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ARTICLE

Population Dynamics and Temporal Trends of Bull Trout in the East Fork Salmon River, Idaho

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Abstract
Because of their long-term listing under the Endangered Species Act, much interest has been placed on estimating population vital rates for Bull Trout *Salvelinus confluentus*, but the biotic and abiotic factors that influence the interannual variability in those vital rates have rarely been evaluated. We used mark–recapture data to estimate fish growth, survival, and trends in abundance for fluvial adult Bull Trout in the East Fork Salmon River, Idaho. Over an 8-year period, a total of 1,205 individual Bull Trout were collected at a weir on the East Fork Salmon River (29 km upstream of its confluence with the Salmon River) during June–September, of which 420 were recaptures from prior years. Bull Trout varied in length from 215 to 756 mm and achieved a slightly larger asymptotic length and a slightly lower rate of growth relative to other fluvial and adfluvial Bull Trout populations. Apparent survival averaged 0.42 across all years, which was similar to previous studies estimating apparent survival for Bull Trout. The number of emigrating anadromous salmonid smolts in the upper Salmon River basin positively influenced East Fork Salmon River Bull Trout growth and survival, and survival was higher in years with lower annual discharge. Assessment of population growth via linear regression analysis indicated that the Bull Trout population was increasing during the study period ($\lambda = 1.08$; 95% confidence interval = 1.03–1.14). Our findings highlight the ecological link between the abundance of wild and hatchery Chinook Salmon *Oncorhynchus tshawytscha*, Sockeye Salmon *O. nerka*, and steelhead *O. mykiss* smolts and growth and survival of adult Bull Trout in systems where these species occur in sympatry.

Bull Trout *Salvelinus confluentus* is a species of char native to western North America that has been listed as threatened by the U.S. Fish and Wildlife Service under the Endangered Species Act since 1999 (USFWS 1999). Bull Trout are large compared with most salmonids, achieving lengths of 700–900 mm and weights of >10 kg, and they commonly live from 8 to 12 years (Sigler and Zaroban 2018). The diet of Bull Trout changes with age, with younger Bull Trout feeding on invertebrates and older Bull Trout tending to be piscivorous. Bull Trout typically mature at 4–7 years of age, with spawning occurring in autumn when water temperatures are below 9°C, primarily in headwater mountain streams.

Understanding the viability of threatened or endangered fish populations or assessing the effectiveness of management strategies or habitat restoration to conserve at-risk species often requires knowledge of population dynamics, such as growth, survival, and recruitment (Morris and Doak 2002). Not surprisingly, population vital rates have been estimated for Bull Trout numerous times, often using the recapture of marked fish to avoid lethal sampling (e.g., Al-Chokhachy and Budy 2008; Erhardt and Scarnecchia 2014; Harris et al. 2016; Hudson et al. 2019). However, most of this work has occurred where Bull Trout populations are relatively weak or vulnerable (USFWS 2008), with few estimates available from relatively healthy or strong populations (but see Beauchamp and Van Tassell 2001 and Erhardt and Scarnecchia 2014). Across their range, Bull Trout status varies dramatically (e.g., Rodtka 2009; Howell and Sankovich 2012; Eby et al. 2014; Meyer et al. 2014). For example, in western Montana, recent trends in abundance for individual Bull Trout populations

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were significantly declining over six times more often than they were significantly increasing (Kovach et al. 2018). Bull Trout population trend data also suggests many Bull Trout populations are declining throughout Alberta (Rodtka 2009). Conversely, in Idaho, recent trends in individual populations were significantly increasing over four times more often than significantly declining (Meyer et al. 2014). Such variation in population trends, coupled with a diversity in life history forms (reviewed in Dunham et al. 2008), suggests that vital rates such as survival and growth may also vary greatly across the range of Bull Trout. Even within individual salmonid populations, growth and survival can be expected to vary annually (Bentley et al. 2012; Carline 2006), though the biotic and abiotic factors that might influence such interannual variability in Bull Trout populations have rarely been evaluated.

To gain a better understanding of the factors that might affect interannual variation in Bull Trout growth and survival, we used a weir for Chinook Salmon *Oncorhynchus tshawytscha* on the East Fork Salmon River in Idaho to also sample fluvial adult Bull Trout as they migrated upstream to their spawning grounds. The specific objectives of the study were to use annual mark–recapture data collected at the East Fork Salmon River weir to evaluate (1) Bull Trout length structure, run timing, fish growth, and survival for this fluvial population; (2) the influence of various biotic and abiotic factors on interannual variation in Bull Trout survival and fish growth; and (3) population growth rate in order to more thoroughly assess the status of this population.

METHODS

The East Fork Salmon River is a tributary of the Salmon River in central Idaho that is approximately 55 km long and drains an area of 1,400 km^2. Discharge in the East Fork Salmon River typically varies from 19.5 to 43.3 m^3/s. The underlying geology of the East Fork Salmon River is predominately comprised of the granitic Idaho batholith, resulting in a relatively unproductive aquatic environment (Sanderson et al. 2009). Land use in the lower portion of the East Fork Salmon River drainage is predominately agriculture, but the upper 25 km of river is relatively undisturbed by human use. In fact, three wilderness areas (i.e., Hemingway–Boulders Wilderness, White Clouds Wilderness, and Jim McClure–Jerry Peak Wilderness) have been designated within the headwaters of the East Fork Salmon River. Additionally, no migration barriers exist within the Salmon River basin. Salmonid species present in the East Fork Salmon River include Bull Trout, Chinook Salmon, steelhead *O. mykiss*, Mountain Whitefish *Prosopium williamsoni*, and Westslope Cutthroat Trout *O. clarkii lewisi*.

