trout biomass and size structure across two time periods (early [2000–2002] and late drought [2005–2007]) in stream reaches with and without *D. geminata*. We discuss the implications of drought and the establishment of *D. geminata* on brown trout populations in the Black Hills.

Methods

Study sites.—We studied three stream reaches in South Dakota’s Black Hills: Spearfish Creek, upper Rapid Creek, and lower Rapid Creek (Figure 1).

Spearfish Creek is an unregulated stream located in the northern Black Hills that drains approximately 360 km² (USGS 2008). The mean annual discharge near Spearfish, South Dakota, was about 1.6 m³/s from 1947 to 2007 (USGS 2008) and was maintained through precipitation and springs. The mean width of Spearfish Creek in the study section (44.40158N, 103.89472W) was approximately 9 m. In addition to naturalized brown trout, naturalized rainbow trout *Oncorhynchus mykiss* were present in this section of the creek. The Rapid Creek drainage covers approximately 1,062 km² (USGS 2008) and includes upper and lower Rapid Creek. The upper Rapid Creek study section is located immediately below the dam at Pactola Reservoir (44.07617N, 103.48445W), which regulates its flow. The mean annual flow below Pactola Dam was about 1.47 m³/s from 1964 to 2007 (USGS 2008), and the mean width in this reach was approximately 11 m. Naturalized brown trout, brook trout, and limited numbers of hatchery rainbow trout

were present in this section of Rapid Creek. The lower Rapid Creek section (44.06371N, 103.27665W) is located within the city limits of Rapid City, South Dakota. The mean annual discharge was 1.87 m³/s from 1964 to 2007 (USGS 2008). The mean stream width was approximately 10 m. White suckers *Catostomus commersonii* were present in this section of Rapid Creek, in addition to naturalized brown trout. On rare occasions, largemouth bass *Micropterus salmoides*, rock bass *Ambloplites rupestris*, green sunfish *Lepomis cyanellus*, mountain suckers *C. platyrhynchus*, and longnose dace *Rhinichthys cataractae* were also found (J. Wilhite, South Dakota Game, Fish and Parks, personal observation).

Stream discharge and water temperature.—Like other areas of the northern Great Plains, the Black Hills experience cyclical climate patterns characterized by extended wet and dry periods (Rosenberry 2003). Several consecutive years of high precipitation during the mid-1990s resulted in dramatic increases in water availability in many of the glacial lakes, wetlands, and streams in South Dakota that peaked in the late 1990s (Selch et al. 2007). Since 2000, annual precipitation in the Black Hills region has generally been below average, leading to an extended drought that lasted until autumn 2008. To characterize the periods of relatively high and low water availability from 2000 to 2007, we evaluated data from two time periods: early drought (2000–2002) and late drought (2005–2007). Mean monthly stream discharge data for Rapid and Spearfish creeks were obtained from U.S. Geological Survey gauging stations (USGS 2008) and used to calculate the mean monthly discharge (m³/s) for each year ($n = 3$) in each time period. For each stream reach, we then compared the mean monthly discharge between the early- ($n = 12$) and late-drought periods ($n = 12$) using a paired t -test ($\alpha \leq 0.05$) to verify that the mean monthly discharge was indeed lower during the late-drought period. Similarly, mean monthly summer (June–August) water temperature data were obtained from the U.S. Geological Survey (USGS 2008) and used to compare the early- and late-drought periods for each study reach.

Brown trout biomass and size distribution.—Brown trout were sampled by backpack electrofishing (Smith-Root LR-24) in the fall (late-August through September) of each year at standardized locations in each study reach. Block nets were deployed at the upstream and downstream ends of a 100-m site to prevent fish from entering or leaving the site during electrofishing. The total lengths (mm) and weights (g) of all of the brown trout caught during these surveys were recorded. Mean stream widths were obtained at each site to estimate the surface area. Three-pass depletion surveys

were conducted, and a maximum-likelihood method was used to estimate the number of brown trout at each site (Hayes et al. 2007). Biomass (kg/ha) estimates were based on the population estimates, the weights of all brown trout sampled from each site (the actual weights of fish that were captured and estimated weights of those not captured), and stream surface area measurements. The Spearfish Creek estimates were derived from sampling at one site every year except 2005. The lower Rapid Creek estimates were calculated from sampling at two sites each year, and the upper Rapid Creek estimates from sampling at three sites each year.

