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Effects of Climate-Related Stream Factors on Patterns of Individual Summer Growth of Cutthroat Trout

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Abstract

Coldwater fishes are sensitive to abiotic and biotic stream factors, which can be influenced by climate. Distributions of inland salmonids in North America have declined significantly, with many of the current strongholds located in small headwater systems that may serve as important refugia as climate change progresses. We investigated the effects of discharge, stream temperature, trout biomass, and food availability on summer growth of Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri*, a species of concern with significant ecological value. Individual size, stream discharge, sample section biomass, and temperature were all associated with growth, but had differing effects on energy allocation. Stream discharge had a positive relationship with growth rates in length and mass; greater rates of prey delivery at higher discharges probably enabled trout to accumulate reserve tissues in addition to structural growth. Temperature effects were positive but not significant, and support in growth models was limited, likely due to the cold thermal regimes of the study area. 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 and highlights the importance of considering multiple factors, including hydrologic regimes, in conservation planning.

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Hydrologic and thermal regimes provide a template for biological processes in lotic ecosystems (Minshall et al. 1983; Poff et al. 1997) and have profound effects on biological communities (Woodward et al. 2010; Comte et al. 2013). Stream discharge and stream temperature are controlled by a complex suite of geomorphic (Harvey and Bencala 1993; Constantz 1998), ecological (Poole and Berman 2001; Malcolm et al. 2004), and climatic factors (Campbell et al. 2011; Isaak et al. 2012). Attributes of stream hydrology (e.g., timing and magnitude of discharge: Hamlet and Lettenmaier 2007) and temperature (e.g., summer minimum and maximum temperatures: Caissie 2006) are strongly affected by regional and local air temperature and precipitation patterns, and shifts in global climatic conditions are projected to substantially alter the temperature and hydrologic regimes of rivers (Arismendi et al. 2013; Barros et al. 2014). Concerns for freshwater fishes, such as salmonids, stem from their narrow thermal tolerances (Brett 1952; Bear et al. 2007) and expected reductions in the amount of suitable habitat (Hari et al. 2006; Wenger et al. 2011). Furthermore, recent studies illustrating how thermal and hydrologic regimes can influence salmonid phenology and life history expression (Kovach et al. 2012; Warren et al. 2012; Otero et al. 2014; Flitcroft et al. 2016) and ultimately individual fitness (e.g., survival: Warren et al. 2009; Lobon-Cervia 2014) suggest salmonids are exceptionally vulnerable to climate-driven stream changes.

Within the Rocky Mountains of North America, the historical distributions of native, potamodromous salmonids have been significantly reduced through extirpations (Thurrow et al. 1997), with strongholds for extant populations predominantly occurring in high-elevation, montane environments (Williams et al. 2009; Isaak et al. 2015). Stream networks in this topographically diverse region have already exhibited symptoms of climate change through alterations in hydrologic and thermal regimes (Isaak et al. 2012; Leppi et al. 2012). Of particular concern for mid-latitude regions in the Rocky Mountains is the summer period, where snowmelt-driven discharge is low and likely to further decrease due to reduced snowpack, warming temperatures, and trends in earlier runoff (Stewart et al. 2005). Concomitantly, stream temperatures are the warmest during the summer and are expected to increase, yielding thermal regimes unsuitable for salmonids in many lower-elevation reaches (Jones et al. 2013; Isaak et al. 2015) and disproportionately intensifying the importance of headwater portions of stream networks (Haak et al. 2010). Accordingly, an understanding of how climate-related factors influence salmonid life history patterns, demographic rates, and fitness is imperative to quantify population resilience and direct conservation efforts under a changing climate (sensu Lawler 2009).

Individual fish growth is an attribute with strong population-level effects (Hutchings 1983) and direct ties to habitat and biotic conditions influenced by climate (Kovach et al. 2016). Salmonids are poikilothermic, and ambient water temperature dictates fish metabolism and therefore growth potential (Elliott 1976; Bear et al. 2007). Stream discharge controls the amount of suitable foraging habitat and periods of low discharge result in reduced available habitat, thus increasing density dependence, a strong driver of salmonid growth (Jenkins et al. 1999; Vollestad et al. 2002). Furthermore, stream discharge influences the rate of prey delivery in the water column, which is critical for drift-feeding salmonids (Nislow et al. 2004; Harvey et al. 2006). In addition to thermal and hydrologic changes, ecosystem productivity is changing across much of North America through changes in growing-season length (Zhu et al. 2012), which can affect salmonid forage and ultimately growth (Weber et al. 2014). The few linkages between climatic factors and salmonid growth have focused on autumn-spawning species in regions with low topographic complexity (Bacon et al. 2005; Xu et al. 2010a), but not species of inland Cutthroat Trout *Oncorhynchus clarkii*, a spring-spawning species with entirely different life history patterns and evolutionary histories, that occur across a broad range of elevations (May et al. 2007).

