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EFFECTS OF CLIMATE AND BIOTIC FACTORS ON LIFE HISTORY CHARACTERISTICS AND VITAL RATES OF YELLOWSTONE CUTTHROAT TROUT IN SPREAD CREEK, WYOMING

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✦ ABSTRACT

The Upper Snake River represents one of the largest remaining strongholds of Yellowstone cutthroat across its native range. Understanding the effects of restoration activities and the diversity of life-history patterns and factors influencing such patterns remains paramount for long-term conservation strategies. In 2011, we initiated a project to quantify the success of the removal of a historic barrier on Spread Creek and to evaluate the relative influence of different climate attributes on native Yellowstone cutthroat trout and non-native brook trout behavior and fitness. Our results to date have demonstrated the partial success of the dam removal with large, fluvial Yellowstone cutthroat trout migrating up Spread Creek to spawn, thus reconnecting this population to the greater Snake River metapopulation. Early indications from mark-recapture data demonstrate considerable differences in life-history and demographic patterns across tributaries within the Spread Creek drainage. Our results highlight the diversity of life-history patterns of resident and fluvial Yellowstone cutthroat trout with considerable differences in seasonal and annual growth rates and behavior across populations. Continuing to understand the factors influencing such patterns will provide a template for prioritizing restoration activities in the context of future challenges to conservation (e.g., climate change).

✦ INTRODUCTION

The Greater Yellowstone Ecosystem is one of the largest intact ecosystems remaining in the lower 48 states (Koel et al. 2005). Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) are a vital component within this system serving as a food source for an estimated 42 species of birds and mammals (Varley and Schullery 1995). Additionally, the subspecies is highly valued as a recreational and cultural resource (Gresswell and Liss 1995, Varley and Schullery 1998).

It is estimated that Yellowstone cutthroat trout occupy approximately 42% of their historic range (May et al. 2007). About 54% of the current occupied stream length is in Wyoming (May et al. 2007). The decline of Yellowstone cutthroat trout has been attributed to the introduction of non-native salmonids and habitat degradation. Land uses such as resource extraction, grazing, and water diversion have impaired habitats and altered hydrologic regimes (Clancy 1988, Varley and Gresswell 1988, Van Kirk and Benjamin 2001). Introduced species, particularly brook trout (*Salvelinus fontinalis*), have led to displacement of native cutthroat trout species (Peterson et al. 2004, Shepard 2004). Rainbow trout (*O. mykiss*) pose a risk of hybridization (Allendorf and Leary 1988) and introgression may become prolific in systems where they co-occur with cutthroat trout (Thurrow et al. 1988, Henderson et al. 2000).

Many of the remaining genetically pure strongholds for this subspecies are on public land in mountainous areas that have not received the level of human disturbance that lower elevation systems have (Varley and Gresswell 1988). This has likely led to the resident life history form being more common than the fluvial form as it has with other salmonids (Nelson et al. 2002). However, headwater populations of Yellowstone cutthroat trout have not received the level of life history research that migratory populations from Yellowstone Lake and larger systems have (Gresswell et al. 1994, 1997, Kaeding and Boltz 2001). Much of the research pertaining to Yellowstone cutthroat trout in small systems has been on status assessments and factors influencing distributions (Kruse et al. 1997, 2000).

In addition to the current threats, global climate change may pose the most serious obstacle to the long term persistence of Yellowstone cutthroat trout (Williams et al. 2009, Haak et al. 2010, Gresswell 2011). Changes in air temperature and weather patterns are anticipated to alter thermal (Isaak et al. 2010, 2012b, Mantua et al. 2010) and hydrologic regimes (Adam et al. 2009). Moreover, many basins throughout the West have already exhibited the effects of climate change with shifts towards earlier timings of runoff in the spring and decreases in summer flows (Isaak et al. 2012a). The concurrent effects on biotic factors such as non-native species distributions (Wenger et al. 2011a, 2011b) and macroinvertebrate prey (Harper and Peckarsky 2006) are anticipated to play major roles in shaping future cutthroat trout distributions. However, there is still a lack of understanding about the influence that abiotic and biotic factors have on the diversity of life histories and population demographics of Yellowstone cutthroat trout.

Current and future management of the subspecies will be heavily focused on maintaining the current distribution as well as restoring populations where feasible (Gresswell 2011). To best direct resources for specific actions it is necessary to understand the extent of fine-scale diversity in populations as well as factors promoting this diversity. In this study we examined the effects of stream temperature, streamflow, food availability, and presence of non-native brook trout on life history characteristics of Yellowstone cutthroat trout in three tributaries in Wyoming. Our specific objectives were to: (1) document movement patterns of Yellowstone cutthroat trout and brook trout; (2) estimate survival rates of Yellowstone cutthroat trout; and (3) evaluate the effect of streamflow, stream temperature, food abundance, and fish densities on growth variability of Yellowstone cutthroat trout.

◆ STUDY AREA

Spread Creek is a third-order tributary to the Snake River in western Wyoming (Figure 1). A portion of the lower basin is located in Grand Teton National Park and the remainder is located on the Bridger-Teton National Forest. The basin is situated in the Mount Leidy Highlands region of the Gros Ventre mountain range. The geology is dominated by relatively unstable sedimentary rock and mass wasting is common (Ryan and Dixon 2007). The climate of this region is characterized by dry summers and cold winters with much of the yearly precipitation occurring as snowfall.