The brown trout in this study were assigned to one of two size categories; fish 199 mm TL or less were classified as juveniles and fish 200 mm or more were classified as adults. Two hundred millimeters is considered the minimum harvestable size by anglers in the Black Hills, and brown trout are typically able to reproduce after reaching this size (South Dakota Game, Fish, and Parks, unpublished data). Biomass was calculated separately for each size-group.

We used a repeated-measures analysis of variance (RMANOVA) to test for differences in mean juvenile and adult biomass between the early- and late-drought periods (PROC MIXED, SAS 9.1; SAS Institute, Cary, North Carolina). Years were nested within the grouping factors (i.e., time periods) to account for the annual variation within stream reaches. Similarly, we used a RMANOVA to compare the size structure of brown trout between the early- and late-drought periods in each stream reach (Neumann and Allen 2007). In this analysis, we tested the hypothesis that the ratio of juvenile to adult brown trout was not different during the two periods. Statistical analyses were performed in SAS 9.1.

Results

All three study sections had significantly lower mean monthly discharge during the late-drought period (Spearfish Creek: $t = 4.42$, $df = 11$, $P = 0.001$; lower Rapid Creek: $t = 6.24$, $df = 11$, $P < 0.0001$; upper Rapid Creek: $t = 4.02$, $df = 11$, $P = 0.002$; Table 1; Figure 2). In contrast, the mean summer stream temperature did not differ significantly between the early- and late-drought periods in any study reach (Spearfish Creek: $t = 0.86$, $df = 2$, $P = 0.48$; lower Rapid Creek: $t = 0.21$, $df = 2$, $P = 0.85$; upper Rapid Creek: $t = 0.03$, $df = 2$, $P = 0.97$; Table 1).

Population estimates for each site and year are reported in Table 2. The mean biomass of adult brown trout was significantly lower in the late-drought period in all three stream sections (Spearfish Creek: $P = 0.02$;

TABLE 1.—Mean summer (June–August) stream temperature, mean annual monthly discharge, mean biomass, and mean adult relative weight (W_r)^a of brown trout in Spearfish Creek, upper Rapid Creek, and lower Rapid Creek during the early- (2000–2002) and late-drought (2005–2007) periods in the Black Hills; SEs are in parentheses.

Stream	Temperature (°C)		Discharge (m ³ /s)		Biomass (kg/ha)				Adult W_r	
					Adult		Juvenile			
	Early	Late	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)	94.3 (0.3)	94.0 (0.4)
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)	93.8 (0.5)	110.9 (2.7)
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)	88.5 (0.4)	97.5 (1.1)

^a Relative weight is an index of condition calculated by dividing the weight of a fish by a length-specific standard weight for that species (Anderson and Neumann 1996).

lower Rapid Creek: $P = 0.01$; upper Rapid Creek: $P = 0.01$; Table 1; Figure 3). For juvenile brown trout in lower Rapid Creek, the mean biomass was significantly lower during the late-drought period ($P = 0.01$; Table 1; Figure 3). In Spearfish and upper Rapid creeks, juvenile biomass was not significantly different between time periods ($P = 0.14$ and 0.08 , respectively; Table 1; Figure 3). However, unlike in the other two study reaches, in upper Rapid Creek the biomass of juvenile brown trout generally increased (Figure 3).

Despite the changes in biomass, the ratio of juvenile to adult fish was similar in two of the three study reaches—lower Rapid Creek ($P = 0.09$) and Spearfish Creek ($P = 0.35$)—during the early- and late-drought periods (Figure 4). However, we observed an increase in the ratio in upper Rapid Creek ($P = 0.0012$).

Discussion

The influence of drought on fish standing stocks has been well documented in a number of studies (Elliot 1987, 2000; Hakala and Hartman 2004). In line with those studies, we observed appreciable declines in the biomass of adult brown trout in our three stream sections from 2000 to 2007. Stream discharge was lower for all three sections during the latter half of the study period, suggesting that lower water availability contributed to the decline in biomass.