This study investigated how variability in climate-related stream factors is linked with summer growth of Yellowstone Cutthroat Trout *O. clarkii bouvieri*, a subspecies with significant ecological and socioeconomic value (Stapp and Hayward 2002). Climate change is anticipated to be a major threat to the long-term persistence of Yellowstone Cutthroat Trout (Gresswell 2011), and headwater stream networks are expected to serve as critical refugia during the warm, summer months (Al-Chokhachy et al. 2013; Isaak et al. 2015). As such, this study focused on headwater stream networks during the summer to reveal how variation in stream temperature, discharge, and food abundance affect Yellowstone Cutthroat Trout growth. Specifically, patterns of growth in mass and length were delineated to better understand how trout allocate energy (Broekhuizen et al. 1994). The results of this study elucidate mechanistic linkages between trout growth and factors influenced by climate change, and help inform conservation and climate adaptation efforts.

METHODS

Study area.— Trout were sampled from three tributaries of Spread Creek, Wyoming, and two tributaries of Shields River, Montana (Figure 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 basins are located in the Greater Yellowstone Area, a topographically diverse region with localized climate variability (Sepulveda et al. 2015) but generally characterized by hot, dry summers and cold winters with most of the annual precipitation occurring as snowfall. Streamflows within the study area are typical for snowmelt-dominated streams in the Rocky Mountains; high spring discharge events occur during May and June and streamflows decline throughout the summer and early autumn (Al-Chokhachy et al. 2017). Both basins are strongholds for Yellowstone Cutthroat Trout, which are present in multiple life history forms (i.e., resident, fluvial) and exhibit genetic purity (May et al. 2007). Native sculpins *Cottus* spp. and nonnative Brook Trout *Salvelinus fontinalis* inhabit portions of both basins. During our study, Brook Trout were present only in Grouse Creek (Spread Creek) and Dugout Creek (Shields River), and densities were relatively low; no other nonnative fishes are present in the study area.

In the Spread Creek basin, fish sampling occurred in Leidy, Grouse, and Rock creeks. Leidy and Grouse creeks are first-order streams and Rock Creek is a second-order stream. The length of stream that bears trout in Rock Creek is 4.5 km and flows from an elevation of 2,500 to 2,200 m where it enters Spread Creek. Grouse and Leidy

creeks flow from elevations of 2,700 to 2,400 m where they enter South Fork Spread Creek, and 5.7 and 5.4 km of stream, respectively, bear trout. Rock Creek flows through a confined valley (sensu Fryirs et al. 2016) with conifers (Coniferae) as the primary riparian vegetation and sporadic willow *Salix* spp. The lower and middle portions of Leidy Creek flow through a partly confined valley containing 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 coniferous-forested upper section. The majority of Grouse Creek flows through a partly confined valley.

In the Shields River basin, fish sampling occurred in Dugout and Lodgepole creeks. Dugout Creek is a second-order stream that flows from an elevation of 2,300 to 1,980 m where it enters the upper Shields River, and the overall length of stream that bears trout is 3.5 km. Lodgepole Creek is a second-order stream that flows from an elevation of 2,200 to 2,000 m before it enters the upper Shields River and has 2.5 km of stream that bears trout. Dugout Creek is primarily characterized by confined valley segments with conifer forest riparian areas. Small sections near the mouth and the upper reaches of Dugout Creek are in partly confined valleys and have willow riparian areas. Lodgepole Creek flows entirely through coniferous forest and has short sections of mixed willow–conifer

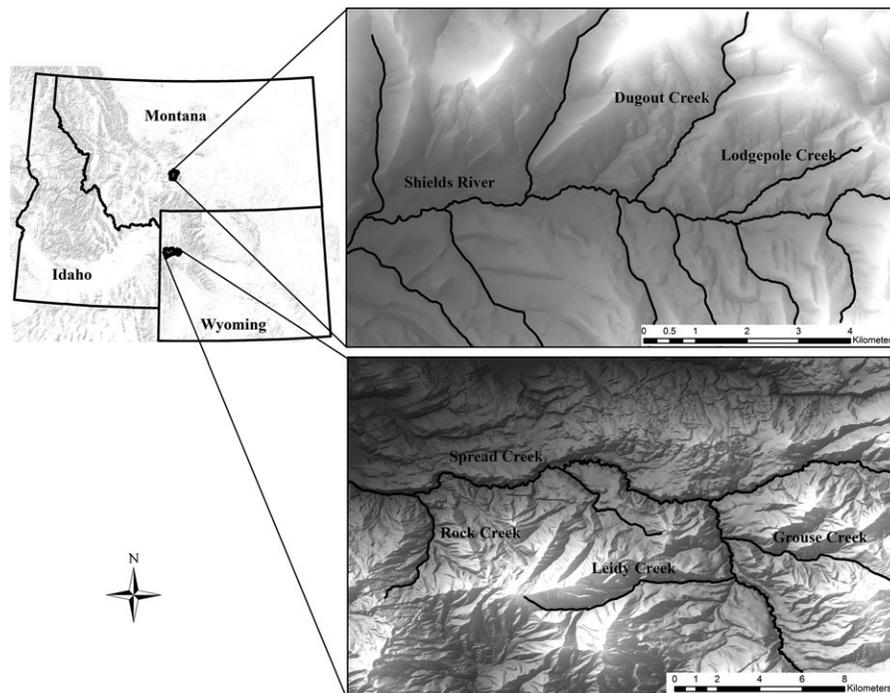


FIGURE 1. Study tributaries of Spread Creek, Wyoming, and Shields River, Montana.

riparian area. The majority of Lodgepole Creek is characteristic of a montane, confined valley stream. Little habitat degradation has occurred in the study streams in the Shields River and Spread Creek basins.

