LIFE HISTORY CHARACTERISTICS AND THE EFFECTS OF CLIMATE ON GROWTH OF YELLOWSTONE CUTTHROAT TROUT IN HEADWATER BASINS

by

Patrick Ryan Uthe

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ABSTRACT

The Yellowstone Cutthroat Trout was historically distributed throughout the Upper Yellowstone and Upper Snake River drainages, but now occupies only 42% of its original range because of habitat degradation and introduced salmonid species. Many of the current strongholds are located on public land in mountainous watersheds with low human disturbance. However, knowledge of life history characteristics of headwater populations is limited. Moreover, streams throughout the Rocky Mountains have already exhibited symptoms of climate change through alterations in thermal and hydrologic regimes, but it is unknown how these changes will affect fish populations. To address these needs, we implemented a mark-recapture study on five populations of trout from Spread Creek, Wyoming, and Shields River, Montana, to estimate annual growth, survival rates, and movement patterns, and document the effects of discharge, temperature, and food availability on summer growth patterns. Survival rates were high compared to survival rates of other Cutthroat Trout subspecies and large trout generally had lower survival rates than small trout. Downstream movements out of streams by tagged trout were substantial. Annual growth rates varied among streams and size classes, but were relatively low compared to populations of Yellowstone Cutthroat Trout from large, low elevation streams. Trout grew more in length than weight in summer, suggesting an investment in structural growth rather than accumulation of reserve tissues. Temperature and discharge had strong effects on summer growth, but the effect of discharge was greater for growth in weight than in length, probably resulting from increased prey availability at high discharges. Temperature interacted with fish length such that small trout responded favorably to increased average daily temperatures near physiological optima and increased growing season length, whereas large trout responded negatively to warming temperatures. These estimates of key demographic parameters are useful in developing management and conservation strategies. Additionally, we documented that even under thermally suitable conditions, discharge can have significant effects on growth, making it important to consider multiple factors affected by climate change when devising climate adaptation strategies for coldwater fishes.

CHAPTER ONE

INTRODUCTION TO THESIS

Loss of aquatic biodiversity is a major conservation concern worldwide (Dudgeon et al. 2006). Habitat degradation and invasions by exotic species are major drivers in the declines of native species distributions (Vitousek et al. 1997). Moreover, climate change is anticipated to exacerbate current stressors by altering local habitat conditions and promoting further expansion of invasive species (Wenger et al. 2011). Salmonids are particularly vulnerable to climate driven stream changes because of their narrow physicochemical tolerances (Brett 1952).

In western North America, inland Cutthroat Trout have experienced significant declines since the 19th century. Historically, the Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* occupied one of the largest geographic ranges of any Cutthroat Trout subspecies, encompassing portions of Montana, Wyoming, Idaho, Utah, and Nevada (Gresswell 2011). However, the current range is restricted to 42% of the original range, with 54% percent of the total occupied stream length located in Wyoming (May et al. 2007). The Yellowstone Cutthroat Trout is a significant ecological resource in the Greater Yellowstone Area, which is one of the largest intact ecosystems in the lower 48 states (Noss et al. 2002). Additionally, the subspecies is a highly valued recreational and cultural resource (Gresswell and Liss 1995).

The decline of Yellowstone Cutthroat Trout has been attributed to habitat degradation (Varley and Gresswell 1988), displacement by introduced Brook Trout *Salvelinus fontinalis* (Kruse et al. 2000; Benjamin and Baxter 2012), and hybridization with non-native Rainbow Trout *O. mykiss* (Campbell et al. 2002; Meyer et al. 2006). As a result, many of the remaining strongholds are located on public land in mountainous areas with little human disturbance (Varley and Gresswell 1988). In addition to the current threats, climate change may pose the most serious challenge to the long term persistence of Yellowstone Cutthroat Trout (Gresswell 2011). Many streams throughout the Rocky Mountain West have already exhibited signs of climate change through alterations in thermal and hydrologic regimes (Isaak et al. 2012). Additionally, ecosystem productivity is changing across much of North America through changes in growing-season length (Zhu et al. 2012), which can affect salmonid forage. Accordingly, an understanding of how climate-related factors affect salmonid populations is imperative.

Headwater populations of Yellowstone Cutthroat Trout will probably become increasingly important under anticipated changes in climate (Al-Chokhachy et al. 2013). Despite this, research on headwater populations has generally focused on status assessments (e.g., Kruse et al. 2000; Meyer et al. 2003, 2006) and factors influencing occupancy (e.g., Kruse et al. 1997). Most life history research has been conducted on migratory populations from Yellowstone Lake and large rivers (e.g., Gresswell et al. 1994, 1997; Kaeding and Boltz 2001; Homel 2013). A paucity of data describes resident and fluvial headwater populations of Yellowstone Cutthroat Trout.

Future management will be heavily focused on maintaining the current distribution as well as restoring populations where feasible (Gresswell 2011). This will require a better understanding of demographic characteristics and behavior from headwater populations across their range. Quantification of key vital rates (e.g., recruitment, survival, immigration, and emigration) is essential for understanding how potential management or conservation strategies will affect populations (Wisdom et al. 2000). Moreover, understanding how these factors differ across size or age classes can help identify potential limiting factors, and therefore, strategies for increasing population persistence (Hilderbrand 2003). Documentation of movement patterns is especially critical because it has bearing on decisions related to fish passage barriers, which are increasingly selected as conservation strategies (Fausch et al. 2006).

We conducted a multi-year, mark-recapture study on five populations of Yellowstone Cutthroat Trout from two headwater drainages. The first chapter of this thesis documents how we determined life history and demographic characteristics. Our specific objectives were to estimate annual growth rates, survival rates, and proportions of tagged trout migrating out of streams. The second chapter of this thesis describes how we explicitly linked multiple climatic stream attributes to trout growth under natural conditions. We investigated the effects of stream temperature, discharge, and food abundance on summer growth to elucidate the mechanisms of climate change effects on Yellowstone Cutthroat Trout. Furthermore, we described both growth in weight and length to determine how climatic factors affect energy allocation. The overarching goal of this research was to provide reliable estimates of basic life history information that have not been documented for headwater populations of Yellowstone Cutthroat Trout, thereby providing necessary and useful information to managers. Overall, our results fill a substantial knowledge gap and provide information on the effects of multiple climate-driven stream factors on trout growth, and therefore fitness.

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CHAPTER TWO

LIFE HISTORY CHARACTERISTICS AND VITAL RATES OF YELLOWSTONE CUTTHROAT TROUT IN TWO HEADWATER BASINS

Contribution of Authors and Co-Authors

Manuscript in Chapter 2

Author: Patrick Uthe

Contributions: Helped conceive study design, implemented study, collected and analyzed data, and authored manuscript.

Co-Author: Robert Al-Chokhachy

Contributions: Helped conceive study design, assisted with data collection, provided guidance on data analysis, and edited manuscript.

Co-Author: Alexander Zale

Contributions: Helped conceive study design, provided technical insights, and edited manuscript

Co-Author: Bradley Shepard

Contributions: Helped conceive study design, assisted with data collection, assisted with data processing, and reviewed manuscript.

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Abstract

The Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* is native to the Rocky Mountains and has declined in abundance and distribution as a result of habitat degradation and introduced salmonid species. Many of its remaining strongholds are in headwater drainages with low human disturbances. Understanding of the life-histories, vital rates, and behaviors of such headwater populations remains limited yet is critical for effectively managing and conserving them. We estimated annual growth in length and weight, annual survival rates, and movement patterns of populations of Yellowstone Cutthroat Trout from three tributaries of Spread Creek, Wyoming, and two tributaries of Shields River, Montana, from 2011 through 2013 using passive integrated transponder (PIT) tag antennas within a mark-recapture framework. Survival rates were relatively high compared to those of other Cutthroat Trout subspecies. Average annual survival rates ranged from 0.32 (SE = 0.04) to 0.68 (SE = 0.05) in the Spread Creek basin and from 0.30 (SE=0.07) to 0.69 (SE=0.10) in the Shields River basin. Downstream movements out of streams by tagged trout were substantial, with as much as 26.5% of a tagging cohort leaving over the course of the study. These estimates of key demographic parameters for headwater populations of Yellowstone Cutthroat Trout provide critical information for developing and assessing potential conservation strategies.

Introduction

Intra-species diversity in life history characteristics is an important consideration for long-term conservation planning (Schindler et al. 2010). Quantification of key vital rates (e.g., recruitment, survival, immigration, and emigration) is essential for developing effective management and conservation strategies (Wisdom et al. 2000). Moreover, understanding how these factors differ among size or age classes can help identify potential limiting factors, and therefore, strategies for increasing population persistence (Hilderbrand 2003). Accurate estimation of these parameters, particularly survival, has been limited by data intensive modeling requirements and the challenges of distinguishing movement from mortality (Bowerman and Budy 2012). With the advent of passive integrated transponder (PIT) tag technology, long-term studies of large sample sizes of individually marked fish can be conducted relatively inexpensively to simultaneously estimate multiple demographic parameters of interest (Gibbons and Andrews 2004; Zydlewski et al. 2006). For many inland salmonid species, this information is lacking or only available for those that are listed under the Endangered Species Act (e.g., Al-Chokhachy and Budy 2008).

Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* historically occupied one of the most extensive geographic ranges among inland Cutthroat Trout subspecies (Gresswell 2011), but now occupy only 42% of the historical range (May et al. 2007). This decline has been attributed to habitat degradation (Varley and Gresswell 1988), displacement by introduced Brook Trout *Salvelinus fontinalis* (Kruse et al. 2000; Benjamin and Baxter 2012), and hybridization with non-native Rainbow Trout *O. mykiss*

(Campbell et al. 2002; Meyer et al. 2006). As a result, many of the remaining genetically pure strongholds of Yellowstone Cutthroat Trout are on public land in mountainous areas with little human disturbance (Varley and Gresswell 1988). Despite the importance of these systems as critical conservation areas, research on headwater populations has generally focused on status assessments (e.g., Kruse et al. 2000; Meyer et al. 2003, 2006) and factors influencing occupancy (e.g., Kruse et al. 1997). Most life history research has been conducted on migratory populations from Yellowstone Lake and large rivers (e.g., Gresswell et al. 1994, 1997; Kaeding and Boltz 2001; Homel 2013). A paucity of data describes resident and fluvial headwater populations of Yellowstone Cutthroat Trout.

Headwater populations of Yellowstone Cutthroat Trout will probably become increasingly important under anticipated changes in climate (Al-Chokhachy et al. 2013). Future management will be heavily focused on maintaining the current distribution as well as restoring populations where feasible (Gresswell 2011), which will require an understanding of demographic characteristics and behaviors of headwater populations range-wide. Moreover, movement patterns will have bearing on decisions related to fish passage barriers, which are increasingly used for conservation (Fausch et al. 2006). To address these needs, we investigated the life history and vital rates of Yellowstone Cutthroat Trout in headwater streams in the Greater Yellowstone Area. Our specific objectives were to estimate annual growth grates, survival rates, and movement patterns of Yellowstone Cutthroat Trout in two headwater basins. Our overarching goal was to provide reliable estimates of basic life history characteristics and vital rates that have not been determined for headwater populations of Yellowstone Cutthroat Trout, thereby providing useful and necessary information to managers.

Methods

Study Area

We conducted a mark-recapture study in three tributaries of Spread Creek, Wyoming, and two tributaries of Shields River, Montana, from 2011 through 2013 (Figure 2.1). All tributaries are small, high elevation streams with low mean daily temperatures throughout the summer growing season (Table 2.1). Spread Creek is a third-order tributary to the Snake River originating in the Gros Ventre Mountains in the Bridger-Teton National Forest and continuing through portions of Grand Teton National Park. The Shields River originates in the Crazy Mountains in the Custer-Gallatin National Forest and joins the Yellowstone River east of Livingston, Montana. Both watersheds are strongholds for Yellowstone Cutthroat Trout with the presence of multiple life-history forms and genetic purity (May et al. 2007). These regions have dry summers and cold winters with much annual precipitation occurring as snowfall.