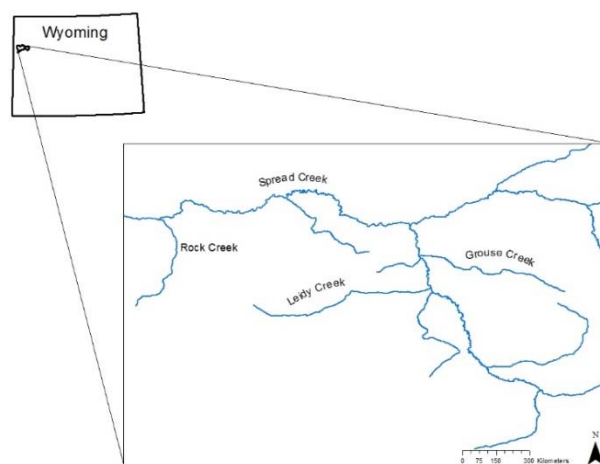


Figure 1. The location of the Spread Creek drainage in Wyoming and the location of the three study tributaries within the basin.

This system supports Yellowstone cutthroat trout, bluehead sucker *Catostomus discobolus*, Utah sucker *C. ardens*, longnose dace *Rhinichthys cataractae*, mottled sculpin *Cottus bairdii*, Paiute sculpin *C. beldingi*, and non-native brook trout.

Sampling was conducted in Rock, Grouse, and Leidy creeks (Figure 1). Leidy and Grouse creeks are 1st-order streams and Rock Creek is a 2nd-order stream. Trout-bearing stream length in Rock Creek is 4.5 km and flows from an elevation of 2500 to 2200m where it enters Spread Creek. Grouse and Leidy creeks flow from elevations of 2700 to 2400m where they enter South Fork Spread Creek. Trout-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 (Figure 2).



Figure 2. Grouse Creek in the Spread Creek drainage (Photo R. Al-Chokhachy).

◆ METHODS

Where necessary, project methods have been approved by the respective permitting authority or oversight committee. Animal capture protocols have been approved by the Montana State University Institutional Animal Care and Use Committee (IACUC). In addition, relevant sampling permits have been issued by Grand Teton National Park and the state of Wyoming.

Fish capture and recapture

Fish sampling was conducted in 100m sampling reaches that were systematically distributed throughout the trout-bearing stream length for an overall sampling coverage of approximately 30% in each stream. Three reaches on Rock, Grouse, and Leidy creeks were block-netted and sampled with three-pass electrofishing to estimate capture efficiency. The remaining reaches were sampled with a single pass. Summer sampling commenced following runoff during the first week of July. All reaches were resampled at the end of September for summer growth estimates.

Fish were collected using a Smith Root LR-24 backpack electrofishing unit operated at voltages between 100 – 500 V, frequencies under 50Hz, and pulse widths less than 4 μ sec. After capture, trout were anesthetized with clove oil. Clove oil is an effective

method of fish anesthetization and is approved by the U.S. FDA, allowing for the immediate release of individuals back to the stream (Anderson et al. 1997). Once it was deemed that fish were sufficiently anesthetized, measurements of total length (\pm 1mm) and weight (\pm 0.01g) were taken on each individual. Newly captured trout with lengths 80-120mm were implanted with a 12mm passive integrated transponder tag (PIT-tag; half-duplex, Oregon RFID, Portland, OR) and individuals with lengths > 120mm were implanted with a 23mm PIT tag. Tags were inserted into the body cavity through a small ventral incision made with a scalpel. The incision was slightly anterior to the pectoral fins. Adipose fins were removed to serve as a secondary tag. Captured individuals missing an adipose fin were placed under a hand-held PIT-tag scanner to check for a tag. If a tag was detected then the unique tag identification number was recorded. If no tag was detected after three attempts, the fish was recorded as having shed the tag and implanted with 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 they fully recovered and then were distributed throughout the sampling reach.

Movement

Prior to fish sampling, we installed passive instream antennae at the mouths of Grouse, Leidy, and Rock creeks. The antennae consisted of two loops laid on the substrate of the stream channel. Loops were separated by 5-10m and allowed for direction of movement to be determined. Detections were recorded by a half-duplex multiplexer (Oregon RFID, Portland, Oregon) powered by two 12-volt batteries charged by a solar panel.

After completion of fish sampling, we used mobile PIT-tag antennae to provide information on recapture and movement for all PIT-tagged individuals. We used continuous surveys in each of the three tributaries. We conducted the mobile surveys using 2 portable hoop antennae (~0.3 m diameter) attached to a pole. This portable unit allowed the operator to cover the stream in a manner analogous to backpack electrofishing and detect fish as the wand passed over a tagged individual. Movement distances were calculated as the distance from the mid-point of the tagging reach to the point of relocation in ArcMap10.1 with the Network Analyst package.