Field sampling.— Adult migratory Bull Trout were collected at an existing Idaho Department of Fish and Game velocity-barrier weir 29 km upstream of the mouth of the East Fork Salmon River (WGS84; 44.115538°, −114.429777°) during June 6 to September 21 each year from 2007 to 2014. Due to the weir, migrating fish must ascend a side-channel fish ladder to navigate upstream. At the upstream end of the ladder is a trap where Bull Trout were captured and held for sampling. The weir and trap effectively captures all upstream-migrating fish, except for any fry that might be able to pass through the trap box pickets. Fish were removed from the trap box with a dip net and placed into holding tanks. Fish placed in holding tanks were anesthetized using MS-222 (tricaine methanesulfonate; 50 mg/L) buffered with sodium bicarbonate. Once anesthetized, Bull Trout were checked for visible marks, scanned for a passive integrated transponder (PIT) tag, and measured for total length to the nearest millimeter. If a tag was not detected, fish were PIT-tagged in the muscular tissue of the operculum with 12-mm, full-duplex tags so that the tag was oriented parallel to the transverse plane of the fish, following Downs et al. (2006). Fish were then placed in fresh water and allowed to recover, after which they were released upstream of the weir.

Environmental variables.— We evaluated the influence of several biotic and abiotic predictor variables on individual annual fish growth and on apparent survival ($\hat{\Phi}$). Average daily discharge (m^3/s) for each water year (October 1 to September 30) was obtained from the United States Geological Survey (gauging station 13307000) located on the Salmon River, Idaho, from which mean water-year discharge was calculated to describe the magnitude of the water year. Discharge in the East Fork Salmon River was not available, and Bull Trout that spawn in the East Fork Salmon River spend the majority of the year in other locations such as the main stem of the Salmon River or other tributaries (Schoby and Keeley 2011); thus, the discharge in the upper Salmon River was used as an index of years with higher or lower streamflow. Discharge (termed *Avgflow*) was included as a predictor variable because streamflow has previously been documented to influence growth (Harvey et al. 2006; Jensen and Johnsen 1999; Letcher et al. 2015; Teichert et al. 2010; Uthe et al. 2019) and survival in salmonids (Al-Chokhachy and Budy 2008; Howell et al. 2016; Letcher et al. 2015; McCormick and High 2020; Richard et al. 2015). Low streamflow also has the potential to limit salmonid populations by reducing habitat quantity and quality (e.g., Magoulick and Kobza 2003), which may impact population survival.

Water temperature was included as a predictor variable because the severity of both summer and winter water temperatures can affect salmonid growth (Armstrong and Nislow 2012; Letcher et al. 2015; Richard et al. 2015; Selong et al. 2001; Uthe et al. 2019) and survival (Jakober et al. 1998; Letcher et al. 2015; Meyer et al. 2014; Selong et al. 2001). Average summer (June–August; termed

SummerTemp) and winter (December–February; termed *WinterTemp*) water temperature was sporadically available for the East Fork Salmon River during this study, but as mentioned above, adult Bull Trout are only in the East Fork Salmon River for a portion of the year. Therefore, as a general index of water temperature in the upper Salmon River basin, a thermograph was installed in the Salmon River at the Sawtooth Fish Hatchery (WGS84; 44.153378°, –114.883750°). The thermograph malfunctioned three times, causing the loss of water temperature data for about 5% of the duration of the study. When water temperature data were unavailable for a particular day, they were predicted from the relationship between air temperature data for Stanley, Idaho and the thermograph water temperature at the hatchery on the same day. Stanley air temperature data was obtained from the National Oceanic Atmospheric Administration Online Weather Data database (Stanley Area). The relationship between Stanley air temperature data and the thermograph water temperature data was estimated by fitting a simple linear regression model using both data sets. In the model, average daily Stanley air temperature was the explanatory variable and average daily thermograph water temperature was the response variable for all days in which both temperatures were available, and the resulting model explained 92% of the variation in Salmon River water temperature data obtained at the hatchery.

The estimated total number of wild and hatchery juvenile anadromous smolts (i.e., Chinook Salmon, steelhead, and Sockeye Salmon *O. nerka*) in the upper Salmon River basin each year (termed *Smolts*) was included as a predictor variable to represent a general measure of Bull Trout food availability. Food availability affects the relative condition of Bull Trout, which in turn influences Bull Trout survival (Al-Chokhachy and Budy 2008). Juvenile salmonid abundance was chosen as a measure of food availability because they seasonally make up a large portion of the diet of migratory Bull Trout in waters with anadromous fish (Furey et al. 2014; Lowery and Beauchamp 2015). The total number of *Smolts* present each year was derived from expanded estimates of Chinook Salmon, Sockeye Salmon, and steelhead emigration using juvenile fish traps and the total number of hatchery smolts releases throughout the upper Salmon River basin. Based on an earlier Bull Trout movement study (Schoby and Keeley 2011), the upper Salmon River basin was considered to include the Salmon River and all tributaries from the confluence of the North Fork Salmon River, Idaho, upstream to the headwaters of the Salmon River.

