Population Characteristics of Brook Trout in Idaho Streams and Alpine Lakes

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Abstract

In western North America, nonnative brook trout (*Salvelinus fontinalis*) frequently threaten native salmonids via competition and hybridization, so fisheries managers often implement eradication programs for conservation purposes. In conjunction with such programs, managers often construct population models to evaluate the effects of different management strategies designed to control the undesirable population, but such models require demographic data (e.g., age, growth, sex ratios, and survival), which are lacking for western brook trout populations. Brook trout were sampled from 12 alpine lakes and two streams in Idaho, with total length varying from 80 to 380 mm and age varying from 1 to 11 yrs. Across all waters, the von Bertalanffy growth parameters $L\infty$ varied from 231 to 490 mm (mean = 345 mm) and K varied from 0.15 to 0.76 (mean = 0.37). Survival estimates, constructed from age-length keys, were corrected for streams with mark-recapture data; for alpine lakes, corrections were made via gill net selectivity data. Survival varied from 0.30 to 0.56 (mean = 0.45), and except for one waterbody, estimates were minimally affected by correcting for capture efficiency. The proportion of the population that was male varied from 0.34 to 0.75 (mean = 0.53). Our results indicate that brook trout population vital rates in Idaho were similar to those observed in their native range, and were surprisingly similar between alpine lake and stream environments.

Keywords: Brook trout, demographics, age, growth

Introduction

Introduced fish species pose one of the greatest threats to native salmonid populations in western North America (Penaluna et al. 2016). Introduced fish species can negatively affect native salmonids through a variety of mechanisms, including direct competition, habitat alteration, hybridization, and predation (Dunham et al. 2002, Kanda et al. 2002, Martinez et al. 2009, Kolar et al. 2010). One species often associated with these negative effects is the brook trout (*Salvelinus fontinalis*). The negative influence of brook trout on native salmonids is typically via competition or hybridization (Dunham et al. 2002, Kanda et al. 2002). Moreover, brook trout can be problematic for fisheries managers due to their propensity to produce "stunted" populations that are undesirable to anglers (Donald and Alger 1989, Hall 1991). Consequently, whether to conserve native species or to improve fishing quality, fisheries managers often attempt to suppress or eliminate brook trout populations outside of their native range.

Managers have used a variety of techniques to suppress or eradicate nonnative brook trout populations, including electrofishing (Thompson and Rahel 1996, Meyer et al. 2006), gill netting (Knapp and Matthews 1998, Pacas and Taylor 2015, Hall 1991), piscicides (Gresswell 1991, Buktenica et al. 2013), introducing sterile predators (Koenig et al. 2015, Messner 2017), and altering sex ratios by introducing conspecifics with two Y chromosomes (Kennedy et al. 2018). Prior to the implementation of suppression or eradication programs, managers often construct population models to evaluate the effects of different management strategies on the undesirable population (e.g., Peterson and Evans 2003, Hansen et al. 2008, Klein et al. 2016, Schill et al. 2017). Such models require demographic data such as age, growth, sex ratios, and survival

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for the population of interest (Macenia and Pereira 2007, Power 2007).

While demographic parameter estimates are readily available from brook trout populations in their native range (e.g., Hoover 1939, McFadden 1961, McFadden et al. 1967, Curry et al. 2003, Robillard et al. 2011, Hoxmeier and Dieterman 2016), estimates from western populations often have limitations. Most have been conducted in beaver ponds (e.g., Rabe 1970), or likely underestimated the age of the fish by using scales for aging (e.g., Bishop 1953, McInery 2017). Given the natural variability in demographic parameters between populations, and that small differences in demographic parameters can have a large effect on the results of population models (Power 2007), further collection of demographics data for brook trout populations in the western United States is warranted. Therefore, the specific objective of this study was to produce estimates of population demographic parameters (i.e., growth, recruitment, longevity, sex ratio, survival, and density) for brook trout in Idaho alpine lakes and streams so that more reliable population models can be constructed for western populations of brook trout.