Stream temperature and streamflow

Pressure transducers (Solinst Canada LTD, Georgetown, Ontario) and temperature data loggers (Onset Computer Corp., Pocasset, Massachusetts) were deployed near the mouth and top of the trout-bearing stream length in each stream to record water temperature (± 0.01 °C) and stage height (± 0.001 m) continuously at hourly intervals. Discharge was measured at least three times over the growing season 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 reaches based on the elevation of the reach mid-point. Temperature data was used to calculate cumulative growing degree days (GDD). Average daily temperatures above 3°C were summed over the growing season to calculate GDD. The minimum temperature of 3°C was chosen because salmonids have exhibited growth down to 3.8°C in laboratory experiments (Elliot 1975) and we wanted to provide a buffer around this threshold to be conservative with the temperature cutoff.

Food availability

Food availability was measured with bi-weekly drift samples collected at one fixed sampling reach near the mouth of each stream from July through September. Each sample occasion consisted of a morning sample starting at one hour after sunrise and an evening sample starting at one hour prior to sunset. This regimen was chosen to capture the beginning of the crepuscular increase in drift density that is an important feeding period for salmonids (Elliott 1967, 1970).

Two drift nets (25 x 45cm, 500 μ m 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 due to clogging. Nets were deployed at least 2cm off the substrate to prevent benthic macroinvertebrates from crawling into the nets and the tops of the nets were always above the water surface to capture drifting terrestrial invertebrates. Flow and water depth were measured directly after setting the nets and prior to retrieving them to calculate the volume of water sampled. The contents of the nets were transferred to storage jars and preserved with 95% ETOH.

In order to account for differences in total energy available due to differences in invertebrate community composition across streams, 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). Energy content was estimated using dry mass-energy equivalents (Curry et al. 1993). There was a strong correlation 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 across streams and years were based on total dry mass of the sample.

Growth analysis

Variation of individual summer growth rates of Yellowstone cutthroat trout was analyzed with linear mixed-effect models. We did not include brook trout in the analysis due to the small sample size and to avoid confounding factors because they were only present in Grouse Creek. Only trout recaptured within the same year were included in the analysis. Growth rates were estimated on a daily basis over the summer growing season as

$$G = (M_2 - M_1) (t)^{-1},$$

where M_1 is initial weight, M_2 is weight at recapture, and t is days between capture and recapture. Variation in growth rates was explored with the general model structure

$$G = RB + TL + MF + GDD + MF \times RB + GDD \times RB + MF \times GDD + MF \times TL + GDD \times TL + RB \times TL,$$

where RB is sample reach 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 streamflow over the period between capture and recapture estimated from the lower level logger in each stream, and GDD is the cumulative growing degree days calculated as the sum of average daily temperatures above 3°C between capture and recapture estimated at the reach the trout was captured in. The effect of food abundance was not included in the model because there were little biologically or statistically significant differences in drifting biomass (mg/m^3) of invertebrates across streams or years (see results). A set of candidate models were developed that were nested structures of the global model to assess support for the hypothesized effects. Analyses were conducted in Program R (R Core Team 2013) using the package nlme (Pinheiro et al. 2013). All models included a nested structure of random effects for stream and sample reach. We used Akaike's information criterion corrected for small sample size (AIC_c) to rank competing models.

Survival analysis

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 recovery and live resightings of tagged individuals between occasions. In addition to survival (S), 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 for the analyses (Table 1.). No recapture events took place in 2011 so all sampling occasions (July 26 – September 16) were combined into the first sampling occasion. Individuals were split into two size classes (80-120mm and >120mm) for analyses. Individuals of the smaller size class were automatically moved into the larger size class in the following year. Stream and size class was incorporated into the analysis as a group variable.

Models were ranked by AIC_c scores. We chose to model emigration as random ($F=F'$) because movement data from the portable PIT antennae surveys revealed that the median range moved by fish was greater than sampling reach lengths which would likely make the probability of a fish being within the sample reach during a sampling event random. To find the best structure for the other parameters we held survival as the global structure and compared different structures of a parameter of interest and selected the best structure based on AIC_c . While comparing structures of a given parameter we kept all other parameter structures modeled as the global structure. Once we found the most supported structure of each parameter we maintained those structures while testing for the best structure to model survival. We assessed over dispersion using the median c-hat procedure in MARK. There was minor evidence of over dispersion (c-hat = 1.344) and all models were adjusted accordingly. We used QAIC_c to rank the candidate survival model structures and calculate the relative QAIC_c weight of each model. We chose to use model averaging to develop the best estimate of survival rate to use for comparisons across streams, size classes, and time intervals.

◆ PRELIMINARY RESULTS

Stream temperature and streamflow

Across the three tributaries, there were considerable differences in discharge during 2012 and 2013 (Figure 3.). Stream discharge was highest in Leidy Creek in 2012 and 2013 (Table 2). Discharge in Grouse Creek was higher than in Rock Creek in 2012, but was very similar during 2013 (Table 2). Summer discharge was lower in 2013 than in 2012 for Leidy and Grouse Creeks, but higher in 2013 than in 2012 in Rock Creek. Stream temperatures were similar in Rock and Grouse Creeks and slightly cooler in Leidy Creek during both years.