For modeling purposes, *Avgflow*, *WinterTemp*, and *Smolts* were assumed to affect Bull Trout growth and survival during the same year. For example, Bull Trout growth and survival from the 2008 to the 2009 spawning run was assumed to have potentially been influenced by the mean daily discharge during the 2009 water year (i.e., October 1, 2008, to September 30, 2009), the winter 2008–2009 mean daily water temperature, and the total number of *Smolts* emigrating in the fall of 2008 and spring and summer of 2009. In contrast, *SummerTemp* was modeled with a 1-year lag; thus, we assumed that summer water temperature in the current year would affect growth and survival in the following year. Had we not lagged *SummerTemp* by 1 year, most (about 80%) of the Bull Trout in any given year would have already passed above the East Fork Salmon River weir (indicating that they survived that year) before even half of the *SummerTemp* data for that year had been collected.

The total number of Bull Trout sampled at the weir the prior year (termed *PriorRunSize*) was included as a predictor variable to evaluate whether increased run size in a particular year produced a density-dependent decline in growth or survival to the following year, as commonly occurs in fish populations (Allen and Hightower 2010; Chundnow et al. 2019; Johnston and Post 2009). Water year (*Time*) was also included as a covariate to account for a year effect.

Data analysis.— Fish growth was estimated by fitting a Fabens modification of the von Bertalanffy growth (VBG) model (Fabens 1965) to length at recapture data for each fish class as follows:

$$L_r = L_m + (L_\infty - L_m)\left[1 - e^{-K(\Delta T)}\right],$$

where L_r is the length of the fish at recapture, L_m is the length of the fish at first capture, L_∞ is the theoretical maximum length a fish could achieve in the population, K is the growth coefficient, and ΔT is the number of years that have passed between the initial capture and the recapture (Ogle et al. 2017). Evaluation of the factors that influenced annual Bull Trout growth increments in the East Fork Salmon River (see below) was conducted using simple linear regression models in which the response variable was the growth rate between capture events. The growth rate was calculated as the change in length between L_m and L_r divided by the amount of time between capture events. For the purpose of evaluating the factors that influence Bull Trout growth, only Bull Trout that were captured in a certain year and then recaptured in the subsequent year were included in the analysis. Simple linear regression models were evaluated in statistical package R (R Core Team 2019).

Estimates of apparent survival ($\hat{\Phi}$) and recapture probability ($\hat{p}$) were calculated using Cormack–Jolly–Seber (CJS) models that were also evaluated in statistical package R, using the RMark function (Laake 2013) to interface with program Mark (White and Burnham 1999). Estimates of true survival could not be calculated because survival rate in these models is confounded with fidelity rate and the spawning frequency of the fish (Pine et al. 2012).

Instead, apparent survival was estimated as follows:

$$\hat{\Phi} = \frac{M_{i+1}}{\hat{M}_i - m_i + R_i},$$

where M_i is the number of marked Bull Trout at the start of sample i, m_i is the number of marked Bull Trout caught in the ith sample, and R_i is the number of Bull Trout caught in the ith sample that are tagged and released (Hayes et al. 2007). Recapture probability was estimated as follows:

$$\hat{p} = \frac{m_i}{\hat{M}_i},$$

where M_i is as defined above and m_i is the number of marked Bull Trout caught in the ith sample. For the purpose of the CJS models, it was assumed that fish spawned and returned to the East Fork Salmon River annually.

A priori growth and survival models included the following: (1) a null model, (2) all single factor models (i.e., *Time*, *Avgflow*, *SummerTemp*, *WinterTemp*, *Smolts*, and *PriorRunSize*), (3) a model including *Avgflow* and *Smolts* and the interaction between *Avgflow* and *Smolts* (*Avgflow* × *Smolts*), (4) a model including *SummerTemp* and *WinterTemp*, and (5) a full model containing all factors. The null model for the growth models included only the length of fish at capture (L_m). Similarly, the null model for the CJS models included no explanatory variables or *Time* [i.e., $\hat{\Phi} = (1)$; $\hat{p}(1)$]. For CJS models, $\hat{p}$ was allowed to vary by *Time* in all models except for the null model. Additionally, L_m was included as a covariate and *Time* was not included as a covariate in all the models evaluating factors that affected individual Bull Trout growth. When modeling the effects of the explanatory variables on both growth and survival, all continuous variables (i.e., *Avgflow*, *SummerTemp*, *WinterTemp*, *Smolts*, *PriorRunSize*, and L_m) were scaled so that the mean of a given explanatory variable was equal to zero and a one-unit increase in the variable was equal to one standard deviation. Because the numeric ranges of continuous variables were vastly different, scaling these variables allowed each variable to contribute equally to the modeling analysis instead of allowing the variables with the largest values to mask the relationships of the variables with smaller values. All models including only one explanatory variable were included to directly evaluate the effect of a given predictor variable on Bull Trout growth or survival. The model containing *Avgflow*, *Smolts*, and *Avgflow* × *Smolts* was included because flow can regulate the availability of juvenile Chinook Salmon, Sockeye Salmon, and steelhead by influencing emigration speed (Smith et al. 2002) and predation efficiency through turbidity (Gregory and Levings 1998). Given the above-mentioned effect of water temperature on survival and growth, the model containing both *SummerTemp* and *WinterTemp* was included to investigate the effects of water temperature on Bull Trout growth and survival during the two time periods in which it is most likely to be a limiting factor. Finally, the model containing all the predictor variables was included to evaluate the possibility that Bull Trout growth and survival was influenced by a combination of all the predictor variables.

