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EFFECTS OF LARGE-SCALE DENSITY REDUCTION ON BROWN TROUT
GROWTH AND MOVEMENT IN SPEARFISH CREEK, SOUTH DAKOTA

BY

TRAVIS REHM

A thesis submitted in partial fulfillment of the requirements for the

Master of Science

Major in Wildlife and Fisheries Sciences

Specialization in Fisheries Science

South Dakota State University

2018

EFFECTS OF LARGE-SCALE DENSITY REDUCTION ON BROWN TROUT
GROWTH AND MOVEMENT IN SPEARFISH CREEK, SOUTH DAKOTA

TRAVIS REHM

This thesis is approved as a creditable and independent investigation by a candidate for the Master of Science in Wildlife and Fisheries Science degree and is acceptable for meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the Department of Natural Resource Management.

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ABSTRACT

EFFECTS OF LARGE-SCALE DENSITY REDUCTION ON BROWN TROUT
GROWTH AND MOVEMENT IN SPEARFISH CREEK, SOUTH DAKOTA

TRAVIS R. REHM

2018

Density-dependent growth is often observed in stream-dwelling Brown Trout *Salmo trutta* populations. In Spearfish Creek, South Dakota, biomass of adult Brown Trout (>200 mm) is about three times greater than that reported for similar Black Hills streams while mean length of adult fish is about 30% less. Here, we evaluate large-scale density reduction as a management tool for improving growth rate of stream-dwelling Brown Trout. We compared age-specific growth of wild Brown Trout in stream sections receiving 50% reductions in fish abundance. We also assessed the effect of fish density manipulation on Brown Trout movement patterns and home range size. We compared gross movement, net movement and home range size of Brown Trout between stream sections with targeted fish removals to sections with natural fish densities. Annual growth in length and weight of older Brown Trout (> age 2) generally increased following fish removals; we observed significantly greater growth for age 3 and 4 fish (162 to 258 %, g/y) in stream sections receiving density reductions. Bioenergetics modeling revealed that total, annual consumption by smaller Brown Trout (ages 1 and 2) was dominated by aquatic invertebrates (91 %) with terrestrial invertebrates comprising only (9%). In contrast, larger Brown Trout (ages 3-6) consumed more terrestrial prey (35%) in order to meet annual energy requirements. In most cases, consumption of aquatic invertebrates by

large Brown Trout was insufficient to meet annual maintenance requirements. As a result, we postulate that growth rate of larger fish is more responsive to density reduction, owing to constraints imposed by availability of aquatic invertebrates. Additionally, we found no evidence that movement patterns or home range size of stream-dwelling Brown Trout differed between sections with natural densities and those where fish density was reduced. There was no relationship between fish density and fish movement parameters or home range size. Brown Trout in Spearfish Creek exhibited limited movement and home range sizes following reductions in fish density. Brown Trout tracked during fall-winter months were observed exhibiting larger gross movement and home range size presumably related to fall spawning activities, although net movement was similar to spring/summer periods – indicating strong site fidelity. A small proportion of radio-tagged (6%) trout exhibited extended movements (> 0.6 km), typical of straying behavior in salmonids. Many factors have been shown to effect variability of movement of stream-dwelling Brown Trout, however, it does not appear that density or large-scale density reduction is among them. Improved growth rate and reductions in intraspecific competition during our study (~1 year) coupled with negligible immigration from natural high-density sections are promising for large-scale density reductions as a management technique to improve the growth of stream-dwelling Brown Trout.

CHAPTER 1

INTRODUCTION

The native range of Brown Trout *Salmo trutta* includes Europe, northern Africa, and western Asia (Page and Burr 1991). Their ability to colonize a variety of freshwater habitats, from small streams to large rivers and lakes, allows Brown Trout to occupy a wide geographical distribution (Klemetsen et al. 2003). Brown Trout are one of the most widely introduced fish species and provide important sport fishing opportunities in North America (Fuller et al. 1999). Brown Trout were first introduced from Germany to the United States in 1883 (Mather 1889; Courtenay et al. 1984); not long after Brown Trout entered the country, they were introduced into Black Hills streams of western South Dakota (1890; Barnes 2007).

Habitat conditions in many streams of the Black Hills provide suitable habitat for Brown Trout to thrive, although salmonids are not native to the region. Cyprinids and catostomids were the only fish species native to the Black Hills (Cordes 2007). Brown Trout have been implicated as a key factor in declining native fish populations as a result of displacement, predation, and interspecific competition (Taylor et al. 1984; Fuller et al. 1999) and the species has come to dominate fish assemblages across many Black Hills streams. The non-indigenous trout was well suited for Spearfish Creek, Black Hills, South Dakota and the creek currently supports a robust population of naturalized Brown Trout. Brown Trout, Rainbow Trout *Oncorhynchus mykiss*, and Brook Trout *Salvelinus fontinalis* are now common throughout the Black Hills and all persist in Spearfish Creek.

Spearfish Creek has become a destination fishery that draws resident and non-resident anglers to pursue wild Brown Trout in this easily accessible fishery (Simpson 2011). Contemporary fisheries management in Spearfish Creek is focused on the wild, naturally reproducing Brown Trout populations, which is not supplemented with hatchery reared fish. Because stocking fish is not used as a management tool, management options are limited to regulatory rules and manipulation of biotic and abiotic factors, which can be challenging when attempting to manipulate sizes and numbers of Brown Trout in Spearfish Creek.

Growth rates and the size range of Brown Trout can vary depending on local conditions. Brown Trout in streams and rivers typically reach sizes ranging from 25-76 cm, however, they can reach sizes of 103 cm (Behnke 2002). Brown Trout persist in environments with water temperatures ranging from 3-26°C, with optimal temperatures for growth ranging from 13-18°C (Elliott and Hurley 2000; Ojanguren et al. 2001; Klemetsen et al. 2003). Growth rates of Brown Trout are known to be density-dependent in lotic systems (Bohlin et al. 2002, Lobon-Cervia 2007, Jenkins et al. 1999). The negative relationship between fish density and growth rate is influenced by reduced feeding rates of individual fish. It may also be exaggerated by decreases in availability of prey, increased aggressive behavior, and reduction in suitable habitat (Klemetsen et al. 2003). The growth-density relationship of Brown Trout is well described by a negative power curve (Jenkins et al. 1999). Both observational and experimental studies have shown that density-dependent growth is a common process that often explains significant variation in size-at-age of stream dwelling Brown Trout (Bohlin et al. 2002; Vollestad et al. 2002; Lobon-Cervia 2005).

Habitat conditions in Spearfish Creek have provided conditions that for Brown Trout abundance and growth to be different than other Black Hills streams. Mean biomass of Brown Trout (>200 mm) was shown to be about three times larger than comparable Black Hills Brown Trout streams (Castle and Rapid creeks; James and Chipps 2016). Similarly, in Spearfish Creek, Brown Trout densities are notably greater (0.2 to 0.7 fish/m²) than those reported for other Black Hills streams (0.006-0.3 fish/m²; Bucholz and Wilhite 2009). However, adult Brown Trout in Spearfish Creek are about 40% smaller than similarly aged fish in Rapid Creek (315 mm; James and Chipps 2016). The mechanism thought to be driving reduced length of Brown Trout in Spearfish Creek is, the previously described, density-dependent growth.

Anglers' perceptions of trout abundance in Spearfish Creek is very positive (Simpson 2011), however, those pursuing larger quarry (i.e. >300 mm) may have little chance at success because very few of these larger fish exist in Spearfish Creek. Managers of Spearfish Creek and comparable fisheries throughout the world currently have little tested methodology for improving growth of stream-dwelling Brown Trout that are limited by density-dependent growth.

One option for improving density-dependent growth is to increase angler harvest, thereby reducing fish density. However, creel surveys in the Black Hills have shown that anglers generally harvest few fish (Simpson 2009), particularly in Spearfish Creek, where annual harvest of Brown Trout is less than 3,200 per year (Simpson 2011). In addition, the social stigmas associated with harvesting wild trout encourage anglers to practice catch and release. Thus, liberalizing harvest regulations will likely have negligible effects on angler harvest in Spearfish Creek.

Experimental manipulation of Brown Trout abundance is an alternative management technique for increasing the growth and size structure of stream-dwelling trout that experience density dependent growth. While fisheries researchers have gained considerable knowledge on how density can affect variation in growth rate among stream-dwelling Brown Trout, only some research investigating the effects of large-scale density reduction has been done. For example, in five Swedish streams, densities of age 1 Brown Trout were reduced, resulting in decreased mean length of age 1 fish the following year, which was attributed this decline in growth to increased survival of age 0 to 2 fish (Nordwall et al. 2001). However, in sections where densities of fish older than age 1 were reduced, mean length of age 2 and 3 Brown Trout increased (Nordwall et al. 2001). After experimental manipulations in Convict Creek, California, a strong, negative relationship between mean weight of age 0 Brown Trout and total trout density was observed (Jenkins et al. 1999). However, among older fish (>age 0), results were equivocal although the relationship between weight gain and fish density was best described by a negative power function (Jenkins et al. 1999). To date, the few studies investigating the effects of density reduction of stream-dwelling Brown Trout have shown increased growth following fish removal, however, results have varied among age classes.

A major consequence of experimental manipulation (i.e., density reduction) could be fish movement into, or out of fish removal sections of stream. Many factors have been shown to influence the movements of stream-dwelling salmonids including: fish size (Clapp et al. 1990; Young 1994; Diana et al. 2004), time of day (Young et al. 1997; Hilderbrand and Kershner 2000), temperature (Petty et al. 2012), season (Young 1996;

Burrell et al. 2000; Schoby and Keeley 2011) condition (Gowan and Fausch 1996), and species (Young et al. 1997). However, the effect of manipulating fish density on movement and home range size is not well documented. For reductions in Brown Trout density to have the desired effects on fish growth, overall movement and home ranges of the targeted fish would ideally be minimal, and immigration from high-density to low-density (i.e., removal sections) areas would ideally be negligible.

Brown Trout are an ideal candidate for experimental manipulations because this species has been shown to exhibit limited daily and seasonal movement and have small home ranges (Bachman 1984, Burrell et al. 2000; James et al. 2007). While observing Brown Trout in Spruce Creek, PA researchers calculated wild fish home range to be 15.6 m². They found that home ranges were established in the first two years of life and changed little throughout a fish's lifetime (Bachman 1984). Home range size of Southern Appalachian Brown Trout ranged from 27.7 m to 98.6 m with the largest home range and movement occurring in the fall associated with spawning activities (Burrell et al. 2000). Recent work in Rapid Creek, South Dakota has shown that Brown Trout averaged yearly gross movements of 506 m and net movements of 49.4 m downstream, with fish exhibiting high site fidelity and little migratory movement excluding fall spawning activities (James et al. 2007).

In areas where movement of Brown Trout in response to population density changes has been observed, it seems that the effects of density changes may be minimal. For example, movement patterns of Brown Trout (>150 mm) in a Michigan stream were similar during a two-year period, even after a significant decrease in population abundance from 209 to 87/ha (Mense 1975). Similarly, after densities of age 0 and \geq age

1 Brown Trout were experimentally reduced (2,500 fish/ha) in 10 stream sections, no difference in movement patterns were observed in reduction and natural density sections (Kaspersson and Höjesjö 2009). Finally, the effects of experimental fish density increases, in Norwegian and Swedish streams, using both wild and hatchery Brown Trout found that movements of Brown Trout were independent of density (Heggenes 1988; Bohlin et al. 2002). The observations of these were performed using low resolution techniques (i.e., mark recapture), and thus have not found direct evidence that fish density and experimental manipulation of fish density affect movement of stream-dwelling Brown Trout. Direct observation of individual trout in response to large-scale density reduction could reveal different results.

While there is considerable knowledge about the mechanisms involved in density-dependent growth, questions about the validity of using large-scale density reductions as a management technique to reduce intraspecific competition and improve growth remain. In this study, we investigated the effects of reducing Brown Trout (>100 mm TL) by 50% (i.e., by number) in 425 m sections of Spearfish Creek, South Dakota. We specifically focused on responses in age-specific growth and movement. Our objectives were to, 1) Compare age-specific growth rate among stream sections with natural densities and those with experimentally-reduced densities of Brown Trout, and 2) Compare movement and home range size among sections with natural densities and those with experimentally reduced densities of Brown Trout. Our research will provide greater understanding of the viability of large-scale density reduction as a management technique for improving growth rate of stream-dwelling salmonids.

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CHAPTER 2

EFFECTS OF LARGE-SCALE DENSITY REDUCTION ON AGE-SPECIFIC
GROWTH OF BROWN TROUT**Abstract**

Density-dependent growth is often observed in stream-dwelling Brown Trout *Salmo trutta* populations. In Spearfish Creek, South Dakota, biomass of adult Brown Trout (>200 mm) is about three times greater than that reported for similar Black Hills streams while mean length of adult fish is about 30% less. Here, we evaluate large-scale density reduction as a management tool for improving growth rate of stream-dwelling Brown Trout. We compared age-specific growth of wild Brown Trout in stream sections receiving 50% reductions in fish abundance and those containing natural densities. Annual growth in length and weight of older Brown Trout (> age 2) generally increased following fish removals; we observed significantly greater growth for age 3 and 4 fish (162 to 258 %, g/y) in stream sections receiving density reductions. Bioenergetics modeling revealed that total annual consumption by smaller Brown Trout (ages 1 and 2) was dominated by aquatic invertebrates (91 %) with terrestrial invertebrates comprising only (9%). In contrast, larger Brown Trout (ages 3-6) consumed more terrestrial prey (35%) in order to meet annual energy requirements. In most cases, consumption of aquatic invertebrates by large Brown Trout was insufficient to meet annual maintenance requirements. As a result, we postulate that growth rate of larger fish is more responsive to density reduction, owing to constraints imposed by availability of aquatic invertebrates. Improved growth rate and reductions in intraspecific competition during our study (~1

year) are promising for large-scale density reductions as a management technique to improve the growth of stream-dwelling Brown Trout.

Introduction

Growth rates of stream-dwelling Brown Trout *Salmo trutta* is often density-dependent owing to factors such as prey abundance, aggressive behavior, and(or) habitat availability (Jenkins et al. 1999, Bohlin et al. 2002, Klemetsen et al. 2003, Lobon-Cervia 2007). Observational and experimental studies have shown that fish density in Brown Trout populations often explains a significant amount of variation in size-at-age (Bohlin et al. 2002; Vollestad et al. 2002; Lobon-Cervia 2005). At high fish density, intraspecific competition for food and space are believed to be associated with reduced growth of Brown Trout (Nordwall et al. 2001). Competition between fish cohorts has also been reported where poorly recruited year classes exhibited faster growth compared to highly recruited cohorts (Lobon-Cervia 2007). Thus, variation among inter-cohort abundance can affect growth throughout the lifetime of a fish (Lobon-Cervia 2007).

Growth rate of stream-dwelling Brown Trout can be altered by manipulating fish density. In Convict Creek, California, Brown Trout densities were increased or decreased in barricaded sections (340-500 m) of the stream to evaluate the growth response of age 0 fish (Jenkins et al. 1999). The authors documented a strong, negative relationship between mean weight of age 0 Brown Trout and total trout density (Jenkins 1999). Among older fish (>age 0), results were equivocal although the relationship between weight gain and fish density was best described by a negative power function (Jenkins et al. 1999). In a similar study, Nordwall et al. (2001) reduced densities of age 1 Brown

Trout in five Swedish streams and found that mean length of age 1 fish declined the following year. Following a reduction in fish density, they attributed the decline in growth of young trout to increased survival of ages 0 to 2 fish. In contrast, in stream sections where fish older than age 1 were removed, the authors observed an increase in the mean length of age 2 and 3 Brown Trout (Nordwall et al. 2001).