Methods

Study Area

Brook trout were sampled in 12 alpine lakes and 2 streams in Idaho (Table 1). Alpine lakes varied from 1.8 to 15.8 ha in area and from 2,092 to 2,423 m in elevation, and were all located in central Idaho. Streams varied from 2.7 to 5.2 m in average stream width and from 2,146 to 2,377 m in elevation. One stream (Dry Creek) was located in central Idaho, and the other (West Fork Rattlesnake Creek) was located in eastern Idaho.

Field Sampling

Twelve alpine lakes were sampled for brook trout with gill nets over one to two nights between 2015 and 2017. Floating Swedish experimental gill nets (3 to 12 nets; 36-m long and 1.8-m deep) consisting of nylon mesh panels of 10.0-, 12.5-, 18.5-, 25.0-, 33.0-, and 38.0-mm bar mesh were set in the afternoon and fished overnight. Based on lake morphometry, nets were set in locations to maximize catch and were retrieved the subsequent morning in the order in which they were set. All nets were set perpendicular to the shoreline with one end tied to the shoreline of the lake.

Two of the lakes could be accessed by vehicle, and thus multiple gears could be deployed to sample fish, including gill nets, fyke nets (2 to 4 nets; 23-m lead, 0.9 × 1.8-m frame, and 1.9-cm bar mesh), angling (during the day), and boat electrofishing (at night). Gill nets were set as described above. Fyke nets were set in the afternoon and fished overnight. Electrofishing at each lake was conducted by navigating the boat around the entire shoreline of the lake, while sampling all available habitat, from dusk until about 0100. Pulsed direct current (DC) was used for electrofishing, with settings of 60 Hz, 25% duty cycle, and 300 to 400 volts, which produced 7 to 10 amps of peak current. Sampling crews during electrofishing were comprised of one person operating the boat and two people on the bow of the boat netting fish, while others waited on shore to gather data on sampled fish after each pass around the lake. Angling was conducted opportunistically using both artificial lures and flies. During the first day and night of sampling in each lake, all captured brook trout were marked with a lower caudal clip and returned to the lake so that recaptured fish could be used to estimate brook trout abundance in each lake.

Both streams (i.e., Dry Creek and West Fork Rattlesnake Creek) were sampled via backpack electrofishing. In Dry Creek, 6.5 km of stream were sampled during July 2016, and 5.2 km of stream were sampled in West Fork Rattlesnake Creek during July 2017. Such long distances were already being sampled as part of an ongoing research project. On the first day, approximately 10 brook trout (≥ 100 mm) were marked with an upper caudal clip at each 0.5 km, so that on the following days, recaptured fish could be used to estimate abundance and capture efficiency. Electrofishing crews consisted of 2 to 3 people (depending on stream flow), with backpack electrofishers moving upstream in tandem sampling all available habitat, and 1 to 3 people with nets and

TABLE 1. Study waters in which brook trout were sampled to estimate population demographics data throughout Idaho including size, elevation, and location.

Waterbody	Surface area (ha)	Average width (m)	Elevation (m)	Latitude	Longitude
		Lakes			
Anderson	3.6	-	2,227	44.887	–115.931
Black	2.6	-	2,149	45.245	–116.199
Disappointment	6.2	-	2,093	45.183	–116.207
Duck	4.9	-	2,177	45.115	–116.157
Hard Creek	3.4	-	2,262	45.172	–116.145
Lloyds	2.9	-	2,092	45.193	–116.164
Martin Lake	1.8	-	2,107	44.303	–115.264
Rainbow	8.8	-	2,175	45.254	–116.197
Rapid	6.6	-	2,206	44.856	–115.913
Seafoam Lake #4	2.7	-	2,423	44.508	–115.126
Snowslide Lake #1	4.9	-	2,188	44.983	–115.934
Upper Hazard	15.8	-	2,265	45.174	–116.135
		Streams			
Dry Creek	-	5.2	2,377	44.127	–113.568
West Fork Rattlesnake Creek	-	2.7	2,146	44.399	–112.076