Models constructed to evaluate factors influencing Bull Trout growth were compared using Akaike information criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002). The top model was considered to be the model with the lowest AIC_c, and any model within 2.0 AIC_c of the top model was also considered to be a plausible model. Assessment of overdispersion was conducted by estimating the dispersion parameter $\hat{c}$ by dividing Pearson's residual deviance by the residual degrees of freedom from the most parameterized model. Models were then considered overdispersed when $\hat{c}$ was greater than one.

Models constructed to evaluate factors influencing Bull Trout survival (i.e., CJS models) were compared using quasi Akaike information criterion corrected for small sample size ($QAIC_c$), with the top model being the one with the lowest $QAIC_c$ value (Burnham and Anderson 2002). Any model from the candidate set of models with a $QAIC_c$ value within 2.0 of the top model was also considered a plausible model. The $QAIC_c$ was used because overdispersion was assessed for the models using the dispersion parameter $\hat{c}$ and it was found to be >1 (i.e., $\hat{c} = 1.85$), indicating that $QAIC_c$ was more appropriate to use than AIC_c for model selection. The estimate of $\hat{c}$ was calculated using a parametric bootstrapping procedure (Cooch and White 2019). Using the statistical package R (R Core Team 2019), 1,000 data sets were simulated using the model in which *Time* was the only predictor variable for both $\hat{\Phi}$ and $\hat{p}$ (Cooch and White 2019). Each simulated data set was then fit using the model with only *Time* as a predictor variable. The $\hat{c}$ for each of the simulated data sets was then estimated by dividing the model deviance by the model degrees of freedom. Simulated $\hat{c}$ was estimated by calculating the average $\hat{c}$ across all 1,000 simulated data sets (simulated $\hat{c}$). The estimate of $\hat{c}$ from the original data set (sample $\hat{c}$) was also calculated by fitting the model with only *Time* as a predictor variable to the original data set and then dividing the model deviance by the model degrees of freedom. The estimate of $\hat{c}$ used to calculate $QAIC_c$ of each model was calculated by dividing the sample $\hat{c}$ by the simulated $\hat{c}$.

To analyze population growth rates (λ), weir count data were fitted with a linear regression model. The sample year was the independent variable and $\log_e$ transformed weir counts of abundance were the dependent variable (Gerrodette 1987; Maxell 1999). The slope of the regression equals the intrinsic rate of change for the population (r), and once exponentiated, the slope of the line is equal to λ. The population was considered to be growing if $\lambda > 1$ (Haddon 2011). Ninety-five percent confidence intervals (CIs) for λ were calculated based on the error surrounding the estimate of λ from the linear regression (i.e., 95% CI = $1.96 \times$ SE).

RESULTS

A total of 1,205 individual Bull Trout was sampled at the weir on the East Fork Salmon River during 2007–2014, of which 420 were recaptured at least once during the study period. Catch of Bull Trout varied from a low of 165 fish in 2008 to a high of 314 in 2013 and averaged 246 fish (SE = 20; Figure 1) per year. Bull Trout varied in length from 215 to 756 mm (Figure 2). Migrating prespawn Bull Trout passed the weir as early as June 7 and as late as September 11, but the spawning run typically peaked between July 1 and July 12. On average, 25% of the spawning run arrived by June 28, 50% arrived by July 6, and 75% arrived by July 14 (Figure 3). Of the 420 fish captured more than once, most were captured in two consecutive years (51%) or three consecutive years (26%) and then were never captured again, and 5% were observed in nonconsecutive years. The maximum number of times a fish was observed was seven times; this occurred for four fish.

The biotic and abiotic factors we measured for their potential influence on Bull Trout growth and survival were relatively consistent during our study (Table 1). Growth analysis indicated that the theoretical maximum length achieved in the population (L_∞) was 877 mm, K was 0.14, and ΔT was 1 year. Comparisons of models

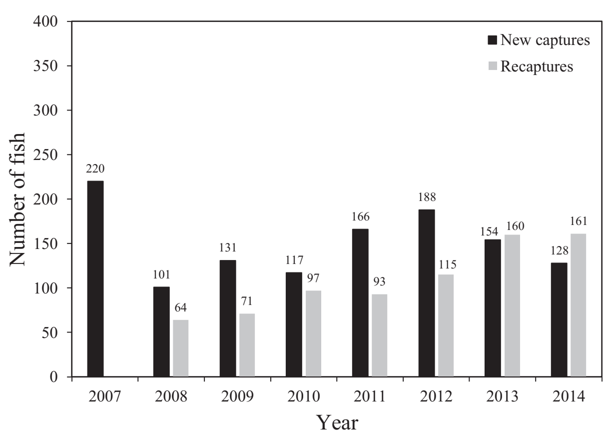

FIGURE 1. The number of Bull Trout sampled at the East Fork Salmon River weir from 2007 to 2014. Recaptured fish were Bull Trout sampled at the weir in previous years that had received a PIT tag.