In Spearfish Creek, Black Hills South Dakota, Brown Trout densities are notably greater (0.2 to 0.7 fish/m²) than those reported for other Black Hills streams (0.006-0.3 fish/m²; Bucholz and Wilhite 2009). Similarly, biomass of adult Brown Trout (>200 mm) is about three times greater than that reported for similar Black Hills streams although mean length of adult fish in Spearfish Creek is about 30% less (James and Chipps 2016). The mechanism believed to be behind reduced growth rates is density dependent growth. Creel surveys of Black Hills streams indicate that most anglers (~85%) view trout as important to their fishing experience and are supportive of restrictive regulations, such as reduced creel limits and size restrictions (Erickson and Galinat 2005). Nonetheless, past studies have shown that Black Hills anglers generally harvest few fish (Simpson 2009), particularly in Spearfish Creek (Simpson 2011). From a management standpoint, targeted efforts to reduce fish density may provide a pragmatic approach for improving fish growth, particularly in cases where harvest rates are low

In this study, we evaluate large-scale density reductions as a management approach for improving growth of stream-dwelling Brown Trout. We quantify effects of large-scale population reductions on abundance and growth of Brown Trout and use bioenergetics modeling to explore mechanisms affecting age-specific growth. Given that slow growth of Brown Trout in Spearfish Creek is more pronounced among adult fish

(>age 2; James and Chipps 2016), we postulated that growth of larger fish will be more responsive to fish removals.

Methods

Study site

Spearfish Creek is located in the northern Black Hills of South Dakota (Figure 2.1). It flows north out of the Black Hills through the town of Spearfish. The creek originates from springs in the Mississippian Madison Limestone and gains and loses surface flow from a shallow alluvial aquifer (Stetler and Sieverding 2001). Spearfish Creek has an annual mean discharge of about 1.53 m³/s (Koth 2007). The creek is characterized by two reaches; the upstream reach includes the headwaters to the lower end of Spearfish Canyon and the downstream reach begins near the town of Spearfish and extends to the confluence with the Redwater River. The two reaches of Spearfish Creek are separated by a de-watered reach, starting at Maurice Intake and ending at Hydro #1 (Figure 2.1). This dewatering is caused by a limestone losing reach in addition to an aqueduct that diverts stream flow at Maurice to a small hydroelectric power plant on the southern edge of the town of Spearfish, resulting in a 12 km dry section between the two reaches. The aqueduct that was built in the late 1800s circumvents a limestone loss zone that extends all around the Black Hills (Koth 2007). Stream substrates are characterized by a calcite precipitate layer owing to high levels of calcium and magnesium in the water (Stetler and Sieverding 2001). The calcite precipitate is more predominate in the Spearfish Canyon portion of the creek than in the downstream reach. The creek is home

to three non-native, but naturalized, salmonid species: Brown Trout, Rainbow Trout *Oncorhynchus mykiss*, Brook Trout *Salvelinus fontinalis* and Cutthroat Trout *O. clarkii*.

For our study, we focused on two reaches; the first reach extends from Maurice Intake upstream to Cheyenne Crossing and constituted the upper reach (canyon reach; Figure 2.1). The second sampling reach extended from the northern city limits of Spearfish, SD upstream to the Hydro #1 facility and represented the lower reach (town reach; Figure 2.1). In these reaches, we selected a total of fourteen, 425 m (~0.25 mile) sampling sections. Sampling sections were selected in consultation with South Dakota Game Fish and Parks (SDGFP) biologists and through analysis of long-term fisheries data to identify stream reaches that were characterized by relatively high Brown Trout density. Ten sections were located in the canyon reach and four sections were selected in the town reach. Seven sections (hereafter called ‘removal’) were randomly selected to receive Brown Trout density manipulations, and during August 2016 we removed 50% of the Brown Trout population. Two removal sections were randomly selected in the town reach and five randomly selected in the canyon reach. Similarly, the remaining seven sampling sections served as controls where trout were sampled but not removed. To minimize the effects of fish movement among sections, we ensured that adjacent sections were separated by at least 425 m (Jenkins et al. 1999). Because of small net movement (< 100 m; Bachman 1984; James et al. 2007) and home range size (40-200 m; Young 1999; Burrell et al. 2000) of Brown Trout, a distance of 425 m was deemed large enough to minimize the probability that natural movement would result in fish being detected in more than one section.

Fish sampling, removal, and PIT tagging

We assessed Brown Trout size, age, abundance, and condition in all fourteen sections during July-August of 2016. Block nets were placed at the lower and upper bounds of each section immediately prior to fish sampling. Nets were used to minimize immigration and emigration of fish in sections during sampling. Stream width (n=11) was measured at transects spaced ~39 m apart at each section. We collected fish in July-August 2016 using two back-pack electrofishing units (LR24 Electrofisher, Smith-Root, Vancouver, Washington). All fish captured were measured (total length, TL, mm) and at least 150 randomly selected fish per section were weighed (g). Three pass electrofishing depletion surveys were used to determine initial size, abundance, and condition at all sections (Bonar et al. 2009). During 2016 we implanted passive integrated transponder (PIT) tags (Biomark, HDX12, Boise, Idaho) into Brown Trout collected from all sections (~150 fish/section) by injecting tags into the abdominal cavity using a UID Identification Solutions implant gun (Multi PIT Tag Injector, Lake Villa, Illinois). All fish that received PIT tags were measured (total length, TL, mm), weighed (g), and the individual PIT tag number was recorded. All fish collected from each electrofishing pass were placed in upstream net pens immediately above the block net until sampling and fish removals (see below) were completed.

We estimated population size of Brown Trout >100 mm in each section using a maximum-likelihood estimator (Junge and Libosvárský 1965; Seber 1982). We included only fish >100 mm because Brown Trout smaller than this length were not fully recruited to our sampling gear (Thompson and Rahel 1996). We used data from three-pass electrofishing depletion counts to calculate fish abundance as:

$$\hat{N} = \frac{6X^2 - 3XY - Y^2 + Y\sqrt{Y^2 + 6XY - 3X^2}}{18(X - Y)},$$

where $X = 2n_1 + n_2$, $Y = n_1 + n_2 + n_3$, and n_i = number of Brown Trout captured on the i^{th} electrofishing pass (Junge and Libosvářský 1965; Seber 1982). Using the average stream width measured at each section, we calculated fish abundance as the number of fish per hectare. After population estimates were calculated for removal sections, we used estimates to inform a 50% removal of all Brown Trout >100 mm. Brown Trout removed from the creek were randomly selected from holding cages using large dip nets and were transported by a hatchery truck to Hanna Pond or Iron Creek Lake where they were released alive. All trout that were not part of removal efforts or used for age analysis (description below) were released back into their respective stream sections.

We returned to all fourteen sections in August-September of 2017 and re-sampled Brown Trout to evaluate effects of density reduction on growth and abundance. We again collected Brown Trout using two back-pack electrofishing units as previously described; all fish were measured for total length (mm) and at least 150 fish per section were weighed (g). We also estimated population size of Brown Trout >100 mm in each section as previously described. All trout captured during 2017 were scanned for PIT tags (Avid, Power Tracker VII, Norco, CA) and those containing PIT tags were measured (total length, TL, mm), weighed (g) and the PIT tag number recorded.

We evaluated changes in abundance of Brown Trout greater than age 1 because our removal efforts (i.e., fish >100 mm) excluded most young of the year Brown Trout in 2016, that subsequently became age 1 fish in 2017. We used a paired t-test to test the

hypothesis that mean, age-specific abundance of Brown Trout did not change within treatments between 2016 and 2017 (i.e., difference=0; R Core Team 2017).

Condition of fishes, with measured length and weight, was calculated as an index, using relative weight (Wege and Anderson 1978; Pope and Kruse 2007). The W_r index for lotic Brown Trout was calculated as,

$$W_r = \left(\frac{W}{W_s} \right) * 100$$

Where W is the fishes weight (g) and W_s is the lotic Brown Trout length-specific standard weight from length weight-regression developed by Milewski and Brown (1994).

Relative weight was calculated for Brown Trout ≥ 140 mm that were measured (TL, mm) and weight (g) during both sampling periods, across all sites. Differences in condition of Brown Trout were analyzed using a two-way analysis of variance (ANOVA) with treatment (control vs removal) and year as grouping factors.

Age analysis

We collected a subsample of Brown Trout from each section during 2016 and 2017 to determine age structure. Fish were euthanized using 150 ppm Fiquel MS-222 (Leary et al. 2013) and their sagittal otoliths removed using the “up through the gills method” (Stevenson and Campana 1992). We embedded otoliths in epoxy (Buehler, EpoxiCure™ 2, Lale Bluff, Illinois) and transversely sectioned each otolith using a low speed isometric saw (Buehler, Model 11-1280-160, Lale Bluff, Illinois). We photographed sectioned otoliths under magnification and aged to consensus, using three readers (Quist and Isermann 2017).

We used ages derived from otolith analysis to construct age-length keys using Fisheries Stock Assessment (FSA) v0.8.12; R v3.3.2 (Ogle 2017; R Core Team 2017). Age-length keys were constructed using 10 mm length bins and we assigned ages to all unaged fish based on the corresponding age-length keys (Ketchen 1949; Isermann and Knight 2005; Ogle 2016). In addition to creating age-length keys, we used length and weight data collected from re-captured PIT-tagged Brown Trout to calculate observed growth rate of fish from 2016 to 2017. Annual growth rate for of PIT-tagged fish was calculated as,

$$G = \frac{Y_2 - Y_1}{T} * 365 ,$$

where G = annual growth rate, Y_2 = length (mm) or weight (g) at recapture, Y_1 = length (mm) or weight (g) at initial capture, and T = days between capture events (Isely and Grabowski 2007). Differences in growth of PIT-tagged fish were analyzed using a two-way analysis of variance (ANOVA) with treatment (control vs removal) and year as grouping factors. Age classes were denoted by initial ages during tagging in 2016; due to low sample size, fish older than age 6 were excluded from the analysis (SAS 2013).

Modeling fish consumption

We used a bioenergetics model to estimate age-specific food consumption by Brown Trout (Dieterman et al. 2004). We estimated food consumption over a 365-day period for age 1-6 Brown Trout in Spearfish Creek. Bioenergetics modeling simulations were performed using Fish Bioenergetics Model 4, version v1.0.3 (Deslauriers et al. 2017). We used information on Brown Trout diet composition and prey energy values reported by James (2011) and James and Chipps (2016) to model food consumption by

fish. To quantify seasonal water temperature in Spearfish Creek, we deployed 8 HOBO Pendant Temperature/Light 64K data loggers (Onset Computer Corporation, Bourne, MA) in locations that spanned our study area. Loggers recorded water temperature every hour from September 26st, 2016 to September 21st, 2017; for modeling purposes, we used bi-weekly average water temperature as model input.

We estimated total food consumption for each cohort based on observed growth rates from 2016 weight-at-age values, obtained through age analysis. We also estimated maintenance requirements of each Brown Trout cohort based on simulations where final weight was equal to initial weight (i.e., no-growth). To explore the relative contribution of aquatic versus terrestrial prey (RC_i) to Brown Trout growth, we expressed total annual prey consumption as a proportion of annual maintenance requirement,

$$RC_i = \frac{Prey_i(kcal)}{Maintenance(kcal)},$$

where RC_i is the proportion of maintenance energy requirements that are met by observed consumption of prey_i, where i represents aquatic or terrestrial prey.

Results

Population density

We collected a total of 12,731 fish in Spearfish Creek from July-August 2016. Brown Trout were the dominant species comprising >98% of the total catch with Rainbow Trout and Cutthroat Trout making up the remainder of the catch. Initial lengths of Brown Trout sampled in 2016 were negatively related to fish densities, with the relationship best describe by a negative power function ($r^2 = 0.63$, $P < 0.001$, Figure 2.2). In the seven removal sections, we reduced Brown Trout density by removing a total of

3,091 fish. We returned to the creek in August-September 2017 and collected a total of 15,741 fish all fourteen sections. Brown Trout were once again the dominant species comprising >98% of the total catch. In 2016, we implanted a total of 2,073 Brown Trout with PIT tags corresponding to ~150 fish/section. PIT-tagged fish ranged in size from 108-444 mm (mean=225 mm; SE=1.14). Of the PIT-tagged Brown Trout, 635 were recaptured in 2017 resulting in a recapture rate of 31%. Recaptured fish ranged in size from 170 to 445 mm (mean=265 mm; SE=1.6).

A year after fish removals were performed, we detected significantly lower abundance of Brown Trout in removal sections ($t = 3.33$, $df = 6$, $p = 0.01$; Table 2.1). In contrast, we did not detect a change in abundance of Brown Trout in our control sections ($t = -0.58$, $df = 6$, $p = 0.57$; Table 2.1). On average, Brown Trout abundance in control sections increased by 135 fish/ha (4%) and decreased in removal sections by 491 fish/ha (20%). Additionally, high recruitment from the 2016 Brown Trout cohort was observed at all sections in 2017, as evidenced by a significant increase in abundance of age 1 fish in removal ($t = -2.51$, $df = 6$, $p = 0.04$; Figure 2.3) and control sections ($t = -3.11$, $df = 6$, $p = 0.02$; Figure 2.3) in 2017.

Condition of Brown Trout was similar in control and removal sections after fish removal ($F_{1,24} = 1.63$, $p = 0.21$; Table 2.2). On average, Brown Trout relative weight in control sections decreased by 1% and decreased in removal sections by 5%.

Age

A total of 858 Brown Trout were aged using otolith analysis. Using estimated ages, age-length keys were created for both reaches (town and canyon) and treatments

(removal and control) during both 2016 and 2017. Confidence intervals (90%) around mean length overlapped for each age cohort collected from control or removal sections in 2016 allowing us to construct a single age-length key for both treatments prior to density removals (Figure 2.4). The keys were applied to all Brown Trout (> 100 mm) to estimate age of fish during both 2016 and 2017.

Growth

Growth rate (mm/y) of age 1 and age 2 Brown Trout was similar in control and removal sections after fish removal (age 1, $F_{1,30} = 0.05$, $p = 0.81$; age 2, $F_{1,207} = 0.92$, $p = 0.33$; Figure 2.5). In contrast, we found that growth rate of age 3 and age 4 Brown Trout in removal sections increased significantly following the population reduction (age 3, $F_{1,161} = 13.35$, $p < 0.001$; age 4, $F_{1,133} = 13.35$, $p < 0.001$; Figure 2.5). Although growth response in older fish (ages 5 and 6) followed similar patterns to that of ages 3 and 4, we found no evidence that growth rate differed between control and removal sections following the population reduction ($p > 0.28$; Figure 2.5).

Growth in weight (g/y) of age 1 and age 2 Brown Trout was similar in control and removal sections following population reduction in 2016 (age 1, $F_{1,30} = 0.75$, $p = 0.39$; age 2, $F_{1,207} = 0.13$, $p = 0.72$; Figure 2.6). Similar to growth in length, we observed significantly greater growth in weight of age 3 and age 4 Brown Trout in removal sections following the population reduction (age 3, $F_{1,161} = 7.84$, $p = 0.005$; age 4, $F_{1,133} = 20.19$, $p < 0.001$; Figure 2.6). Although growth responses in older fish (ages 5 and 6) were similar to those of ages 3 and 4 again, we found no evidence that growth rate significantly differed between control and removal sections following the population reduction ($p > 0.23$; Figure 2.6).

Fish consumption

Energy derived from aquatic invertebrate prey greatly exceeded maintenance requirements for ages 1 and 2 fish (189-261%; Figure 2.7). Total food consumption exceeded maintenance requirements for ages 3-6 Brown Trout (109-161%; Figure 2.7) however, at a substantially smaller margin than younger cohorts. For ages 1-2 Brown Trout, consumption of aquatic invertebrate prey accounted for most of their energy acquisition (91%) with terrestrial prey making up a much smaller proportion (9%; Figure 2.7). Energy derived from aquatic prey ranged from just exceeding maintenance requirements (108-111%; Figure 2.7) to insufficient in meeting annual energy demands of age 3-6 Brown Trout. To increase energy intake beyond maintenance requirements and allow for somatic growth, Brown Trout relied more on terrestrially-derived prey composing a much larger proportion of consumed energy (35%), whereas aquatically-derived prey represented a smaller proportion (65%) of consumed energy compared to younger cohorts.