buckets (19 L). Pulsed DC was used for backpack electrofishing, with settings of 60 Hz, 25% duty cycle, and 500 to 700 volts, which produced 0.5 to 1.0 amps of peak current. Data collected from captured fish in all lakes and streams included species, total length (TL; mm), the presence of marks, and mesh size when applicable. In the majority of alpine lakes, brook trout were the only species encountered. However, in two lakes, rainbow trout (*Oncorhynchus mykiss*) were also present. In the two streams, Yellowstone cutthroat trout (*O. clarkii bouvieri*) were present but in low numbers. For all waterbodies, species other than brook trout were identified, measured, and released.

Data Analysis

For each lake and stream, sagittal otoliths were removed from up to 10 wild brook trout per 10-mm length bin, preserved dry in 1.5-mL microcentrifuge tubes, and stored indoors away from direct sunlight. Dried whole otoliths were viewed and photographed in immersion oil using reflected light at 25X power using a Leica (Model DC 500) digital camera and a Leica (Model DM 4000B) compound microscope. Using the photographs of each otolith, presumptive annuli were enumerated by two independent readers, unaware of fish length, to determine the age of the fish. When the two readers were not in agreement with regard to the age of a fish, fish length was included for consideration to resolve the discrepancy and determine the consensus age.

Age estimates from otoliths were used to estimate a number of demographic parameters for each population, including growth, survival, longevity, and recruitment. Estimates of growth were calculated by fitting a von Bertalanffy growth function (VBGF; von Bertalanffy 1938) to length-at-capture data for each fish using the formula:

$$L_t = L_\infty\left[1 - e^{-K(t-t_0)}\right]$$

where L_t is the length of brook trout at a given age (t), $L\infty$ is the theoretical maximum average length that the population can achieve, K is the Brody growth coefficient, t is the age, and t_0 is the theoretical age when length equals 0 mm (Quist et al. 2012, Ogle et al. 2017).

To estimate survival, aged fish were grouped into 20-mm length bins and age-length keys were constructed for each waterbody. However, estimates of survival based on age-length keys must be corrected for the selectivity of the sampling

TABLE 2. Model equations for selectivity models used to estimate the relative selectivity of the entire net for brook trout sampled via experimental gill nets throughout Idaho. Values included in parentheses are model constants. Included in model equations is the fish length (1) and the size of the gill net mesh j (m_j).

Model	Selection curve equation [s_j (l)]
Bimodal (k_1, k_2, k_3, k_4, c)	$\exp\left(-\frac{(l - k_1 - m_j)^2}{2k_2^2 \times m_j^2}\right) + c\exp\left(\frac{(l - k_3 - m_j)^2}{2k_4^2 \times m_j^2}\right)$
Log normal (μ,σ)	$\frac{m_j}{1 \times m_1}\exp\left(\mu - \frac{\sigma^2}{2} - \frac{\left(\log(l) - \mu - \log\left(\frac{m_j}{m1}\right)\right)^2}{2\sigma^2}\right)$
Normal location (k_1, σ)	$\exp\left(-\frac{(1 - k_j \times m_j)^2}{2\sigma^2}\right)$
Normal scale (k_1, k_2)	$\exp\left(-\frac{(1 - k_j \times m_j)^2}{2k_2^2 \times m_j^2}\right)$

gear used to collect the fish (Miranda and Colvin 2017). In our study, selectivity corrections to the age-length keys varied by water type and sampling method. For example, age-length keys developed for each alpine lake were corrected by constructing gill net selectivity curves using the SELECT method (Millar and Holst 1997, Millar and Fryer 1999, Shoup and Ryswyk 2016) in statistical package R (R Core Team 2020). One selectivity curve was developed from the combined catch at all the alpine lakes sampled only via gillnet. Selectivity curves were used to estimate the relative selectivity (S_l) of the entire gillnet by fitting brook trout catch data (i.e., fish length and the mesh size in which it was captured) to four log-linear models (i.e., bimodal, log-normal, normal location, and normal scale; Table 2) using a maximum-likelihood approach (Millar and Holst 1997, Shoup and Ryswyk 2016, Klein et al. 2019). For modeling purposes, fish were grouped into 20-mm length bins, catch was assumed to be a Poisson random variable, and effort was assumed to be equal among mesh sizes (Klein et al. 2019). Model fit was evaluated by assessing model deviance, and the model with the smallest estimate of deviance was assumed to be the top model (Millar and Holst 1997, Shoup and Ryswyk 2016, Klein et al. 2019). Using the top model, gill net relative selectivity (S_l) was calculated using the formula:

$$S_l = \Sigma_j\left(\frac{s_j(l)}{max_l}\right)$$

where $s_j(1)$ represents the probability of retention in mesh size j for length bin 1, and max_1 represents the maximum selectivity across all length bins (Shoup and Ryswyk 2016, Klein et al. 2019). Catch data were then corrected by dividing by the raw catch of a given length bin by the S_l for that length bin. Fish < 80 mm were not included in these analyses because we were unable to effectively sample fish of that size with gill nets.

Age-length keys at waterbodies with mark-recapture data, including the two lakes with multiple sampling gears as well as both streams, were corrected using mark-recapture data for each length bin. Capture efficiency was estimated as the number of marked fish caught in the recapture pass in each length bin divided by the total number of marked fish in that length bin. Catch data were then corrected by dividing the raw catch of a given length bin by the capture efficiency for that length bin. Length bins for mark-recapture data were created so that each bin included a minimum of three recaptured fish (Robson and Regier 1964). Using only the gillnet catch of lakes sampled with multiple gears, a second set of corrected age-length keys were created by applying the estimates of S_l from the lakes sampled solely with gillnets to the catch. For lakes sampled with multiple gears, survival estimates derived from each method of correcting age-length keys were compared to evaluate the similarity of the estimates. Due to the low capture efficiency of fish < 80 mm in lakes sampled with multiple gears and fish < 100 mm in streams, these size classes were excluded from the analyses for the respective water type.

For all the corrected age-length keys, the Chapman-Robson estimator and the "peak plus one" criteria were used to estimate the instantaneous mortality rate (Z; Chapman and Robson 1960, Smith et al. 2012). Total annual survival (S) was estimated as $S = e^{-z}$ (Ricker 1975). Based on plots of corrected catch by age, we determined the youngest age class fully recruited to the sampling gears, and prior to estimating Z and S, we removed catch data for age classes not fully recruited. Such plots revealed that in lakes sampled solely with gill nets, age-2 and older fish were fully recruited to the gear, whereas in lakes sampled with multiple gears, and in streams, fish age-1 and older were fully recruited to the gear.

The recruitment coefficient of determination (RCD) was used to estimate recruitment variability for each population (Isermann et al. 2002). The RCD is the coefficient of determination (r^2) resulting from a catch curve style regression model in which log transformed catch at age data is the response variable and age is the explanatory variable (Quist 2007). Populations exhibiting stable recruitment have RCD estimates closer to 1.0 and populations with inconsistent recruitment producing RCD estimates closer to zero.

Abundance was estimated for the two alpine lakes sampled with multiple gears and for both streams using mark-recapture data and the modified Peterson estimator from the FSA package (Ogle 2020) in statistical package R (R Core Team 2020). Separate abundance estimates were made for the smallest size groups possible having at least three recaptured fish per group to satisfy model assumptions (Robson and Regier 1964). Estimates of abundance for each length bin were calculated using the formula:

$$\hat{N} = \frac{(M+1)(n+1)}{(m+1)} - 1$$

where $\hat{N}$ is the population estimate for the given length bin, M is the number of marked fish in the given length bin, *n* is the number of fish captured during the recapture pass in the given length class, and m is the number of recaptured fish in a given length bin.