Fish capture and recapture.—Sampling occurred biannually (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 stream sections that were systematically distributed with a frequency of one site every 0.2–0.5 km. Single-pass electrofishing was conducted in the majority of sample sections, but multiple-pass electrofishing was conducted in a subset of sections to estimate capture efficiencies. 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 μ s (Dwyer et al. 2001) were used to capture fish. After capture, trout were anesthetized with clove oil. After fish were sufficiently anesthetized, measurements of TL (± 1 mm) and mass (± 0.5 g) were taken on each individual. In the Spread Creek basin, trout with lengths of 80–120 mm were implanted with 12-mm PIT tags (half-duplex, Oregon RFID, Portland, Oregon) and individuals 120 mm and longer were implanted with 23-mm PIT tags. In the Shields River basin, trout with lengths of 80–130 mm were implanted with 12-mm PIT tags and individuals 130 mm and longer were implanted with 23-mm PIT tags. Tags were inserted into the body cavity through a small ventral incision made with a scalpel posterior to the origin of the pectoral fins. Adipose fins were removed to serve as secondary marks. Trout with clipped adipose fins were scanned with a hand-held PIT tag scanner to check for tags. If no tag was detected after three attempts, the fish was considered to have shed its tag and a new tag was implanted. Shed rate was low over the course of the study (4%). After processing, individuals were placed in a live well in the stream (plastic tub with holes, which allowed current to flow through) until they were fully recovered and then distributed evenly throughout the sampling section. A tag effect was not observed, as evidenced by a lack of a significant trend between growth rate and days between sampling periods ($P = 0.393$).

Temperature and discharge.—Pressure transducers (Solinst Canada, Georgetown, Ontario) and temperature data loggers (Onset Computer, Pocasset, Massachusetts) were deployed near the mouth and upper limit of salmonid distribution in each stream to record water temperature ($\pm 0.01^\circ\text{C}$) and stage height (± 0.001 m) continuously at hourly intervals between the fish-sampling periods. Discharge was measured a minimum of three times between July and November at each pressure transducer to develop stage–discharge relationships. The frequency of measurements was sufficient for developing relationships during the study period because the investigation occurred after peak

discharge and through base discharge in autumn (Spread Creek basin: $R^2 = 0.88$ – 0.99 ; Shields River basin: $R^2 = 0.71$ – 0.99). Lapse rates were estimated from the lower and upper loggers to interpolate mean daily stream temperatures at all tagging sections based on the elevation of the mid-point of the stream section.

Food availability.—Food availability was measured with biweekly drift samples collected at one fixed sampling site near the mouth of each stream from July through September in 2012 and 2013. In 2012, six sampling events were conducted in Grouse, Leidy, and Rock creeks, and five sampling events were conducted in Dugout and Lodgepole creeks. In 2013, three sampling events were conducted in Grouse, Leidy, and Rock creeks, and only one sampling event was conducted in Dugout and Lodgepole creeks, which occurred during early August. Sampling occasions consisted of morning samples starting 1 h after sunrise and evening samples starting 1 h before sunset. We used this approach to capture the beginning of the crepuscular increase in drift density that is an important feeding period for salmonids (Elliott 1967).

Two drift nets (25 \times 45 cm, 500- μ m mesh) were deployed adjacently in the thalweg of a fast-water channel unit. Nets remained in the channel for approximately 1 h 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 before retrieving them to calculate the volume of water sampled. We estimated the volume of water by multiplying the width of the net (25 cm) by the average velocity and average water depth during the sampling period. Net contents were transferred to storage jars and preserved with 95% ethanol.

The contents of storage jars were sorted to remove macroinvertebrates from detritus. Macroinvertebrate samples from 2012 were identified to the taxonomic level of order and then dried in an oven at 103°C for 4 h (Mason et al. 1983) to account for differences in total energy available caused by differences in invertebrate assemblage composition among streams. Drift composition was relatively similar among streams and primarily consisted of individuals of the orders Ephemeroptera, Plecoptera, Diptera, and Tricoptera, with additional inputs of terrestrial individuals of the orders Coleoptera, Hemiptera, Hymenoptera, Araneae, and Collembolla. Energy content was estimated using taxa-specific, dry mass–energy equivalents (Curry et al. 1993). A strong relationship existed between total energy estimated from order-specific caloric content and total dry mass of the sample ($R^2 = 0.9$), suggesting that differences in macroinvertebrate composition among streams did not result in differences of total energy

available to trout. Therefore, drift samples from 2013 were oven-dried and weighed without partitioning taxonomic groups. Food availability comparisons among streams and years were based on the total dry mass of the samples. We calculated drift concentration as the dry mass of samples divided by the volume of water sampled (Miller and Judson 2014) and drift rate as the dry mass of samples divided by the length of time the drift nets were deployed.