Discussion

A better understanding of the mechanisms that influence fish growth has important implications for sport fish management. The results of our investigation offer further evidence for the case of density-dependent growth and that large-scale density reduction could be a viable management technique for improving growth in stream-dwelling salmonids. However, our large-scale density reduction provided differing effects on growth between cohorts of Brown Trout. Density reductions improved growth in both length and weight of age 3 and 4 Brown Trout. However, we did not detect similar improvements in growth rate for younger cohorts. Similarly, in a Swedish stream,

densities of Brown Trout age 1 were reduced by 97% but mean length of age-1 Brown declined the following season (Nordwall et al. 2001). However, the authors did observe an increase in mean length for age 2 and 3 Brown Trout (Nordwall et al. 2001). Fish density manipulations in Convict Creek, California revealed a strong negative relationship between density and individual mass of age 0 Brown Trout but were less conclusive for older trout (Jenkins et al. 1999). In a study investigating effects of inter-cohort abundance on juvenile Brown Trout growth, young of the year fish grew significantly faster when the abundance of older cohorts (\geq age 1) was low (Kaspersson and Höjesjö 2009). In a comparable study, experimentally increased biomass of Brown Trout using both wild and hatchery fish had a negative effect on growth rate of resident fish (Bohlin et al. 2002). While growth rate in Brown Trout populations can be density-dependent, reduction of total fish density can have variable effects on cohort-specific growth rate, as we observed in Spearfish Creek Brown Trout.

Our ability to detect changes in growth rate for Brown Trout older than age 4 could be explained by the asymptotic nature of fish growth and(or) small sample size. As growth rate becomes asymptotic with age in fish, the ability to influence short-term (i.e., 1 year) changes in growth become more difficult. Such growth patterns are well described by the von Bertalanffy growth function (von Bertalanffy 1938), the most commonly used function when modeling fish growth (Quist and Isermann 2017). As fish age and obtain large sizes, our abilities to improve growth rate through reduced intraspecific competition may diminish. On average, growth of fish $>$ age 2 increased when trout density was reduced although greater variability and smaller sample sizes among older fish may have masked differences in growth. It is also possible that with the

dominance hierarchy displayed by stream-dwelling salmonids, with older individuals occupying the most profitable feeding positions (Bachman 1984; Hughes 1992), fish density has little to no effect on food consumption.

Brown Trout length-at-age is similar in Spearfish and Rapid creeks, two comparable Black Hills streams, for age 1 and 2 fish. However, age 3 Brown Trout in Spearfish Creek are about 40% smaller than age 3 fish in Rapid Creek (315 mm; James and Chipps 2016). Similarly, mean biomass of Brown Trout greater than 200 mm is about three times greater in Spearfish than Rapid Creek (James and Chipps 2016). It appears that Brown Trout in Spearfish Creek, as they approach age 3, exhibit reduced growth caused by high fish density (density-dependent growth). Prey size and availability are crucial factors affecting fish growth (Elliott 1975a; Elliott 1975b) and as fish increase in size they need to consume larger prey items to continue growth (Klemetsen et al. 2003). The ability to continually grow throughout a fish's lifetime typically hinges on whether or not larger prey items are available as the fish grows, if not, growth typically slows (Gorman and Nielson 1982; Klemetsen et al. 2003). Using a combined foraging and bioenergetics model to predict growth over the lifetime of drift-feeding Brown Trout, prey size structure was found to significantly influence fish growth and growth rate of Brown Trout > age 3 substantially declined (Hayes et al. 2000).

Aquatic invertebrate communities in Spearfish Creek are dominated by small prey items (James and Chipps 2016). Brown Trout in Spearfish Creek exhibit an ontogenetic diet shift from mainly small aquatic invertebrates (e.g., Ephemeroptera and Diptera) as age 1-2 fish, to larger, terrestrially-derived prey at ages 3 and older (James and Chipps 2016). A potential reason for the shift to terrestrial prey may be the lack of suitable

aquatic invertebrate prey for larger Brown Trout. Such a shift in prey use is necessary for growth as larger fish require more energy. Thus, availability of large, aquatic invertebrates may be a limiting factor affecting growth of larger trout (i.e., ages 3 and 4). Bioenergetics modeling supported the notion that aquatic prey may be a limiting resource for older fish, and thus could influence density-dependent growth. In larger, older fish, maintenance requirements were barely met and in some cases could not be met by foraging solely on aquatic invertebrates – a striking contrast to patterns seen in ages 1 and 2 fish. Brown Trout ages 3-6 were forced to rely on terrestrially-derived prey sources in order to obtain or maintain their larger sizes. Our modeling results indicate that density-dependent growth was most pronounced among cohorts that experienced the greatest food-resource limitation.

The effects of a dominance hierarchy displayed by stream-dwelling salmonids may also be factor behind differing effects of density removals. Dominance hierarchies in Brown Trout populations are well documented where older and larger individuals occupy the more profitable feeding positions (Bachman 1984; Hughes 1992). Age specific habitat segregation has been observed frequently in stream-dwelling salmonids (Bohlin 1977; Bachman 1984; Bremset and Berg 1999) where younger fish are forced to compete for territories in marginal habitats. In an observational study, researchers found that behavioral dominance was strongly correlated with age for wild and hatchery Brown Trout and was found to be linearly dependent on body size (Bachman 1984). Fish occupying the most optimal feeding position always exhibited the highest specific growth rate (Faush 1984). Older, larger individuals in Spearfish Creek should occupy the most

profitable feeding positions. These positions should also receive the largest benefit from increases in prey resources due to density removals.

Our findings provide evidence that the effects of reduced intraspecific competition due to large-scale density reductions will not be significantly affected by immigration of Brown Trout. We observed reduced abundance in removal sections indicating that we were able to effectively decrease intraspecific competition during the study period. This sustained reduction in abundance (~ 1yr) indicates that either increased rates of survival and(or) immigration from surrounding areas were negligible or at low enough rates to sustain reduced abundance for a period of ~1 year. These findings support corresponding work in Spearfish Creek where fish immigration into removal sections was found to be negligible (see Chapter 3). With fish occurring in 16 m reaches above or below a removal sections, at most about 8% of the total section area, expected to move into areas with reduced fish density (see Chapter 3). Growth benefits of large-scale density reductions may also depend on the home range of individuals in removal sections and the surrounding portions of stream. Brown Trout in Spearfish Creek removal sections occupy small home ranges (95 m; see Chapter 3), similar to those previously documented by stream-dwelling Brown Trout (Heggenes 1988; Burrell et al. 2000; James et al. 2007). These small observed movements and home ranges suggest that movement patterns of Brown Trout should not significantly alter experimentally reduced densities. In contrast, in a Swedish stream, natural densities of Brown Trout age 0 and \geq age 1 were reduced and a higher biomass and number of immigrant fish were found in removal sections when compared to those with natural densities (Kaspersson and Höjesjö 2009).

We observed increased growth and lower fish abundance in removal sections, although the longevity of these effects remains unknown. The greatest limitation of our study is the unknown effects beyond 1 year and if a single density reduction event has the ability to improve growth of stream-dwelling fish for multiple years. If large-scale density reductions can prove to be effective beyond a single year they would be markedly more attractive to managers as a technique to improve growth of stream-dwelling fish. Continued assessment of these large-scale density reductions will be paramount in determining the full benefit (i.e., growth improvement) and duration (reduced intraspecific competition) of these activities.

In 2017, we observed high abundance of age 1 Brown Trout in Spearfish Creek, particularly in the canyon reach. However, we detected no evidence that recruitment varied between control and removal sections. In contrast, several studies have observed high recruitment immediately following fish removals (Hamrin and Persson 1986; Tonn et al. 1992; Persson et al. 1993) that can either restore populations to pre-reduction levels or create cyclical population swings. Additionally, in Convict Creek, California, after reductions in abundance of age 1 Brown Trout, young of the year Brown Trout increased the following year (Jenkins et al. 1999). In Swedish streams, reduced Brown Trout densities (\geq age 1) led to significant increases of age 1 trout the following year (Nordwall et al. 2001). While fish density can be negatively related to recruitment, we did not detect any evidence of increased recruitment due to large-scale density fish removal. It is possible that effects of density reduction were overshadowed by other factors that have been shown to affect Brown Trout recruitment in streams (i.e., streamflow; Nuhfer et al. 1994, Nicola et al. 2009). Streamflow averaged 1.87 m³/s during the study period and

1.81 m³/s during the winter months of November 2016 - March 2017 (U.S. Geological Survey 2016). Spearfish Creek did not experience any low-flow events during the entirety of the study period and flows remained relatively stable with low frequency and duration of high flow events, conditions promoting high survival and recruitment of Brown Trout (Nicola et al. 2009).

Large-scale density reduction appears to be a viable management technique for improving growth rates of stream-dwelling salmonids that suffer from density-dependent growth. Density reduction provided increased growth in both length and weight for age 3 and 4 Brown Trout. Additionally, bioenergetics modeling provided an explanation as to why larger Brown Trout were more susceptible to density-dependent growth. Due to the lack of large aquatically-derived prey, larger Brown Trout were forced to rely on terrestrially-derived prey, a seasonally and spatially variable prey source, to meet their energy requirements. These results underscore the importance of considering factors that might be limiting growth in the population (i.e., prey resources), and relatedly, those cohorts most affected by limited resources. Identifying those cohort(s) where density-dependent growth is believed to be most pronounced could help focus efforts on targeted reduction of specific sizes/ages of fish that minimize the cost:benefit ratio of large-scale fish removal efforts.

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Table 2.1. – Population estimates of Brown Trout (> age 1) collected from removal or control sections in Spearfish Creek, SD in 2016 and 2017.

Population Treatment	Reach	Section Elevation (m)	Fish / ha		% change
			2016	2017	
Removal	Town	1,082	1,215	1,003	-17
	Town	1,130	2,086	2,092	0.3
	Canyon	1,373	2,837	2,051	-28
	Canyon	1,465	2,875	2,502	-13
	Canyon	1,516	2,475	2,220	-10
	Canyon	1,536	2,056	948	-54
	Canyon	1,609	1,215	1,003	-17
	Average			2,108	1,688
Control	Town	1,104	1,710	1,208	-29
	Town	1,116	1,421	1,092	-23
	Canyon	1,480	2,378	3,396	43
	Canyon	1,486	1,850	2,764	49
	Canyon	1,553	2,040	1,810	-11
	Canyon	1,565	2,887	3,092	7
	Canyon	1,589	2,507	2,375	-5
	Average			2,113	2,248

Table 2.2. – Relative weight of Brown Trout (> 140 mm) collected from removal or control sections in Spearfish Creek, SD in 2016 and 2017. Values in parentheses represent one standard error.

Population Treatment	Reach	n	Wr		% change
			2016	2017	
Removal	Town	2	98.6 (3.68)	100.8 (4.52)	2
	Canyon	5	96.3 (0.67)	93.5 (1.04)	-3
	All Sections	7	96.9 (1.02)	95.6 (1.82)	-1
Control	Town	2	100.7 (1.18)	99 (3.71)	-2
	Canyon	5	99.4 (1.14)	93.5 (0.6)	-6
	All Sections	7	99.8 (0.86)	95.1 (1.35)	-5

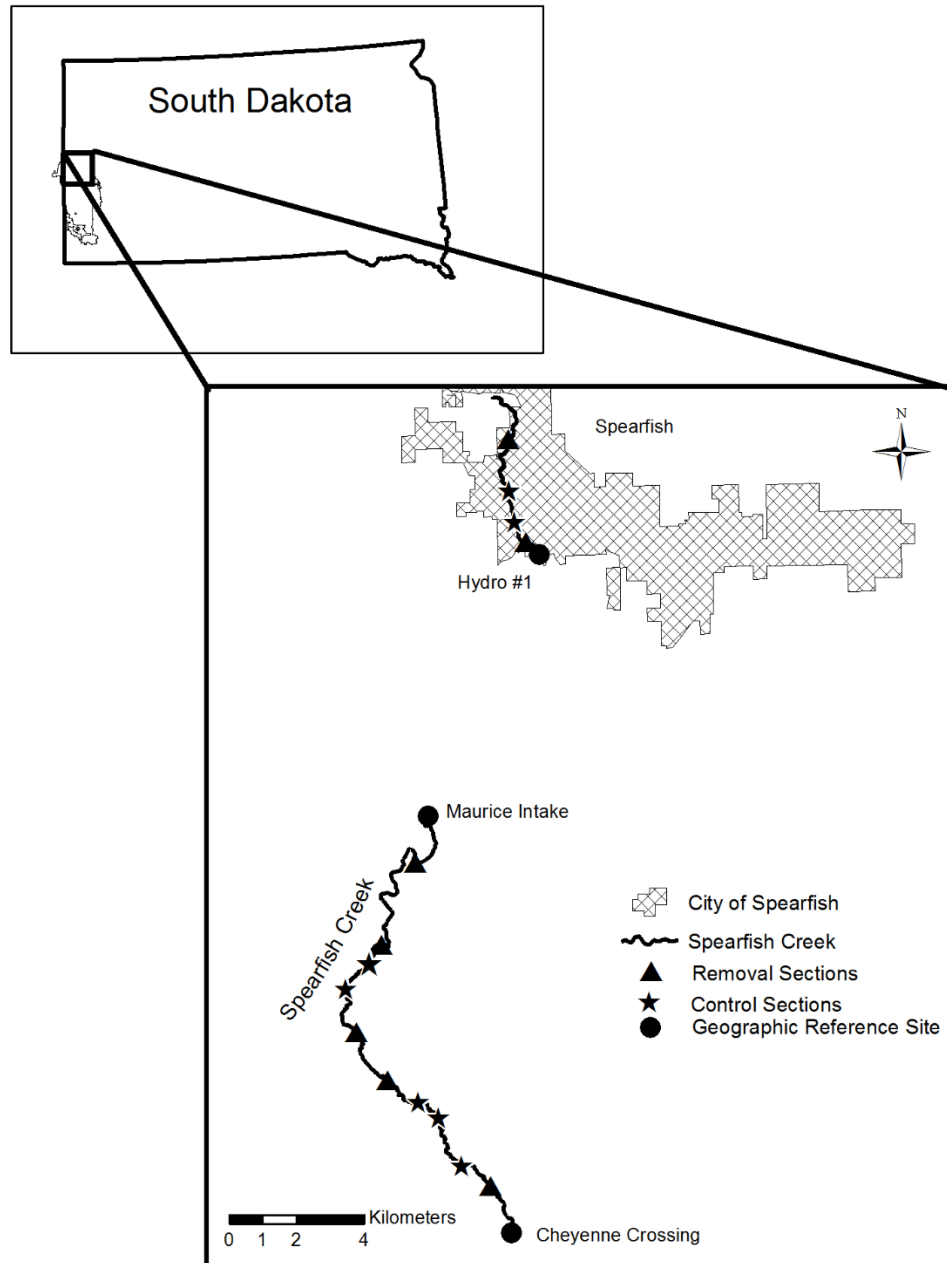


Figure 2.1. – Spearfish Creek, Black Hills, South Dakota; triangles depict removal sections, stars depict control sections and circles depict geographic reference sites. Areas within the inset marked with cross-hatching indicate Spearfish city boundaries. The outline within South Dakota and within the inset depicts the boundary of the Black Hills.