Food availability

There were little biologically relevant or statistically significant differences between the drifting biomass of invertebrates during the summer months across the three streams (Figure 4). In Leidy Creek the average invertebrate biomass in the drift was 0.18 mg/m³ (SD = 0.10) in the morning and 0.26 mg/m³ (SD = 0.12) in the evening during 2012 and was 0.55 mg/m³ (SD=0.58) in the morning and 0.39 mg/m³ (SD=0.14) in the evening during 2013. In Grouse Creek, the average drifting biomass was 0.14 mg/m³ (SD = 0.12) in the morning and 0.50 mg/m³ (SD = 0.53) in the evening during 2012 and was 0.30 mg/m³ (SD=0.15) in the morning and 0.67 mg/m³ (SD=0.35) in the evening during 2013. In Rock Creek, the average drifting biomass was 0.15 mg/m³ (SD = 0.10) in the morning and 0.20 mg/m³ (SD = 0.14) in the evening during 2012 and was 0.24 mg/m³ (SD= 0.08) in the morning and 0.16 mg/m³ (SD=0.07) in the evening during 2013.

Growth

Average growth rates varied among streams and between years (Figure 5). In general, brook trout in Grouse Creek consistently demonstrated high growth when compared to Yellowstone cutthroat trout in Grouse Creek and each of the other tributaries. In 2012, there were no significant differences between growth rates of brook trout and Yellowstone cutthroat trout in Grouse Creek, nor between cutthroat trout in Grouse and Leidy Creeks. Yellowstone cutthroat trout in Rock Creek had significantly lower growth rates than observed in both Grouse and Leidy Creeks. There were no significant differences in growth rates of cutthroat trout across the three tributaries in 2013.

Table 1 – Sampling dates and methods used to capture, recapture, and resight trout in Grouse, Rock, and Leidy creeks. During primary sampling occasions live captures and recaptures were done with backpack electrofishing units and live resights during intervals between primary occasions were done with passive instream antennae (PIA) at the mouths of each creek as well as portable PIT antennae (PPA) surveys in the three streams.

Sampling Date	Resight Interval (months)	Number Marked	Live Recaptures	Live Resights	Dead Recoveries	Sampling Method
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			293	4	PIA + PPA
Jul 1 – 18, 2013		140	41			Electrofish
	3			235	37	PIA + PPA
Oct 5-11, 2013		192	50			Electrofish
				154	16	PIA + PPA

Table 2 - The average (standard deviation) daily discharge (m^3/s) and stream temperature ($^{\circ}C$) measured near the mouths of Grouse, Leidy, and Rock Creeks during the period of July 1 to September 30 in 2012 and 2013.

Stream	2012		2013	
	Temperature	Discharge	Temperature	Discharge
Grouse Creek	9.99 (2.81)	0.08 (0.02)	10.25 (2.84)	0.06 (0.02)
Leidy Creek	9.11 (2.13)	0.34 (0.09)	9.15 (2.23)	0.17 (0.05)
Rock Creek	9.92 (2.65)	0.02 (0.02)	10.48 (2.68)	0.07 (0.02)

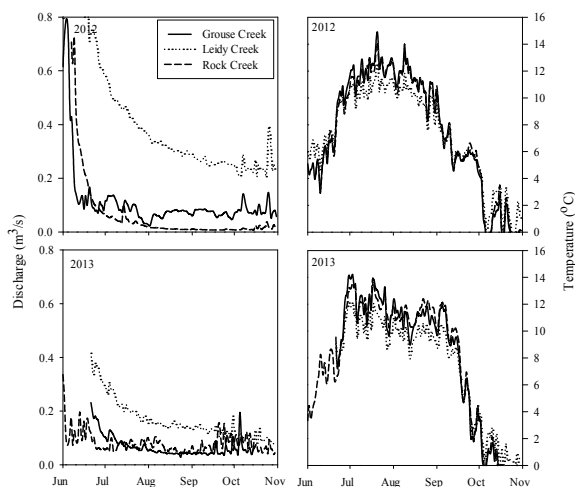


Figure 3. Average daily discharge (left) and average daily temperature (right) in Grouse, Leidy, and Rock creeks during the summer of 2012 (top) and 2013 (bottom).

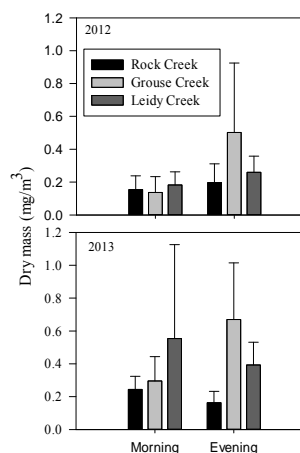


Figure 4. Average dry mass of invertebrates drifting in the water column during the morning and evening sampling events in the three tributaries in 2012 (top) and 2013 (bottom). Error bars represent 95% confidence intervals.