Statistical analyses.— Summer growth rates of individual Yellowstone Cutthroat Trout ($n = 181$) were used in analyses. Sample sizes varied among streams (Grouse Creek: $n = 19$; Rock Creek: $n = 33$; Leidy Creek: $n = 23$; Dugout Creek: $n = 49$; Lodgepole Creek: $n = 57$). Only trout recaptured within the same year were included in the analyses, and we treated individual recaptures independently given the considerable interval between marking and recapture (79–100 d). Growth rates were estimated over the summer growing season using the following equation:

$$G_{L,W} = (R - M)/(T_2 - T_1),$$

where G is growth rate (mm/d or g/d), L is length, W is mass, R is length or mass at recapture, M is length or mass at marking, T_1 is the date of marking, and T_2 is the date of recapture.

Variation of individual summer growth rates was analyzed with linear mixed-effect models using the nlme package in Program R (R Development Core Team, Vienna; available: www.r-project.org). Preliminary analyses indicated a strong correlation between discharge and drift across streams ($r = 0.88$; see Figure 3A), and few biologically or statistically significant differences existed in drifting biomasses of invertebrates among streams or years (see Figure 3B); as such we did not include the effect of food availability in the growth models. A candidate set of models was developed to describe the fixed effects of discharge, temperature, density, and fish length on variation of individual summer growth rates of trout. Individual fish were considered independent observations given that resident trout typically do not school after early life stages when sufficient cover is present, the decline of family effects after age 1 (Hansen et al. 1997; Neville and Peterson 2014), and the considerable heterogeneity in trout metabolic rates and growth (Xu et al. 2010a; Sloat and Reeves 2014). Basin, stream, and sample section were considered random effects in the analyses. This analytical approach was used given the consistency with similar studies investigating salmonid growth rates (Xu et al. 2010a). Variation in growth was explored with the general model structure,

$$G = SB + TL + MD + MT + MT \times TL,$$

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, MD is mean daily discharge between capture and recapture estimated from the lower level logger in each stream, and MT is the mean daily temperature between capture and recapture estimated at the section the trout was tagged in. We considered an interaction between temperature and fish length given the potential differences in metabolic and growth rates across temperatures in salmonids (Rodnick et al. 2004). Consideration of interactions between discharge and fish length and discharge and temperature were precluded by the lack of a range of fish lengths and temperatures at all levels of stream discharge. 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 (AIC_c) to rank competing models. All models included nested random effects for basin, stream, and sample section.

RESULTS

Discharge varied throughout the course of the study (Table 1). While stream temperatures fluctuated as a result of short-term weather patterns and minimal differences across years, mean daily temperatures during the trout growing season were not remarkably different across streams and years (Table 1; Figure 2). Average food availability within streams was similar between years (Figure 3B). Few statistically significant differences in average food availability existed among streams. The drift rate was strongly correlated with stream discharge ($r = 0.88$; Figure 3A).

The magnitude of growth differed across metrics and size-classes (Figure 4). Growth rate in length for trout < 150 mm (median = 0.165 mm/d) was significantly higher (Mann–Whitney $U = 2628.5$, $P < 0.001$) than in trout ≥ 150 mm (median = 0.0983 mm/d). However, growth in mass was minimal for trout < 150 mm (median = 0.024 g/d) and trout ≥ 150 mm (median = 0.000 g/d), and no difference was observed between the two groups (Mann–Whitney $U = 3499.0$, $P = 0.30$). A considerable number of trout < 150 mm (37%) and trout ≥ 150 mm (53%) demonstrated zero or negative growth rates in mass during the sample period.

Discharge, stream temperature, section biomass, and fish length were all included in the top models of summer growth in length and mass (Table 2). Fish length was included in all of the top models of growth rate in length ($\sum W_i = 1.00$). Considerable support existed for discharge ($\sum W_i = 0.65$), but less support was evident for the importance of stream temperature ($\sum W_i = 0.47$) and section biomass ($\sum W_i = 0.23$). The random-effects results from the top model of growth rate in length

TABLE 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.

Stream	2012			2013		
	Minimum	Maximum	Mean (SD)	Minimum	Maximum	Mean (SD)
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 (m³/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)