The negative effects of the drought were similar for all of the salmonids in our study sections. In lower Rapid Creek, brown trout represented more than 99% of salmonid species during both time periods, so comparisons with other salmonids were not possible in this reach. In Spearfish Creek, the proportions of adult brown trout and rainbow trout were similar in the early- (brown trout, 68%; rainbow trout, 32%) and late-drought periods (70%; 30%), indicating that the drought affected both species similarly. In upper Rapid Creek, adult brown trout represented 77% of the salmonids during the early-drought period (rainbow trout, 18%; brook trout, 5%), compared with 56% (30%; 14%) in the late-drought period. It was difficult to make comparisons in this reach because rainbow trout stocking occurred in the late-drought period.

Drought affects the organisms in flowing water in numerous ways. These include reducing habitat availability and altering food resources, which can lead to emigration from drought-impacted areas (Magoulick and Kobza 2003) or the alteration of fish densities and size- or age-structures (Lake 2003). Mean stream depth, for example, has been shown to be important in determining the carrying capacity of a habitat for stream fishes (Lobón-Cerviá 2007). Pool habitat is important for lotic brown trout. Generally speaking, as discharge decreases stream margins become dewatered and pool habitat is reduced in some streams. In a study in southern Ontario streams, Bowlby and Roff (1986) found higher trout biomass

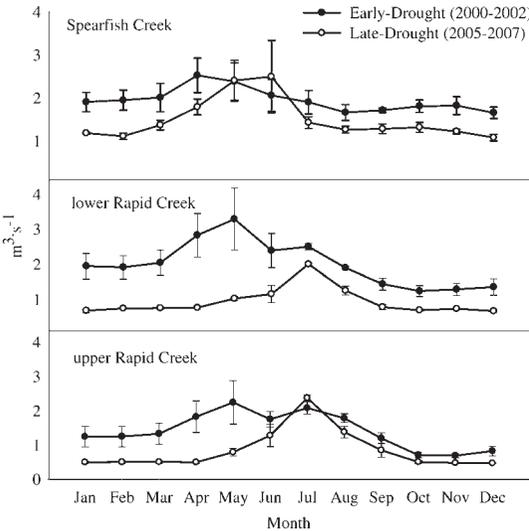


FIGURE 2.—Mean monthly discharge (m³/s) in Spearfish Creek, lower Rapid Creek, and upper Rapid Creek during the early- and late-drought periods; the error bars denote SEs.

TABLE 2.—Population estimates (number/100 m [95% confidence intervals in parentheses]) for juvenile (J) and adult (A) brown trout sampled in upper Rapid Creek, lower Rapid Creek, and Spearfish Creek in 2000–2002 and 2005–2007.

Year	Site	Age	Upper Rapid Creek	Lower Rapid Creek	Spearfish Creek ^a
2000	1	J	21 (16–36)	216 (214, 220)	162 (140, 184)
		A	37 (36–40)	185 (185, 186)	114 (105, 125)
	2	J	42 (42–43)	694 (623, 765)	
		A	35 (34–39)	198 (181, 215)	
	3	J	107 (82–137)		
		A	89 (89–91)		
2001	1	J	53 (28–121)	141 (139, 145)	78 (72, 87)
		A	58 (58–58)	201 (200, 204)	127 (126, 130)
	2	J	81 (72–93)	223 (186, 260)	
		A	53 (53–55)	143 (142, 146)	
	3	J	222 (110–383)		
		A	62 (62–63)		
2002	1	J	31 (25–41)	306 (293, 319)	142 (90, 209)
		A	38 (38–39)	140 (139, 143)	107 (104, 112)
	2	J	68 (48–101)	370 (357, 383)	
		A	28 (28–28)	64 (64, 64)	
	3	J	84 (71–101)		
		A	37 (36–40)		
2005	1	J	597 (478–716)	222 (221, 224)	
		A	2 (2–3)	30 (29, 33)	
	2	J	237 (168–306)	475 (424, 526)	
		A	17 (17–18)	51 (51, 52)	
	3	J	437 (336–538)		
		A	5 (5–5)		
2006	1	J	678 (520–836)	169 (159, 179)	54 (54, 56)
		A	3 (3–5)	36 (34, 41)	34 (34, 35)
	2	J	215 (179–251)	438 (412, 464)	
		A	7 (7–7)	8 (8, 8)	
	3	J	304 (270–338)		
		A	4 (4–4)		
2007	1	J	417 (391–443)	249 (217, 281)	78 (69, 90)
		A	4 (4–4)	41 (41, 42)	35 (35, 36)
	2	J	147 (146–150)	380 (337, 423)	
		A	8 (8–10)	9 (9, 10)	
	3	J	308 (221–395)		
		A	6 (6–7)		

^a No data available for 2005.

in areas with more pools. Similarly, the availability of pool habitat has been shown to have a predictable effect on trout biomass in southern Ontario streams (Stoneman and Jones 2000). Although we did not quantify habitat availability in our study, we postulate that it decreased as drought conditions persisted and was linked to the reductions in trout biomass.