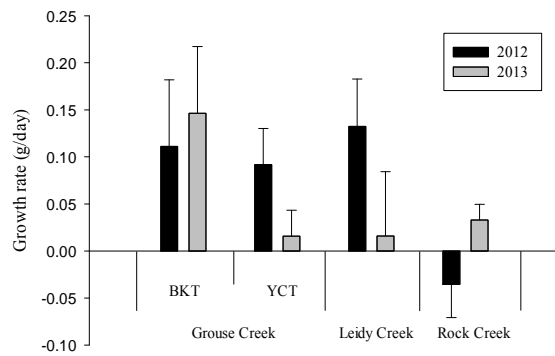


Figure 5. Average growth rates (g/day) in Grouse, Leidy and Rock Creeks for brook trout (Grouse Creek only) and Yellowstone cutthroat trout in 2012 and 2013. Error bars represent 95% confidence intervals.

Growth rates of brook trout in 2013 were significantly greater than Yellowstone cutthroat trout in Grouse Creek. Cutthroat trout in Grouse Creek exhibited significantly lower growth rates in 2013 than in 2012. Cutthroat trout in Leidy Creek also had a decrease in growth rates from 2012 to 2013, but this was not significant. In Rock Creek, cutthroat trout had significantly higher growth rates in 2013 than in 2012.

Stream temperature, streamflow, and fish length were all strongly associated with variation in summer growth rates as the most supported model contained the main effects of these factors (Table 3). There were also significant interactions between streamflow and temperature, streamflow and length, and temperature and length. At all temperatures within the range observed throughout the study, higher streamflow was associated with higher growth rates (Figure 6). Increased accumulation of degree days throughout the growing season was associated with decreased growth rates. The effect of streamflow was greater at lower accumulations of degree days. The effects of streamflow and temperature were greater for larger fish than smaller fish. There was minimal support for a reach biomass effect as the best model containing this effect was 2.58 AIC_c units away from the top model and only had 16% of the support in the data (Table 3).

Movement

Monthly displacement distances were different across seasons and streams (Figure 7). The range of movement in Rock Creek declined considerably after high flows subsided in July, but trout in Leidy and Grouse creeks continued to exhibit a high range of mobility throughout the summer and fall. Yellowstone cutthroat trout in Grouse Creek were more mobile than brook trout except for the fall

interval when they exhibited very similar movement patterns.

In general, Grouse Creek had the greatest amount of fish moving in and out of the stream during both years, Leidy Creek had the least amount of movement, and Rock Creek had considerable variability across years (Figure 8). In 2013 there was a substantial difference in the number of fish detected moving over the antennae in each stream.

There were 57 trout (44 cutthroat and 13 brook trout) detected in Grouse Creek, 24 trout (22 cutthroat and 2 brook trout) detected in Leidy Creek, and 32 cutthroat trout detected in Rock Creek. Frequency of detections differed across months and across streams. Cutthroat trout in Grouse Creek had peak movements in July and October as well as consistent movements throughout the summer. Movements over the Rock Creek antennae peaked in July then remained low for the remainder of the season. Leidy Creek had the least amount of detections as well as no clear seasonal pattern.

Survival

There was overwhelming support for a model that contained the additive effects of size class, time interval, stream, and the interaction of size class and time interval ($W_i = 97.3\%$, Table 4). However, model-averaged survival estimates were not significantly different between size classes or across streams (Figure 9). During all time intervals monthly survival rates between size classes were not significantly different in any stream. During the summer of 2013, trout >120mm had significantly lower monthly survival rates compared with the other time intervals, whereas trout 80-120mm did not exhibit significantly lower survival rates (Figure 9). When estimates were expanded over the seasonal interval, survival rates for both size classes were generally lower in winter than in summer except for the summer of 2013 which was the lowest survival for individuals >120 mm (Figure 10).

Table 3- Set of linear mixed-effect models developed for comparison of growth rates (g/day) of Yellowstone cutthroat trout in three tributaries of Spread Creek, WY. Asterisks denote interactive effects. All models include nested random effects for reach and stream. K is the number of parameters for each model; AIC_c is Akaike's information criterion, corrected for small sample size; ΔAIC_c is the difference between a given model and the most supported model; W_i is the Akaike weight of the model. Model terminology is as follows: RB (reach biomass, g/m²), MF (mean streamflow, m³/s), TL (total length of individual at tagging, mm), and GDD (growing degree days).

Model	Structure	K	AIC_c	ΔAIC_c	W_i
1	MF + GDD + TL + MF*GDD + MF*TL + GDD*TL	10	-181.9	0	0.60
2	RB + MF + TL + GDD + MF*RB + MF*GDD + MF*TL + GDD*TL	12	-179.3	2.58	0.16
3	RB + MF + TL + GDD + MF*RB + MF*GDD + GDD*TL	11	-178.0	3.91	0.08
4	RB + MF + TL + GDD + MF*RB + MF*GDD + MF*TL + GDD*TL + RB*GDD	13	-176.4	5.51	0.04
5	RB + MF + TL + GDD + MF*RB + MF*GDD + MF*TL + GDD*TL + RB*GDD + RB*TL	14	-175.7	6.21	0.03