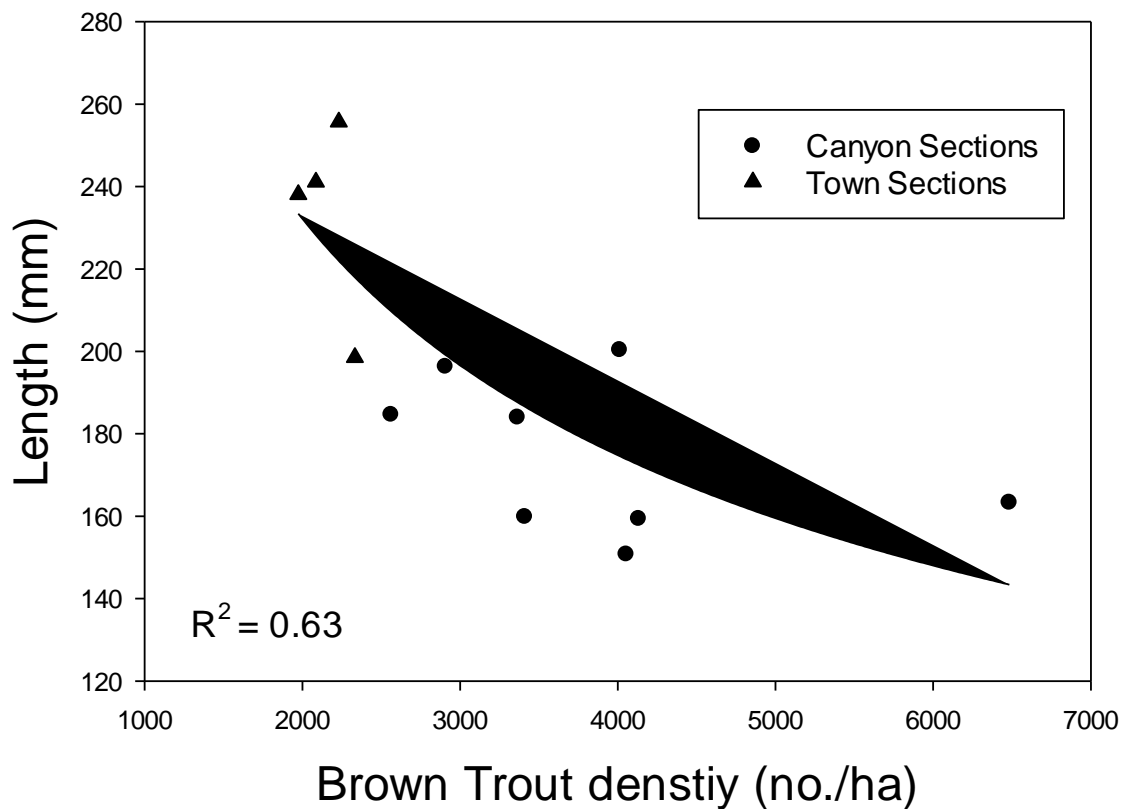


Figure 2.2. – Mean length of Brown Trout as function of fish density at fourteen sections in Spearfish Creek, SD, 2016. Line represents power curve fitted to the data (Mean Length (mm) = $5227.37(\text{no./ha})^{-0.41}$). Triangles depict town sections and circles depict canyon sections.

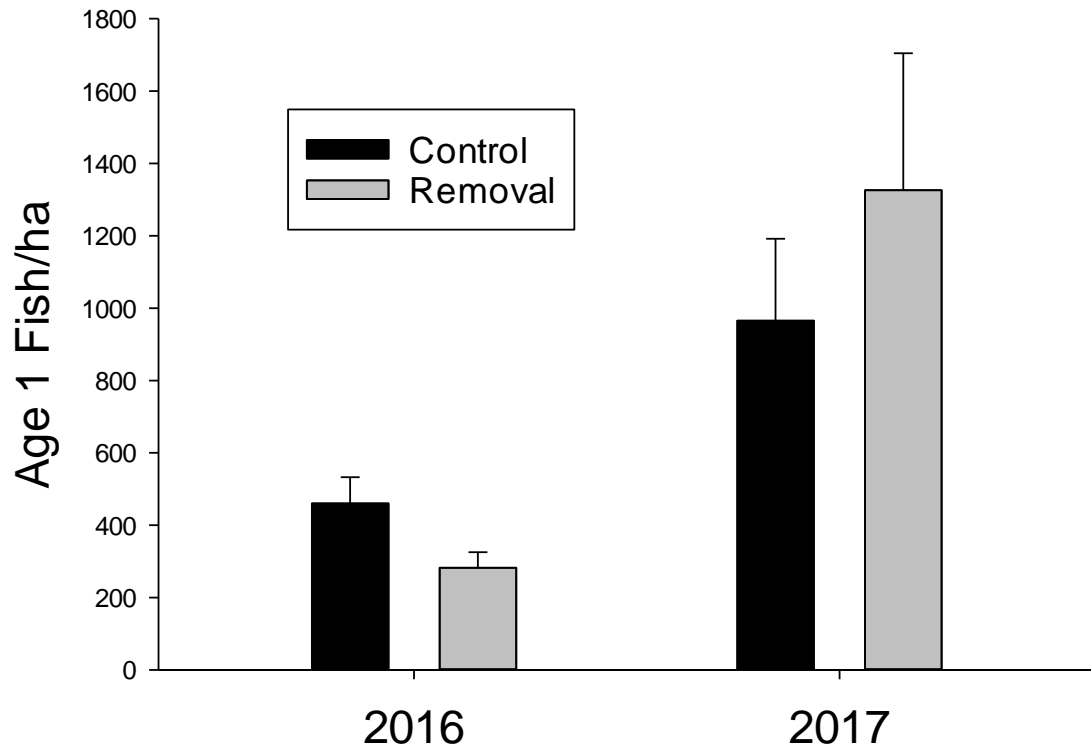


Figure 2.3. – Mean abundance of age 1 Brown Trout sampled in control and removal sections during both the 2016 and 2017 sampling periods

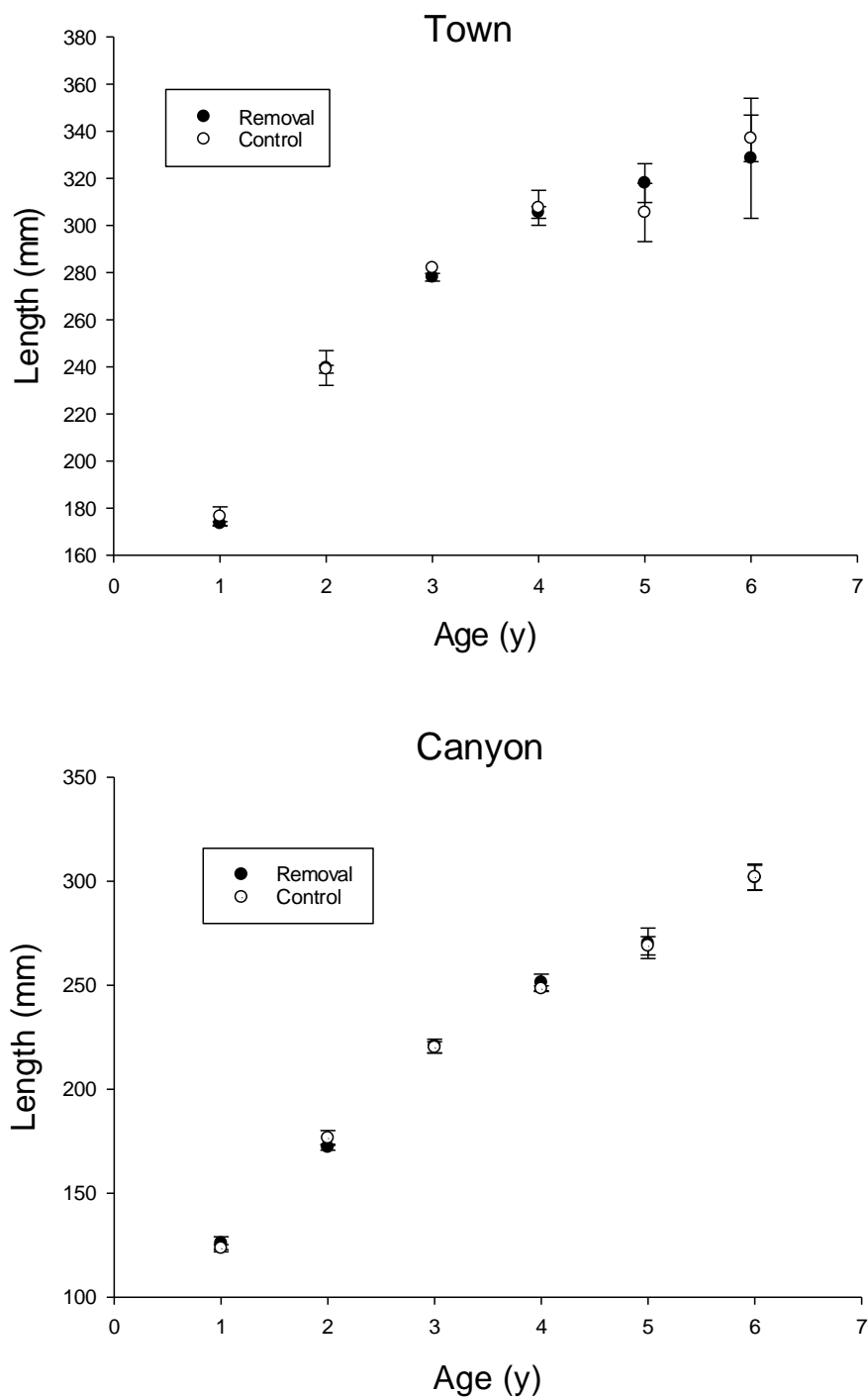


Figure 2.4. – Mean length at age by treatment group in town (top) and canyon (bottom) reaches of Spearfish Creek, SD, 2016. Error bars represent 90 % confidence intervals.

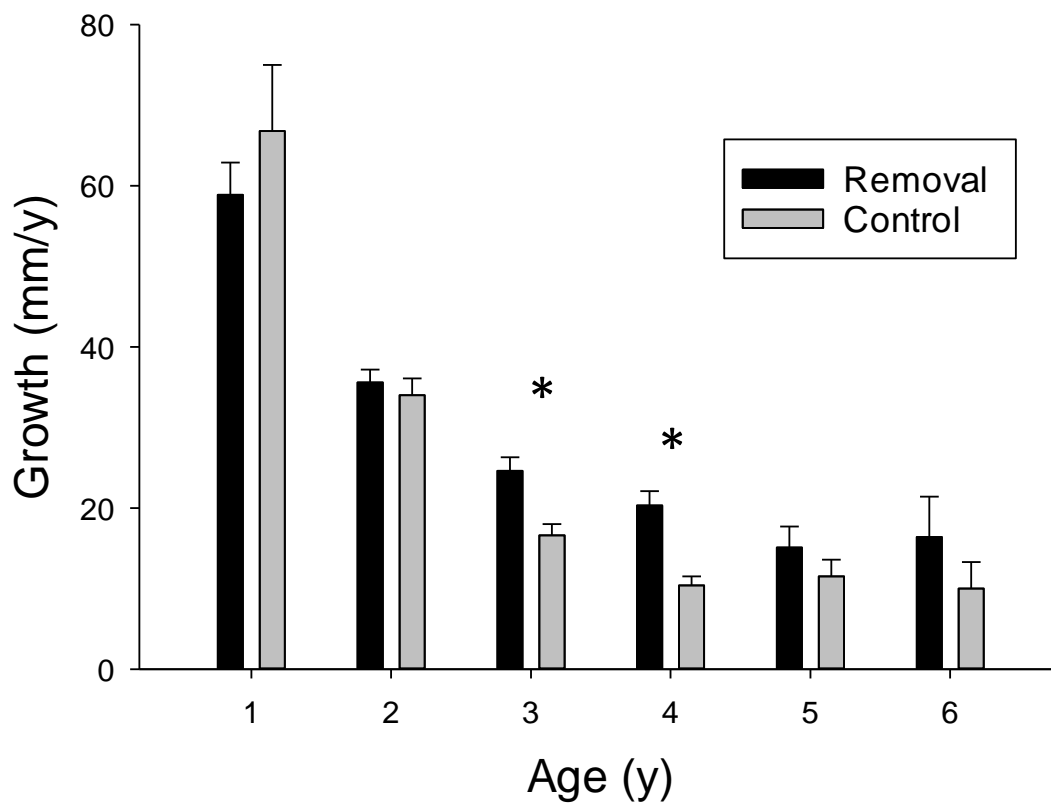


Figure 2.5. – Mean annual growth rate (mm/y) of PIT-tagged Brown Trout in Spearfish Creek, SD. Growth rates for age 1-6 fish are shown for removal (solid bars) and control sections (gray bars). Error bars represent 1 S.E. and * denotes significant differences between treatment groups.

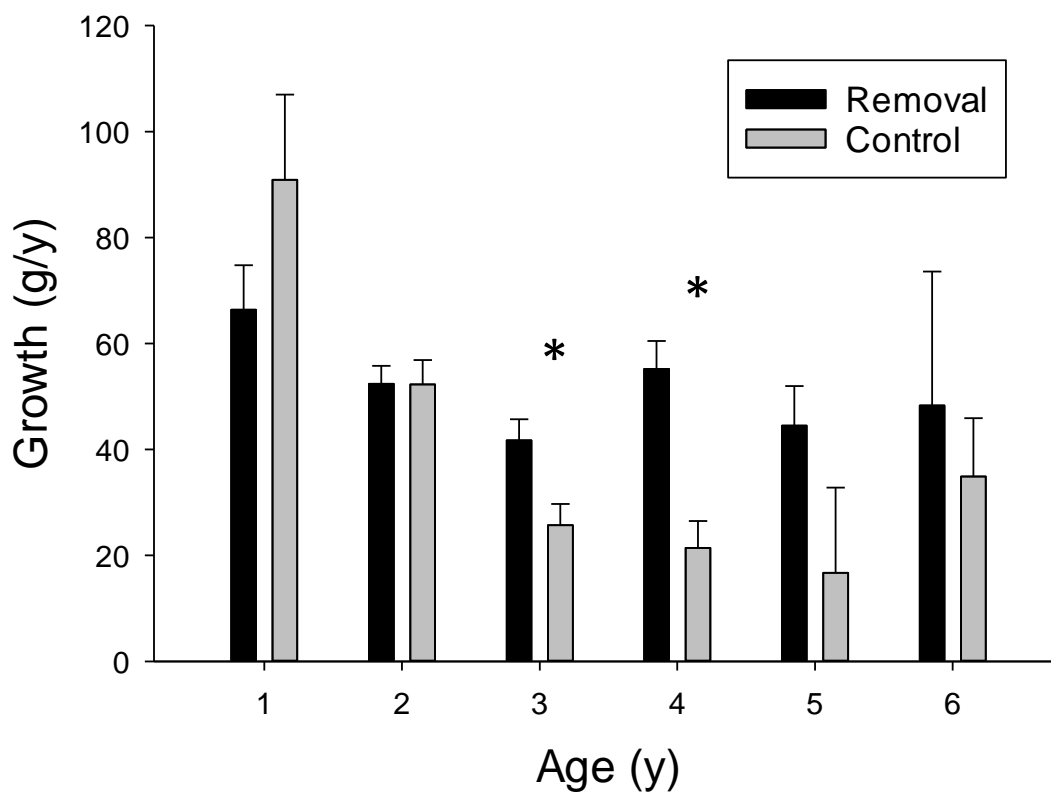


Figure 2.6. – Mean annual growth rate (g/y) of PIT-tagged Brown Trout in Spearfish Creek, SD. Growth rates for age 1-6 fish are shown for removal (solid bars) and control sections (gray bars). Error bars represent 1 S.E. and * denotes significant differences between treatment groups.