Because summer stream temperatures were similar throughout the study period, water temperature probably had little effect on biomass. There are several possible reasons why water temperatures did not rise in any of our study sections during the late-drought period. First, the mean summer air temperature near our study sites did not change appreciably between the two periods (21.9°C [SE = 1.6] versus 23.0°C [1.5]; National Oceanic and Atmospheric Administration <http://www.noaa.gov/>). In addition, factors specific to each stream section probably acted to limit temperature increases. Spearfish Creek is located at the bottom of a steep-walled canyon and has dense canopy cover in many areas. The water in upper Rapid Creek originates

from hypolimnetic releases from Pactola Reservoir (>30 m deep), so its temperature is similar year-round. And in lower Rapid Creek, Canyon Lake tends to stabilize the water temperature owing to the residence time of water in the reservoir.

Our results show that size structure did not change in lower Rapid and Spearfish creeks but that the ratio of juvenile to adult brown trout increased in upper Rapid Creek. Because the ratios in lower Rapid and Spearfish creeks did not change (even though total standing stock declined), it appears that recruitment to both the juvenile and adult size-classes remained relatively constant between time periods in these two stream sections. By contrast, the recruitment of juvenile brown trout in upper Rapid Creek increased while that to adult sizes was nearly zero at times during the late-drought period (Figure 4). During that period, the mean biomass of juvenile brown trout was noticeably higher in upper Rapid Creek (73 kg/ha, or more than five times as great as that in the early-drought period [14 kg/ha]). It is possible that the low, stable discharges

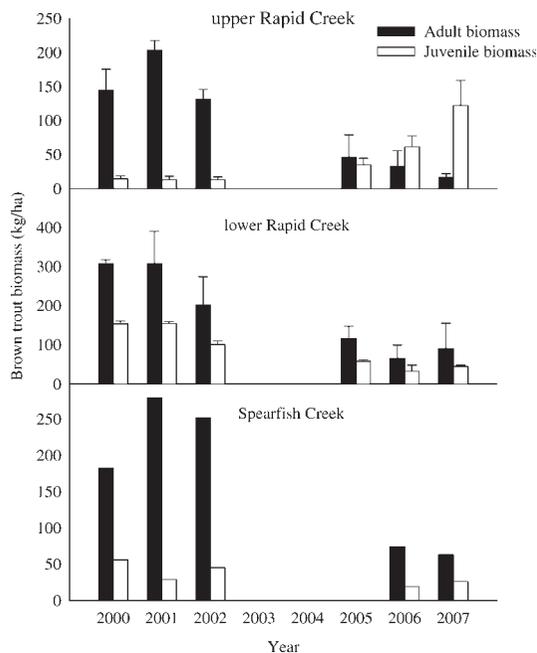


FIGURE 3.—Mean annual biomass (error bars denote SEs) of juvenile and adult brown trout in lower Rapid Creek and upper Rapid Creek and annual biomass of juvenile and adult brown trout in Spearfish Creek, 2000–2007.

during the latter part of the drought created a higher amount of juvenile habitat and thus contributed to higher reproductive success in upper Rapid Creek. Meanwhile, adult habitat (i.e., pools) could have decreased during the late-drought period, which would have negatively impacted older size- and age-classes (Bowlby and Roff 1986; Stoneman and Jones 2000; Lobón-Cerviá 2007).