Species compositions are similar across watersheds. Spread Creek contains Yellowstone Cutthroat Trout, Bluehead Sucker *Catastomus discobolus*, Utah Sucker *C. ardens*, Longnose Dace *Rhinichthys cataractae*, Mottled Sculpin *Cottus bairdii*, Paiute Sculpin *C. beldingi*, and non-native Brook Trout. Species in the upper Shields River drainage are Yellowstone Cutthroat Trout, Mottled Sculpin, Longnose Dace, and non-native Brook Trout.

Fish Capture and Recapture

Mark-recaptures.—We used a systematic sampling design in each tributary to account for longitudinal differences in fish distributions. Sample sections were 100 m in length and distributed at a frequency of one site every 0.2-0.5 km. Only one sampling event occurred in 2011 (July - August), but sampling occurred bi-annually in 2012 and 2013 (July - August and September - October).

We used single-pass electrofishing for the majority of sample sections, but conducted multiple passes in a subset of sample sections to estimate capture efficiencies. We sampled each section using Smith-Root® BP-15, BP-12, or LR-24 backpack electrofishing units operated at voltages in the range of 100 to 600 V, frequencies under 50 Hz, and pulse widths less than 2 µsec (Dwyer et al. 2001). We measured total lengths (± 1 mm) and weights (± 0.5 g) of all captured individuals with lengths 80 mm and longer. In the Spread Creek drainage, we tagged trout 80-119 mm long with 12-mm passive integrated transponder tags (PIT tag; half-duplex, Oregon RFID®, Portland, OR) and trout 120 mm and longer with 23-mm PIT tags. In the Shields River drainage, we tagged trout 80-129 mm long with 12-mm PIT tags and individuals 130 mm and longer with 23-mm PIT tags. We inserted tags into the body cavity through a small ventral incision made with a scalpel anterior to the pectoral fins. We removed adipose fins to serve as secondary marks. We used a hand-held PIT-tag scanner to check for tags in trout with clipped adipose fins. If we detected a tag, we recorded the unique tag identification number, but if we failed to detect a tag after three attempts, we considered it a shed tag and implanted a new tag. Tag retention rates were high (96%).

Passive Recaptures.—We installed passive instream PIT antennas near the mouths of all streams prior to fish sampling. In the Spread Creek basin, antennas were deployed in 2012 and 2013. In the Shields River basin, antennas were deployed in 2011-2013. Antennas operated continuously from late-May during runoff until the autumn when water temperatures dropped and ice started to form, which was usually in October. Each antenna consisted of two loops laid on the substrate of the stream channel and separated by 5 to 10 m to allow determination of the direction of movement and increase the chance of detecting a tagged trout (Zydlewski et al. 2006). Detections were recorded by a half-duplex multiplexer (Oregon RFID®, Portland, Oregon) powered by two 12-volt batteries charged by a solar panel.

Active Recaptures.—We used portable PIT-tag antennas to provide information on recapture of PIT-tagged individuals and to effectively sample marked fish outside of our electrofishing sample sections within tributaries to minimize bias caused by fish movements. We used continuous surveys in each tributary so that each stream was sampled from the highest known distribution of salmonids down to its mouth. We conducted the surveys using two portable hoop antennas (about 0.3 m in diameter) attached to poles. The operators covered the stream in a manner analogous to backpack electrofishing and detected fish as the wands passed over tagged individuals (sensu Roussel et al. 2000). When a tag was detected, we thoroughly agitated the substrate to determine if it was in a live fish or either shed or from a dead fish.

Growth

We estimated annual growth rates of individuals marked during summer sampling occasions and recaptured the following summer and individuals marked during autumn sampling occasions and recaptured the following the autumn. Fish detected leaving streams of tagging origins between capture and recapture were not included. Individual growth was calculated through empirical measures of change in length and weight between the time of capture and recapture (e.g., Budy et al. 2007). To account for differences in time between marking and recapture, we calculated daily growth rates and scaled to 365 days using the following equation:

$$G_{l,w} = \frac{c - m}{d} * 365,$$

where G is annual growth rate (mm or g), l is length, w is weight, c is length or weight at recapture, m is length or weight at marking, and d is the number of days at large. We estimated annual growth of 98 trout. Growth intervals (days at large) ranged from 326 to 395 days. We used a one-way analysis of variance (ANOVA) to test for differences in growth among streams for trout with lengths less than 100 mm, lengths 100-149 mm, and lengths of 150 mm and longer at a significance level of $\alpha = 0.05$. We were unable to include trout with lengths less than 100 mm from Leidy Creek and trout with lengths 150 mm and greater in Dugout Creek in the ANOVA because of small sample sizes ($n = 1$).

Survival Analyses

We used a Barker model in Program MARK (White and Burnham 1999) to estimate survival rates of Yellowstone Cutthroat Trout. This model incorporates information from recapture occasions as well as dead recoveries and live resights of tagged individuals between occasions (Barker 1997) and provides less biased estimates of survival (S) than apparent survival estimated using a Cormack-Jolly-Seber Model (Bowerman and Budy 2012). The Barker model estimates recapture probability (p), the probability of recovering the tag of a dead individual between occasions (r), the probability of recapturing an individual alive between occasions (R), the probability of recapturing an individual alive before it dies between occasions (R'), the probability that an animal at risk of capture at time t is at risk of capture at time $t + 1$ (F), and the probability that an animal not at risk of capture at time t is at risk of capture at time $t + 1$ (F').

We used data from 2011 through 2013. Because no recapture events took place in 2011, all sampling (July 26 – September 6) was combined into the first sampling occasion. The arrangement of sampling occasions and numbers of individuals captured, recaptured, and recovered dead are presented per the example of Bowerman and Budy (2012) (Table 2.2). We estimated survival rates of 975 trout in the Spread Creek basin and 335 trout in the Shields River basin (Table 2.2). In the Spread Creek basin, physical recaptures during electrofishing surveys were low with only 13.5% (n = 132) of trout recaptured at least once. However, live resights with both portable PIT antennas and instream passive antennas were high with 64.8% (n = 632) of trout detected at least once. Electrofishing recaptures were higher in the Shields River basin with 26.3% (n = 88) of trout recaptured at least once. Live resights were lower than in the Spread Creek basin with only 39.7% (n = 133) of trout detected at least once.

Individuals were segregated into two size classes for analyses (Spread Creek Basin: 80-119 mm and ≥ 120 mm; Shields River Basin: 80-129 mm and ≥ 130 mm). The small size class included age-1 and some age-2 trout and the large size class included some age-2 trout and age-3 and older trout. Individuals of the smaller size class were automatically moved into the larger size class during the following year. Stream and size class were treated as grouping variables in the analysis. We tested for temporal variation using three separate approaches: 1) testing for differences across sample periods where a parameter varied by time interval (t); 2) year effects where we set parameters equal for occasions occurring within 2011, 2012, or 2013; and 3) season effects where we set parameters equal for occasions occurring within the summer (July – October) or winter (October – July).

We chose to model emigration from electrofishing sample sections as random ($F = F'$) because movement data from the portable PIT antenna surveys showed the median range moved by fish was greater than section lengths, which would make the probability of a fish being within the sample section during a sampling event random. We chose to model r as constant because of the relatively low proportion of dead recoveries observed throughout the study (Table 2.2). We also modeled R' as constant. All tag detections not from live fish were considered dead recoveries because of the low tag-shedding rate (4%). Individuals detected moving downstream over a stationary antenna were considered emigrants from their respective stream and removed from the model likelihood following that interval (sensu Horton and Letcher 2008). To find the best structure for recapture and resight parameters (*R* and *p*), we held survival as the global structure and compared different structures of the parameter of interest and selected the best structure based on AIC_c. When comparing structures of a given parameter, we kept the other parameter structures modeled as the global structure. After we found the most supported structure of each parameter, we maintained those structures while testing for the best structure of survival. We then assessed model fit of the global structure of survival along with the most supported structures of the other parameters using the median $\hat{c}$ procedure in MARK. Little evidence of over-dispersion existed (Spread Creek basin: $\hat{c} = 1.400$, Shields River basin: $\hat{c} = 1.409$). Therefore, we used AIC_c to rank the candidate survival model structures and calculate the relative AIC_c weight of each model. We used model averaging to maximize the information within the multi-model framework (Burnham and Anderson 2002). We extrapolated model-averaged monthly survival rates to estimate mean annual survival rates for each size class in each stream and used the delta method to estimate variances of mean annual survival rates (Powell 2007).

Movement Patterns

We quantified the number of tagged trout leaving each stream. In the Spread Creek basin, movements were estimated in 2012 and 2013. In the Shields River basin, we estimated movements from 2011 through 2013. We calculated movements by size class because detection efficiencies differ for 12-mm and 23-mm PIT tags passing over instream antennas (Hewitt et al. 2010). As described above, individuals were counted as moving when first detected passing downstream over a stationary antenna. Fish classified as moving were counted only once during the course of the study.

Results

Growth

Trout from all streams grew slowly; average growth rates were less than 59 mm/year and 50 g/year (Table 2.3). Annual growth differed among streams and size classes. Mean growth rates in length of all size classes were significantly different among streams (< 100 mm, ANOVA, $F = 20.8$, df = 3, 24, $P < 0.001$; 100-149 mm, $F = 9.1$, df = 4, 37, $P < 0.001$; ≥ 150 mm, $F = 8.1$; df = 3, 22, $P < 0.001$). Mean growth rates in weight of trout with lengths less than 100 mm and lengths 110-149 mm were significantly different among streams (< 100 mm, $F = 7.5$, df = 3, 24, $P = 0.001$; 100-149 mm, $F = 7.4$, df = 4, 37, $P < 0.001$), but mean growth rates in weight of trout with lengths 150 mm and greater were not ($F = 1.9$, df = 3, 22, $P = 0.156$).

Survival

Survival rates were high. Mean annual survival rates in Grouse Creek were 0.68 (SE = 0.05) for trout 80-119 mm and 0.58 (SE = 0.04) for trout with lengths 120 mm and greater. In Leidy Creek, mean annual survival rates were 0.44 (SE = 0.08) for trout 80-119 mm and 0.32 (SE = 0.04) for trout with lengths 120 mm and greater. In Rock Creek, mean annual survival rates were 0.62 (SE = 0.05) for trout 80-119 mm and 0.51 (SE = 0.04) for trout with lengths 120 mm and greater. The top model of survival in the Spread Creek basin contained the additive effects of size class, time interval, stream, and the interaction of size class and time interval (Akaike weight (W_i) = 97.8 %, Table 2.4). Two of the five top models contained an interaction between size class and time interval or year suggesting differences between size classes varied through time (total W_i = 98.8 %). Differences between size classes did not differ among streams because of the lack of support for an interaction between size class and stream (total W_i = 1.8 %). Small trout in Grouse and Rock creeks had higher monthly survival rates than large trout in three of the four time intervals, whereas small trout in Leidy Creek had higher survival rates than large trout in only two time intervals (Figure 2.2).

Mean annual survival rates in Dugout Creek were 0.47 (SE = 0.11) for trout 80-129 mm and 0.30 (SE = 0.07) for trout with lengths 130 mm and greater. Mean annual survival rates in Lodgepole Creek were 0.69 (SE = 0.10) for trout 80-129 mm and 0.52 (SE = 0.07) for trout with lengths 130 mm and greater. The top model of survival in the Shields River basin contained the additive effects of size class, stream, and year (W_i = 34.1%, Table 2.4). Three of the five top models contained a stream by size class interaction suggesting the difference between size classes was different between streams (total W_i = 44.3%). We found minor support for models containing interactions between size class and time (total W_i = 30.6%) and interactions between stream and time (total W_i = 30.6%). Small trout in Dugout and Lodgepole creeks had higher monthly survival rates than large trout during all time intervals (Figure 2.2).