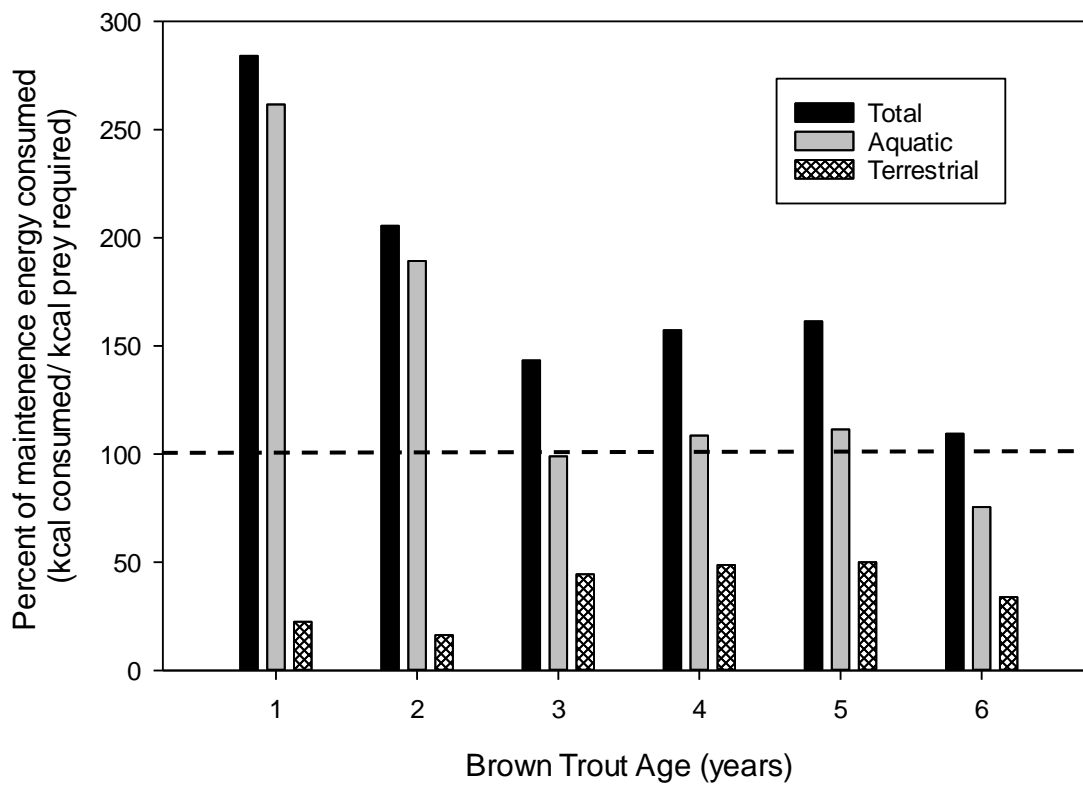


Figure 2.7. – Age specific consumption by Brown Trout in Spearfish Creek, SD. Bar values represent total food consumption, consumption of aquatic invertebrates or consumption of terrestrial invertebrates as a proportion of annual maintenance requirements (see text for details). The dashed, horizontal line represents annual maintenance requirement for each age cohort (i.e., no growth). Bar values are based on observed growth rates and show whether annual maintenance requirements were 1) met (dashed line), 2) not met (below dashed line) or 3) exceeded (above dashed line) for each food category.

CHAPTER 3

EFFECTS OF LARGE-SCALE DENSITY REDUCTION ON MOVEMENT AND
HOME RANGE OF BROWN TROUT**Abstract**

We assessed the effect of fish density manipulation on Brown Trout movement patterns and home range size. We compared individual movement, net movement and home range size of Brown Trout between stream sections with targeted fish removals (50% reduction) to those with natural fish densities in Spearfish Creek, South Dakota. We found no evidence that movement patterns or home range size of stream-dwelling Brown Trout differed between sections with natural densities and those where fish density was reduced. There was no relationship between fish density and fish movement parameters or home range size. Brown Trout in Spearfish Creek exhibited limited movement and home range sizes following reductions in fish density. Brown Trout tracked during fall-winter months were observed exhibiting larger individual movement and home range size presumably related to fall spawning activities, although net movement was similar to spring/summer periods – indicating strong site fidelity. A small proportion of radio-tagged (6%) trout exhibited extended movements (> 0.6 km), typical of straying behavior in salmonids. Many factors have been shown to effect variability of movement of stream-dwelling Brown Trout, however, it does not appear that fish density is among them.

INTRODUCTION

Stream-dwelling fishes often exhibit restricted movements, occupying small home range sizes and showing high site fidelity (Gerking 1959; Cargill 1980; Bachman 1984). However, large variability in movements and home range size between species and water bodies has been documented (Gerking 1959; Gowan et al. 1994; Smithson and Johnston 1999; Hilderbrand and Kershner 2000; Rodríguez 2002). Though home range size in stream-dwelling salmonids is reportedly small for many species, there is notable variation among studies. Observations of stream-dwelling Rainbow Trout *Oncorhynchus mykiss* show home range sizes ranging from 165 m (Cargill 1980) to 606 m (Young et al. 1997). Home range size of Brook Trout *Salvelinus fontinalis* varies with stream size and can be an order of magnitude greater in larger tributary streams (Petty et al. 2012). Brook Trout observed in high-elevation streams commonly traveled distances of at least 50 m (up to 3380 m), with most tracking periods being just a few months (Gowan and Fausch 1996). Small, stream-dwelling Cutthroat Trout *O. clarki* home ranges have been assessed ranging from 4 m (Heggenes et al. 1991) to 223 m (Young 1996). However, larger river-dwelling Cutthroat Trout and Bull Trout *S. confluentus* have been observed occupying home ranges of 67 km and 68 km, respectively (Schoby and Keeley 2011)

Many factors have been shown to influence the movements of stream-dwelling salmonids and include fish size, time of day, temperature, season, and condition. In south-central Wyoming streams, Brown Trout *Salmo trutta* >340 mm inhabit larger home ranges and move further distances than Brown Trout <340 mm (Young 1994). Brown Trout >400 mm exhibit strong site fidelity in home sites during daylight hours with fish making larger nocturnal movements (Clapp et al. 1990; Diana et al. 2004). Cutthroat

Trout in Beaver Creek, Idaho-Utah and Brown Trout in Silver Creek, Idaho, demonstrate a significant diel pattern, moving more during crepuscular periods and night (Young et al. 1997; Hilderbrand and Kershner 2000). Brook Trout inhabiting the upper Shavers Fork of the Cheat River, West Virginia move to seek out cooler microhabitats, as a means of thermoregulation, during times of stressful temperatures (Petty et al. 2012). Brown Trout, Colorado River Cutthroat Trout, Bull Trout and Westslope Cutthroat Trout all show significant variation in movement and activity associated with season, commonly related with spawning activities (Young 1996; Burrell et al. 2000; Schoby and Keeley 2011). Furthermore, Brook Trout in poorer condition in high-elevation Colorado streams make longer movements than the rest of population (Gowan and Fausch 1996).

Stream-dwelling Brown Trout have been characterized as a sedentary species owing to their high site fidelity and limited movement (Bachman 1984, Burrell et al. 2000; Knouft and Spotila 2002). Brown Trout also commonly inhabit small home ranges (Heggenes 1988; Burrell et al. 2000; James et al. 2007). However, some research indicates that larger individuals (>400mm) exhibit greater movement, often occurring during night or crepuscular periods with fish returning to their home 'sites' during daylight hours (Clapp et al. 1990; Diana et al. 2004). While observing Brown Trout in Spruce Creek, PA researchers calculated wild fish home range to be 15.6 m². They found that home ranges were established in the first two years of life and changed little throughout a fish's lifetime (Bachman 1984). Home range size of Southern Appalachian Brown Trout ranged from 27.7 m to 98.6 m with the largest home range and movement occurring in the fall associated with spawning activities (Burrell et al. 2000). In contrast, 64% of Brown Trout tracked over an 11-month period in the Motupiko River, New

Zealand moved less than 1 km, however movement up to 41 km was observed (Young et al. 2010). Recent work in Rapid Creek, South Dakota has shown that Brown Trout averaged yearly gross movements of 506 m and net movements of 49.4 m downstream, with fish exhibiting high site fidelity and little migratory movement excluding fall spawning activities (James et al. 2007).

While several factors have been shown to influence stream-dwelling salmonid movements, the effect of fish density or large-scale density reduction on movement patterns are not well documented. In Spearfish Creek, SD, growth rate of Brown Trout has been linked to fish abundance, with density ranging from 1,590 to 3,593 Brown Trout >100 mm/ha and averaging 2,648 Brown Trout >100 mm/ha (See Chapter 2). At densities of 262 fish/ha and 209 fish/ha > 15 cm, fish abundance reportedly has no influence on movement patterns of Brown Trout in Michigan and Norwegian streams (Mense 1975; Heggenes 1988). In this study, we quantify effects of large-scale, population reductions on movement patterns of Brown Trout in Spearfish Creek, SD. Given the sedentary behavior of Brown Trout, we postulate that movement and home range size will be similar between control sections and removal sections where 50% of the population was removed.

METHODS

Study site

Spearfish Creek is located in the northern Black Hills of South Dakota (Figure 3.1). It flows north out of the Black Hills through the town of Spearfish. The creek originates from springs in the Mississippian Madison Limestone and gains and loses

surface flow from a shallow alluvial aquifer (Stetler and Sieverding 2001). Spearfish Creek has an annual mean discharge of about 1.53 m³/s (Koth 2007). The creek is characterized by two reaches; the upstream reach includes the headwaters to the lower end of Spearfish Canyon and the downstream reach begins near the town of Spearfish and extends to the confluence with the Redwater River. The two reaches of Spearfish Creek are separated by a de-watered reach, starting at Maurice Intake and ending at Hydro #1 (Figure 3.1). This dewatering is caused by a limestone losing reach in addition to an aqueduct that diverts stream flow at Maurice to a small hydroelectric power plant on the southern edge of the town of Spearfish, resulting in a 12 km dry section between the two reaches. The aqueduct, built in the late 1800s circumvents a limestone loss zone that extends all around the Black Hills (Koth 2007). Stream substrates are characterized by a calcite precipitate layer owing to high levels of calcium and magnesium in the water (Stetler and Sieverding 2001). The calcite precipitate is more predominate in the Spearfish Canyon portion of the creek than in the downstream reach. The creek is home to three non-native, but naturalized, salmonid species: Brown Trout, Rainbow Trout, Brook Trout, and Cutthroat Trout.

For our study, we focused on two reaches; the first reach extends from Maurice Intake upstream to Cheyenne Crossing and constituted the upper reach (canyon reach; Figure 3.1). The second sampling reach extended from the northern city limits of Spearfish, SD upstream to the Hydro #1 facility and represented the lower reach (town reach; Figure 3.1). In these reaches, we selected a total of fourteen, 425 m (~0.25 mile) sampling sections. Sampling sections were selected in consultation with South Dakota Game Fish and Parks (SDGFP) biologists and through analysis of long-term fisheries

data to identify stream reaches that were characterized by relatively high Brown Trout density. Ten sections were located in the canyon reach and four sections were selected in the town reach. Seven sections (hereafter called ‘removal’) were randomly selected to receive Brown Trout density manipulations, and during August 2016 we removed 50% of the Brown Trout population. Two removal sections were randomly selected in the town reach and five randomly selected in the canyon reach. Similarly, the remaining seven sampling sections served as controls where trout were sampled but not removed. To minimize the effects of fish movement among sections, we ensured that adjacent sections were separated by at least 425 m (Jenkins et al. 1999). Because of small net movement (< 100 m; Bachman 1984; James et al. 2007) and home range size (40-200 m; Young 1999; Burrell et al. 2000) of Brown Trout, a distance of 425 m was deemed large enough to minimize the probability that natural movement would result in fish being detected in more than one section.

Density reduction

We assessed Brown Trout size, age, abundance, and condition in all fourteen sections in two reaches of Spearfish Creek during the summers of 2016 and 2017 (see Chapter 2). Block nets were placed at the lower and upper bounds of each section immediately prior to fish sampling. Nets were used to minimize immigration and emigration of fish in the sections during sampling. Stream width (n=11) was measured at transects spaced ~39 m apart at each section. We collected fish in July-August 2016 using two back-pack electrofishing units (LR24 Electrofisher, Smith-Root, Vancouver, WA). All fish captured were measured (total length, TL, mm) and at least 150 randomly selected fish per section were additionally weighed (g). Three pass electrofishing

depletion surveys were used to determine initial size, abundance, and condition at all sections (Bonar et al. 2009). During sampling events all fish from each electrofishing pass were retained in net pens immediately above the upstream block net, until sampling and density reductions were completed. Additionally, in the seven removal sections we reduced Brown Trout density (>100 mm) by 50% (see Chapter 2: for complete description). We returned to all fourteen sections in August-September of 2017 and re-sampled Brown Trout to evaluate effects of density reduction on growth and abundance. We collected Brown Trout using two back-pack electrofishing units as previously described, and measured (total length, TL, mm) and at least 150 fish per section were additionally weighed (g). We also estimated population size of Brown Trout >100 mm in each section (see Chapter 2).

Radio-tagging

To evaluate movement patterns radio tags were implanted in adult Brown Trout in Spearfish Creek, fish were collected using standardized methods via back-pack electrofishing (Smith-Root, LR24 Electrofisher, Vancouver, Washington; Bonar et al. 2009). A total of 38 Brown Trout were surgically implanted with radio transmitters (Advanced Telemetry Systems, Model F1550 implant transmitter, Isanti, MN) in the abdominal cavity (Table 3.1). The F1550 implant transmitters have an air weight of 2.2 g and an expected battery life of 68-158 days. Surgeries were performed streamside and fish were returned directly to the site of capture upon recovery from anesthesia. Prior to surgical implantation of radio transmitters, fish were anesthetized using 100 mg/L Finquel MS-222 (Tricaine Methanesulfonate). Brown Trout that received radio transmitters ranged from 215-337 mm total length (TL) and weighed between 111 and

389 g (Table 3.1). Fish selected for tagging met weight requirements complying with the general rule that tags weigh less than 2% of its body mass to ensure that fish were not negatively affected by the added weight of transmitters (Winter 1983, 1996; Cooke et al. 2012; Table 3.1).

Brown Trout were placed in a water bath containing the anesthetic until fish lost equilibrium (Summerfelt and Smith 1990). Once anesthetized, fish were measured (total length, TL, mm), weighed (g) and positioned ventral side up in wetted soft foam V-shaped surgery table. Gills were irrigated with stream water containing MS-222 at 100 mg/L throughout the duration of the surgical procedure. A 20 mm incision was made right of the ventral midline using a disposable #10 scalpel blade. The radio transmitters were then inserted into the abdominal cavity and the shielded-needle technique (Ross and Kleiner 1982) was used to execute the exit of the antenna from the body cavity posterior to the incision. The incision was closed using 2-3 simple interrupted sutures (Oasis, nylon monofilament 4-0 sutures, Glendora, California). Immediately following the surgical procedure, fish were placed into a stream-side water bath and allowed to recover (5-10 minutes) until they regained equilibrium and normal swimming abilities. Once fish fully recovered from anesthesia and appeared to be in good condition, they were released back into the stream at the point of capture.

Eighteen Brown Trout received transmitters between August 16-September 2, 2016, which we refer to as fall-winter fish. Twenty additional Brown Trout received transmitters between March 6-7, 2017, which we refer to as spring-summer fish. To compare movement of fish between control and removal sections, we tagged at least one fish per section during both tagging periods, in both town and canyon reaches.

Radio telemetry methods

Fish locations were obtained using radio telemetry, from August 17, 2016 to July 17, 2017. Fish were tracked 3-5 times per week from August 17- November 10, 2016, then weekly until July 17, 2017. Due to inclement weather, fish were not located during two separate weeks during the winter months (January-February 2017). All fish were tracked through the life of their transmitters or until the tracking end date August 17, 2017 when only seven transmitters were still sending a signal. Fish locations were recorded from the edge of the stream bank using the zero-point tracking method described by Cooke et al. (2012). In addition to GPS coordinates, time of day, date, and water temperature were also recorded. Locations of fish were identified using a Lotek wireless receiver (Biotracker, Newmarket, Ontario Canada) paired with a three-element folding Yagi antenna (AF Antronics Inc., Model F150-3FB 14318, Urbana, Illinois). Fish locations were documented using Survey123 for ArcGIS on a Samsung tablet (Model SM-T550, Seoul, South Korea) connected via Bluetooth with BadElf GNSS Surveyor handheld GPS (Model BE-GPS-3300, Tariffville, Connecticut). GPS accuracy was assumed to be ± 2.5 m based on manufactures specifications.

PIT-tagging and recapture

During 2016, passive integrated transponder tags (PIT) were implanted into ~150 Brown Trout per section (n=14 sections; Biomark, HDX12, Boise, Idaho). Tags were injected into the abdominal cavity using a UID Identification Solutions implant gun (Multi PIT Tag Injector, Lake Villa, Illinois). All fish that received PIT tags were measured (total length, TL, mm), weighed (g), and the individual PIT tag number was

recorded. All fish captured during 2017 were scanned for PIT tags (Avid, Power Tracker VII, Norco, California) and recaptured PIT tagged fish were measured (total length, TL, mm), weighed (g), and the individual PIT tag number and location was recorded.