While these factors could be responsible for the size structure and biomass differences in upper Rapid Creek during the late-drought period, another possible factor is the presence of *D. geminata*, which only occurs in the upper Rapid Creek study reach. The recent spread and establishment of nuisance *D. geminata* blooms has prompted much concern in North America and New Zealand (Kilroy 2004; Branson 2006; Spaulding and Elwell 2007). Recent studies have shown that the invertebrate composition shifts from larger taxa (i.e., Ephemeroptera, Plecoptera, and Trichoptera) to smaller taxa such as Diptera in areas impacted by *D. geminata* (Shelby 2006; Larson 2007; Shearer et al. 2007; Kilroy et al. 2009; Gillis and Chalifour 2010). Moreover, the total invertebrate abundance generally increases in areas where *D. geminata* is present (Kilroy et al. 2009; Gillis and Chalifour 2010). An increase in the number of smaller invertebrate taxa (i.e., in the abundance of

food) could explain the higher number of juvenile brown trout in Rapid Creek. Studies conducted by Shearer et al. (2007) suggest that the growth of brown trout would not be negatively affected by *D. geminata*, even though taxonomic differences and changes in the size structure of invertebrates were observed at sites at which it was present. We observed a marked increase in the relative weight of the brown trout in upper Rapid Creek (Table 1), which could be explained by density-dependent factors, increased invertebrate abundance (associated with *D. geminata*), or both.

It is unlikely that the changes in the fish distributions associated with the early- and late-drought periods are related to the movements of brown trout. A telemetry study of brown trout in Rapid Creek showed that they exhibit limited movement except during spawning (James et al. 2007). In a year-long tracking study in 2000 and 2001, they were relocated an average of 49 m from their original tagging locations; although they moved up to 1,100 m during the spawning period in October and early November, they subsequently returned to their prespawning locations (James et al. 2007). Although movement is possible in Spearfish Creek because the stream is unimpeded by physical barriers (dams and waterfalls), movement is more limited in Rapid Creek—upstream migration is blocked by Pactola Dam, while movement in lower Rapid Creek is precluded upstream by the dam at Canyon Lake in Rapid City and downstream by unsuitably warm water temperatures (Erickson 2005).

Increased angler harvest could also be a factor in the reduced biomass of brown trout, but this is unlikely. The upper Rapid Creek study section has historically been managed as a no-harvest fishery. A 1.6-km section of lower Rapid Creek was also managed by the same regulations, but the remainder of Rapid Creek was open to brown trout harvest (daily limit = 5 per day, 1 trout >356 mm TL). The Spearfish Creek study section was also open to brown trout harvest. However, creel survey data showed that harvest rates of brown trout exceeding 200 mm were low. Voluntary catch and release is common among the trout anglers who fish these streams, and less than 1% of the estimated adult brown trout population caught by anglers in Rapid and Spearfish creeks is harvested (South Dakota Game, Fish, and Parks, unpublished data). Thus, it is unlikely that the declines in brown trout biomass are related to differential harvest rates between the two time periods.

Our findings show that drought conditions were linked to appreciable declines in the biomass of adult brown trout in Black Hills streams. However, the changes in size structure were noticeably different in upper Rapid Creek than in the other two study sections. Because the drought coincided with the establishment