The recapture probability (p) varied by size and season in the Spread Creek basin. During summer, p was 0.15 (SE = 0.03) for trout 80-119 mm and 0.11 (SE = 0.02) for trout with lengths 120 mm and greater. During autumn, p was 0.24 (SE = 0.03) for trout

80-119 mm and 0.17 (SE = 0.02) for trout with lengths 120 mm and greater. The probability of recapturing an individual alive between occasions (*R)* was higher than *p* and varied by time interval. The probability *R* was 0.13 (SE = 0.02) in the first time interval, 0.31 (SE = 0.02) in the second interval, 0.14 (SE = 0.01) in the third interval, 0.37 (SE = 0.03) in the fourth interval, and 0.68 (SE = 0.15) in the fifth interval. The probability of recapturing an individual alive before it dies between occasions (*R*') was low at 0.003 (SE = 0.006). The probability of recovering the tag of a dead individual between occasions (*r*) was 0.09 (SE = 0.01).

The recapture probability (*p*) varied by stream in the Shields River basin. In Dugout Creek, *p* was 0.21 (SE = 0.05). In Lodgepole Creek, *p* was 0.42 (SE = 0.05). The probability *R* varied by season. In winter, *R* was 0.10 (SE = 0.01) and in summer, *R* was 0.14 (SE = 0.02). The probability *R'* was 0.03 (SE = 0.01). The probability *r* was similar to the Spread Creek basin at 0.10 (SE = 0.03).

Movement Patterns

Proportions of tagged trout leaving streams varied among years and streams (Tables 2.5 and 2.6). Proportions of tagging cohorts detected leaving streams throughout the entire study period were relatively high with a maximum of 26.5% observed leaving Grouse Creek (Table 2.6). Movement proportions of size classes were not markedly different within streams. In the Spread Creek basin, which had instream antennas deployed in 2012 and 2013, the proportions of tagged fish that left during the study were 19.3% in Grouse Creek, 4.6% in Leidy Creek, and 11.1% in Rock Creek. In the Shields River basin, which had instream antennas deployed in 2011, 2012, and 2013, the proportions of tagged fish that left during the study were 16.2% in Dugout Creek and 11.8% in Lodgepole Creek.

Discussion

Yellowstone Cutthroat Trout in headwater streams grew slowly, but had relatively high survival rates. The growth rates we observed are consistent with growth patterns of Cutthroat Trout in other headwater basins (Corsi 1988; Hilderbrand and Kershner 2004; Fraley and Shepard 2005; Budy et al. 2007; Belk et al. 2009). Although growth rates were low in all streams, significant differences in growth existed among streams, which probably resulted from differences in abiotic and biotic conditions (Vollestad and Olsen 2008; Xu et al. 2010; Baerum et al. 2013). Our survival estimates encompass the range reported for Cutthroat Trout, but the maximum observed rate of 0.69 is higher than other published estimates (Peterson et al. 2004; Budy et al. 2007). In particular, Bonneville Cutthroat Trout *O. c. utah* in a tributary of the Logan River had mean annual survival rates less than 0.40 (Budy et al. 2007) and Colorado River Cutthroat Trout *O. c. pleuriticus* in high elevation streams had mean survival rates ranging from 0.23 to 0.57 (Peterson et al. 2004). Although most of the populations we investigated had survival rates near the upper end of published ranges, survival rates were as low as 0.30 in Dugout Creek, which may have resulted from competition with an expanding population of non-native Brook Trout (Peterson et al. 2004).

Growth and survival patterns of Cutthroat Trout in small, high elevation streams differ from those in large, low elevation streams. Yellowstone Cutthroat Trout in main-stem rivers achieved longer maximum lengths and had significantly greater lengths at age than trout in tributaries (Leeseberg and Keeley 2014). In the Logan River, growth rates of Bonneville Cutthroat Trout were as high as 0.5 g/day and average growth rates were 0.25 g/day for age-1 trout, 0.15 g/day for age-2 trout, and 0.075 g/day for age-3 and older trout (Budy et al. 2007). Large streams provide food resources to promote high growth rates and adequate habitat to support large fish, whereas the small streams we investigated have short growing seasons, sub-optimal (too cold) thermal regimes (Bear et al. 2007), and low food availability throughout much of the growing season (Sotiropoulos et al. 2006; Leeseberg and Keeley 2014), which probably caused the low growth rates we observed. Bonneville Cutthroat Trout survival rates increased with age (Budy et al. 2007), but we found that survival rates of small trout were greater than those of large trout. In the small tributaries we investigated, size may not confer survival advantages (Carlson et al. 2008), and might be disadvantageous because large fish are more susceptible to predation (Lima and Dill 1990; Munch and Conover 2003) and resource limitations (Xu et al. 2010a).

Life history diversity among individuals within populations can affect vital rates. Migratory stocks of Yellowstone Cutthroat Trout exhibited greater lengths at age compared with resident stocks within the same basin (Thurow et al. 1988), suggesting an advantage for moving out of tributaries for portions of the year. Migration in potadromous salmonids presents a tradeoff between increased growth in more productive stream sections (Stolarski and Hartman 2010) and mortality costs associated with movement (Jonsson and Jonsson 1993). Fecundity is strongly related to size in salmonids

(Downs et al. 1997; Hendry et al. 2001), providing fitness advantages for increased growth in lower parts of a watershed (Leeseberg and Keeley 2014), but comes with migration costs from predation (Larsson 1985). Our survival estimates apply only to individuals that resided within the tributary of tagging for the entire period at liberty. Residents may have higher survival rates and mature earlier than migrants (Jonsson and Jonsson 1993, Meyer et al. 2003a), but sacrifice reproductive potential by growing less. In small streams, individuals may be unable to make up the costs of reproduction within a given year, forcing them to adopt a life history pattern of alternate year spawning instead of repetitive spawning (Johnston and Post 2009).

The proportions of trout leaving streams suggest that movements among tributaries and main-stem rivers are important aspects of population dynamics in these headwater drainages. Both basins are non-fragmented stream networks and support individuals exhibiting fluvial and resident life histories (Al-Chokhachy et al. 2014; Shepard et al. 2014). Migratory behavior is common for inland salmonids that inhabit environments with patchy distributions of necessary resources to complete life history requirements (Northcote 1997). Small, high elevation streams have challenging environmental conditions during the summer and winter seasons. In summer, low base discharges limit habitat and forage availability (Harvey et al. 2006), which may cause some individuals to risk migration to find adequate resources. Additionally, small streams may not provide sufficient over-wintering habitat, forcing some fish to make substantial downstream movements to find suitable habitats lower in drainages (Brown and Mackay 1995; Jakober et al. 1998). Competition may also elicit emigration in small streams during periods of low discharge because densities increase in the limited amount of suitable habitats. Whitespotted Char *S. leucomaenis* emigrated in response to long-term flow reductions (Nakamura 2013). Proportions of tagged trout leaving tributaries were high, yet survival rates of trout within tributaries were also high, suggesting the presence of source-sink dynamics (Pulliam 1988). If climate change marginalizes stream conditions in low elevation portions of watersheds (Isaak and Rieman 2013), headwater populations may become increasingly important to the long-term persistence of populations within basins by providing sources of individuals to migrate downstream and inhabit sub-optimal portions of stream networks. Given that small amounts of immigration can greatly increase population persistence (Stacey and Taper 1992; Hilderbrand 2003), movement patterns and stream connectivity should be important considerations in conservation of headwater populations.

Limitations

We acknowledge limitations of our survival estimates. Even though we explicitly accounted for emigration to achieve an estimate of true survival rather than apparent survival, we did not have antennas operating continuously throughout the study. Furthermore, antennas had imperfect detection when operating. We installed antennas in late spring near the start of run-off and removed them in autumn, just prior to ice-up. We may have failed to detect trout making pre-winter downstream movements (Jakober et al. 1998). However, we removed antennas in autumn when average daily temperatures were below 2°C, which is lower than temperatures expected to initiate over-wintering downstream migrations of Cutthroat Trout (4-6°C, Jakober et al. 1998). The survival estimates in Leidy Creek are probably biased low because of undetected movements into Leidy Lake at the headwaters of the stream. Lack of an antenna at the lake outlet precluded accounting for fish migrating into the lake.

Because of the presence of multiple life history forms in both basins, we were unable to determine the origins of tagged fish. Our movement estimates may have included tagged, sexually mature fish of unknown origin that migrated into our tributary streams. Additionally, we do not know whether small trout moving out of streams were offspring of migratory fish or if they were resident fish leaving in response to resource limitations. Even if the estimates do not represent emigration of the resident components of the populations, they provide information on fish movement among tributaries and main-stem stream segments within headwater basins. We quantified only downstream movements, but investigation of upstream movements into tributaries is necessary to evaluate the contribution of migratory individuals and spawning immigrants in the context of isolation, genetic diversity, population growth rates, and overall persistence of resident tributary populations (Morita and Yamamoto 2002).

Conclusions

Yellowstone Cutthroat Trout in headwater basins grew slowly and generally survived at high rates. High movement rates out of tributaries by both small and large trout suggested that mobility is common in these headwater systems and is an important consideration for isolation strategies. Survival rates were also high, suggesting that these tributary populations may be functioning as source populations within the basins. Given the benefits and tradeoffs associated with different life histories, identifying non-fragmented drainages with multiple life history forms and implementing conservation strategies that promote their diversity may help minimize extinction risks.

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Table 2.1. Physical characteristics of tributaries sampled in Spread Creek, Wyoming, and Shields River, Montana. Wetted width and gradient are means of electrofishing sample sections. Temperatures and discharges are means of daily means from July through September at the mouth of each stream during 2012 and 2013.

Stream	Lower elevation (m)	Upper elevation (m)	Length with trout (km)	Number of sample sections	Wetted width (m)	Gradient (%)	Temperature (°C)		Discharge (m^3/s)	
							2012	2013	2012	2013
					Spread Creek basin					
Grouse Creek	2400	2700	5.7	18	2.7	4.3	9.99	10.25	0.076	0.058
Leidy Creek	2400	2700	5.4	17	2.9	3.7	9.11	9.15	0.343	0.166
Rock Creek	2220	2500	4.5	14	2.4	5.1	9.92	10.48	0.022	0.071
					Shields River basin					
Dugout Creek	1980	2300	3.5	7	2.9	4.4	10.19	10.60	0.047	0.027
Lodgepole Creek	2000	2200	2.5	7	1.8	4.5	9.39	9.82	0.019	0.006

Table 2.2. Sampling dates and methods used to capture, recapture, and resight trout in Spread Creek, Wyoming, and Shields River, Montana. Live captures and recaptures on primary sampling occasions were done with backpack electrofishing units and live resights during intervals between primary occasions were done with passive instream antennas (PIA) at the mouths of each creek as well as portable PIT antenna (PPA) continuous surveys throughout the entire length of the study streams.

Sampling period	Resight interval (months)	Number marked	Live recaptures	Live resights	Dead recoveries	Sampling method
Spread Creek basin						
Jul 26 – Sep 6, 2011		115				Electrofish
	10			51	2	PIA + PPA
Jul 2-18 , 2012		217	8			Electrofish
	3			170	1	PIA + PPA
Sep 22 – Oct 5, 2012		311	51			Electrofish
	9			294	4	PIA + PPA
Jul 1 – 18, 2013		140	41			Electrofish
	3			220	35	PIA + PPA
Oct 5-11, 2013		192	48			Electrofish
	1			157	15	PIA + PPA
Total		975	148	892	57	
Shields River basin						
Aug 1 – 26, 2011		90				Electrofish
	10			48	1	PIA + PPA
Jul 10-20 , 2012		54	11			Electrofish
	3			49	4	PIA + PPA
Sep 17 – Oct 19, 2012		70	16			Electrofish
	9			71	12	PIA + PPA
Jul 8 – Aug 19, 2013		55	27			Electrofish
	3			12	0	PIA + PPA
Sep 19 – Oct 10, 2013		66	32			Electrofish
	1			0	0	PIA + PPA
Total		335	86	180	17	

Table 2.3. Mean (SD) daily growth rates and annual growth rates of three size classes of Yellowstone Cutthroat Trout from tributaries of Spread Creek, Wyoming, and Shields River, Montana, 2011-2013.