Data analysis

The spatial distribution of radio-tagged trout was analyzed using ArcGIS. This allowed us to calculate mean individual movement, net movement, and home range size of tagged Brown Trout. Mean individual movement was calculated by averaging all movements regardless of up or downstream directional movement for each fish. Net movement was calculated by summing all movements, where upstream movements were positive values and downstream movements were negative values for each fish. Finally, home range was calculated by measuring the distance between the most upstream point and the most downstream point of a fish's location, similar to methods used by Young (1994), Burrell et al. (2000), and Ertel et al. (2017). Fish locations were overlaid on a GIS layer with satellite imagery, so that Spearfish Creek was visible. Distances between each consecutive by calendar date fish location were calculated in stream meters for each radio-tagged fish. If locations were not directly on the creek image, due to GPS error, the point was moved to the stream point directly perpendicular to the fish location. Mean individual movement, net movement, and home range were used as metrics for movement and fidelity of trout. If sections contained multiple radio-tagged fish, movement metrics were averaged among fish in that section prior to comparisons of control and removal treatments. Differences in mean individual movement, net movement, and home range size were analyzed using a two-way analysis of variance with treatment (control and removal) and time period (fall-winter and spring-summer) as

grouping factors. Pearson's correlation analysis was used to explore relationships between average fish density (2016-2017) and mean individual movement, net movement and home range size. Prior to analysis, the first week of recorded fish locations were excluded due to erratic behavior of fish post-surgery (Mesing and Wicker 1986). Five fish were also excluded from analysis due to apparent mortality. An additional fish was excluded from analysis that made a substantial outlying movement. This fish made small movements and exhibited high site fidelity for ~2 months post radio tagging followed by a 2376 m movement upstream. The fish then resumed small movements and high site fidelity at the new location through the life of the radio tag. We believe its exclusion better represents the typical movement patterns of Brown Trout in Spearfish Creek.

Locations of recaptured PIT-tagged fish were used to compare fish movement and site fidelity between control and removal sections. Using recapture locations, we compared the proportion of PIT-tagged fish that were recaptured from (1) their initial tagging location (i.e., section), (2) an adjacent section that was immediately upstream or downstream of their initial tagging location, or (3) a non-adjacent section that was upstream or downstream from their initial location. We used a Pearson's chi-squared test to compare the distribution of recapture locations between treatment groups. Analyses were conducted using Program R (R Core Team 2017).

Results

Density reduction

In 2016, we collected 12,731 fish via backpack electrofishing from all fourteen sections along Spearfish Creek (Table 3.2.). Initial lengths of Brown Trout sampled in

2016 were negatively related to fish densities, with the relationship best described by negative power function ($r^2 = 0.63$, $P < 0.001$; Figure 3.2). In the seven removal sections, we reduced Brown Trout density by removing a total of 3,091 fish. We returned to the creek in August-September 2017 and collected a total of 15,741 fish all fourteen sections. Comparison of Brown Trout densities showed that fish density declined significantly in removal sections from 2016 to 2017 but did not decrease in control sections (See Chapter 2; Table 3.2).

Radio telemetry

A total of 778 fish locations were recorded from August 17, 2016 to July 17, 2017. Average length of the tracking period for the fall-winter period was 174 days and 115 days for the spring-summer period. Overall, radio-tagged Brown Trout exhibited small individual movements (Figure 3.3), high site fidelity (Figure 3.4), and small home range size (Figure 3.5). Mean individual fish movement was similar between removal (14.8 m, $n=13$, SE 2.1) and control (12.6 m, $n=13$, SE=1.3) sections ($F_{1,23} = 0.92$, $p = 0.34$). Mean net movement was (-15.2 m, $n = 13$, SE = 30.8) or (7.9 m, $n = 13$, SE = 12.1) for removal and control sections, respectively, and did not differ between treatments ($F_{1,23} = 0.92$, $p = 0.49$). Home range size also did not differ between removal (95 m, $n = 13$, SE = 35) or control (81.2 m, $n = 13$, SE = 15.8) sections ($F_{1,23} = 0.92$, $p = 0.70$; Table 3.3).

Mean individual movement during the fall-winter period (16.1 m, $n = 14$, SE = 1.9) was significantly greater than during the spring-summer period (10.9 m, $n = 12$, SE = 1.2; $F_{1,23} = 4.88$, $p = 0.03$). Mean net movement was (-10.5, $n = 14$, SE = 30.1) or (4.4 m,

$n = 12$, $SE = 8.2$) for fall-winter and spring-summer periods, respectively, and did not vary significantly between sampling periods ($F_{1,23} = 0.19$, $p = 0.66$). Mean home range size for the fall-winter period (119.9 m, $n=14$, $SE = 32.4$) was greater than that observed for the spring-summer period (51 m, $n=12$, $SE = 8.7$; $F_{1,23} = 3.53$, $p = 0.07$, Table 3.3).

We found no evidence that mean individual ($r = 0.16$, $p = 0.43$) or net movement ($r = 0.02$, $p = 0.91$) was correlated with Brown Trout density (fish/ha). Similarly, we also found no evidence that home range size ($r = -0.05$, $p = 0.77$) was correlated with density of Brown Trout.

PIT tagging and recapture

During the 2016 sampling period, we implanted a total of 2,073 Brown Trout with PIT tags, fish ranged in size from 108-444 mm (mean=225 mm; $SE=1.14$). Of the PIT-tagged fish, a total of 635 (31%) were recaptured during the 2017 sampling period. Recaptured fish ranged in size from 170-445 mm (mean=265 mm; $SE=1.66$). We found no evidence that recapture locations differed between control and removal sections (Figure 3.6; $\chi^2 = 4.87$, $df = 2$, $p = 0.09$). Recaptured fish also provided more evidence of small net movements of Brown Trout with 92% of fish tagged in control sections and 96% of fish tagged in removal sections being re-captured at their original tagging section (Figure 3.6).

Discussion

Density-dependent growth is a characteristic trait among many Brown Trout populations, but interestingly, fish density had little to no influence on immigration or emigration patterns as documented by our study. Significant reductions of Brown Trout

densities as high as 1,804 fish/ha had no measurable influence on movement patterns of individual fish. Brown Trout (>150 mm) movement patterns that were anecdotally recorded in a Michigan stream were similar during a two-year period, despite a significant decrease in population abundance from 209 to 87/ha (Mense 1975). In a related study, Heggenes (1988) experimentally increased stream-dwelling Brown Trout density by 242 fish/ha (i.e., intraspecific competition), but found no evidence of altered movement patterns. Brown Trout abundance in two Swedish streams was experimentally increased by 61-150% and researchers increased abundance using wild caught fish in four sections and hatchery fish in another four. They found movements of Brown Trout to be independent of density, suggesting that fitness costs of leaving an area and searching for a more profitable alternative were high (Bohlin et al. 2002). In another study, natural densities of Brown Trout age 0 and \geq age 1 were experimentally removed (2,500 fish/ha) from Swedish stream sections. Researchers found no difference in Brown Trout movements between sections contain reduced fish densities and those containing natural fish densities (Kaspersson and Höjesjö 2009). Our research collaborates past findings that density of Brown Trout does not influence movement patterns.

Marine reserves are commonly used to conserve and protect fish communities from overfishing in marine environments. These reserves exclude fish harvest in their boundaries. Fish movement beyond the boundary of these reserves decreases their benefit, exposing fish to harvest (Grüss et al. 2011). Species with low mobility benefit most from marine reserves, with increasing abundance compared to more mobile species (Chapman and Kramer 1999). A major positive mechanism proposed during creation of marine reserves is the idea of density dependent spill over, where net export of adult fish

has a positive influence on adjacent fisheries. However, demonstrations of density dependent spill over functioning in marine reserves has been difficult (Willis et al. 2003; Hilborn et al. 2004), particularly for low mobility species that reap the greatest benefits from these no harvest areas (Willis et al. 2001). These marine reserves function similarly to natural high-density areas adjacent to removal sections in Spearfish Creek. Analogous to findings in marine environments we did not detect density dependent spill over into reaches that received large-scale density reduction, adding more evidence that fluctuating densities does not change established movement patterns of fishes.

Brown Trout in Spearfish Creek displayed limited movement, small home range, and exhibited a high degree of site fidelity. Of all radio-tagged Brown Trout 81% had observed home ranges less than 100 m and as small as 20 m. The large number of recapture PIT-tagged fish found in their original tagging location provided us with supporting evidence of high site fidelity and small net movements. These findings support previously described movement of stream-dwelling Brown Trout (Burrell et al. 2000; Knouft and Spotila 2002; Young et al. 2010). Brown Trout in the River Gwyddon, South Wales, exhibited similar movements with the majority of Brown Trout moving less than 15 m and rarely exceeding 50 m (Harcup et al. 1984). Southern Appalachian Brown Trout occupy similar home ranges, ranging from 27 m to 98 m (Burrell et al. 2000). Net movement (-3.65 m) of Brown Trout in Spearfish Creek was similar to that reported for Brown Trout in Rapid Creek, SD (-49.4 m; James et al. 2007). An important assumption of this fish movement data is that transmitters do not influence fish movement. Four radio tagged fish were recaptured after the tracking period had ended. All of these fish retained

their transmitters had grown, and appeared to be in good condition, implying that radio tag implantation likely had little influence on movement behavior.

Extended movements for an individual fish often involve biological costs, including risk of predation and excess energy expenditure (Yoder et al. 2004; Závorka et al. 2015). The decision to move involves a tradeoff between fitness benefits and costs (Závorka et al. 2015; Dingle and Drake 2007). Závorka et al. (2015) proposed that more active individuals (e.g., larger movements) adopt a high gain/high cost strategy that can be an advantageous life history strategy in high food availability environments. However, this high gain/high cost strategy can be detrimental under lower food availability situations, where energy intake does not outpace expenditure. On the contrary, less active individuals adopt a low gain/low cost strategy (less movement) allowing them to continue to grow under more variable environmental conditions. With density of Brown Trout (>100 mm) in Spearfish Creek averaging 2,648 fish/ha (range 1,590 to 3,593 fish/ha) and growth of Brown Trout linked to fish density (See Chapter 2), we argue that Spearfish Creek's environmental conditions are suboptimal (i.e., high fish density, limited resources). These suboptimal conditions should select for Brown Trout that follow a low gain/low cost life history strategy (Elliott 1989; Northcote 1992). With naturalized Brown Trout present in Spearfish Creek since 1890 (Barnes 2007), there has been ample time for local stocks to adapt to these sub-optimal conditions. We would expect selection to favor a life history that exhibits small movements and home range size, similar to those observed during this study.

In a meta-analysis of 66 different fish species, home range size was shown to be positively correlated with fish size (Woolnough et al. 2009). Additionally, field studies

have shown that Brown Trout have been recorded moving large distances outside the spawning season have been primary large individuals (>400 mm) and movements have been associated with active foraging (Clapp et al. 1990; Diana et al. 2004). The authors suggest that actively foraging trout target larger prey items (i.e., fish; Diana et al. 2004) and that movement may increase considerably in larger-bodied trout (Clapp et al. 1990). Brown Trout > 400 mm in Spearfish Creek are very rare (0.001%), which might explain limited movement patterns observed in our study.

Finally, food habits studies of Brown Trout in Spearfish Creek show that they consume primarily small invertebrates and terrestrial insects, with no large invertebrate prey or fish in the diet (James and Chipps 2016). These results support a drift feeding strategy (Hayes et al. 2000) over active foraging for Brown Trout inhabiting Spearfish Creek. Individuals that adopt a low cost/low gain life history strategy should gain a competitive advantage using a drift-feeding strategy. Thus, we would expect the most successful individuals to exhibit high site fidelity that occupy the most profitable feeding positions. These diet compositions, environmental conditions, and size of fish all support the general movement patterns (small movements and home range size) we observed by Spearfish Creek Brown Trout.

While small movements and small home ranges appear to be common among Brown Trout in Spearfish Creek, we did observe a small portion of individuals displaying more mobile and exploratory behaviors. An individual radio-tagged fish exhibited this pattern for ~2 months post radio tagging, then made a 2,376 m movement upstream and resumed small movements and high site fidelity in the new location. To a lesser extent, a second fish showed a similar behavior. A small proportion of the population exhibiting

these straying behaviors would be advantageous on a population level (i.e., colonizing local extirpated streams). For example, movements of stream-dwelling Creek Chub *Semotilus atromaculatus*, Blackspotted Topminnow *Fundulus olivaceus*, Green Sunfish *Lepomis cyanellus*, and Longear Sunfish *L. megalotis* were monitored in Little Glazypeau Creek, Arkansas and researchers found the majority of all monitored species to be sedentary with a small portion of the fish exhibiting exploratory movement behaviors (Smithson and Johnston 1999). Most Cutthroat Trout (61%) in Beaver Creek, Idaho-Utah, exhibit high site fidelity, whereas fewer (39%) made movements of relatively long distances, with several radio-tagged Cutthroat Trout exhibiting both mobile and sedentary behaviors (Hilderbrand and Kershner 2000), similar to those we observed in Spearfish Creek. Analogous behaviors in Brown Trout inhabiting small home ranges for months, traveling large distances, then resuming small movements once again for extended periods of time have been observed (Harcup et al. 1984; Young et al. 2010). Similar behaviors by Brown Trout were also observed in the River Gwyddon, South Wales, where the population was described as primarily containing individuals that exhibit high site fidelity with limited movement with a small portion of the population exhibiting large movements (Harcup et al. 1984). Of our radio-tagged fish, 2/33 (6%) exhibited this extended movement patterns.

Season has been shown to be factor that explains a large amount of variability in fish movement (Young 1996; Schoby and Keeley 2011). Brown Trout exhibit larger movements in Valley Creek, Minnesota (Clapp et al. 1990) and Chattooga River Watershed, South Carolina (Burrell et al. 2000) during fall-winter months. We observed a similar increase in movement and home range during the fall-winter months, with

individual movement for fall-winter tagged fish, averaging 5.2 m further than spring-summer tagged fish. We also detected a larger home range for fish in the fall-winter period ($p < 0.10$) with an average home range size that was 69 m larger than observed in spring-summer. We believe increased movement is related to spawning activity (James et al. 2007). Interestingly, while individual movement and home range size increased in the fall, we did not observe a concomitant increase in net movement. This suggests that Brown Trout return to their 'home' section of stream post-spawning activities. Brown Trout in Rapid Creek, South Dakota, display similar movements moving significantly more in fall months and regularly returned within a few meters of their pre-spawn locations (James et al. 2007).

Movement and home range size of Brown Trout were not affected by large scale density reduction, and as a result, we found no relationship between fish density and movement patterns. Given their high site fidelity, stream-dwelling Brown Trout – perhaps more so than other salmonids, are a good candidate species for density manipulations with the purpose of improving growth rate.

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Table 3.1. – Characteristics of Brown Trout implanted with radio transmitters in Spearfish Creek 2016 and 2017. Values in parentheses are one standard error

Season	Period	N	Length (mm)		Weight (g)		Transmitter: Weight ratio	
			Mean	Range	Mean	Range	Mean	Range
Fall-Winter	August-April	18	265 (8)	219-337	203 (18)	111-389	0.012 (0.001)	0.006-0.019
Spring-Summer	March-July	20	268 (6)	225-315	199 (13)	121-266	0.012 (0.001)	0.007-0.018

Table 3.2. – Population estimates of Brown Trout (> age 1) collected from removal or control sections in Spearfish Creek, SD in 2016 and 2017.

Population Treatment	Reach	Section Elevation (m)	Fish / ha		% change
			2016	2017	
Removal	Town	1,082	1,215	1,003	-17
	Town	1,130	2,086	2,092	0.3
	Canyon	1,373	2,837	2,051	-28
	Canyon	1,465	2,875	2,502	-13
	Canyon	1,516	2,475	2,220	-10
	Canyon	1,536	2,056	948	-54
	Canyon	1,609	1,215	1,003	-17
	Average			2,108	1,688
Control	Town	1,104	1,710	1,208	-29
	Town	1,116	1,421	1,092	-23
	Canyon	1,480	2,378	3,396	43
	Canyon	1,486	1,850	2,764	49
	Canyon	1,553	2,040	1,810	-11
	Canyon	1,565	2,887	3,092	7
	Canyon	1589	2,507	2,375	-5
	Average			2,113	2,248

Table 3.3. – Mean individual, net, and home range for both treatment groups and periods. Values in parentheses represent one standard error.