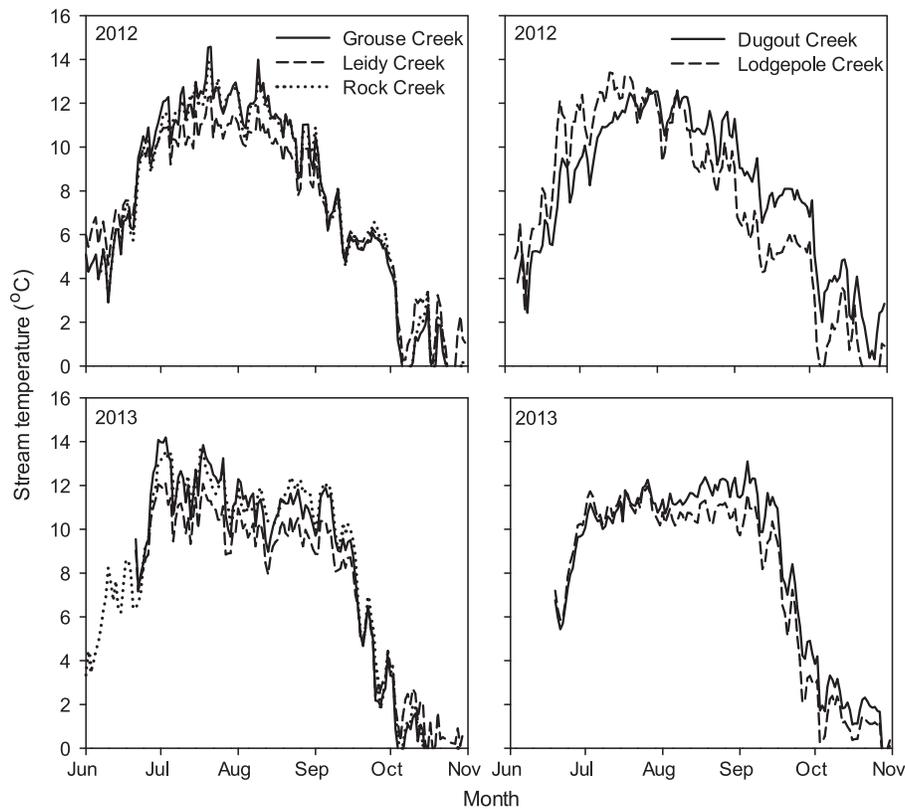


FIGURE 2. Mean daily stream temperatures calculated from hourly intervals during 2012 (top panels) and 2013 (bottom panels) in tributaries of Spread Creek, Wyoming (left panels), and Shields River, Montana (right panels).

suggested little difference across basins ($SD < 0.001$), with stream section ($SD = 0.06$) and stream ($SD = 0.04$) accounting for more of the variability among individuals (Table 3). Results from the most-supported model

indicated growth rate in length was negatively related to fish length ($\beta = -0.001$, $SE < 0.001$) and positively related to discharge ($\beta = 0.354$, $SE = 0.192$; see Appendix Tables A.1 and A.2 for results from all models).

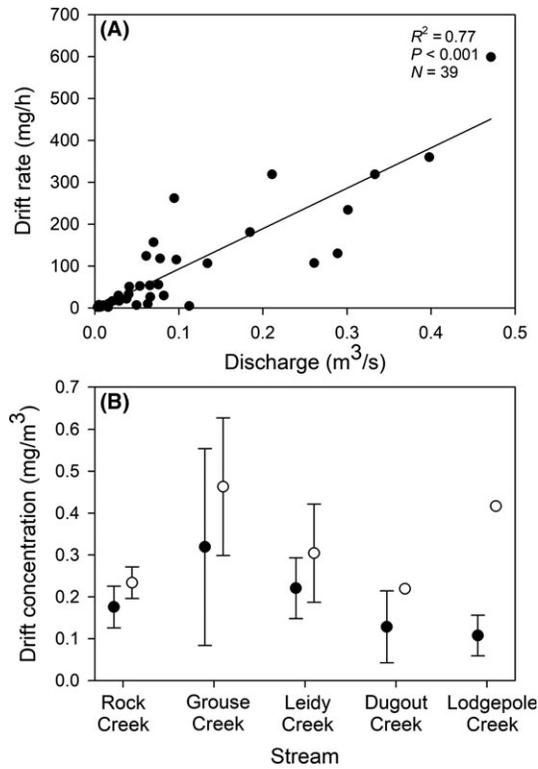


FIGURE 3. (A) Relationship between drift rate and discharge for samples pooled across all study streams and (B) average summer drift concentrations in each stream during 2012 (closed circles) and 2013 (open circles). Only one sampling event occurred in Dugout and Lodgepole creeks in 2013. Error bars represent 95% CIs.

Stream discharge was included in all of the candidate models describing growth rate in mass ($\sum W_i = 1.00$). Trout biomass within the sample section ($\sum W_i = 0.48$) and fish length ($\sum W_i = 0.43$) were included in a subset of the candidate models, while stream temperature was only included in models with the lowest overall weights ($\sum W_i = 0.26$). Results for the random effects were generally similar to those for the most-supported model describing trout growth rate in length (Table 3). The most-supported model describing trout growth rate in mass indicated a positive relationship with discharge ($\beta = 0.474$, $SE = 0.136$) and a negative relationship with trout biomass in sample sections ($\beta = -0.007$, $SE = 0.004$).