In all study waters, a random sample of fish ≥ 150 mm were visually observed for the presence of ovaries or testes to determine the sex ratio. Confidence intervals (CIs) on sex ratios were calculated as:

$$p \pm 1.96\sqrt{\frac{pq}{n}}$$

where p is the proportion of male brook trout from the sample, q=1 – p, and *n* is the sample size (Zar 1996).

Results

Lakes

A total of 1,121 brook trout were sampled in alpine lakes (Table 3). An additional 36 brook trout were sampled at Lloyds Lake, which were not included for any analyses (except to estimate gill net selectivity) because otoliths were not collected from these fish. Brook trout in alpine lakes varied in length from 80 to 380 mm (Figure 1, Figure 2), with average length being smallest in Upper Hazard Lake (149 mm) and largest in Seafoam Lake #4 (240 mm; Table 4). Age was estimated for 1,114 brook trout and varied from 1 to 11 yrs. Mean length-at-capture by age class varied from 95 to 181 mm at age 1 (mean = 121 mm), 136 to 206 mm at age 2 (mean = 156 mm), 189 to 280 mm at age 3 (mean = 223 mm), and 210 to 312 mm at age 4 (mean = 257 mm). Based on average length-at-capture data for each age class, $L\infty$ varied from 231 to 490 mm (mean = 345 mm) and K varied from 0.15 to 0.76 (mean = 0.37; Table 5). Estimates of $L\infty$ and K could not be made for Upper Hazard Lake because only one fish was captured in the fourth age class in the lake, which precluded fitting a VBGF to the data.

Evaluation of selectivity models for gill net catch data indicated that the top model was lognormal (Table 6). Gill net relative selectivity averaged 0.84 across size classes, with relative selectivity lowest for the 80-mm length bin (0.49) and highest for the 280-mm length bin (1.00; Table 7 and Figure 3). In lakes sampled with multiple gears, relative selectivity was lowest for brook trout between 80 and 159 mm in Martin Lake and

TABLE 3. Population demographic parameter estimates for various brook trout populations throughout Idaho. Demographic parameters include the instantaneous mortality rate (Z), annual survival (S), and the recruitment coefficient of determination (RCD). Also included is the sample size (*n*). Standard errors are shown in parentheses. For capture methods, BE is backpack electrofishing, CB is a combination of gears (i.e., gill nets, fyke nets, angling, and boat electrofishing), and GN is gillnet.

			Uncorrected			Corrected		
Waterbody	Capture method	*n*	Z	S	RCD	Z	S	RCD
Lakes								
Anderson Lake	GN	102	0.66 (0.17)	0.51 (0.04)	0.72	0.68 (0.17)	0.51 (0.03)	0.75
Black Lake	GN	79	0.75 (0.09)	0.47 (0.04)	0.93	0.78 (0.09)	0.46 (0.04)	0.94
Disappointment Lake	GN	79	0.58 (0.15)	0.56 (0.04)	0.89	0.62 (0.14)	0.54 (0.04)	0.92
Duck Lake	GN	88	0.76 (0.21)	0.46 (0.05)	0.50	0.80 (0.19)	0.44 (0.05)	0.67
Hard Creek Lake	GN	57	0.71 (0.11)	0.49 (0.05)	0.94	0.78 (0.09)	0.46 (0.05)	0.97
Martin Lake	CB	162	0.65 (0.18)	0.52 (0.04)	0.82	0.86 (0.19)	0.42 (0.03)	0.89
Martin Lake	GN	60	0.57 (0.28)	0.56 (0.04)	0.68	0.58 (0.26)	0.56 (0.04)	0.84
Rainbow Lake	GN	89	0.74 (0.04)	0.47 (0.04)	0.99	0.78 (0.03)	0.46 (0.04)	0.99
Rapid Lake	GN	60	0.81 (0.11)	0.44 (0.06)	0.74	0.88 (0.12)	0.41 (0.06)	0.74
Seafoam Lake # 4	CB	136	0.59 (0.14)	0.55 (0.04)	0.84	0.59 (0.14)	0.55 (0.01)	0.83
Seafoam Lake # 4	GN	111	0.55 (0.14)	0.58 (0.03)	0.78	0.60 (0.13)	0.55 (0.03)	0.83
Snowslide Lake #1	GN	64	0.84 (0.23)	0.42 (0.05)	0.60	0.87 (0.22)	0.41 (0.05)	0.66
Upper Hazzard Lake	GN	34	1.07 (0.13)	0.32 (0.10)	0.92	1.14 (0.13)	0.30 (0.09)	0.93
Streams								
Dry Creek	BE	4,011	0.57 (0.11)	0.56 (0.01)	0.89	0.70 (0.05)	0.49 (0.04)	0.97
West Fork Rattlesnake Creek	BE	1,015	0.80 (0.29)	0.45 (0.11)	0.93	0.85 (0.28)	0.43 (0.01)	0.95