			Growth in Length		Growth in Weight	
Stream	Size class (mm)	*n*	Daily (mm/day)	Annual (mm/year)	Daily (g/day)	Annual (g/year)
			Spread Creek basin			
Grouse Creek	< 100	3	0.08 (0.01)	29.8 (5.0)	0.03 (0.01)	10.4 (3.4)
	100-149	9	0.12 (0.04)	45.3 (14.7)	0.08 (0.03)	27.8 (10.9)
	≥ 150	3	0.08 (0.03)	27.7 (11.6)	0.07 (0.03)	26.2 (12.0)
Leidy Creek	< 100	1	0.11 (--)	39.7 (--)	0.04 (--)	14.5 (--)
	100-149	5	0.16 (0.05)	58.4 (19.6)	0.11 (0.05)	39.6 (17.5)
	≥ 150	5	0.11 (0.05)	40.1 (19.0)	0.14 (0.03)	49.9 (10.8)
Rock Creek	< 100	7	0.08 (0.02)	28.2 (6.2)	0.02 (0.01)	8.3 (3.2)
	100-149	6	0.07 (0.01)	26.4 (5.2)	0.03 (0.01)	11.5 (3.2)
	≥ 150	7	0.05 (0.03)	17.5 (9.6)	0.06 (0.04)	22.3 (14.6)
			Shields River basin			
Dugout Creek	< 100	6	0.15 (0.01)	53.7 (4.3)	0.06 (0.02)	21.7 (7.8)
	100-149	3	0.12 (0.01)	44.7 (4.9)	0.11 (0.03)	41.9 (10.5)
	≥ 150	1	0.11 (--)	40.9 (--)	0.07 (--)	24.3 (--)
Lodgepole Creek	< 100	12	0.09 (0.02)	34.0 (7.2)	0.03 (0.01)	12.5 (5.0)
	100-149	19	0.07 (0.03)	25.7 (12.3)	0.06 (0.03)	22.1 (9.5)
	≥ 150	11	0.03 (0.02)	10.9 (7.5)	0.08 (0.07)	30.9 (26.5)

Table 2.4. Five top candidate Barker mark-recapture models used to estimate survival rate (*S*) of Yellowstone Cutthroat Trout in Spread Creek, Wyoming, and Shields River, Montana, 2011-2013 (size is one of two size class [80-119 mm or ≥ 120 mm in Spread Creek, 80–129 mm or ≥ 130 mm in Shields River]; *t* = time interval, . = constant [intercept only], + = additive parameter; * = interaction effect). The number of parameters estimated by the model (*K*), Akaike’s information criterion corrected for small-sample size (AIC_c), Akaike weight (W_i), and likelihood of each model are shown. Barker model parameters are described in the Methods.

Model structure	*K*	AICc	W_i	Model likelihood
Spread Creek basin				
$S_{(\text{size + stream} + t + \text{size}*t)}$ $p_{(\text{size + season})}$ $r_{(.)}$ $R_{(t)}$ $R_{(.)}$ F=F’	22	4213.7	0.978	1.000
$S_{(\text{steam + size + year + stream*size + size*year})}$ $p_{(\text{size + season})}$ $r_{(.)}$ $R_{(t)}$ $R_{(.)}$ F=F’	20	4222.7	0.011	0.011
$S_{(\text{steam + size + year + stream*size})}$ $p_{(\text{size + season})}$ $r_{(.)}$ $R_{(t)}$ $R_{(.)}$ F=F’	18	4223.6	0.007	0.007
$S_{(\text{steam} + t)}$ $p_{(\text{size + season})}$ $r_{(.)}$ $R_{(t)}$ $R_{(.)}$ F=F’	17	4225.6	0.003	0.003
$S_{(\text{size + stream} + t)}$ $p_{(\text{size + season})}$ $r_{(.)}$ $R_{(t)}$ $R_{(.)}$ F=F’	18	4227.3	0.001	0.001
Shields River basin				
$S_{(\text{size + stream + year})}$ $p_{(\text{stream})}$ $r_{(.)}$ $R_{(\text{season})}$ $R_{(.)}$ F=F’	11	1225.6	0.341	1.000
$S_{(\text{size + stream + year + size*stream + size*season + stream*season})}$ $p_{(\text{stream})}$ $r_{(.)}$ $R_{(\text{season})}$ $R_{(.)}$ F=F’	13	1227.1	0.158	0.464
$S_{(\text{ size + stream + year + size*stream + size*year + stream*year })}$ $p_{(\text{stream})}$ $r_{(.)}$ $R_{(\text{season})}$ $R_{(.)}$ F=F’	16	1227.3	0.148	0.433
$S_{(\text{size + stream + year + size*stream})}$ $p_{(\text{stream})}$ $r_{(.)}$ $R_{(\text{season})}$ $R_{(.)}$ F=F’	12	1227.4	0.137	0.403
$S_{(\text{size + stream} + t)}$ $p_{(\text{stream})}$ $r_{(.)}$ $R_{(\text{season})}$ $R_{(.)}$ F=F’	13	1228.9	0.066	0.193

Table 2.5. Numbers of Yellowstone Cutthroat Trout (80–119 mm in Spread Creek, Wyoming, and 80–129 mm in Shields River, Montana) tagged in each study stream by year and the numbers and percents that were detected moving downstream past passive instream antennas located at the mouths of each stream by year.

Stream	Tag year	Number tagged	Number detected by year				Percent detected by year			
			2011	2012	2013	Total	2011	2012	2013	Total
			Spread Creek basin							
Grouse Creek[a]	2011	17		2	0	2		11.8	0.0	11.8
	2012	64		4	9	13		6.3	14.1	20.3
	2013	47			7	7			14.9	14.9
Leidy Creek[a]	2011	9		0	0	0		0.0	0.0	0.0
	2012	55		0	0	0		0.0	0.0	0.0
	2013	42			0	0			0.0	0.0
Rock Creek[a]	2011	12		0	0	0		0.0	0.0	0.0
	2012	111		0	18	18		0.0	16.2	16.2
	2013	60			6	6			10.0	10.0
			Shields River basin							
Dugout Creek	2011	27	5	1	1	7	18.5	3.7	3.7	25.9
	2012	34		1	3	4		2.9	8.8	11.8
	2013	58			4	4			6.9	6.9
Lodgepole Creek	2011	8	0	0	1	1	0.0	0.0	12.5	12.5
	2012	38		1	7	8		2.6	18.4	21.1
	2013	16			0	0			0.0	0.0

[a] No antennas were deployed during 2011

Table 2.6. Numbers of Yellowstone Cutthroat Trout (≥ 120 mm in Spread Creek, Wyoming, and ≥ 130 mm in Shields River, Montana) tagged in each study stream by year and the numbers and percents that were detected moving downstream past passive instream antennas located at the mouths of each stream by year.

	Tag	Number	Number detected by year				Percent detected by year			
Stream	year	tagged	2011	2012	2013	Total	2011	2012	2013	Total
					Spread Creek basin					
Grouse Creek[a]	2011	26		2	0	2		7.7	0.0	7.7
	2012	98		15	11	26		15.3	11.2	26.5
	2013	84			15	15			17.9	17.9
Leidy Creek[a]	2011	21		1	0	1		4.8	0.0	4.8
	2012	119		5	5	10		4.2	4.2	8.4
	2013	60			3	3			5.0	5.0
Rock Creek[a]	2011	30		2	0	2		6.7	0.0	6.7
	2012	81		3	7	10		3.7	8.6	12.3
	2013	39			1	1			2.6	2.6
					Shields River basin					
Dugout Creek	2011	30	3	4	0	7	10.0	13.3	0.0	23.3
	2012	27		4	2	6		14.8	7.4	22.2
	2013	15			3	3			20.0	20.0
Lodgepole Creek	2011	25	0	2	2	4	0.0	8.0	8.0	16.0
	2012	25		0	4	4		0.0	16.0	16.0
	2013	32			0	0			0.0	0.0

[a] No antennas were deployed during 2011

Figures

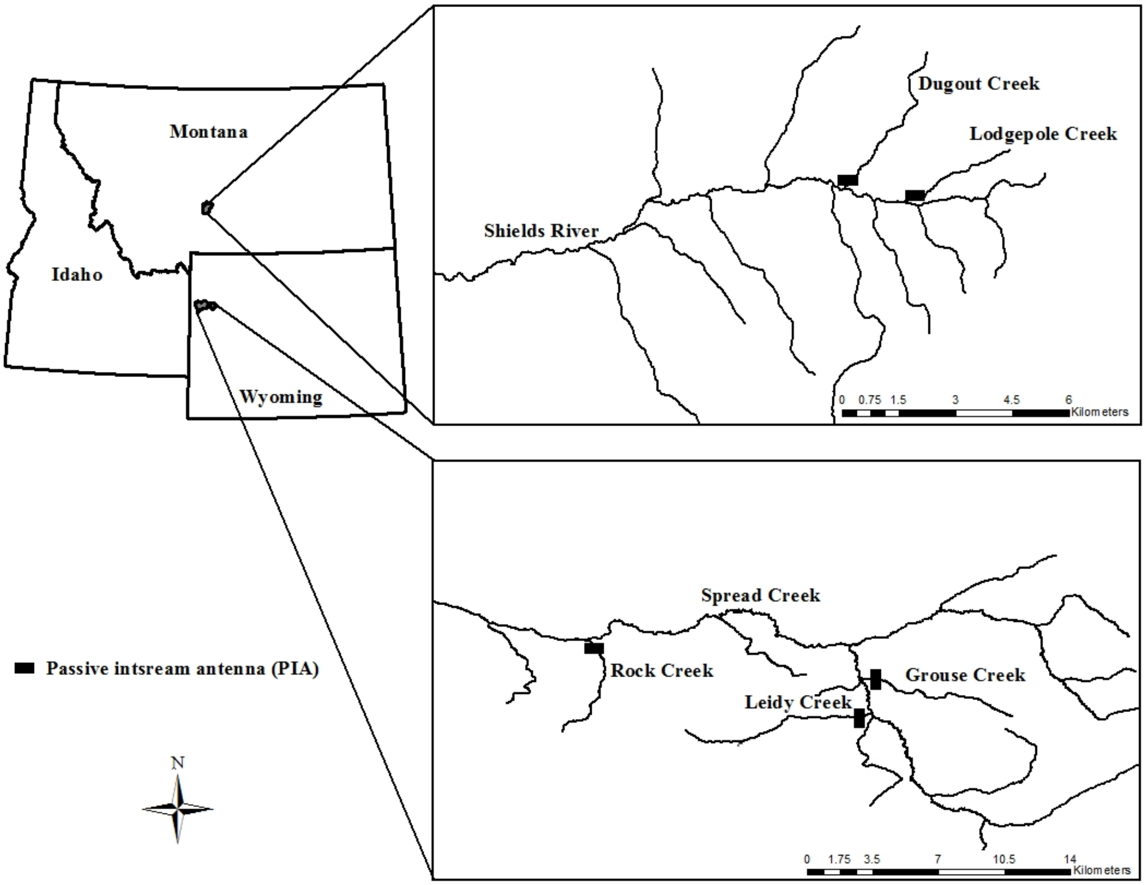

Figure 2.1. Study streams in the Shields River and Spread Creek basins with locations of passive instream antennas.