DISCUSSION

The results of this study demonstrate the challenges involved with the conservation of salmonids, a group of fishes expected to be particularly vulnerable to changing climatic conditions (Jonsson and Jonsson 2009; Kovach et al. 2016). We focused on individual growth given its importance for salmonid survival and population

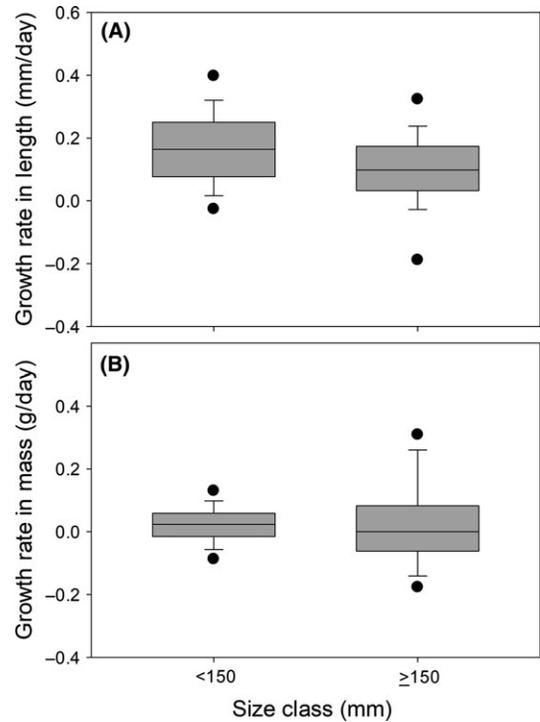


FIGURE 4. Growth rate in (A) length and (B) mass of Yellowstone Cutthroat Trout <150 mm (80–150 mm) and ≥ 150 mm; horizontal line illustrates the median values, boxes represent the 25th and 75th percentiles, whiskers represent the 10th and 90th percentiles, and points demonstrate the 5th and 95th percentiles.

dynamics (Hutchings 2006). During the summer season, the factors influencing salmonid growth can be complex (Harvey et al. 2005), but growth is typically governed by temperature (e.g., Lobon-Cervia and Rincon 1998), stream discharge (e.g., Teichert et al. 2010), forage (e.g., Nislow et al. 2004), fish density or biomass (e.g., Vollestad et al. 2002), and local habitat conditions (e.g., Harvey et al. 2005). Our study focused on streams with limited habitat degradation, allowing us to evaluate how attributes altered under changing climatic conditions may affect individual summer growth rates of Yellowstone Cutthroat Trout.

High elevation stream networks 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; Xu et al. 2010b; Hvidsten et al. 2015). Results indicated that trout, especially smaller trout, invested more in structural growth (length) than in accumulation of reserve tissue during the summer and early fall (i.e., mass: Broekhuizen et al. 1994). Prey abundance in headwater streams fluctuates seasonally; high abundance occurs during early summer when discharges are high (Leeseberg and Keeley 2014). Therefore, trout probably allocate ingested energy towards easily synthesized reserves as

TABLE 2. Linear mixed-effect models developed for comparison of summer growth rates 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), MD (mean discharge, m^3/s), TL (total length of individual at tagging, mm), MT (mean temperature, $^{\circ}C$).

Model	Structure	K	Likelihood likelihood	AIC_c	W_i
Growth in length					
1	TL + MD	7	114.80	-214.94	0.26
2	TL + MD + MT	8	115.19	-213.55	0.13
3	TL	6	113.01	-213.53	0.13
4	TL + MT	7	114.01	-213.37	0.12
5	TL + MD + SB	8	114.94	-213.04	0.10
6	TL + MD + MT + TL \times MT	9	115.81	-212.56	0.08
7	TL + MT + TL \times MT	8	114.40	-211.96	0.06
8	TL + SB	7	113.14	-211.63	0.05
9	TL + MD + MT + SB	9	115.26	-211.46	0.05
10	TL + MD + MT + SB + TL \times MT	10	115.85	-210.41	0.03
Growth in mass					
1	MD + SB	7	163.04	-311.43	0.26
2	MD	6	161.79	-311.09	0.22
3	TL + MD + SB	8	163.41	-309.99	0.13
4	TL + MD	7	162.28	-309.92	0.12
5	MD + MT	7	161.80	-308.95	0.08
6	TL + MD + MT + TL \times MT	9	163.61	-308.17	0.05
7	TL + MD + MT + SB + TL \times MT	10	164.63	-307.96	0.05
8	TL + MD + MT + SB	9	163.41	-307.77	0.04
9	TL + MD + MT	8	162.29	-307.75	0.04
10	SB	6	157.02	-301.56	0.00

TABLE 3. Parameter estimates for the most supported models of individual summer growth in length and growth in mass 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	0.301	0.040	129	7.561	<0.001
Length	-0.001	<0.001	129	-5.652	<0.001
Discharge	0.354	0.192	129	1.839	0.068
Growth in mass^b					
Intercept	0.020	0.019	129	1.033	0.304
Discharge	0.474	0.136	129	3.483	<0.001
Section biomass	-0.007	0.004	129	-1.688	0.094

^aRandom effect SD: basin \leq 0.001, stream = 0.040, section = 0.060, residual = 0.118.

^bRandom effect SD: basin \leq 0.001, stream = 0.022, section = 0.042, residual = 0.092.

opposed to structural tissue to maximize the benefits of the short period of high food availability (Broekhuizen et al. 1994). However, entering winter in poor condition can reduce reproductive potential of adults (Scott 1962) and decrease overwinter survival of juveniles (Biro et al.

2004). The low growth in mass during the summer and cold temperatures in our study area during the winter ($<1^{\circ}C$) also suggests the importance of growth during the spring. Trout lose reserves during winter such that mature individuals are confronted with a tradeoff between reproductive investment and depleted reserve restoration (Stearns 1976; 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 postspawn mortality (Jonsson et al. 1991; Morita and Yokota 2002).