270 and 329 mm in Seafoam Lake #4, and highest for brook trout between 250 and 359 mm in Martin Lake and 80 and 269 mm in Seafoam Lake #4 (Table 7). Corrected estimates of S varied between 0.30 (Upper Hazard Lake) and 0.56 (Martin Lake; Table 3). In general, correcting age-length keys for selectivity had little impact on survival estimates (Table 3). However, at Martin Lake, uncorrected and corrected estimates of S were similar when using gill net selectivity to correct the age-length key, whereas when the age-length key was corrected by mark-recapture data from multiple gear types, the corrected estimate of S was much lower than the uncorrected estimate. At Seafoam Lake #4, both corrections to the age-length key resulted in estimates of S similar to the uncorrected estimates.

Recruitment was generally stable among lakes (mean RCD = 0.84), but recruitment variability was highest in Snowslide Lake #1 (RCD = 0.66) and

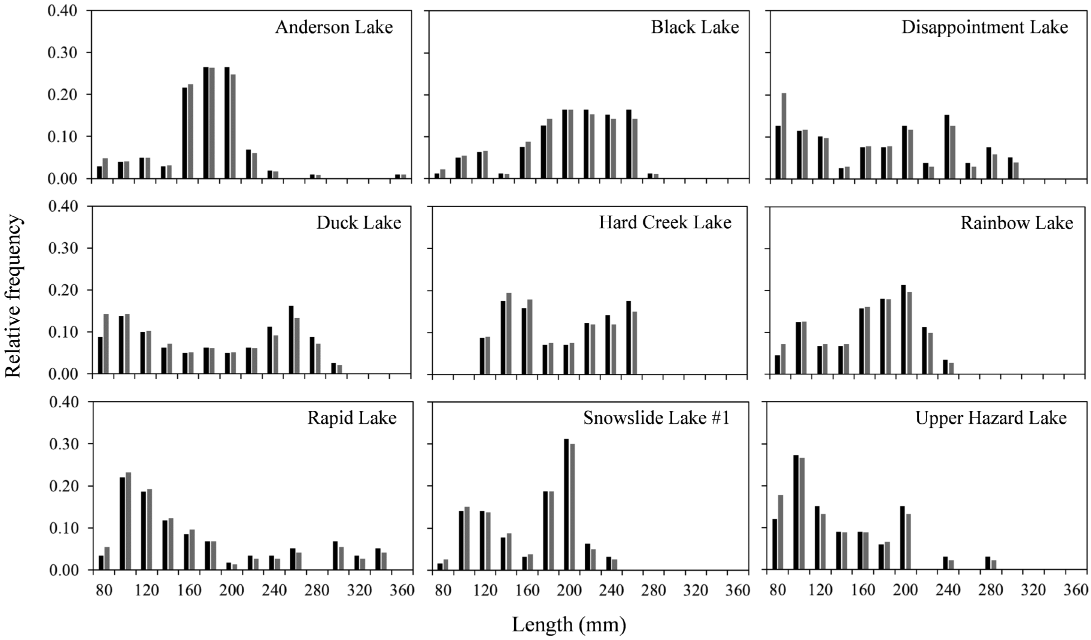

Figure 1. Length frequency distribution of brook trout sampled in various lakes throughout Idaho during 2015 and 2017. Black bars represent uncorrected catch data, and gray bars represent catch data that have been corrected for the size selectivity of the sampling gear.

lowest in Rainbow Lake (0.99; Table 3). Based on mark-recapture data, abundance was estimated to be 528 brook trout ≥ 80 mm (293 ha^{-1}) in Martin Lake and 578 brook trout ≥ 80 mm (214 ha^{-1}) in Seafoam Lake #4.