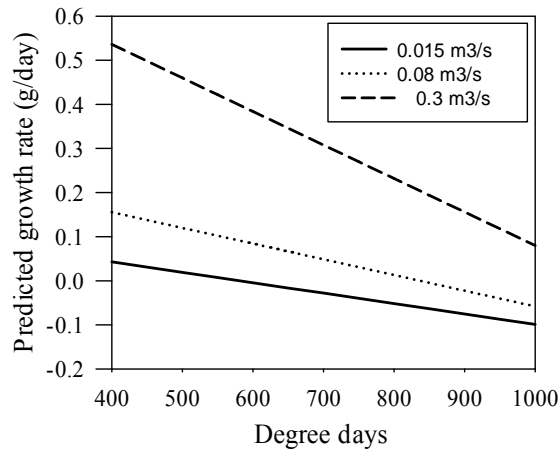


Figure 6. Variation in growth rate (g/day) in relation to temperature for three levels of discharge. Inference is from the best supported model and predicted growth is based on a fish length of 150mm. The relationship between growth rate and temperature is shown for the minimum (solid line; 0.015 m³/s), median (dotted line; 0.08m³/s), and maximum (dashed line; 0.3 m³/s) streamflows observed in this study.

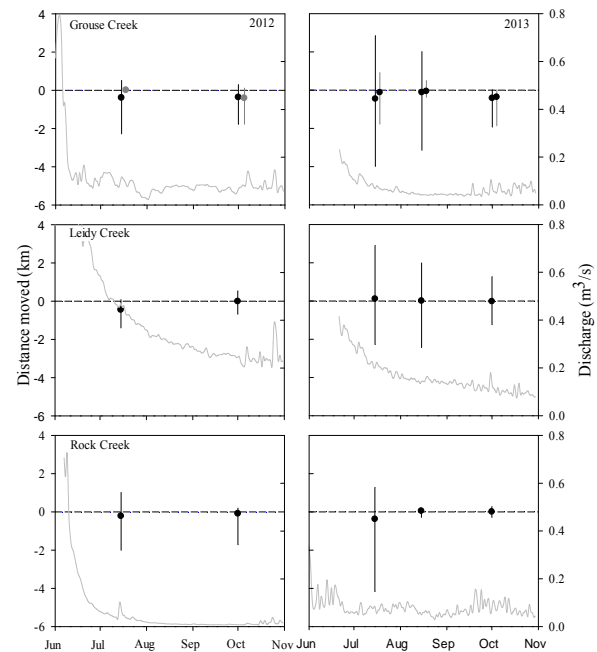


Figure 7. Monthly displacement distances (left y- axis) of Yellowstone cutthroat trout (black vertical lines) and brook trout (dark grey) and mean daily discharges (right y-axis) in 2012 (left column) and 2013 (right column). The circles represent the mean displacement distance during the interval and the vertical lines represent minimum and maximum distances moved; negative values represent distances moved downstream and positive values represent distances moved upstream. Note that the fall movement interval in 2012 is from July to November and in 2013 is from September to November.

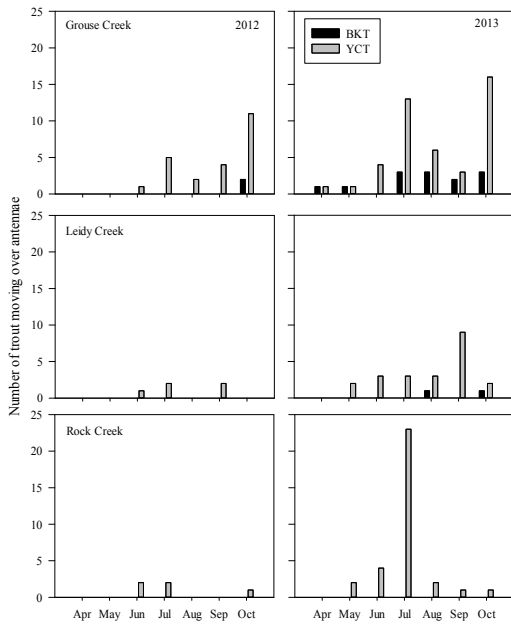


Figure 8 - Number of tagged Yellowstone cutthroat trout (grey bars) and brook trout (black bars) moving over the stationary antennae by month in 2012 (left column) and 2013 (right column). Note that no brook trout have been detected in Rock Creek. These are counts of the last known detection of a unique tag number within a year.

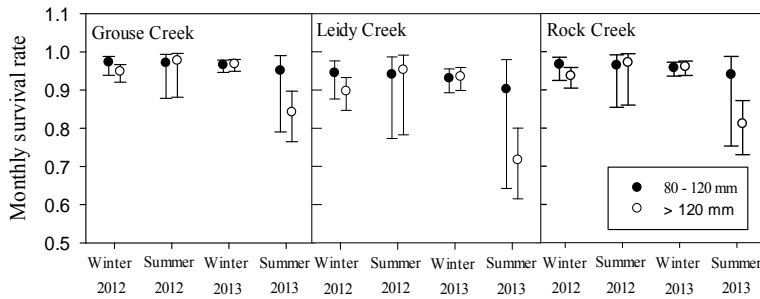


Figure 9. Model-averaged estimates of monthly survival rate (95% confidence interval) calculated from mark–recapture analyses of two Yellowstone cutthroat trout size-classes (80-120 mm, black circles; >120 mm open circles) in three tributaries of Spread Creek, WY, 2011–2013. The winter 2011 interval is from September 1, 2011 – June 30, 2012; the summer 2012 interval is from July 1 – September 30; the winter 2012 interval is from October 1st 2012- June 30th 2013; and the summer 2013 interval is from July 1st 2013 – September 30th 2013.