Stream discharge was an important component of trout growth in length and mass, a pattern consistent with previous findings for salmonids and other riverine fishes (Railsback and Rose 1999; Nislow et al. 2004; Tonkin et al. 2017). Because stream-dwelling Cutthroat Trout are predominantly drift feeders (Nakano et al. 1992), the implications of discharge likely resulted, in part, from high drifting prey availability at high discharges (Figure 3A) (Miller and Judson 2014). Furthermore, drifting invertebrates travel shorter distances during periods of low discharge, which can further reduce prey availability at foraging locations (Danehy

et al. 2011). Significant decreases in rates of prey delivery depress growth rates of closely related Rainbow Trout *O. mykiss* under the 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). Higher discharge can also yield increased energetic expenditures associated with movement and feeding (Fausch 1984; Rand et al. 2006), yet salmonids commonly regulate habitat selection behaviorally to enhance growth and fitness. Profitable habitat selection and increased prey delivery are likely mechanisms for the positive relationship between discharge and growth (Davidson et al. 2010; Xu et al. 2010a). Increased availability of habitat and cover at high discharges can also affect growth by reducing physiological stress (McCormick et al. 1998) associated with predator avoidance (Järvi 1990) and crowding (Pickering and Stewart 1984). Decreases in late summer discharges associated with a changing climate (Al-Chokhachy et al. 2017) may further prevent trout from accumulating prewinter reserves. Declines in reserves may limit juveniles from attaining adequate energy for reproductive development, thus forcing them to delay maturation in favor of somatic growth (Bohlin et al. 1994).

Trout biomass within sample sections was negatively related to trout growth in mass, but no clear relationship was observed with growth in length. The lack of an effect of biomass on growth in length is surprising given previous findings demonstrating the negative effects of biomass and density on salmonid growth in length (Jenkins et al. 1999; Bohlin et al. 2002; Imre et al. 2004). The negative relationship between section biomass and trout growth in mass may have resulted from density-dependent mechanisms due to competition for resources (Lobon-Cervia 2005; Hartson and Kennedy 2014). The effect of biomass on growth in mass is also indicative of self-thinning, where the capacity of stream sections is limited in terms of the overall biomass sustained (Elliott 1993; Dunham and Vinyard 1997).

The effect of temperature on trout growth was relatively minor, which is not surprising given the relatively consistent thermal regimes in our study area (Figure 2). The positive effect of temperature (but not significant, $P > 0.10$; Appendix) on trout growth in all candidate models suggests that increased average daily temperatures near physiological optima or increased growing season lengths may cause increased growth, which corroborates predictions in headwater streams from the Greater Yellowstone Area (Al-Chokhachy et al. 2013) based on a temperature-dependent growth model (Bear et al. 2007). 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), a pattern consistent with laboratory experiments (Elliott 1975).

Predicting the effects of future stream changes on Cutthroat Trout growth will require a better mechanistic understanding of the observed relationships. Differences in quantities and qualities of foraging locations among streams were not accounted for because habitat surveys were not included in the sampling design. Therefore, it is unclear 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; Kennedy et al. 2008) and decreased competition at high discharges (Chapman and Bjornn 1969). Furthermore, the study duration was insufficient to investigate whether trout from different populations responded differentially to the factors we investigated (*sensu* Alvarez et al. 2006).

Overall, these findings demonstrate that even under thermally suitable conditions, discharge can greatly affect trout growth patterns in summer. Our results are concerning given recent indications of declining trends in summer discharge throughout the region (Leppi et al. 2012; Al-Chokhachy et al. 2017) and anticipated reductions in snowpack associated with warming temperatures and climate shifts in the Rocky Mountains (Mote 2003; Barros et al. 2014). Decreases in winter snowpack and warming temperatures are expected to result in earlier spring runoff and further decreases in summer base discharge (Pederson et al. 2011; Ficklin et al. 2013), which may have greater consequences than warming stream temperatures for headwater populations. Declines in discharge will be exacerbated where warming temperatures and ensuing trout metabolic rates increase (Jonsson et al. 2013; Myrvold and Kennedy 2015), particularly as macroinvertebrate drift decreases and competition for resources increases. For species such as Yellowstone Cutthroat Trout that have current distributions primarily 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). The findings of this study and those of other field-based investigations (Nislow et al. 2004; Xu et al. 2010a) demonstrate the need to consider multiple factors when devising conservation strategies for coldwater fishes in response to climate change.

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Appendix: Details of Models Developed to Describe Yellowstone Cutthroat Trout Growth Rate

TABLE A.1. Model rank based on AIC_c scores, model structure, model parameter, estimate (SE), degrees of freedom of model (df), *t*-value, and *P*-value for significance of parameters in models describing trout growth rate in length.