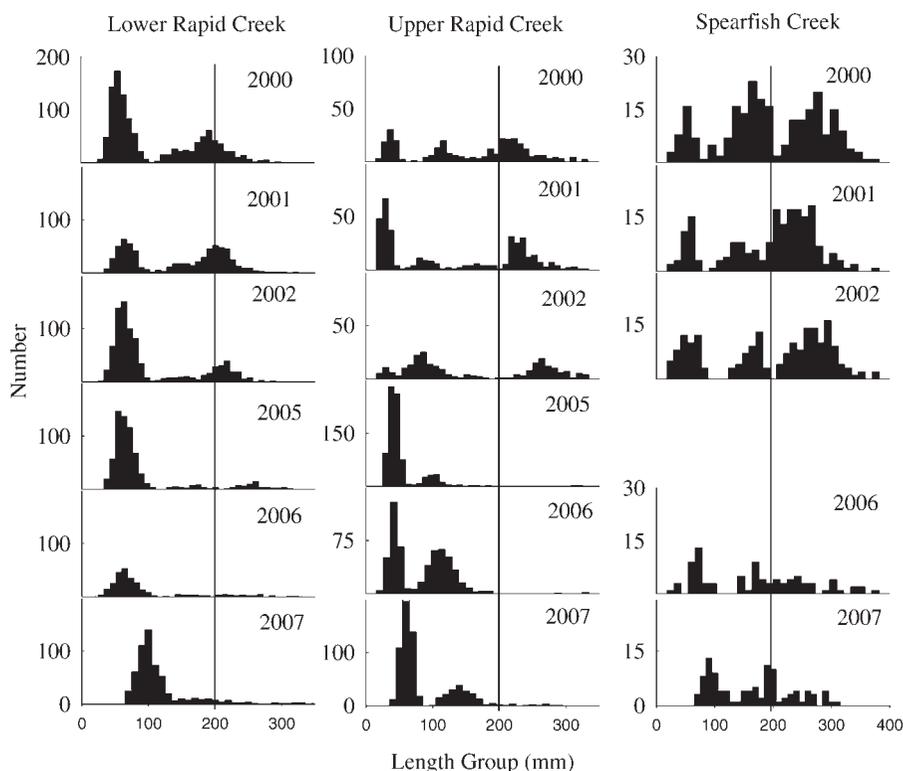


FIGURE 4.—Length-frequency histograms for brown trout in lower Rapid Creek, upper Rapid Creek, and Spearfish Creek, 2000–2007.

of *D. geminata* in upper Rapid Creek, it is difficult to determine how and to what extent *D. geminata* influenced trout abundance. Nonetheless, the declines in adult biomass associated with drought conditions were consistent across study reaches, regardless of the presence or absence of *D. geminata*. Further work in areas impacted by *D. geminata* would provide important insight into how this rapidly expanding nuisance species influences the growth, survival, and production of brown trout.

Management Implications

Global climate change has the potential to negatively impact water resources in the near future. For example, simulation modeling has predicted major reductions in water volume and a shortening of hydroperiods in prairie wetland complexes of the prairie pothole region of central North America (Johnson et al. 2010). If the results of this modeling are accurate, droughts may become more frequent and less water availability could lead to the reduction of habitat in rivers and streams. Reduction in habitat could result in lower fish population sizes and reduced size structure (Bowlby and Roff 1986; Elliot 1987, 2000; Stoneman and Jones

2000; Lake 2003; Magoulick and Kobza 2003; Hakala and Hartman 2004).

Because of these potential challenges, fisheries managers need to consider habitat limitations and maximize the use of the available water (i.e., habitat) in the streams they manage. Increasing the amount of low-water habitat (i.e., pools) in streams may be one way to provide refugia for fish during harsh conditions and increase the survival of adult trout, thus reducing the negative effects of low-water conditions. In tailwater systems, fisheries managers could collaborate with dam operators and their constituents to develop minimum-discharge thresholds that would satisfy the needs of both fisheries managers and dam operators during low-water conditions.