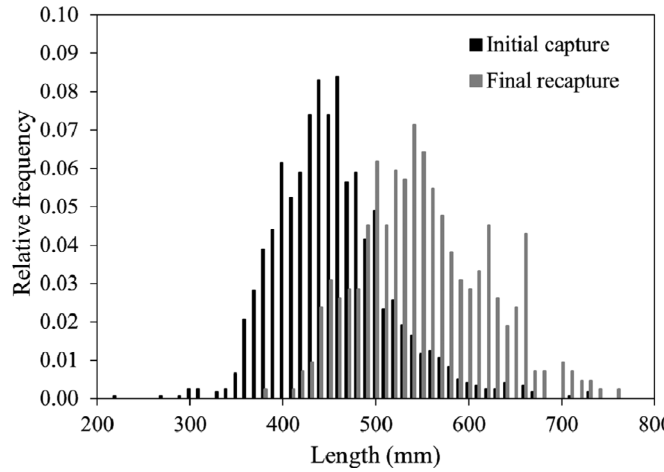

FIGURE 2. Length distributions of Bull Trout sampled at the East Fork Salmon River weir at the time the fish was first observed (initial capture) and at the last time the fish was observed (final recapture) during 2007–2014. Length data for fish that were only observed once were not included in final recapture data.

evaluating factors that influenced the growth of individual Bull Trout indicated that the model that included *Smolts* and L_m as the explanatory variables was the top model (AIC_c = 1,868.2, df = 209, $r^2 = 0.19$; Table 2). The next closest model was not within 2.0 AIC_c and therefore not considered a top model. Based on parameter estimates for the top model, Bull Trout growth increased as *Smolts* increased and decreased as L_m increased (Table 3).

Model selection revealed that the top model for estimating apparent survival was the model in which *Avgflow*, *Smolts*, and *Avgflow* × *Smolts* were included as explanatory variables for $\hat{\Phi}$ and $\hat{p}$ was allowed to vary by *Time* ($QAIC_c$ = 1,345.3; Table 4). Parameter estimates from this model indicated that Bull Trout survival decreased as *Avgflow* increased and S*molts* decreased; the interaction term *Avgflow* × *Smolts* had no effect on survival (i.e., 95% CIs on the parameter estimates overlapped zero; Table 3). The next closest model included *PriorRunSize* as a lone predictor variable ($QAIC_c$ = 1,346.2), which indicated that Bull Trout survival increased as *PriorRunSize* increased. The models including S*molts* ($QAIC_c$ = 1,346.3) and *Avgflow* ($QAIC_c$ = 1,347.2) as lone predictors were also considered top models (i.e., $QAIC_c$ value within 2.0 of the top model), but the parameter estimates indicated the same relationship between *Smolts* and *Avgflow* as the top model. Based on the top model, $\hat{\Phi}$ varied from a low of 0.39 during 2008–2009 to a high of 0.52 during 2009–2010 and 2012–2013 and averaged 0.42 (95% CI = 0.39–0.44; Table 5). Recapture probability varied from a low of 0.79 during 2007–2008 to a high of 1.00 during 2011–2012. Over the course of the entire study period, recapture probability averaged 0.93 (95% CI = 0.90–0.96). Lastly, population growth rate analysis indicated that the fluvial Bull

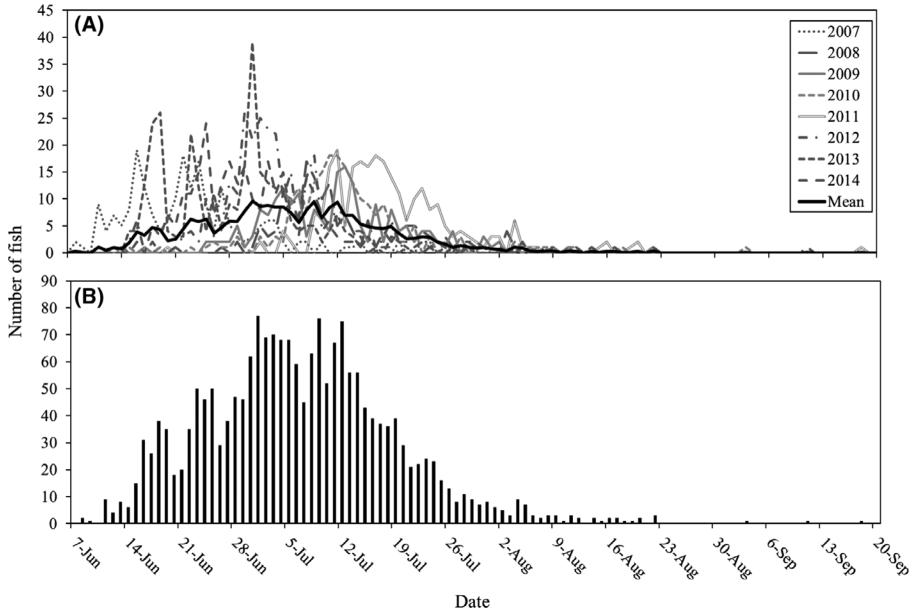

FIGURE 3. Timing of Bull Trout sampled at the East Fork Salmon River weir in Idaho from 2007 to 2014. Panel **(A)** includes the total number of Bull Trout sampled daily each year and the average number of Bull Trout sampled on a given day across all study years. Panel **(B)** includes the total number of Bull Trout sampled on a given day over the course of the study.

TABLE 1. Summary statistics for continuous variables for use in models predicting the growth and survival of migratory Bull Trout in the East Fork Salmon River captured and subsequently recaptured at a weir (2007–2014). See Methods for definitions of the environmental variables.

Environmental variable	Mean (SD)	Minimum	Maximum
Avgflow (m^3/s)	85.3 (14.6)	61.1	107.8
PriorRunSize (number of fish)	246 (54.7)	165	314
Smolts (millions of fish)	7.66 (0.8)	6.44	8.49
SummerTemp (°C)	13.0 (0.7)	12.1	14.1
WinterTemp (°C)	1.8 (0.2)	1.6	2.2

Trout population in the East Fork Salmon River was increasing during the study period (i.e., $\lambda = 1.08$, 95% CI = 1.03–1.14).