Rank	Structure	Parameter	Estimate	SE	df	<i>t</i> -value	<i>P</i> -value
1	TL + MD	Intercept	0.3012	0.0398	129	7.56	<0.001
		TL	-0.0012	0.0002		-5.65	<0.001
		MD	0.3539	0.1925		1.84	0.068
2	TL + MD + MT	Intercept	0.2165	0.0896	128	2.41	0.017
		TL	-0.0012	0.0002		-5.58	<0.001
		MD	0.2987	0.2049		1.46	0.147
		MT	0.0096	0.0089		1.08	0.282
3	TL	Intercept	0.3226	0.0407	130	7.92	<0.001
		TL	-0.0012	0.0002		-5.48	<0.001
4	TL + MT	Intercept	0.2070	0.0910	129	2.27	0.025
		TL	-0.0011	0.0002		-5.46	<0.001
		MT	0.0127	0.0088		1.45	0.151
5	TL + MD + SB	Intercept	0.3077	0.0416	128	7.40	<0.001
		SB	-0.0029	0.0059		-0.50	0.619
		TL	-0.0012	0.0002		-5.62	<0.001
		MD	0.3545	0.1927		1.84	0.068
6	TL + MD + MT + TL × MT	Intercept	0.0669	0.1665	127	0.40	0.689
		TL	-0.0001	0.0010		-0.09	0.926
		MD	0.3270	0.2053		1.59	0.114
		MT	0.0258	0.0176		1.47	0.145
		TL × MT	-0.0001	0.0001		-1.07	0.285
7	TL + MT + TL × MT	Intercept	0.0824	0.1672	128	0.49	0.623
		TL	-0.0003	0.0010		-0.25	0.801
		MT	0.0263	0.0176		1.49	0.138
		TL × MT	-0.0001	0.0001		-0.89	0.378
8	TL + SB	Intercept	0.3292	0.0425	129	7.75	<0.001
		SB	-0.0029	0.0059		-0.50	0.619
		TL	-0.0012	0.0002		-5.46	<0.001
9	TL + MD + MT + SB	Intercept	0.2240	0.0944	127	2.37	0.019
		SB	-0.0018	0.0061		-0.29	0.772
		TL	-0.0012	0.0002		-5.57	<0.001
		MD	0.3010	0.2054		1.47	0.145
		MT	0.0093	0.0092		1.01	0.315
10	TL + MD + MT + SB + TL × MT	Intercept	0.0742	0.1706	126	0.43	0.665
		SB	-0.0015	0.0061		-0.24	0.808
		TL	-0.0001	0.0010		-0.10	0.920
		MD	0.3285	0.2059		1.60	0.113
		MT	0.0254	0.0178		1.42	0.157
		TL × MT	-0.0001	0.0001		-1.06	0.290

TABLE A.2. Model rank based on AIC_c scores, model structure, model parameter, estimate (SE), degrees of freedom of model (df), t -value, and P -value for significance of parameters in models describing trout growth rate in mass.

Rank	Structure	Parameter	Estimate	SE	df	t -value	P -value
1	MD + SB	Intercept	0.0200	0.0194	129	1.03	0.304
		SB	-0.0071	0.0042		-1.69	0.094
		MD	0.4736	0.136		3.48	<0.001
2	MD	Intercept	0.0042	0.0152	130	0.28	0.783
		MD	0.4669	0.1315		3.55	<0.001
3	TL + MD + SB	Intercept	0.0416	0.0297	128	1.40	0.164
		SB	-0.0069	0.0043		-1.60	0.113
		TL	-0.0002	0.0002		-0.96	0.339
		MD	0.4927	0.1383		3.56	<0.001
4	TL + MD	Intercept	0.0289	0.0277	129	1.05	0.298
		TL	-0.0002	0.0002		-1.08	0.283
		MD	0.4888	0.1343		3.64	<0.001
5	MD + MT	Intercept	-0.0126	0.0572	129	-0.22	0.826
		MT	0.0020	0.0065		0.30	0.763
		MD	0.4590	0.1415		3.24	0.002
6	TL + MD + MT + TL \times MT	Intercept	-0.1599	0.1269	127	-1.26	0.210
		TL	0.0011	0.0008		1.33	0.185
		MD	0.5118	0.1433		3.57	<0.001
		MT	0.0204	0.0135		1.51	0.135
		TL \times MT	-0.0001	0.0001		-1.58	0.116
7	TL + MD + MT + SB + TL \times MT	Intercept	-0.1277	0.1288	126	-0.99	0.323
		SB	-0.0065	0.0043		-1.50	0.136
		TL	0.0010	0.0008		1.28	0.201
		MD	0.5224	0.1461		3.58	<0.001
		MT	0.0181	0.0136		1.33	0.185
8	TL + MD + MT + SB	TL \times MT	-0.0001	0.0001	127	-1.51	0.134
		Intercept	0.0403	0.0668		0.60	0.548
		TL	-0.0002	0.0002		-0.98	0.331
		MD	0.4942	0.1462		3.38	0.001
		MT	0.0002	0.0067		0.03	0.975
9	TL + MD + MT	SB	-0.0069	0.0045	128	-1.56	0.122
		Intercept	0.0147	0.0638		0.23	0.818
		TL	-0.0002	0.0002		-1.08	0.282
		MD	0.4818	0.1439		3.35	0.001
		MT	0.0017	0.0066		0.25	0.800
10	SB	Intercept	0.0550	0.0207	130	2.66	0.009
		SB	-0.0074	0.0042		-1.77	0.080