Sex ratio estimates varied widely, ranging from 34% to 75% male (Table 8). However, CIs around individual estimates overlapped 50% for all but two lakes. Mean sex ratio across all lakes was 53% male.

Streams

During stream sampling, a total of 5,026 brook trout were sampled (Table 3). Length structure of brook trout was larger in Dry Creek (average length = 193 mm; range = 100 to 346 mm) than in West Fork Rattlesnake Creek (average length = 158 mm; range = 100 to 285 mm; Table 4 and Figure 2). Age was estimated for 338 fish and varied between 1 and 6 years in both stream systems (Table 4). Mean length-at-capture by age class varied from 128 to 134 mm at age 1 (mean = 131 mm), 172 to 201 mm at age 2 (mean = 189 mm), 220 to 231 mm at age 3 (mean = 226 mm), and 239 to 267 mm at age 4 (mean = 253 mm), and was consistently larger across all age classes in Dry Creek (Table 4). Evaluation of growth models indicated that $L\infty$ was larger in West Fork Rattlesnake Creek (330 mm) than in Dry Creek (315 mm), but K was larger in Dry Creek (0.46) than in West Fork Rattlesnake Creek (0.28; Table 5).

Size selectivity analysis indicated that selectivity was lowest for brook trout between 100 and 139 mm in Dry Creek and 150 and 159 mm in West Fork Rattlesnake Creek, and highest for brook trout between 280 and 299 mm in Dry Creek and 160 and 169 mm in West Fork Rattlesnake Creek (Table 7). Corrected estimates of S and RCD differed slightly in Dry Creek (i.e., S = 0.49; RCD = 0.97) and West Fork Rattlesnake Creek (i.e., S = 0.43; RCD = 0.95; Table 3). Similar to findings in alpine lakes, corrected estimates of population dynamic parameters for streams were similar to uncorrected estimates (Table 3). Estimated abundance of brook trout was 8,474 fish ≥ 100 mm (25/100 m^2) in Dry Creek and 1,869 fish ≥ 100 mm (13/100 m^2) in the West Fork Rattlesnake Creek. Sex ratio analysis indicated that brook