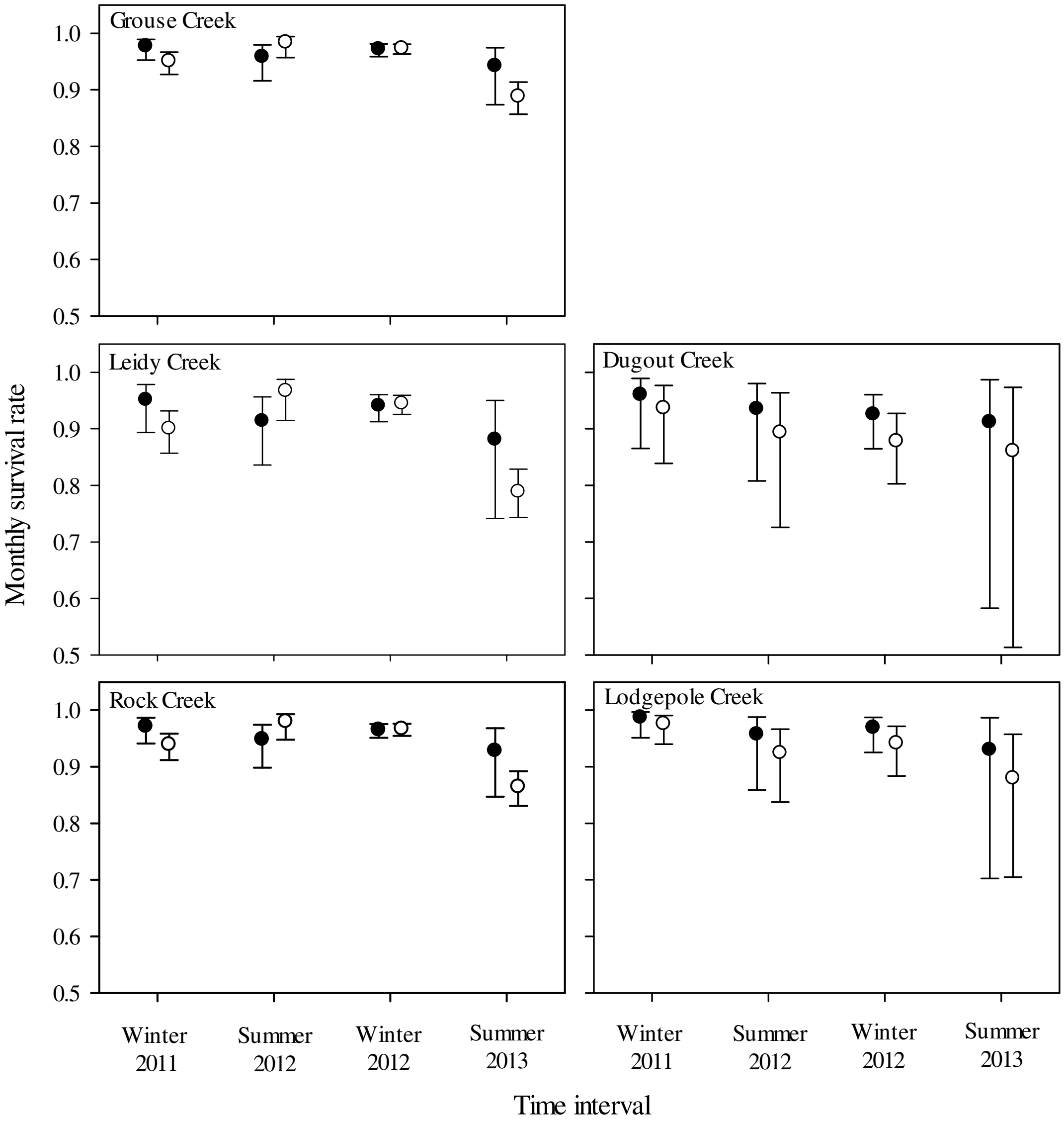

Figure 2.2. Model-averaged estimates of monthly survival rate (± 95% confidence interval) calculated from Barker mark-recapture analyses of two size classes of Yellowstone Cutthroat Trout in Spread Creek, Wyoming (left), and Shields River, Montana (right), 2011-2013. Size classes are 80-119 mm (closed circle) and ≥ 120 mm (open circle) in Spread Creek basin and 80-129 mm (closed circle) and ≥ 130 mm (open circle) in Shields River basin.

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CHAPTER THREE

EFFECTS OF CLIMATE-DRIVEN STREAM FACTORS ON SUMMER GROWTH PATTERNS OF YELLOWSTONE CUTTHROAT TROUT

Contribution of Authors and Co-Authors

Manuscript in Chapter 3

Author: Patrick Uthe

Contributions: Helped conceive study design, implemented study, collected and analyzed data, and authored manuscript.

Co-Author: Robert Al-Chokhachy

Contributions: Helped conceive study design, assisted with data collection, provided guidance on data analysis, and edited manuscript.

Co-Author: Bradley Shepard

Contributions: Helped conceive study design, assisted with data collection, and reviewed manuscript.

Co-Author: Alexander Zale

Contributions: Helped conceive study design, provided technical insights, and edited manuscript

Co-Author: Jeffrey L. Kershner

Contributions: Helped conceive study design, provided technical insights, and reviewed manuscript.

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Patrick Uthe, Robert Al-Chokhachy, Bradley Shepard, Alexander Zale, and Jeffrey L. Kershner
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Abstract

Coldwater fishes are sensitive to stream conditions governed by climate. Distributions of inland salmonids in North America have declined significantly such that many of the current strongholds are located in small headwater systems that will serve as important refugia as climate change progresses. We investigated the effects of discharge, stream temperature, and food abundance on summer growth of Yellowstone Cutthroat Trout, *Oncorhynchus clarkii bouvieri* a species of concern with significant ecological value. Discharge and temperature were both associated with growth, but had differing effects on energy allocation. Greater rates of prey delivery at higher discharges probably enabled trout to accumulate reserve tissues in addition to structural growth. Temperature interacted with fish length such that large fish responded less favorably to increases in average daily temperatures and the length of the summer growing season. The strength of the discharge effect on growth suggests that climate adaptation strategies for coldwater fishes that focus solely on thermal characteristics may be misleading.

Introduction

Climate provides a template for biological processes in lotic ecosystems (Minshall et al. 1983). Salmonids are coldwater fishes that are particularly sensitive to environmental conditions because of their narrow physicochemical tolerances (Brett 1952). Thermal and hydrologic controls on phenology and life history expression (Kovach et al. 2012) can ultimately affect individual fitness, making salmonids exceptionally vulnerable to climate-driven stream changes.

The distribution of native, potamodromous salmonids in North America has been significantly reduced through historical extirpations, with strongholds for extant populations predominantly occurring in high-elevation, montane environments (Williams et al. 2009). Stream networks in the topographically diverse Northern Rocky Mountains (NRM) of the United States have already exhibited symptoms of climate change through alterations in hydrologic and thermal regimes (Isaak et al. 2012). Additional climatic shifts in the NRM will continue to decrease late summer discharges and increase temperatures, probably disproportionately increasing the importance of headwater stream networks, which have a low risk of thermally induced extirpation (Haak et al. 2010). Accordingly, an understanding of how climate-related factors influence salmonid life-history patterns, demographic rates, and fitness is imperative.

Individual fish growth is an attribute with strong population-level effects (Hutchings 1993) that is directly related to habitat conditions influenced by climate. Water temperature dictates fish metabolism and therefore growth potential (Bear et al. 2007), whereas stream discharge controls the amount of suitable foraging habitat and the rate of prey delivery in the water column (Nislow et al. 2004; Harvey et al. 2006). Additionally, ecosystem productivity is changing across much of North America through changes in growing-season length (Zhu et al. 2012), which can affect salmonid forage. The few linkages between climatic factors and salmonid growth have focused on autumn spawning species in regions with low topographic complexity (Bacon et al. 2004; Xu et al. 2010), but not species of inland cutthroat trout, which have entirely different life history patterns and evolutionary histories. Climate change is one of the greatest threats to the long term persistence of Yellowstone Cutthroat Trout, *Oncorhynchus clarkii bouvieri* (Gresswell 2011), a taxon with significant ecological value (Stapp and Hayward 2002). We investigated the effects of stream temperature, discharge, and food abundance on summer growth to elucidate the mechanisms of climate change effects on Yellowstone Cutthroat Trout. Specifically, we describe patterns of growth in mass and length to determine how trout are allocating energy (Broekhuizen et al. 1994).

Methods

Study Area

We sampled trout from three tributaries of Spread Creek, Wyoming, and two tributaries of Shields River, Montana (Figure 3.1). Spread Creek is a 3rd-order tributary to the Snake River originating in the Gros Ventre Mountains in the Bridger-Teton National Forest and continuing through portions of Grand Teton National Park. The Shields River originates in the Crazy Mountains in the Custer-Gallatin National Forest and joins the Yellowstone River east of Livingston, Montana. The climates of these regions are characterized by dry summers and cold winters with much annual precipitation occurring as snowfall. Species compositions are similar between watersheds. Spread Creek contains Yellowstone Cutthroat Trout, Bluehead Sucker, *Catastomus discobolus*, Utah Sucker, *C. ardens*, Longnose Dace, *Rhinichthys cataractae*, Mottled Sculpin, *Cottus bairdii*, Paiute Sculpin, *C. beldingi*, and non-native Brook Trout *Salvelinus fontinalis*. Species in the upper Shields River drainage are Yellowstone Cutthroat Trout, Mottled Sculpin, Longnose Dace, and non-native Brook Trout.

In the Spread Creek basin, fish sampling occurred in Leidy, Grouse, and Rock creeks. Leidy and Grouse creeks are 1st-order streams and Rock Creek is a 2nd-order stream. Fish-bearing stream length in Rock Creek is 4.5 km and flows from an elevation of 2500 m to 2200 m where it enters Spread Creek. Grouse and Leidy creeks flow from elevations of 2700 m to 2400 m where they enter South Fork Spread Creek. Fish-bearing stream length is 5.4 km in Leidy Creek and 5.7 km in Grouse Creek. Rock Creek flows through a confined valley with conifers as the dominant riparian vegetation. The lower and middle portions of Leidy Creek flow through a wide valley dominated by a willow riparian zone. The upper portion consists of a short, high-gradient coniferous forest section and a meadow-like reach directly below Leidy Lake. Grouse Creek has a mixed willow/conifer riparian zone in the lower and middle sections and a conifer forested upper section. The majority of Grouse Creek flows through an unconfined valley.

In the Shields River basin, fish sampling occurred in Dugout and Lodgepole creeks. Dugout Creek is a 2nd-order stream that flows from an elevation of 2300 m to 1980 m where it enters the Upper Shields River. It has 3.5 km of fish-bearing stream length. Lodgepole Creek is a 2nd-order stream that flows from an elevation of 2200 m to 2000 m where it enters the Upper Shields River. It has 2.5 km of fish-bearing stream length. The riparian area of Dugout Creek is characterized primarily by conifer forest. Small meadow areas with willows are present near the mouth and towards the upper reaches of the stream. Lodgepole Creek flows entirely through coniferous forest.

Fish Capture and Recapture

Sampling occurred bi-annually (July-August and September-October) from 2011 through 2013 in the Shields River basin and from 2012 through 2013 in the Spread Creek basin. Fish were sampled in 100-m sections that were systematically distributed with a frequency of one site every 0.2-0.5 km. We used single-pass electrofishing for the majority of sample sections, but conducted multiple-pass electrofishing in a subset of sections to estimate capture efficiencies. We used Smith-Root® BP-15, BP-12, or LR-24 backpack electrofishing units operated at voltages in the range of 100 to 600 V, frequencies under 50 Hz, and pulse widths less than 2 µsec (Dwyer et al. 2001) to capture fish. After capture, trout were anesthetized with clove oil. After fish were sufficiently anesthetized, measurements of total length (± 1 mm) and weight (± 0.5 g) were taken on each individual. In the Spread Creek drainage, trout with lengths 80-120 mm were implanted with 12-mm passive integrated transponder tags (PIT tag; half-duplex, Oregon RFID, Portland, Oregon) and individuals 120 mm and longer were implanted with 23-mm PIT tags. In the Shields River drainage, trout with lengths 80-130 mm were implanted with 12-mm PIT tags and individuals 130 mm and longer were implanted with 23-mm PIT tags. We inserted tags into the body cavity through a small ventral incision anterior to the pectoral fins made with a scalpel. Adipose fins were removed to serve as secondary marks. We used a hand-held PIT-tag scanner to check for tags in trout with clipped adipose fins. If we detected a tag, we recorded the unique tag identification number, but if we failed to detect a tag after three attempts, we considered it a shed tag and implanted a new tag. Shed rate was low over the course of the study (4%). After processing, individuals were placed in a live well (plastic tub with holes that allow current to flow through) until fully recovered and then distributed throughout the sampling section. We did not observe a tag effect as evidenced by lack of a significant trend between growth rate and days at large ($P = 0.393$).