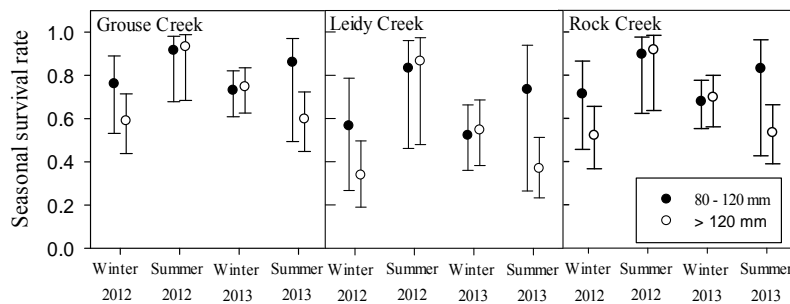


Figure 10. Model-averaged estimates of seasonal survival rate (95% confidence interval) over each time intervals calculated from mark–recapture analyses of two Yellowstone cutthroat trout size-classes (80-120 mm, black circles; >120 mm open circles) in three tributaries of Spread Creek, WY, 2011–2013. The winter 2011 interval is from September 1, 2011 – June 30, 2012; the summer 2012 interval is from July 1 – September 30; the winter 2012 interval is from October 1st 2012- June 30th 2013; and the summer 2013 interval is from July 1st 2013 – September 30th 2013.

Table 4 - Summary of model selection among Barker mark–recapture models used to estimate Yellowstone cutthroat trout survival rate (S) across two size-classes in three tributaries of Spread Creek, WY, 2011 – 2013. The Barker model includes six parameters: S ; capture probability (p), which was modeled as varying by size and stream; probability of recapturing a fish between sampling occasions (R), which was modeled as varying by time interval (t); probability of recapturing a fish before it dies between sampling occasions (R'), which was modeled as varying by season; probability of resighting a dead animal (r), which was modeled as varying with season; and the probability that a fish at risk of capture in time t is also at risk of capture in time $t+1$ (F), which was set equal to probability that a fish not at risk of capture in time t is at risk of capture in time $t+1$ (F') because it was assumed that emigration from the tagging reach was random. Quasi - Akaike's information criterion corrected for small-sample size (QAICc), the difference between a given model and the best supported model (Δ QAICc), number of parameters estimated by the model (K), Quasi-Akaike weight (W_i), and likelihood of each model are shown.

Model structure of S	K	QAICc	Δ QAICc	W_i	Model likelihood
size + stream + t + size*time	24	3118.79	0	0.97	1
stream + t	19	3126.88	8.10	0.02	0.0174
size + stream + t	20	3128.05	9.26	0.01	0.0097
Size + stream + year + size*stream	20	3135.15	16.36	0.00	0.0003

◆ DISCUSSION

Knowledge of intra-species diversity in life history characteristics and vital rates is an important consideration for long-term conservation planning (Schindler et al. 2010). In this study we documented variability in growth, movement, and survival of Yellowstone cutthroat trout from three tributaries within an intact headwater basin. Additionally, we quantified important stream factors and linked variability in growth rates to differences in stream temperatures and streamflows. We also compared growth rates and movement patterns between brook trout and Yellowstone cutthroat trout within one stream.

Growth

Salmonid growth is strongly regulated by stream temperature due to the direct control it exerts on metabolism (Swift 1961, Brett 1964). Studies conducted in a laboratory setting have revealed strong relationships between temperature and growth (Elliot 1975, Bear et al. 2007), but attempts to assess laboratory derived temperature relationships in a field setting have yielded mixed results (Lobón-Cerviá and Rincón 1998, Johnson et al. 2006, Xu et al. 2010a). We found that temperature had a significant effect on Yellowstone cutthroat trout growth, but it depended on fish length and streamflow. A similar relationship has been documented for variability of summer growth rates of brook trout in the Eastern U.S. (Xu et al. 2010a).

We found that increased streamflow was strongly associated with higher growth rates. Harvey et al. (2006) documented suppression of rainbow trout growth rates when streamflow was diverted from study reaches within a California stream. The mechanistic relationship between growth and streamflow is likely due to the control streamflow has on availability of suitable foraging habitat (Nislow et al. 2004).

Although we were unable to analyze growth variability for brook trout or test for an effect of brook trout presence on Yellowstone cutthroat trout growth due to confounding variables and small sample size, we found that brook trout had higher average growth compared with Yellowstone cutthroat trout within the same stream as well as populations in the other tributaries. Other studies have documented negative effects of introduced salmonid species on growth rates of native trout. Seiler and Keeley (2009) found cutthroat trout growth rates were significantly lower in sympatry with cutthroat-rainbow hybrids than in allopatry. McHugh and Budy (2005) observed Bonneville cutthroat trout *O. c. utah* had lower growth rates in sympatry with brown trout than in allopatry. In a laboratory experiment, brook trout significantly depressed growth rates of bull trout (McMahon et al. 2007). Further investigation is necessary to investigate the effect of brook trout density on Yellowstone cutthroat trout growth rates and what interaction it has with the other factors we investigated in this study.