TABLE 2. Simple linear regression models for predicting the growth of migratory Bull Trout in the East Fork Salmon River captured and subsequently recaptured at a weir (2007–2014). See text for covariate descriptions and model explanations. Also included are AIC_c values, the difference between each model and the top model (ΔAIC_c), the number of parameters in the model (*K*), and model weights (w_i).

Model	*K*	AIC_c	ΔAIC_c	w_i
$Smolts + L_m$	4	1,868.2	0.00	0.77
$Avgflow + Smolts + Avgflow \times Smolts + L_m$	6	1,871.2	3.00	0.17
$Avgflow + PriorRunSize + Smolts + SummerTemp + WinterTemp + L_m$	8	1,875.5	7.34	0.02
L_m	3	1,877.5	9.33	0.01
$Avgflow + L_m$	4	1,877.6	9.39	0.01
$PriorRunSize + L_m$	4	1,877.6	9.47	0.01
$SummerTemp + L_m$	4	1,877.8	9.66	0.01
$WinterTemp + L_m$	4	1,878.2	10.07	0.01
$SummerTemp + WinterTemp + L_m$	5	1,879.9	11.75	0.00

DISCUSSION

Because of their long-term Endangered Species Act listing and their reputation as an indicator species of clean, cold water in relatively pristine lotic and lentic habitats, Bull Trout have been the subject of myriad studies over the past 20 years on their status, habitat requirements, and population dynamics. A by-product of these investigations has been the generation of vital rate estimates for Bull Trout across much of their range (Table 6), though prior to the present study, estimates of Bull Trout growth and survival in central Idaho have been lacking. Our results suggest that in the East Fork Salmon River, Bull Trout achieve a slightly larger asymptotic length (L_∞) and a slightly lower rate of growth (*K*) relative to the other fluvial and adfluvial Bull Trout populations for which

TABLE 3. Parameter estimates from the top simple linear regression model (growth models) predicting the growth of migratory Bull Trout. Also included are parameter estimates from the top Cormack–Jolly–Seber models (survival models) predicting the apparent survival ($\hat{\Phi}$) and recapture probability ($\hat{p}$) of migratory Bull Trout. Fish were captured and subsequently recaptured at a weir on the East Fork Salmon River, Idaho (2007–2014). See text for covariate descriptions and model explanations. Also included are lower (LCI) and upper (UCI) 95% confidence intervals.

Parameter	Estimate	LCI	UCI
Top growth model			
Intercept	56.11	53.46	58.76
Smolts	4.66	1.95	7.35
L_m	–7.77	–10.47	–5.07
Top survival model			
$\hat{\Phi}$(Intercept)	–0.06	–0.16	0.05
$\hat{\Phi}$(*Avgflow*)	–0.18	–0.30	–0.06
$\hat{\Phi}$(*Smolts*)	0.14	0.05	0.22
$\hat{\Phi}$(*Avgflow*) × (*Smolts*)	–0.18	–0.37	0.02
$\hat{p}$(Intercept)	1.70	0.48	2.16
$\hat{p}$(2008–2009)	0.19	–0.48	1.76
$\hat{p}$(2009–2010)	0.29	–0.35	2.17
$\hat{p}$(2010–2011)	1.47	0.14	3.40
$\hat{p}$(2011–2012)	32.92	–15,543.13	15,603.20
$\hat{p}$(2012–2013)	1.67	0.65	3.44
$\hat{p}$(2013–2014)	15.32	–2,291.07	2,320.46
Second-best survival model			
$\hat{\Phi}$(Intercept)	–0.79	–1.37	–0.21
$\hat{\Phi}$(*PriorRunSize*)	0.003	0.000	0.005
$\hat{p}$(Intercept)	1.11	0.37	1.85
$\hat{p}$(2008–2009)	0.65	-0.39	1.70
$\hat{p}$(2009–2010)	1.46	0.24	2.68
$\hat{p}$(2010–2011)	1.95	0.40	3.51
$\hat{p}$(2011–2012)	17.00	–27,491.02	2,783.11
$\hat{p}$(2012–2013)	2.31	0.96	3.66
$\hat{p}$(2013–2014)	2.66	–4.17	9.48

TABLE 4. Cormack–Jolly–Seber models for estimating apparent survival ($\hat{\Phi}$) and recapture probability ($\hat{p}$) of migratory Bull Trout in the East Fork Salmon River captured and subsequently recaptured at a weir (2007–2014). See text for covariate descriptions and model explanations. Also included are $QAIC_c$ values, the difference between each model and the top model ($\Delta QAIC_c$), the number of parameters in the model (K), and model weights (w_i).