Temperature and Discharge

Pressure transducers (Solinst Canada LTD, Georgetown, Ontario) and temperature data loggers (Onset Computer Corp., Pocasset, Massachusetts) were deployed near the mouth and upper limit of salmonid distribution in each stream to record water temperature (± 0.01 °C) and stage height (± 0.001 m) continuously at hourly intervals. Discharge was measured a minimum of three times between July and November at each pressure transducer to develop stage-discharge relationships. We estimated lapse rates from the lower and upper loggers to interpolate stream temperatures at all tagging sections based on the elevation of the section mid-point. Temperature data were used to calculate cumulative growing degree days greater than 3°C (hereafter called degree days). Degree days rather than mean temperature over the growing season were used because the thermal profiles of the streams exhibited subtle differences that were not captured by a seasonal mean (Figure 3.2). The 3°C degree-day threshold was chosen because salmonid growth at temperatures as low as 3.8°C has been documented in laboratory experiments (e.g. Elliott 1975) and we wanted to maintain a buffer around this temperature because maximum daily temperatures in these streams exceeded 4°C when average daily temperatures were at 3°C. Degree days were calculated by summing the mean daily temperature minus the 3°C threshold for the period between tagging and recapture of an individual (e.g., Lawrence et al. 2012).

Food Availability

Food availability was measured with bi-weekly drift samples collected at one fixed sampling site near the mouth of each stream from July through September in 2012 and 2013. Between three and six events occurred in each stream during each year, except in Dugout and Lodgepole creeks, which only had one sampling event during 2013 at the beginning of August. Sampling occasions consisted of morning samples starting one hour after sunrise and evening samples starting one hour prior to sunset. This regimen captured the beginning of the crepuscular increase in drift density that is an important feeding period for salmonids (Elliott 1967)**.**

Two drift nets (25 × 45 cm, 500-µm mesh) were deployed adjacently in the thalweg of a fast-water channel unit. Nets remained in the channel for one hour to maximize the volume of water sampled without risking backflow caused by clogging. Nets were deployed at least 2 cm above the substrate to prevent benthic macroinvertebrates from crawling into the nets. The tops of the nets were always above the water surface to capture drifting terrestrial invertebrates. Water velocity and depth were measured directly after setting the nets and prior to retrieving them to calculate the volume of water sampled. Net contents were transferred to storage jars and preserved with 95% ETOH.

Samples from 2012 were identified to the taxonomic level of order and then dried in an oven at 103°C for four hours (Mason et al. 1983) to account for differences in total energy available caused by differences in invertebrate assemblage composition among streams. Energy content was estimated using dry mass-energy equivalents (Curry et al. 1993). A strong correlation existed between total energy estimated from order-specific caloric content and total dry mass of the sample ($R^2 = 0.9$). Therefore, drift samples from 2013 were oven dried and weighed without partitioning taxonomic groups. Food availability comparisons among streams and years were based on total dry mass of samples.

Statistical Analyses

We investigated summer growth of individual Yellowstone Cutthroat Trout (n = 181). Only trout recaptured within the same year were included in the analysis. Growth was estimated over the summer growing season using the following equation:

$$G_{L,W} = (R - M),$$

where G is total growth (mm or g), L is length, W is weight, R is length or weight at recapture, and M is length or weight at marking.

Variation of individual summer growth was analyzed with linear mixed-effect models using the *nlme* package in Program R (R Development Core Team 2013). We developed a candidate set of models to describe the effects of discharge, temperature, density, and fish length on variation of individual summer growth of trout. Variation in growth was explored with the general model structure:

$$G = \mathrm{SB} + \mathrm{TL} + \mathrm{MF} + \mathrm{DD} + \mathrm{DD} \times \mathrm{TL},$$

where SB is sample section biomass calculated as total first pass biomass divided by average stream-specific capture efficiency, TL is the initial total length of the individual, MF is mean discharge between capture and recapture estimated from the lower level logger in each stream, and DD is the cumulative degree days between capture and recapture estimated at the section the trout was tagged in. Candidate models with nested structures of the global model were developed to assess support for the hypothesized effects. We used Akaike's information criterion corrected for small sample size ($\mathrm{AIC_c}$) to rank competing models. All models included nested random effects for basin, stream, and sample section. The effect of food abundance was not included in the model because few biologically or statistically significant differences existed in drifting biomasses of invertebrates among streams or years (Figure 3.3). Temperature was expected to interact with fish length (Figure 3.4). Consideration of interactions between discharge and fish length and discharge and temperature were precluded by lack of a range of fish lengths and temperatures at all levels of stream discharge.

Results

Discharge differed throughout the course of the study (Table 3.1). Mean daily temperatures during the growing season were not remarkably different across streams and years (Table 3.1), but degree days during the growing season varied as a result of short-term weather patterns and inter-annual differences in seasonal temperature shifts (Figure 3.2).

A significant association existed between growth in weight and degree days for small trout (Figure 3.4a), but not for large trout (Figure 3.4b). The association between growth in length and accumulation of degree days was similar for small (Figure 3.4c) and large trout (Figure 3.4d). Stream discharge was strongly associated with growth in weight (Figure 3.4e) and length (Figure 3.4f). Discharge, degree days, and fish length were all included in the top models of summer growth in length and weight (Table 3.2). The strength of the discharge effect was greater for growth in length than growth in weight (Figure 3.5). Significant interactions existed between degree days and fish length for growth in length and weight (Table 3.3). The strength of the degree day effect was greater for growth in length than growth in weight (Figure 3.6). Predicted growth from the top models was positively correlated with observed growth in weight ($R^2 = 0.56$, $P < 0.001$) and length ($R^2 = 0.65$, $P < 0.001$).

Discussion

Our results demonstrate the challenges with the conservation of salmonids—high elevation streams are likely to act as critical thermal refugia under anticipated climate changes, yet discharge within these ecosystems can strongly affect energy allocation, and concomitantly, fitness (Scott 1962). Both observed data and modeling results indicated that juvenile and adult trout invested more in structural growth (length) than in accumulation of reserve tissue (weight) (Broekhuizen et al. 1994). Prey abundance in headwater streams fluctuates seasonally—high abundance occurs during early summer when discharges are high (Bacon et al. 2004; Leeseberg and Keeley 2014). Therefore, trout probably allocate ingested energy towards easily synthesized reserves as opposed to structural tissue to maximize the benefits of the short period of high food availability (Broekhuizen et al. 1994). Entering winter in poor condition can reduce reproductive potential of adults (Scott 1962) and decrease over-winter survival of juveniles (Biro et al. 2004). Trout lose reserves during winter such that mature individuals are confronted with a tradeoff between reproductive investment and depleted reserve restoration (Reznick 1983) when compensatory growth occurs during the following spring (Broekhuizen et al. 1994). The tradeoff can affect population dynamics through decreased fecundity or increased post-spawn mortality (Jonsson et al. 1991). As climate change continues to decrease late summer discharges, trout may be further prevented from accumulating pre-winter reserves causing juveniles to lack adequate energy for reproductive development forcing them to delay maturation in favor of somatic growth (Bohlin et al. 1994).

The strength of the discharge effect was greatest for growth in weight, which probably resulted from high prey availability at high discharges (Figure 3.3). Significant decreases in rates of prey delivery depress growth rates of closely related Rainbow Trout, *Oncorhynchus mykiss*, under direct manipulation of discharges (Harvey et al. 2006). Moreover, variation in growth of Atlantic Salmon, *Salmo salar*, was best explained by natural variability in annual discharges, which affected the availability of suitable foraging habitat (Nislow et al. 2004). The strength of the temperature effect was greatest for growth in length, indicating trout exposed to temperatures and growing season lengths at the upper end of the range we observed were accumulating less reserves than trout exposed to fewer thermal units over the growing season.

The temperature effect was positive for small trout, suggesting that increased average daily temperatures near physiological optima or increased growing season lengths may cause increased growth, which corroborates predictions from the Greater Yellowstone Ecosystem (Al-Chokhachy et al. 2013) based on a temperature-dependent growth model (Bear et al. 2007). However, the temperature effect lost strength and shifted direction for larger individuals, suggesting that without a concurrent increase in prey delivery, increases in temperature or duration of the growing season may reduce energetic profitability. Interestingly, the predicted fish length at which the temperature effect shifted direction was at a larger size for growth in length than growth in weight, implying the energetic consequences of warming may be magnified for the largest individuals. These relationships conform to expectations given that thermal regimes in our study streams are below or near optimal for Cutthroat Trout (Bear et al. 2007) and that temperature-growth relationships for salmonids in the wild are highly dependent on food availability (Bacon et al. 2005).

Predicting the effects of future stream changes on trout growth will require a better mechanistic understanding of the relationships we observed. We did not include habitat surveys in our sampling design, making us unable to account for differences in quantities and qualities of foraging locations among streams. Therefore, we are unsure if the positive discharge effect was caused entirely by the increased prey we documented at high discharges or resulted from a combination of other variables, such as foraging habitat availability controlled by discharge (Nislow et al. 2004) and decreased competition at high discharges (Chapman and Bjornn 1969). Furthermore, our study duration was insufficient to investigate if trout from different populations responded differentially to the factors we investigated (sensu Álvarez et al. 2006). Additional research that builds on our study will provide a better understanding of the complexities of multiple abiotic and biotic stream factors on trout growth and afford more power to predict trout response to stream changes.

Overall, our findings demonstrate that even under thermally suitable conditions, discharge can greatly affect growth patterns. Consequently, future decreases in mountain snowpack (Isaak et al. 2012) and subsequent decreases in summer base discharges may have greater consequences than warming temperatures for headwater populations. For species such as Yellowstone Cutthroat Trout, the current distributions of which are limited to systems with short growing seasons and suboptimal thermal profiles, a better understanding of seasonal growth patterns will aid assessments of the importance of shoulder seasons, which are likely to be greatly altered as climate change progresses (Isaak et al. 2012; Zhu et al. 2012; Al-Chokhachy et al. 2013). Our findings and those of other field-based investigations (Nislow et al. 2004; Xu et al. 2010) demonstrate the need for consideration of multiple factors when devising conservation strategies for cold-water fishes in the face of climate change.

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Table 3.1. Minimum, maximum, and mean (SD) daily stream temperatures and discharges from July through September in three tributaries of Spread Creek, Wyoming, and two tributaries of Shields River, Montana, 2012-2013.