Movement	Treatment	
	Removal (n=13)	Control (n=13)
Mean Individual (m)	14.8 (2.1)	12.6 (1.3)
Net (m)	-15.2 (30.8)	7.9 (12.1)
Home Range (m)	95 (35)	81.2 (15.8)
Movement	Period	
	Fall-Winter (n=14)	Spring-Summer (n=12)
Mean Individual (m)	16.1 (1.9)	10.9 (1.2)
Net (m)	-10.5 (30.1)	4.4 (8.2)
Home Range (m)	119.9 (32.4)	51 (8.7)

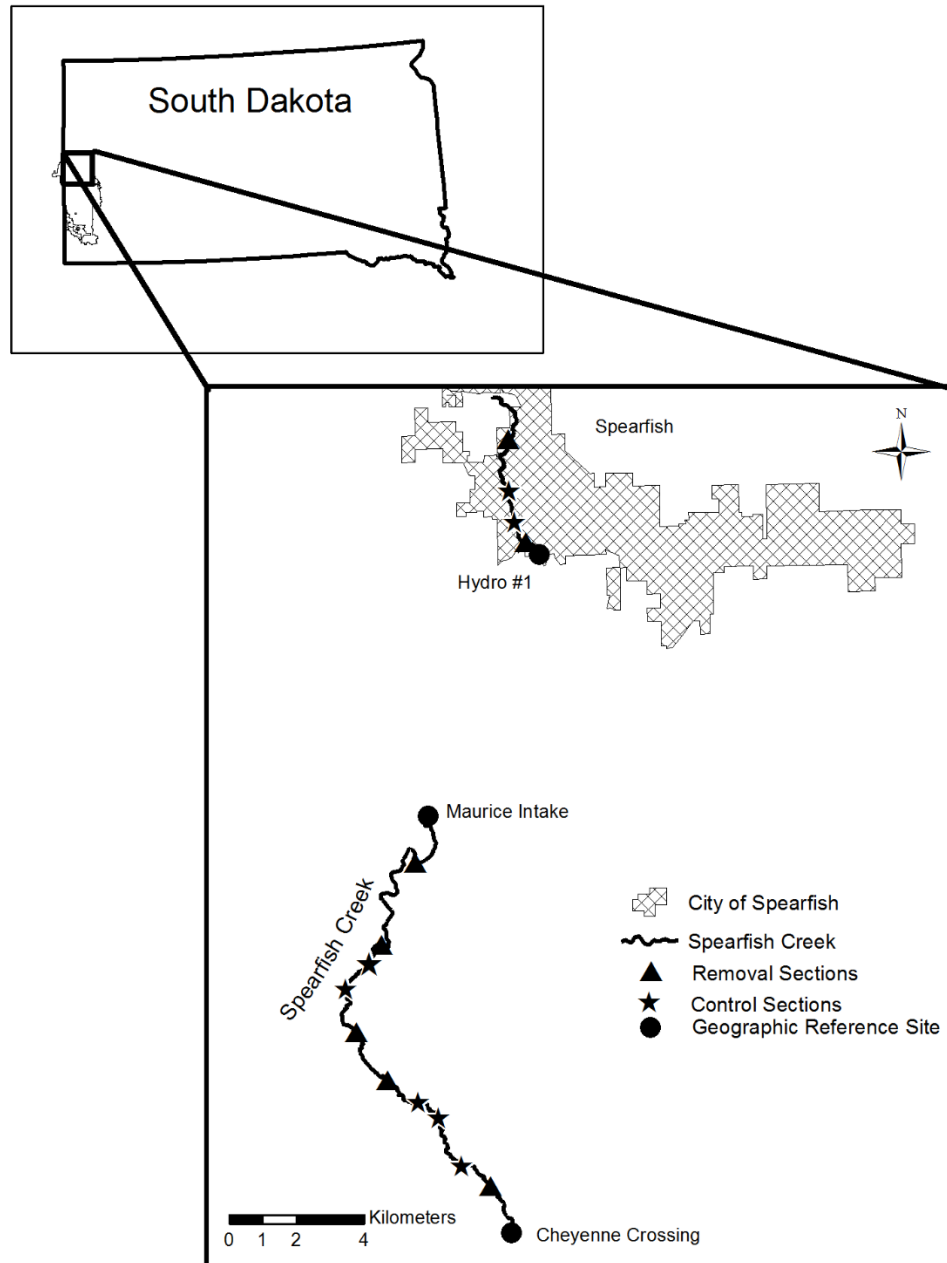


Figure 3.1. – Spearfish Creek, Black Hills, South Dakota; triangles depict removal sections, stars depict control sections and circles depict geographic reference sites. Areas within the inset marked with cross-hatching indicate Spearfish city boundaries. The outline within South Dakota and within the inset depicts the boundary of the Black Hills.

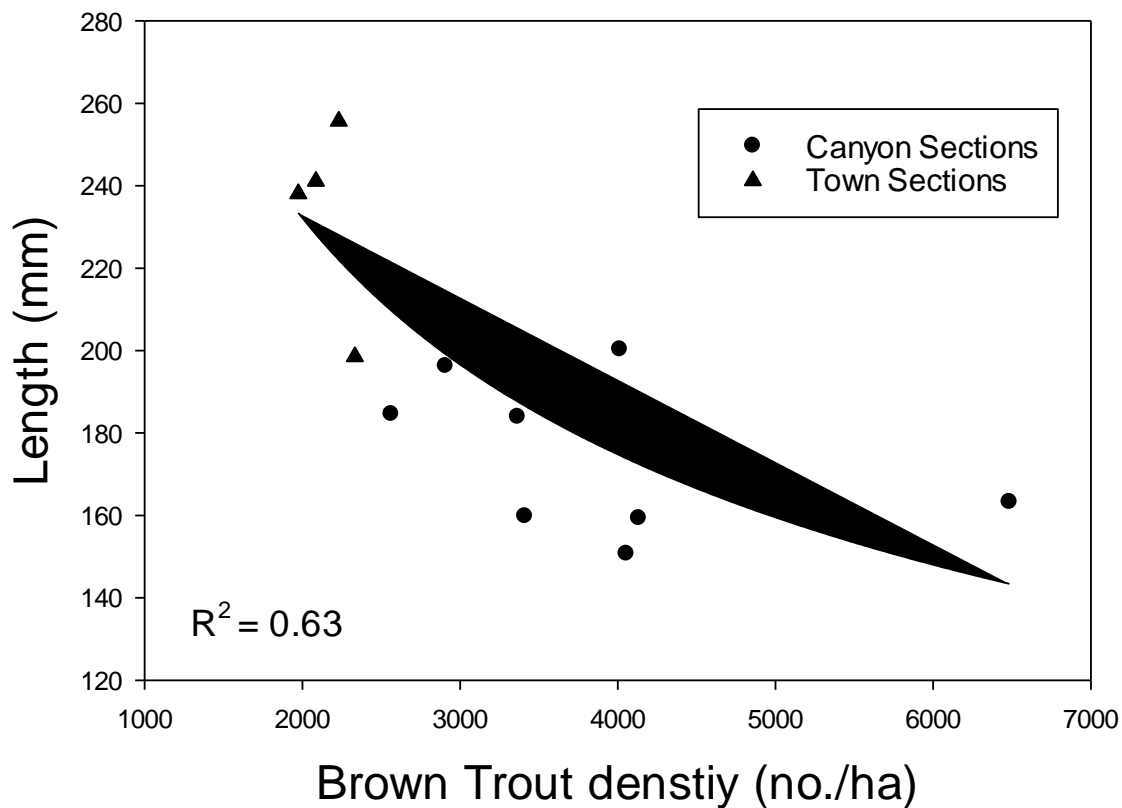


Figure 3.2. – Mean length of Brown Trout as function of fish density at fourteen sections in Spearfish Creek, SD, 2016. Line represents power curve fitted to the data (Mean Length (mm) = $5227.37(\text{no./ha})^{-0.41}$). Triangles depict town sections and circles depict canyon sections.

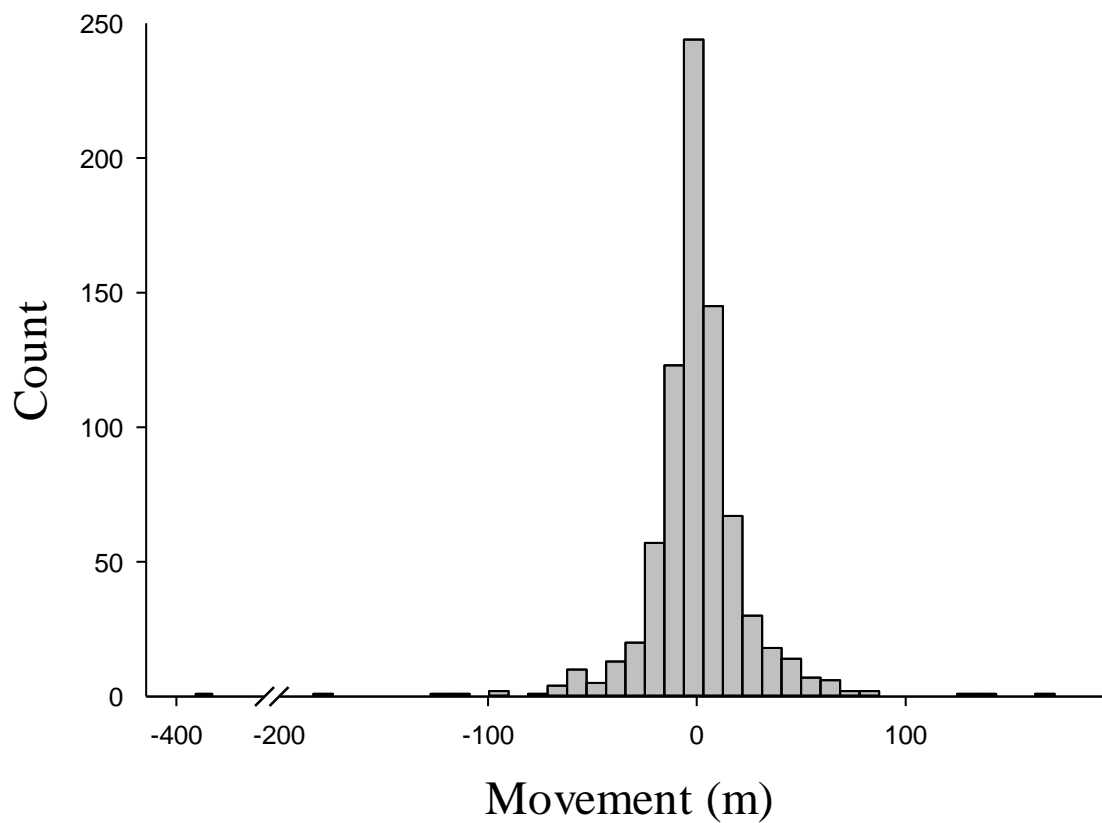


Figure 3.3. – Frequency of individual Brown Trout movements ($n=778$) recorded from August 17, 2016 to July 17, 2017. Positive values indicate upstream movements and negative values indicate downstream movements.

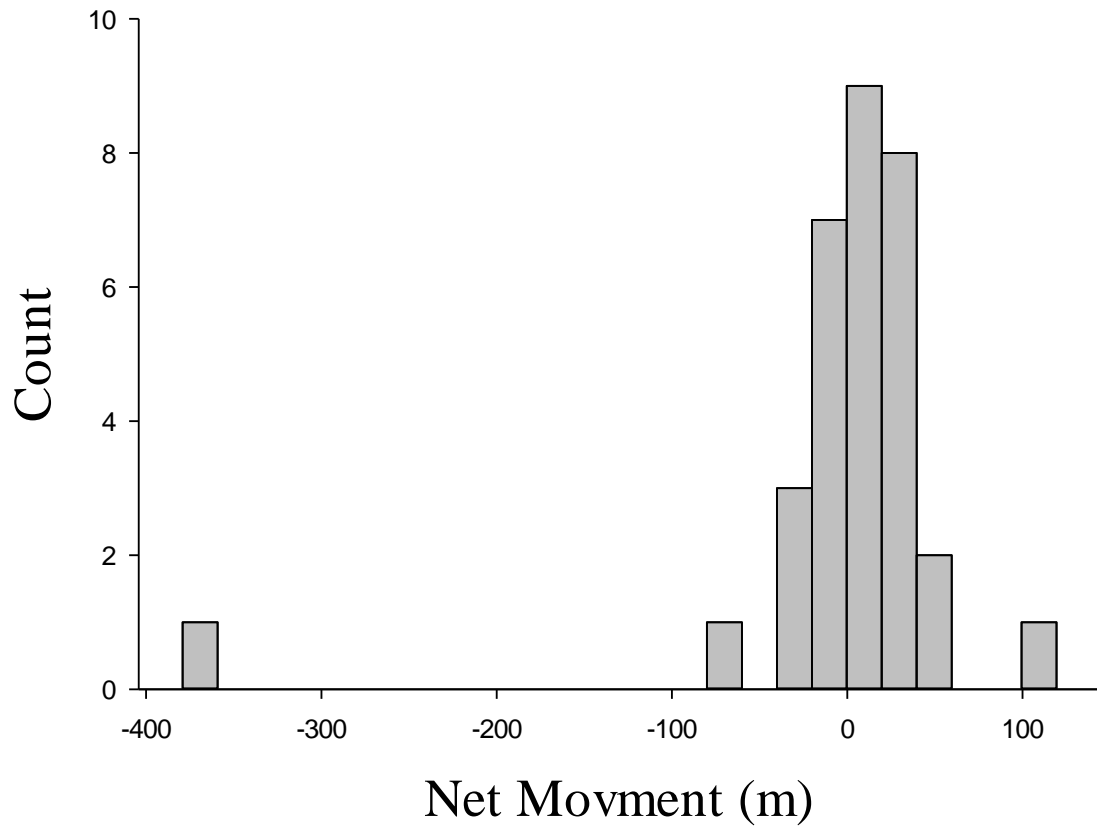


Figure 3.4. – Frequency of Brown Trout net movement (n= 32) recorded from August 17, 2016 to July 17, 2017. Positive values indicate upstream movements and negative values indicate downstream movements.

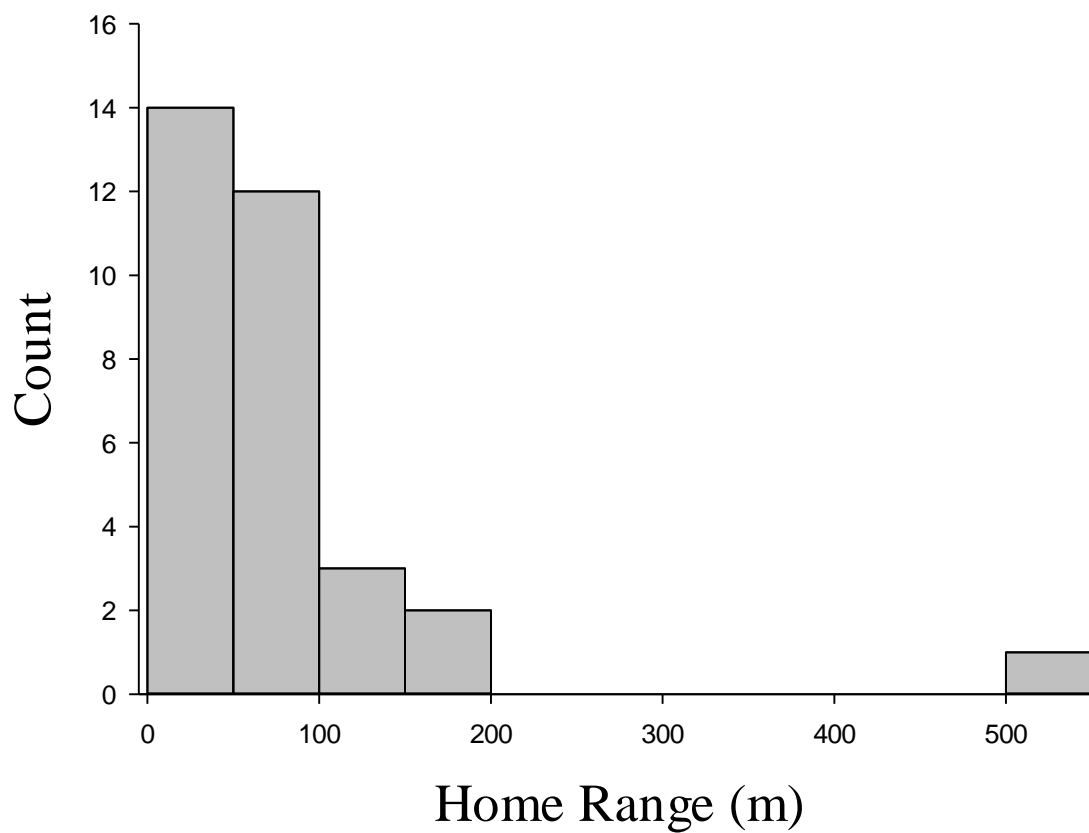


Figure 3.5. – Frequency of Brown Trout home range size (n= 32) recorded from August 17, 2016 to July 17, 2017.