Model	K	$QAIC_c$	$\Delta QAIC_c$	w_i
$\hat{\Phi}$(*Avgflow* + *Smolts* + *Avgflow* × *Smolts*) $\hat{p}$(*Time*)	11	1,345.3	0.00	0.30
$\hat{\Phi}$(*PriorRunSize*) $\hat{p}$(*Time*)	9	1,346.2	0.98	0.19
$\hat{\Phi}$(*Smolts*) $\hat{p}$(*Time*)	9	1,346.3	1.06	0.18
$\hat{\Phi}$(*Avgflow*) $\hat{p}$(*Time*)	9	1,347.2	1.96	0.11
$\hat{\Phi}$(*Time*) $\hat{p}$(*Time*)	14	1,347.7	2.47	0.09
$\hat{\Phi}$(*SummerTemp*) $\hat{p}$(*Time*)	9	1,349.3	4.03	0.04
$\hat{\Phi}$(1) $\hat{p}$(1)	2	1,349.6	4.37	0.03
$\hat{\Phi}$(*WinterTemp*) $\hat{p}$(*Time*)	9	1,349.8	4.54	0.03
$\hat{\Phi}$(*SummerTemp* + *WinterTemp*) $\hat{p}$(*Time*)	10	1,350.9	5.61	0.02
$\hat{\Phi}$(*Time* + *Avgflow* + *PriorRunSize* + *Smolts* + *SummerTemp* + *WinterTemp*) $\hat{p}$(*Time*)	19	1,357.9	12.69	0.00

growth has been estimated using the Fabens modification to the VBG model. Direct comparison of growth parameters between the standard VBG model and Fabens modification may be inappropriate because the two methods do not have identical interpretations of the growth parameters (Francis 1988; Ogle et al. 2017). However, studies using both methods for Bull Trout have produced very similar VBG parameter estimates (Table 6). Taken collectively, there is a distinct negative correlation between L_∞ and K for these individual Bull Trout populations (Pearson's correlation coefficient: $r = –0.65$), as would be expected theoretically given the relationship between L_∞ and K (Beverton and Holt 1959). The relatively unproductive underlying geology in the upper Salmon River basin (Sanderson et al. 2009) may explain the below-average rate of growth for adult Bull Trout in the East Fork Salmon River. However, growth studies in fluvial Bull Trout populations are generally lacking, and additional studies of growth in fluvial populations of Bull Trout would help better place our results in context with other populations across their range.

While Bull Trout growth in the East Fork Salmon River differed from previous studies, estimates of apparent survival across years (mean $\hat{\Phi} = 0.42$) were surprisingly similar to previous estimates for a variety of fluvial and adfluvial Bull Trout populations (e.g., Al-Chokhachy and Budy 2008; Al-Chokhachy et al. 2019; Beauchamp and Tassel 2001; Howell et al. 2016; Hudson et al. 2019), which taken collectively have ranged from 0.35 to 0.47 and averaged 0.43. Apparent survival is an underestimate of true survival for Bull Trout because site fidelity and annual spawning rates are generally not 100% for this species (e.g., Barnett and Paige 2013; Rieman and Allendorf 2001), and fish that are actually alive but go undetected are recorded as mortalities, leading to underestimates of $\hat{\Phi}$. Inclusion of subadult fish (i.e., fish <350 mm; Erhardt and Scarnecchia 2014) in our study could have biased our estimate of adult Φ relative to other studies, assuming that survival differed between the two life stages (Rieman and Allendorf 2001). However, considering that subadults comprised only a small portion of the overall catch (i.e., 16 fish or 0.8% of all fish captures), it is unlikely their inclusion affected estimates of Φ. Estimates of absolute survival are rare for Bull Trout populations but have been reported to be 0.54–0.66 in Lake Pend Oreille (Vidergar 2000; McCubbins et al. 2016). It may seem surprising that $\hat{\Phi}$ is so similar for

TABLE 5. Estimates of apparent survival ($\hat{\Phi}$) and recapture probability ($\hat{p}$) of the top Cormack–Jolly–Seber model for migratory Bull Trout in the East Fork Salmon River captured and subsequently recaptured at a weir (2007–2014). The top model included *Avgflow*, *Smolts*, and *Avgflow* × *Smolts* as explanatory variables for $\hat{\Phi}$, and $\hat{p}$ was allowed to vary by *Time*. See text for covariate descriptions and model explanations.

	$\hat{\Phi}$		$\hat{p}$	
Time period	Estimate	95% CI	Estimate	95% CI
2007–2008	0.36	0.30–0.44	0.85	0.67–0.94
2008–2009	0.44	0.36–0.51	0.87	0.74–0.94
2009–2010	0.55	0.50–0.61	0.96	0.74–0.95
2010–2011	0.41	0.36–0.46	0.96	0.86–0.99
2011–2012	0.47	0.44–0.50	1.00	0.00–1.00
2012–2013	0.52	0.47–0.57	0.97	0.90–0.99

relatively vulnerable (e.g., Howell et al. 2016; $\hat{\Phi} = 0.43$) and relatively healthy (this study; $\hat{\Phi} = 0.42$) Bull Trout populations, considering that adult survival is a primary factor in population growth rate (Morris and Doak 2002). However, population growth is a function not only of adult survival, but also of juvenile survival, fish growth, longevity, age at maturity, and fecundity. In fact, previous studies have suggested that population growth in freshwater fisheries is particularly sensitive to changes in juvenile fish survival (Ng et al. 2016; Brauer et al. 2019).