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References

- Bowlby, J. N., and J. C. Roff. 1986. Trout biomass and habitat relationships in southern Ontario streams. *Transactions of the American Fisheries Society* 115:503–514.
- Branson, J. 2006. *Didymosphenia geminata* economic impact assessment. New Zealand Institute of Economic Research, Wellington.
- Chapman, D. W., and E. Knudsen. 1980. Channelization and livestock impacts on salmonid habitat and biomass in western Washington. *Transactions of the American Fisheries Society* 109:357–363.
- Elliot, J. M. 1987. Population regulation in contrasting populations of trout *Salmo trutta* in two Lake District streams. *Journal of Animal Ecology* 56:83–98.
- Elliot, J. M. 2000. Pools as refugia for brown trout during two summer droughts: trout responses to thermal and oxygen stress. *Journal of Fish Biology* 56:938–948.
- Erickson, J. 2005. Stress responses of brown trout *Salmo trutta* within an urbanized reach of stream in the Black Hills of South Dakota. Doctoral dissertation. South Dakota School of Mines and Technology, Rapid City.
- Gillis, C., and M. Chalifour. 2010. Changes in the macrobenthic community structure following the introduction of the invasive alga *Didymosphenia geminata* in the Matapedia River (Quebec, Canada). *Hydrobiologia* 647:63–70.
- Hakala, J. P., and K. J. Hartman. 2004. Drought effect on stream morphology and brook trout (*Salvelinus fontinalis*) populations in forested headwater streams. *Hydrobiologia* 515:203–213.
- Hayes, D. B., J. R. Bence, T. J. Kwak, and B. E. Thompson. 2007. Abundance, biomass, and production. Pages 327–374 in C. S. Guy and M. L. Brown, editors. *Analysis and interpretation of freshwater fisheries data*. American Fisheries Society, Bethesda, Maryland.
- Jager, H. I., W. Van Winkle, and B. D. Holcomb. 1999. Would hydrologic climate changes in Sierra Nevada streams influence trout persistence? *Transactions of the American Fisheries Society* 128:222–240.
- James, D. A., J. W. Erickson, and B. A. Barton. 2007. Brown trout seasonal movement patterns and habitat use in an urbanized South Dakota stream. *North American Journal of Fisheries Management* 27:978–985.
- Johnson, C. W., B. Werner, G. R. Guntenspergen, R. A. Voldseth, B. Millett, D. E. Naugle, M. Tulbure, R. W. H. Carroll, J. Tracy, and C. Olawsky. 2010. Prairie wetland complexes as landscape functional units in a changing climate. *Bioscience* 60:128–140.
- Kilroy, C. 2004. A new alien diatom, *Didymosphenia geminata* (Lyngbye) Schmidt: its biology, distribution, effects, and potential risks for New Zealand freshwaters. National Institute of Water and Atmospheric Research, Project ENS05501, Report CHC2004-128, Christchurch, New Zealand.
- Kilroy, C., S. T. Larned, and B. J. F. Biggs. 2009. The nonindigenous diatom *Didymosphenia geminata* alters benthic communities in New Zealand rivers. *Freshwater Biology* 54:1990–2002.
- Lake, P. S. 2003. Ecological effects of perturbation by drought in flowing waters. *Freshwater Biology* 48:1161–1172.
- Larson, A. M. 2007. Effects of nuisance blooms of *Didymosphenia geminata* on benthic community composition in Rapid Creek, South Dakota. South Dakota Department of Environment and Natural Resources, Biological Assessment Interim Report, Pierre.
- Lobón-Cerviá, J. 2007. Numerical changes in stream-resident brown trout (*Salmo trutta*): uncovering the roles of density-dependent and density-independent factors across space and time. *Canadian Journal of Fisheries and Aquatic Sciences* 64:1429–1447.
- Magoulick, D. D., and R. M. Kobza. 2003. The role of refugia for fishes during drought: a review and synthesis. *Freshwater Biology* 48:1186–1198.
- Neumann, R. M., and M. S. Allen. 2007. Size structure. Pages 375–421 in C. S. Guy and M. L. Brown, editors. *Analysis and interpretation of freshwater fisheries data*. American Fisheries Society, Bethesda, Maryland.
- Rosenberry, D. O. 2003. Climate of the Cottonwood Lake area: hydrological, chemical, and biological characteristics of a prairie pothole wetland complex under highly variable climate conditions—the Cottonwood Lake area, east-central North Dakota. U.S. Geological Survey, Professional Paper 1675.
- Selch, T. M., C. W. Hoagstrom, E. J. Weimer, J. P. Duehr, and S. R. Chipps. 2007. Influence of fluctuating water levels on mercury concentrations in adult walleye. *Bulletin of Environmental Contamination and Toxicology* 79:36–40.
- Shearer, K. A., J. Hay, and J. W. Hayes. 2007. Invertebrate drift and trout growth potential in didymo (*Didymosphenia geminata*)-affected reaches of the Mararoa and Oreti rivers: April and August 2006. Cawthron Institute, Report 1214 to Ministry of Agriculture and Forestry Biosecurity, Nelson, New Zealand.
- Shelby, E. L. 2006. An assessment and analysis of benthic macroinvertebrate communities associated with the appearance of *Didymosphenia geminata* in the White River below Bull Shoals Dam. Arkansas Department of Environmental Quality, Summary Report, Little Rock.
- Spaulding, S., and L. Elwell. 2007. Increase in nuisance blooms and geographic expansion of the freshwater diatom *Didymosphenia geminata*: recommendations for response. U.S. Environmental Protection Agency, Denver, Colorado, and Federation of Fly Fishers, Livingston, Montana.
- Stoneman, C. L., and M. L. Jones. 2000. The influence of habitat features on the biomass and distribution of three species of southern Ontario stream salmonines. *Transactions of the American Fisheries Society* 129:639–657.
- USGS (U.S Geological Survey). 2008. Water resource and stream flow data, 1943–2007. Available: <http://www.usgs.gov/>. (January 2008.)