	2012			2013		
Stream	Minimum	Maximum	Mean	Minimum	Maximum	Mean
			Temperature (°C)			
Grouse Creek	4.68	14.58	9.99 (2.81)	1.94	14.20	10.25 (2.84)
Leidy Creek	5.01	12.31	9.11 (2.13)	2.37	12.09	9.15 (2.23)
Rock Creek	4.55	13.89	9.92 (2.65)	1.78	13.75	10.48 (2.68)
Dugout Creek	6.54	12.63	10.19 (1.72)	4.08	13.10	10.60 (2.00)
Lodgepole Creek	4.28	13.41	9.39 (2.87)	2.07	11.95	9.82 (2.31)
			Discharge (m^3/s)			
Grouse Creek	0.024	0.136	0.076 (0.024)	0.036	0.127	0.058 (0.022)
Leidy Creek	0.244	0.586	0.343 (0.089)	0.103	0.307	0.166 (0.047)
Rock Creek	0.008	0.100	0.022 (0.019)	0.029	0.155	0.071 (0.023)
Dugout Creek	0.023	0.120	0.047 (0.023)	0.015	0.046	0.027 (0.009)
Lodgepole Creek	0.003	0.138	0.019 (0.026)	0.005	0.011	0.006 (0.001)

Table 3.2. Linear mixed-effect models developed for comparison of summer growth of Yellowstone Cutthroat Trout in three tributaries of Spread Creek, Wyoming, and two tributaries of Shields River, Montana. All models include nested random effects for section, stream, and basin. *K* is the number of parameters in each model; AIC_C is Akaike's information criterion, corrected for small sample size; and W_i is the Akaike weight of the model. Model terminology is as follows: SB (section biomass, g/m^2), MF (mean discharge, m^3/s), TL (total length of individual at tagging, mm), DD (degree days).

Model	Structure	*K*	Model	AICc	W_i
	Growth in length				
1	TL + MF + DD + DD*TL	9	-577.37	1173.80	0.47
2	TL + DD + DD*TL	8	-578.94	1174.73	0.30
3	SB + TL + MF + DD + DD*TL	10	-577.36	1176.01	0.16
4	TL + MF + DD	8	-581.10	1179.04	0.03
5	TL + DD	7	-582.40	1179.45	0.03
6	SB + TL + MF + DD	9	-581.04	1181.13	0.01
7	TL + MF	7	-598.13	1210.90	0.00
	Growth in weight				
1	TL + MF + DD + DD*TL	9	-563.08	1145.21	0.52
2	SB + TL + MF + DD + DD*TL	10	-562.31	1145.92	0.36
3	TL + MF	7	-567.79	1150.24	0.04
4	SB + TL + MF	8	-566.73	1150.29	0.04
5	TL + MF + DD	8	-567.64	1152.12	0.02
6	SB + TL + MF + DD	9	-566.61	1152.28	0.02
7	SB + MF	7	-570.57	1155.79	0.00

Table 3.3. Analysis of individual summer growth in length and growth in weight of Yellowstone Cutthroat Trout in Spread Creek, Wyoming, and Shields River, Montana.

Factor	Estimate	SE	df	*t*-value	*p*- value
Growth in length [a]					
Intercept	1.084	4.126	127	0.263	0.793
Length	-0.020	0.021	127	-0.956	0.341
Discharge	18.195	10.345	127	1.759	0.081
Degree days	0.041	0.007	127	5.736	< 0.001
Length:degree days	< -0.001	< 0.001	127	-2.723	0.007
Growth in weight [b]					
Intercept	-4.655	3.433	127	-1.356	0.178
Length	0.024	0.019	127	1.268	0.207
Discharge	44.545	8.711	127	5.114	< 0.001
Degree days	0.019	0.007	127	2.818	0.006
Length: degree days	< -0.001	< 0.001	127	-3.003	0.003

[a] Random effect SD: basin = 0.001; stream = 4.274; section = 2.559; residual = 5.346

[b] Random effect SD: basin = 0.001; stream = 1.997; section = 3.339; residual = 4.790

Figures

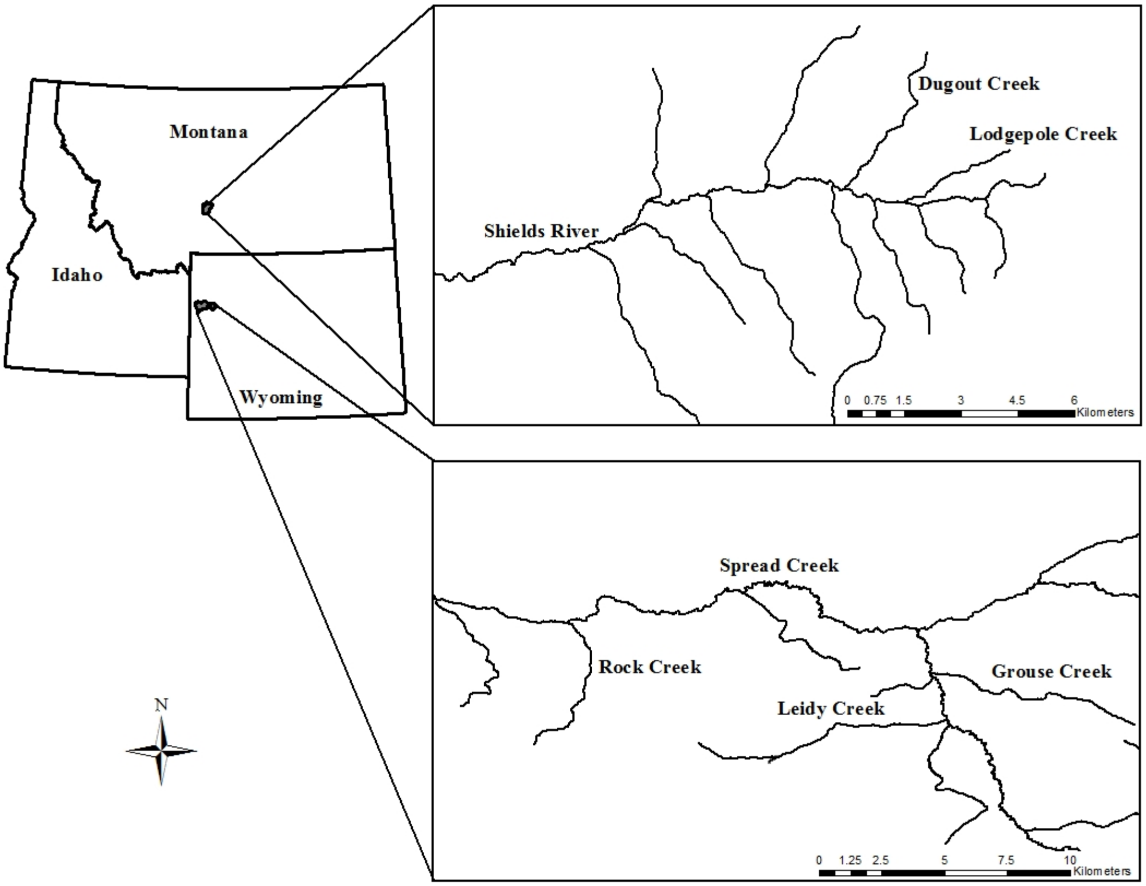

Figure 3.1. Study tributaries of Spread Creek, Wyoming, and Shields River, Montana.

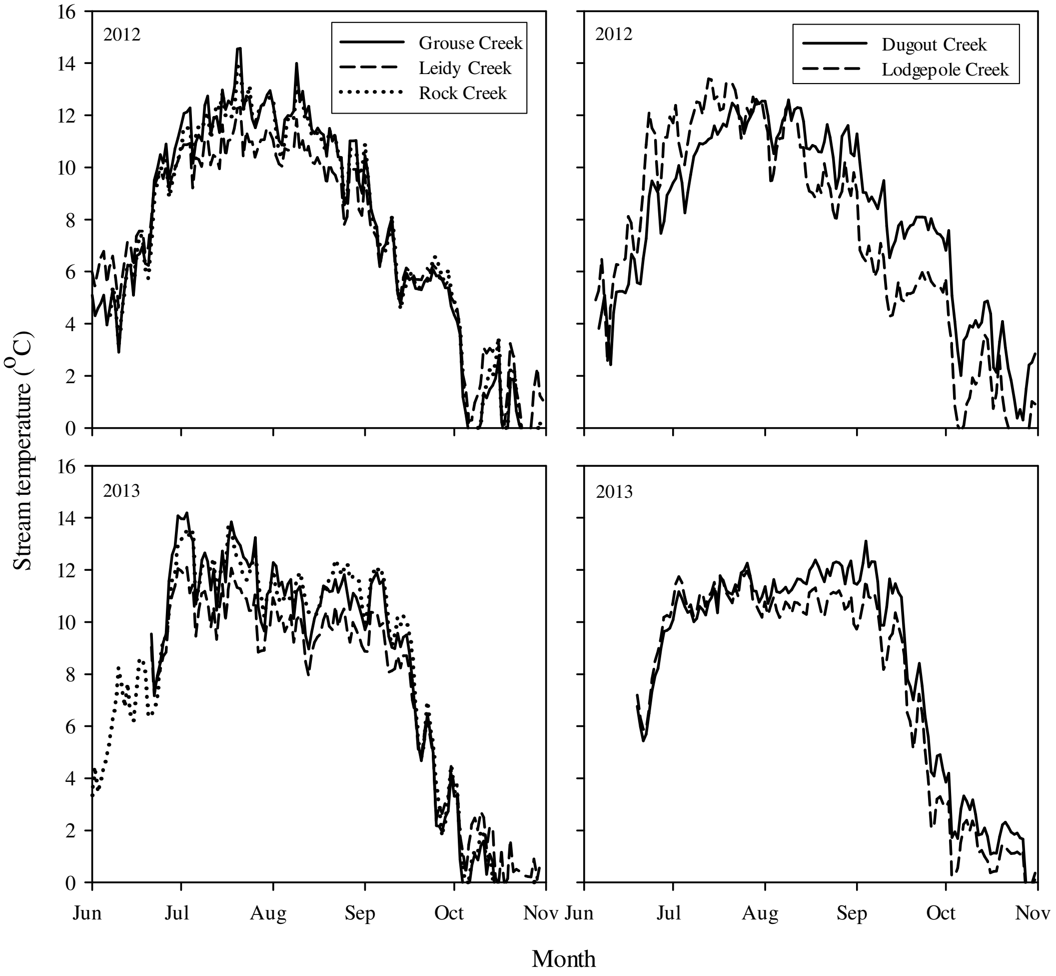

Figure 3.2. Mean daily stream temperatures during 2012 (top) and 2013 (bottom) in tributaries of Spread Creek, Wyoming (left), and Shields River, Montana (right).

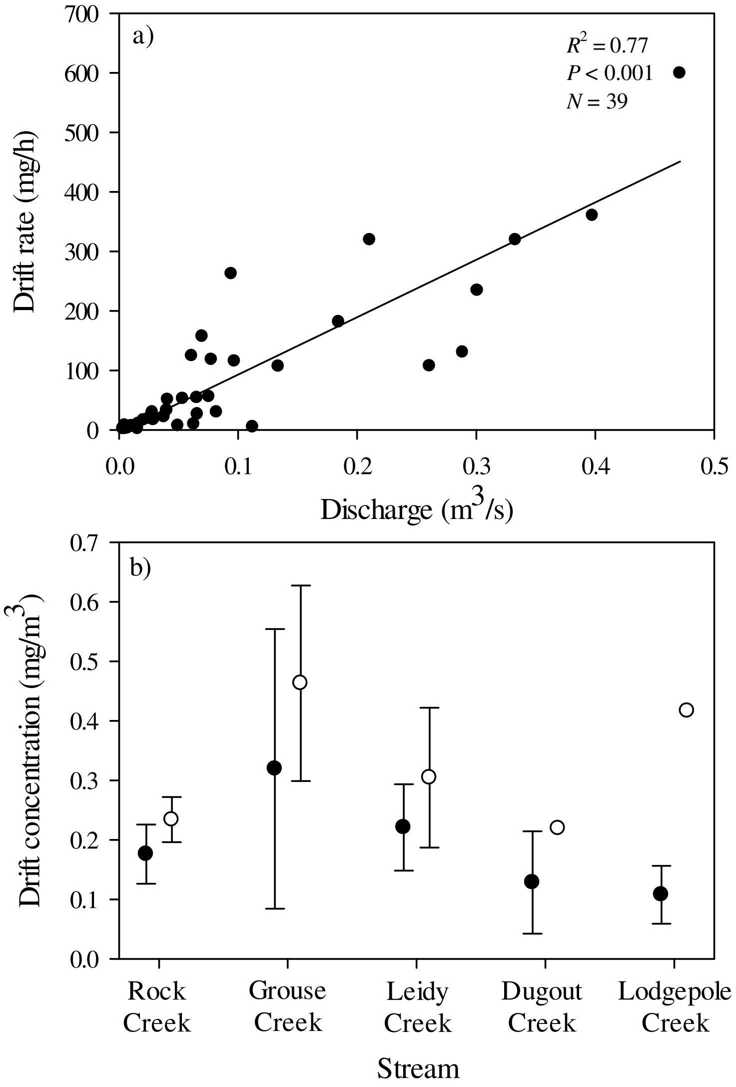

Figure 3.3. (a) Relationship between drift rate and discharge. (b) Average summer drift concentrations in each stream during 2012 (closed circles) and 2013 (open circles). Only one sampling event occurred in Dugout and Lodgepole creeks in 2013. Error bars represent 95% confidence intervals.