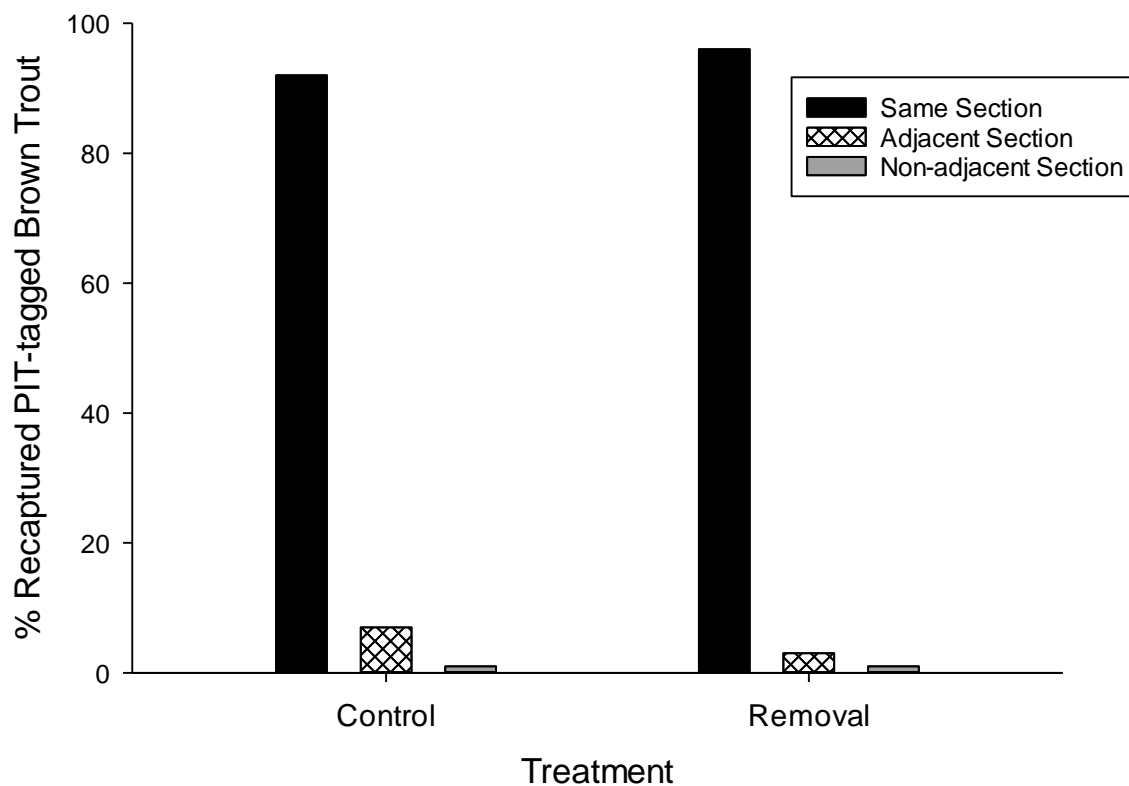


Figure 3.6. – Percent of PIT-tagged Brown Trout recaptured from (1) the same section they were initially tagged (black bars), (2) an adjacent section upstream or downstream from their initial location (cross-hatched bars) or (3) a non-adjacent section upstream or downstream from their initial location (gray bars).

CHAPTER 4

SUMMARY AND RECOMMENDATIONS

My research has provided a greater understanding of the viability of large-scale density reduction as a management technique for improving growth rate of stream-dwelling Brown Trout. I also documented the effects of density reduction on age-specific growth, abundance, and movement of Brown Trout in Spearfish Creek, South Dakota. Furthermore, my results give managers direction on further research and the use of density manipulation as a technique to improve growth of stream-dwelling salmonids influenced by density dependent growth.

My investigation offers further evidence of density dependent growth in stream-dwelling salmonids, with Brown Trout inhabiting sections that received large-scale density reductions exhibiting higher growth rates than those in natural density sections. However, large-scale density reductions provided differing effects on growth between cohorts of Brown Trout. Density reductions improved growth in both length and weight of age 3 and 4 Brown Trout. I did not detect these same improved growth rates for older and younger cohorts. The limited effect on growth of older cohorts can be explained by the slowing and greater variability in growth as fish age and(or) a small sample size. In Spearfish Creek growth begins to asymptote at age 5. As fish approach L_{∞} , our abilities to improve growth rate and detect differences in growth through reduced intraspecific competition may diminish, especially, over small time periods (i.e., 1 year)

I propose that the lack of response in growth for younger cohorts is likely due to an ontogenetic diet shift coupled with the dominance hierarchy displayed in steam-

dwelling salmonids. Brown Trout in Spearfish Creek experience a shift from diets mainly composed of small prey items (Ephemeroptera) to larger prey items (terrestrial macroinvertebrates), at about 200 mm. With a lack of large, aquatically-derived prey items, this shift to terrestrial prey sources is likely required to continue somatic and gonadal growth. Susceptibility to density dependent growth in older cohorts of Brown Trout was demonstrated using a bioenergetics model. In larger, older fish energetic maintenance requirements were barely met, and in some cases, could not be met by foraging solely on aquatic invertebrates – a striking contrast to patterns seen in ages 1 and 2 fish. Brown Trout ages 3-6 rely on terrestrially-derived prey sources, a seasonally and spatially variable prey source, to obtain and maintain their larger sizes. The lack of large, aquatically-derived prey items and reduced energy obtained from aquatically-derived sources provides persuasive evidence to the differing effects of large-scale density reduction on separate cohorts of Brown Trout.

I demonstrated that density reductions provided relief of intraspecific competition over the entire study period (~ 1 year). Removal sections showed a decrease in fish abundance during the sampling period, whereas control sections showed no significant change in abundance. Reduced trout abundance in removal sections indicated that either increased rates of survival and(or) immigration from natural high-density areas to new low-density areas (removal sections) were negligible.

My research also furthered the understanding of the effect fish density and large-scale density reduction on movements and home ranges of stream-dwelling fishes. Significant reductions of Brown Trout densities as high as 1,804 fish/ha had no measurable influence on movement patterns of Brown Trout. I also demonstrated that

fish density had little to no influence on immigration or emigration. Movements of radio tagged and PIT-tagged Brown Trout both yielded no evidence of differing movements patterns in response to differing densities. Many factors have been shown to affect the variability in fish movement; however, it does not appear that density is among them.

I also quantified mean individual movement, net movement, and home range size of Brown Trout in Spearfish Creek. Brown Trout displayed limited movement, small home ranges, and exhibited a high degree of site fidelity. These findings were consistent to prior research on stream-dwelling Brown Trout movement. Sedentary species like Brown Trout are a good candidate species for density manipulations with the purpose of improving growth rate, allowing reduced intraspecific competition to persist with little immigration and emigration.

While small movements and home ranges appeared to be common among Brown Trout in Spearfish Creek, I did observe a small portion of individuals (6%) displaying extended movement patterns. A small proportion of the population made up of these straying individuals would be advantageous on a population level (i.e., colonizing new habitat). Numerous populations of stream-dwelling fishes have been observed with a small portion of individuals exhibiting this straying behavior and we do not believe that these individuals will substantially affect immigration and emigration rates.

Finally, season has been shown to be an important factor that explains a large amount of variability in fish movement. I observed an increase in individual movement and home range during the fall-winter months. I believe these movement increases are related to spawning activities. These individual movements and increased home ranges

did not appear to increase net movements. This suggests that Brown Trout return to their 'home' section of stream post-spawning activities, again highlighting the high site fidelity exhibited by stream-dwelling Brown Trout. These seasonal increases in movement with fish returning to their home section of stream post-spawning has been documented in other Black Hills streams (Rapid Creek).

Large-scale density reductions appear to be a viable management technique for improving growth rates of stream-dwelling Brown Trout and likely many stream-dwelling fishes that suffer from density dependent growth. However, the effects have yet to be studied beyond a single year. Continuing assessment of these large-scale density reductions will be paramount in determining the full benefit (i.e., growth improvement) and duration (reduced intraspecific competition) of these activities.

It would be wise for fisheries managers to maintain annual surveys to track changes in growth and abundance between treatment sections. I recommend continuing yearly population estimates in both control and removal sections to determine if improved growth rate in removal sections is maintained. Continued PIT-tagging and recapture of tagged fish will give managers a cost-effective method for tracking growth in both control and removal sections. Assessments could be performed at smaller scales (i.e. 100 m) in current removal and control sections to save time and money. Continued assessment will help determine the full benefit and duration of large-scale density reductions.

As both growth rate and abundance in removal sections will likely return to levels comparable to those in control sections, additional removals will be required to maintain

improved growth associated with reductions in intraspecific competition. As previously stated, investigating the complete duration of benefits of large-scale density reduction will inform how frequently density reductions will be required to continue improved growth. If managers decide that large-scale density reduction is a cost-effective and socially significant technique to improve growth of stream-dwelling fishes, I would recommend periodic density removals (i.e. every 2 years) as abundance within removal sections returns to natural levels.

If density reductions are to be commonly employed as a management technique, I would also recommend that fisheries managers target improved growth in relatively low-mobility species (i.e., Brown Trout). My results underscore the importance of considering factors that might be limiting growth in the population (i.e., prey resources), and relatedly, those cohorts most affected by limited resources. Identifying those cohort(s) where density-dependent growth is believed to be most pronounced could help focus efforts on targeted reduction of specific sizes/ages of fish that minimize the cost:benefit ratio of large-scale removal efforts.

In Spearfish Creek, South Dakota I recommend targeting fish removal efforts on age 3-4 Brown Trout. These cohorts appear to be the most effected by density-dependent growth and show the greatest benefits of removal efforts. Finally, while I targeted removal of 50% of the Brown Trout > 100 mm in removal sections, my results suggest that higher percent removals may be required to observe abundance reductions closer to 50% in subsequent sampling events. I postulate that removals of 75% of the age 3-4 Brown Trout will be more effective at increasing growth in Spearfish Creek.

Future research should focus on the effects of large-scale density reductions beyond a single year. The greatest limitation of our study is the unknown effects beyond 1 year and if a single density reduction event has the ability to improve growth of stream-dwelling fish for multiple years. If large-scale density reductions can prove to be effective beyond a single year they would be markedly more attractive to managers as a technique to improve growth of stream-dwelling fish.

APPENDIX

Appendix A. Age-specific survival of Brown Trout in Spearfish Creek, SD

A.1. – Canyon Reach- 2016 all sections (n=10).

Age	Mean density (no./ha)	S.E.	Annual survival (S, %)	Annual mortality (M, %)	Instantaneous mortality (Z)
1	431	54.6	n/a	n/a	n/a
2	843	97.3	n/a	n/a	n/a
3	493	67.1	58	42	0.54
4	330	46.2	67	33	0.4
5	78	11.3	24	76	1.43
6	26	5.7	33	67	1.11

A.2. – Town Reach- 2016 all sections (n=4)

Age	Mean density (no./ha)	S.E.	Annual survival (S, %)	Annual mortality (M, %)	Instantaneous mortality (Z)
1	221	33.9	n/a	n/a	n/a
2	464	77.2	n/a	n/a	n/a
3	279	62.6	60	40	0.51
4	141	43.9	51	49	0.67
5	87	32.7	62	38	0.48
6	64	21.8	74	26	0.30

Appendix B. Age-specific size and growth of Brown Trout in Spearfish Creek, SD

B.1. – Canyon Reach- 2016 all sections (n=10)

Age	Mean Length (mm)	S.E.	Mean Weight (g)	S.E.	Growth increment (mm/y)	Growth increment (g/y)	Annual instantaneous growth rate, length	Annual instantaneous growth rate, weight
1	125	1.1	27	1.4	n/a	n/a	n/a	n/a
2	174	1.3	65	1.8	49	38	0.33	0.88
3	221	1.2	122	2.7	47	57	0.24	0.63
4	250	1.3	168	2.9	29	46	0.12	0.32
5	270	2.5	236	16.5	20	68	0.08	0.34
6	302	2.5	271	16.7	32	35	0.11	0.14

B.2. – Town Reach- 2016 all sections (n=4)

Age	Mean Length (mm)	S.E.	Mean Weight (g)	S.E.	Growth increment (mm/y)	Growth increment (g/y)	Annual instantaneous growth rate, length	Annual instantaneous growth rate, weight
1	175	1.4	63	1.3	n/a	n/a	n/a	n/a
2	239	1.9	157	5.4	64	94	0.31	0.91
3	280	1.2	238	9.6	41	81	0.16	0.42
4	307	2	306	15.6	27	68	0.09	0.25
5	312	5.2	325	21.3	5	19	0.02	0.06
6	333	7.2	419	31	21	94	0.07	0.25

Appendix C. von Bertalanffy growth functions for Brown Trout in Spearfish Creek, SD

The von Bertalanffy growth function was used to estimate length at age (L_t , in mm) for Brown Trout in Spearfish Creek as,

$$L_t = L_{inf} [1 - e^{-K(t-t_0)}],$$

Where L_{inf} is the theoretical, maximum size in millimeters (mm), K is the growth constant, t_0 is a fitted parameter (i.e., theoretical age that a fish would have a length=0), and t is age of fish (in years).

The reciprocal of this equation can be used to estimate the age (t , in years) of a Brown Trout for a given length (L_t) as,

$$t = -1/K * \ln(1 - L_t/L_{inf}) + t_0$$

Moreover, L_t can be predicted from Brown Trout weight (W , in g) as,

$$L_t = aW^b,$$

where a and b are regression parameters.

C.1. – von Bertalanffy parameter estimates derived from Brown Trout collected in the canyon and town reach of Spearfish Creek, 2016.

Von Bertalanffy parameter	Data Source			
	2016 _{Canyon}		2016 _{Town}	
	Est.	95% CI	Est.	95% CI
L_{inf}	349	341 – 357	337	333 - 341
K	0.28	0.26 – 0.29	0.52	0.49 - 0.55
T_0	-0.57	-0.63 – -0.51	-0.29	-0.36 - -0.21

Source: 2016_{canyon} = Brown Trout collected for age analysis in the canyon reach from July-August, 2016 (n=223); 2016_{town} = Brown Trout collected for age analysis in the Town reach from July-August, 2016 (n=179).

C.2 – Age-at-size estimates for Brown Trout collected from Spearfish Creek, SD, 2016. Data sources were 2016_{Canyon} for the canyon reach and 2016_{Town} for the town reach.

Reach			
Canyon		Town	
Length (mm)	Age estimate	Length (mm)	Age estimate
80	0	80	0
90	0	90	0
100	1	100	0
110	1	110	0
120	1	120	1
130	1	130	1
140	1	140	1
150	1	150	1
160	2	160	1
170	2	170	1
180	2	180	1
190	2	190	1
200	2	200	1
210	3	210	2
220	3	220	2
230	3	230	2
240	4	240	2
250	4	250	2
260	4	260	3
270	5	270	3
280	5	280	3
290	6	290	3
300	6	300	4
310	7	310	5
320	8	320	5
330	10	330	7
340	12	340	7