Our results suggest that the number of emigrating anadromous salmonid smolts—which have been documented to be a major food source for adult Bull Trout in central Idaho (Schoby and Keeley 2011) and in the Chilko River, British Columbia (Furey et al. 2014)—positively influenced both the growth and the survival of adult Bull Trout in the East Fork Salmon River. Moreover, in years with lower discharge, Bull Trout survival increased. Lower streamflow does slow emigration travel time for smolts and reduces turbidity (Gregory and Levings 1998; Notch et al. 2020), which inherently would benefit foraging success of piscivorous salmonids. However, the fact that the *Smolts* × *Avgflow* interaction term was not significant (i.e., the 95% CIs around the parameter estimate overlapped zero) suggests that lower streamflow was not altering Bull Trout foraging success, at least not over the range of flows that we observed. Nevertheless, foraging conditions for adult Bull Trout in central Idaho may become even more favorable as climate change continues to reduce the magnitude and duration of high streamflows during late spring to early summer (Mote et al. 2005) when the majority of smolt emigration occurs (e.g., Copeland and Venditti 2009; Trushenski et al. 2019). However, given that the effects of climate change on coldwater ecosystems are somewhat unpredictable (Isaak et al. 2012), how climate change will affect adult Bull Trout survival and growth in central Idaho is a matter of conjecture (Lynch et al. 2016). Moreover, current annual smolt emigration from central Idaho, even including hatchery releases, is likely a fraction of historical abundance (Thurow et al. 2020), suggesting that forage availability for Bull Trout in the upper Salmon River basin has been greatly reduced for decades. Nevertheless, Bull Trout continue to thrive in the upper Salmon River basin and the rest of central Idaho (Meyer et al. 2014) for a variety of reasons, one of which is undoubtedly the immense numbers of hatchery smolts released in the basin (e.g., Sullivan et al. 2018), with release time occurring before adult Bull Trout leave foraging areas for their annual spawning migration.

TABLE 6. Comparisons of parameter estimates from the standard von Bertalanffy growth (VBG) model and Fabens modification to that model for various populations of Bull Trout, where L_∞ is the theoretical maximum length a fish could achieve in the population and K is the growth coefficient. For water bodies, EF is East Fork, SF is South Fork, and NF is North Fork. Values followed by an asterisk indicate that the value is an average.

Water body	Life history	L_∞ (mm)	K	Method	Reference
EF Salmon River, Idaho	Fluvial	877	0.14	Fabens	This study
Lower Kananaskis Lake, Alberta	Adfluvial	768*	0.19	Fabens	Johnston and Post (2009)
NF Clearwater River, Idaho	Adfluvial	644	0.21	Fabens	Erhardt and Scarnecchia (2013)
SF Walla Walla River, Oregon and Washington	Fluvial	624*	0.37*	Fabens	Harris et al. (2016)
Lake Pend Oreille, Idaho	Adfluvial	965	0.09	VBG	Vidergar (2000)
Lower Kananaskis Lake, Alberta	Adfluvial	800	0.32	VBG	Post et al. (2003)
NF Clearwater River, Idaho	Adfluvial	644	0.12	VBG	Erhardt and Scarnecchia (2014)
SF Walla Walla River, Oregon and Washington	Fluvial	828*	0.10*	VBG	Harris et al. (2016)
Lake Pend Oreille, Idaho	Adfluvial	1,036*	0.10*	VBG	McCubbins et al. (2016)
Chilko River, British Columbia	Adfluvial	691	0.27	VBG	Kanigan (2017)
NF Lewis River, Washington	Adfluvial	907	0.16	VBG	Al-Chokhachy et al. (2019)
Lewis River, Washington	Adfluvial	907	0.15	VBG	Hudson et al. (2019)

Additionally, hatchery fish are generally more vulnerable to predation than are wild fish (reviewed by Weber and Fausch 2003). Our findings highlight the ecological linkage between Chinook Salmon, Sockeye Salmon, and steelhead smolts and adult Bull Trout that is likely present whenever these species are sympatric.

The lack of an effect of *SummerTemp*, *WinterTemp*, and *PriorRunSize* on the individual growth and survival of fluvial adult Bull Trout returning each year to the East Fork Salmon River to spawn could be due to any number of reasons. First, while Bull Trout are among the most cold-adapted of all aquatic vertebrates in central Idaho (Isaak et al. 2016), water temperatures remain particularly cold in the upper Salmon River basin, providing ideal rearing conditions for both juvenile and adult fish. Moreover, water temperature (both summer and winter) fluctuated the least of all biotic and abiotic factors we included in the present study, which may have prevented any water temperature effects on Bull Trout growth or survival from materializing. Second, the upper Salmon River basin is a highly connected riverscape (Schoby and Keeley 2011), which allows Bull Trout to seasonally select locations with the most favorable conditions for growth and survival. Such movement also diminishes the likelihood that a stationary water temperature thermograph will accurately characterize the actual temperatures experienced by adult Bull Trout occupying various tributaries and main-stem reaches of the upper Salmon River basin. The lack of a density-dependent effect on growth and the minimal effect on survival was not surprising given that (1) the Bull Trout population in the East Fork Salmon River was experiencing population growth during the study period and (2) this population has been estimated to be below carrying capacity (Meyer et al. 2014).

Our study contributes to the literature regarding the effects of biotic and abiotic factors affecting the growth and survival of adult fluvial Bull Trout, but additional studies are clearly needed to more fully identify factors limiting such vital rates under a variety of conditions and in populations exhibiting an array of life history strategies. While our analyses included several biotic and abiotic factors likely to influence Bull Trout populations, other environmental variables or species interactions that we did not consider may also play a role. Nevertheless, our findings provide evidence of a clear link between the abundance of wild and hatchery Chinook Salmon, Sockeye Salmon, and steelhead smolts and adult Bull Trout growth and survival where they coexist; as such, future studies of the factors affecting Bull Trout growth and survival with and without the coexistence of Chinook Salmon, Sockeye Salmon, and steelhead would be particularly useful.

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