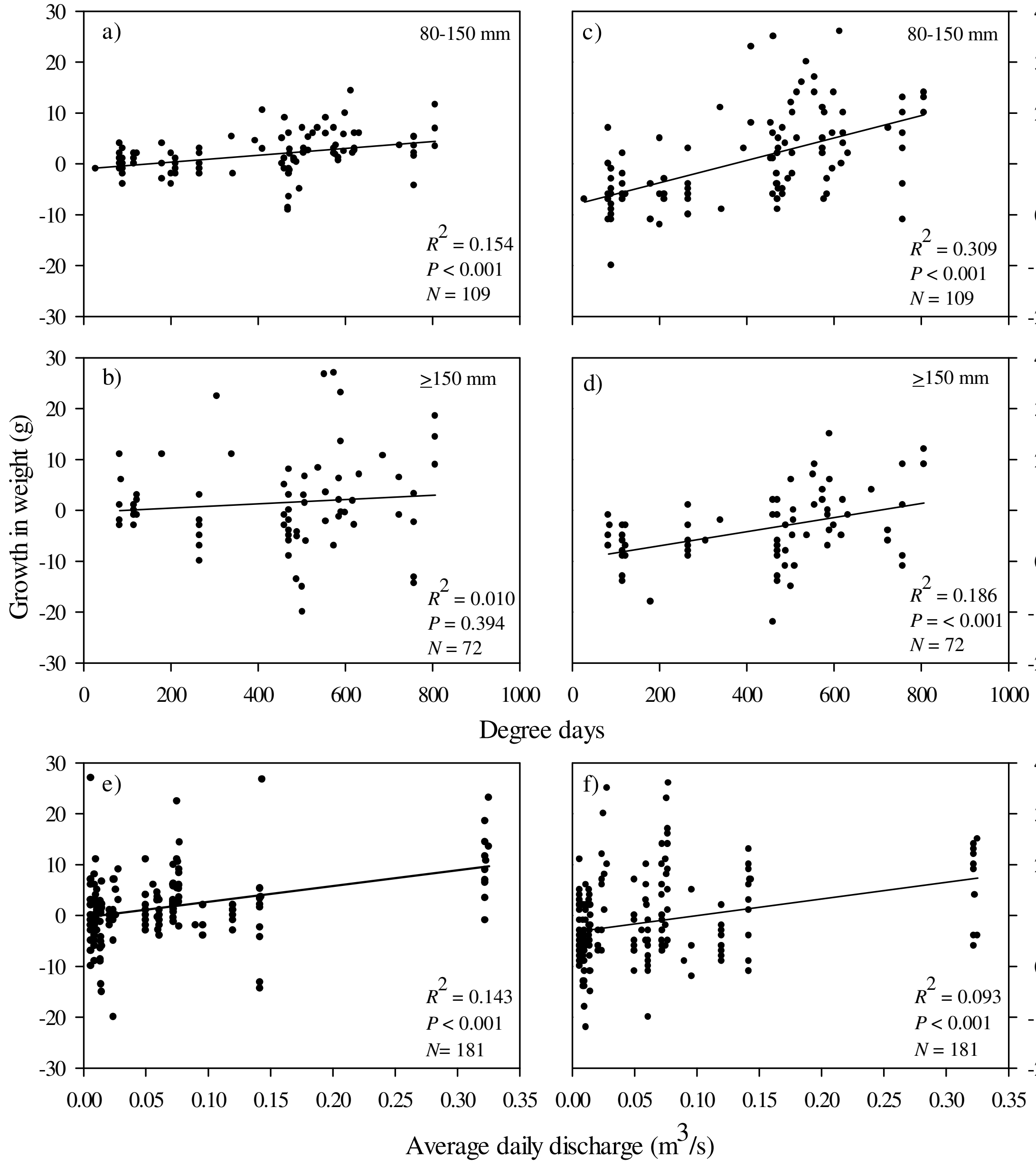

Figure 3.4. Relationships between degree days and summer growth in weight of Yellowstone Cutthroat Trout 80-150 mm (a) and ≥ 150 mm (b); relationships between degree days and summer growth in length of trout 80-150 mm (c) and ≥ 150 mm (d); relationships between average daily discharge and growth in weight (e) and growth in length (f) of trout of all lengths.

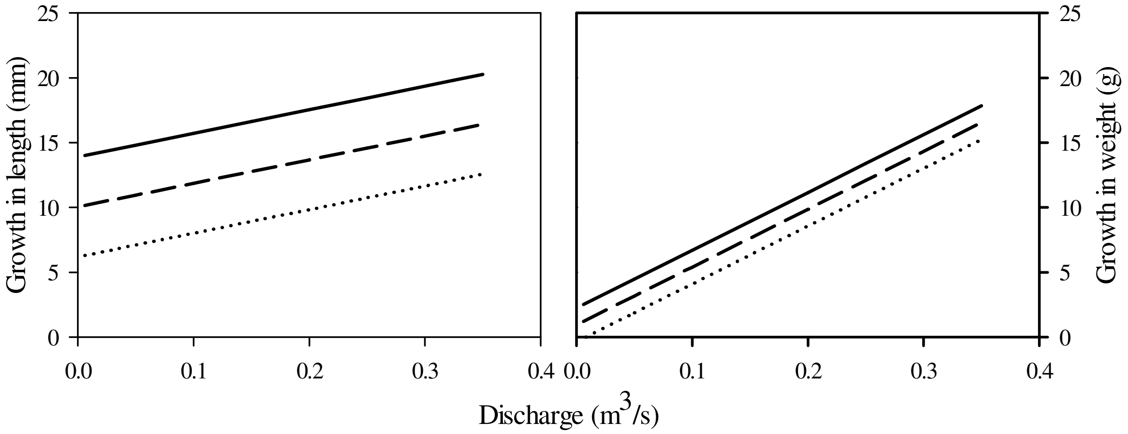

Figure 3.5. Predicted relationships between discharge and growth in length (left) and growth in weight (right) for trout with lengths 100 mm (solid lines), 150 mm (dashed lines), and 200 mm (dotted lines) (inference from model number 1 in Table 3.2.).

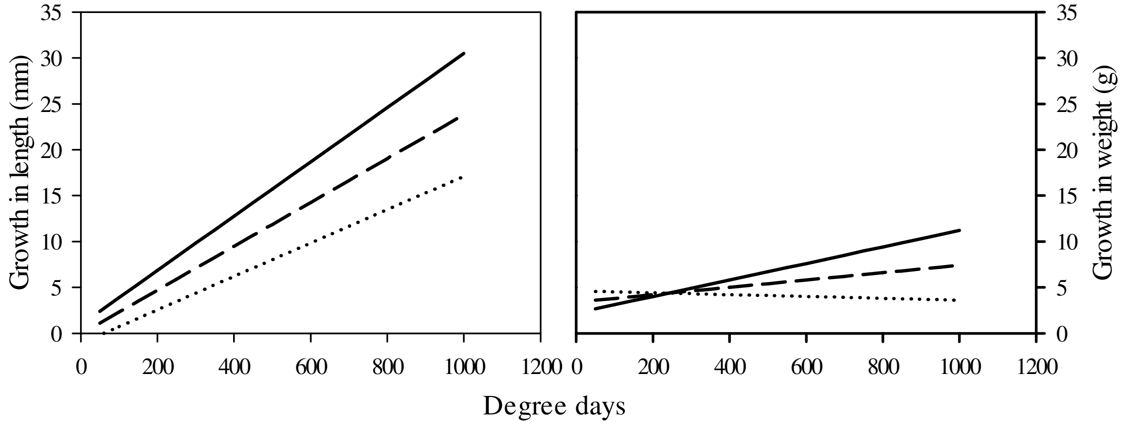

Figure 3.6. Predicted relationships between degree days and growth in length (left) and growth in weight (right) for trout with lengths 100 mm (solid lines), 150 mm (dashed lines), and 200 mm (dotted lines) (inference from model number 1 in Table 3.2.).

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CHAPTER FOUR

CONCLUSIONS

Headwater populations represent current and probable future strongholds of many native salmonids in the northern Rocky Mountains (Williams et al. 2009; Haak et al. 2010). Our objectives were to describe life history characteristics, estimate vital rates, and investigate the effects of climate attributes on summer growth rates of Yellowstone Cutthroat Trout in headwater basins. In Chapter 2, we estimated annual growth rates, survival rates, and proportions of tagged trout that migrated out of streams. We found annual survival rates were high compared to estimates of other Cutthroat Trout subspecies. We also found that small trout generally had greater survival rates than large trout, which is contrary to survival patterns of Bonneville Cutthroat Trout (Budy et al. 2007). In the small tributaries we investigated, large size may be disadvantageous because larger fish are probably more susceptible to predation (Lima and Dill 1990; Munch and Conover 2003) and resource limitations (Xu et al. 2010) than smaller fish. Growth rates were similar to those of populations of other Cutthroat Trout subspecies in headwater streams, but lower than those of Yellowstone Cutthroat Trout in large, low-elevation streams. The low growth rates observed in our study were probably a result of short growing seasons, sub-optimal thermal regimes (Bear et al. 2007), and low food availability throughout much of the growing season in high elevation drainages (Sotiropoulos et al. 2006; Leeseberg and Keeley 2014). We also observed high proportions of tagged trout migrating out of streams. Because we were unable to determine origin of trout tagged in tributaries and both basins contain multiple life-history forms, the high rates of movement were probably a combination of fluvial fish migrating back to the main-stem rivers after spawning, offspring of migratory individuals emigrating from tributaries, and resident individuals emigrating to more suitable locations to meet resource requirements (Brown and Mackay 1995; Northcote 1997; Jakober et al. 1998).

In Chapter 3, we investigated the effects of climatic stream factors on summer growth patterns of Yellowstone Cutthroat Trout. We found that discharge and temperature had strong effects on summer growth patterns. The strength of the discharge effect was greatest for growth in weight, which probably resulted from high prey availability at high discharges (Harvey et al. 2006). The temperature effect was positive for small trout, suggesting that increased average daily temperatures near physiological optima or increased growing season lengths cause increased growth. However, the temperature effect lost strength and shifted direction for larger individuals, suggesting that without a concurrent increase in prey delivery, increases in temperature or duration of the growing season may reduce energetic efficiency. These relationships conform to expectations given that thermal regimes in my study streams were below or near optimal for Cutthroat Trout (Bear et al. 2007) and that temperature-growth relationships for salmonids in the wild are highly dependent on food availability (Bacon et al. 2005).

Further research is needed to develop more precise survival estimates as well as investigate how climatic streams factors affect population level processes. Future growth investigations are necessary to determine if tributary populations respond differentially to changing thermal and hydrologic conditions (i.e., stream by discharge or stream by temperature interactions), which will aid in refining climate risk assessments. Overall, our results provide basic life history information that is useful in developing management and conservation strategies. Our results also demonstrate the importance of considering stream discharge, in addition to thermal suitability, when developing conservation strategies for cold-water fishes.

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