Survival

Salmonids have age-structured populations, in which survival rates are dependent on size and age class (Xu et al. 2010b). Small increases in survivorship of juvenile age classes can elicit substantial responses in population growth, which can increase chances of persistence (Hilderbrand 2003). We did not detect significant differences between survival rates of two sizes of Yellowstone cutthroat trout. During the summer of 2013 the estimate of survival for larger trout was considerably lower than survival of smaller trout, but detection of a statistically significant difference was precluded by the imprecise survival estimate of smaller fish due to a small sample size of tagged trout in that size class. The decrease in survival of adult trout may be from low streamflows in 2013. Even though Rock Creek had slightly higher discharge in 2013, all three streams have been in a drought cycle and the associated decreases in baseflow may have negatively impacted survival of larger trout. Xu et al. (2010b) found that decreased streamflows reduced summer survival rates of brook trout in larger size classes.

Interestingly, we did not detect significant differences in survival across streams despite different hydrologic and thermal regimes. Although these differences are associated with variation in growth they may not be different enough to elicit changes in survival. Temperatures in these streams are generally optimal as the maximum average daily temperature throughout the summer never approached the critical upper thermal limit of 19.6°C, reported for the similar subspecies westslope cutthroat trout (Bear et al. 2007). Also, we may not be detecting effects on survival due to the size classes we investigated. Peterson et al. (2004) documented biotic and abiotic effects on survival of juvenile Colorado River cutthroat trout, but for age-2 and older there were no detectable effects on survival.

Movement

Movement can influence individual success by moving to more suitable locations and it can influence population dynamics through immigration and emigration. It wasn't until recently that mobility in headwater trout populations was found to be common, contrary to early thoughts (Gowan et al. 1994). We documented a wide range of movement patterns, with some fish exhibiting high mobility. There were trout present in each stream that moved distances greater than 3km. In Rock Creek displacement distances declined greatly after July. In Grouse and Leidy creeks, the widest range of movement was in July as well, but there was still a broad amount of mobility

through the late summer and fall. The high mobility documented during the July interval may be from trout making post-spawning movements. Other studies have found cutthroat trout movements to be greatest during the spawning season and decline considerably following post-spawning movements (Young 1996, Hilderbrand and Kershner 2000, Schrank and Rahel 2004).

It is largely documented that discharge is a key factor eliciting spawning movement for cutthroat trout (Brown and Mackay 1995b, Schmetterling 2001), but the role it plays in affecting movement patterns during other seasons remains poorly studied. We found mobility was greatest earlier in the summer when flows were higher as well as in streams with higher discharge profiles. Trout in Grouse and Leidy creeks had higher average displacement distances than trout in Rock Creek and this pattern was most pronounced after high flows subsided. Although Rock Creek had similar average discharge compared with Grouse Creek in 2013 it is characteristically a low discharge profile stream. This sharp decline in mobility on the descending limb of the hydrograph may be indicative of local adaption to a low discharge profile. Individuals that make long range movements may do so during higher flows to minimize risk of predation. In Grouse and Leidy Creeks baseflows are generally higher and individuals may be at less risk of predation and use mobility later in the summer to better exploit optimal foraging habitats within the streams (Gowan and Fausch 2002).

We observed a wider range of movement distances within each stream in 2013 compared with 2012 which may be due to a much larger sample size of tagged individuals during 2013. The average distances moved during each interval were not very different between years within each stream. Although we did not observe pronounced movement differences in response to inter-annual variability in discharge as was observed with Bonneville cutthroat (Schrank and Rahel 2006), we did see the general trend of higher mobility in response to higher flows when comparing across streams.

We found an increase in trout moving over the stationary antennae in Grouse and Leidy creeks during the fall, but not in Rock Creek. There was a slight peak in detections at the antennae in Leidy Creek during September and during October in Grouse Creek. These movements may be individuals seeking suitable over-winter habitat as westslope cutthroat have been documented making extensive fall movements coinciding with declining temperatures and formation of stream ice (Brown and Mackay 1995a, Jakober et al. 1998). There is documentation of

variation in fall movements among different subspecies as Bonneville cutthroat trout (Hilderbrand and Kershner 2000) and Colorado River cutthroat trout (Young 1998) did not display autumn movements. It is interesting that we found a similar pattern of variability across different populations of the same subspecies.

◆ CONCLUSIONS

Our research documented variability in growth and movement patterns as well as quantified survival rates of Yellowstone cutthroat trout. We found strong and interactive effects of streamflow and stream temperature on trout growth rates. Higher streamflows mediated the effects of increasing summer stream temperatures, whereas low streamflows exacerbated the impacts of warming temperatures. This underscores the importance of considering multiple climate-driven stream factors when predicting the effects of climate change on trout populations. We also found considerable differences in movement patterns within the basin that may be related to differences in stream discharge profiles. These results suggest that intra-basin variability in life history characteristics and vital rates should be considered when developing and implementing conservation strategies.

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