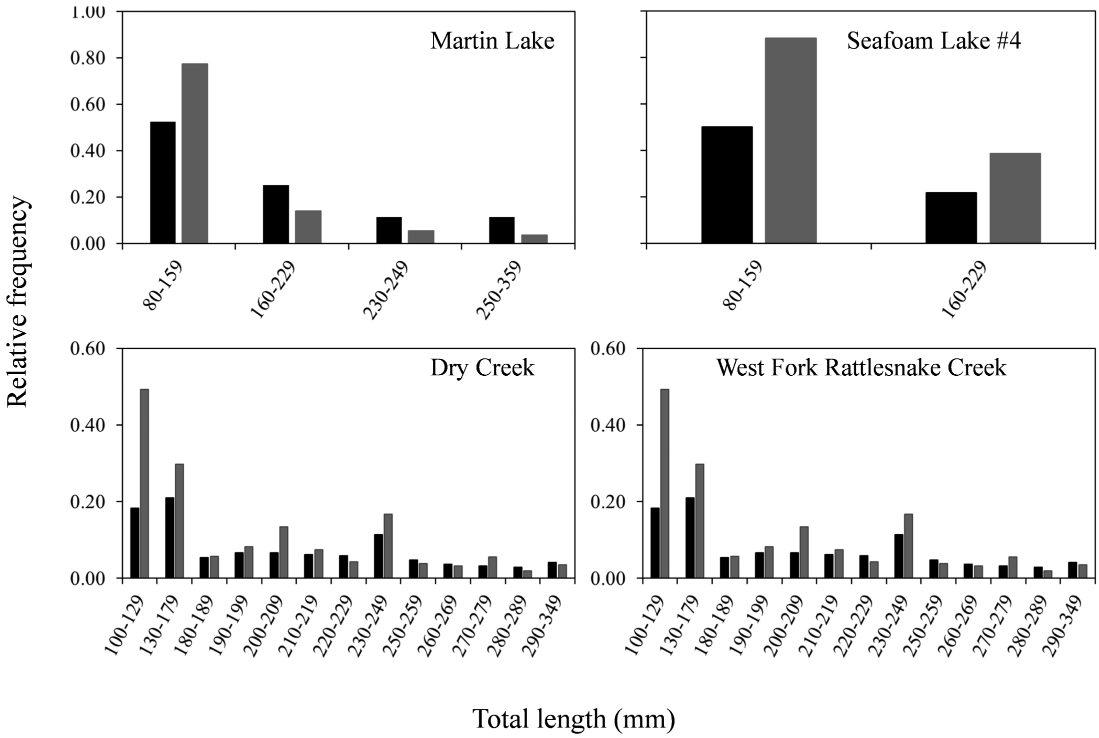

Figure 2. Length frequency distribution of brook trout sampled in two Idaho lakes and two streams during 2016 and 2017. Black bars represent uncorrected catch data, and gray bars represent catch data that have been corrected for the size selectivity of the sampling gear.

trout in Dry Creek were 52% male and in West Fork Rattlesnake Creek were 44% male (Table 8).

Discussion

Our results indicate that nonnative brook trout populations in Idaho exhibit vital rates that are similar to those observed in their native range (e.g., Hoover 1939, McFadden 1961, Curry et al. 2003, Robillard et al. 2011, Hoxmeier and Dieterman 2016). Moreover, vital rates were surprisingly similar between alpine lakes and streams. Of all the vital rate estimates, perhaps most surprising was the similarity in estimates of $L\infty$ and K between the alpine lakes (mean $L\infty$ = 349 mm; mean K = 0.37) and streams (mean $L\infty$ = 323 mm; mean K = 0.37). For other char that occupy both alpine lake and riverine environments, such as bull trout (*Salvelinus confluentus*), growth is typically slower in alpine lakes (Herman 1997, Parker et al. 2007) than in streams (Roth et al. 2021). Brook trout appear to be very plastic phenotypically, and equally adapted to occupy either environment, making them ideal aquatic invaders (Adams et al. 2001, Dunham et al. 2002). However, estimates of $L\infty$ and K differ considerably between eastern (mean $L\infty$ = 441 mm; mean K = 0.23; Table 5) and western populations of brook trout (mean $L\infty$ = 349 mm; mean K = 0.38; Table 5), likely due to the tendency of brook trout populations to become stunted in western waters (Donald and Alger 1989, Hall 1991).

Estimates of S based on catch curves assumes that the catch is representative of the population, and violating that assumption can result in inaccurate estimates of S (Ricker 1975). In the current study, we observed little difference between uncorrected and corrected estimates of S for brook trout in Idaho caught with either gill nets or elec-

TABLE 4. Mean length-at-age (at capture) for brook trout sampled in various waterbodies throughout Idaho. Also included is the sample size (*n*).

		Mean length (mm) at age (SE in parentheses):							
Waterbody	*n*	1	2	3	4	5	6	7	11
Lakes									
Anderson Lake	92	118.0 (9.3)	175.0 (3.7)	193.5 (3.9)	210.2 (4.4)	225.3 (12.4)	-	-	376.0 (-)
Black Lake	78	132.4 (8.8)	205.3 (5.7)	227.5 (7.4)	255.8 (2.9)	252.3 (12.0)	262.0 (-)	-	-
Disappointment Lake	63	95.4 (2.7)	136.1 (6.2)	212.6 (5.5)	257.9 (5.5)	293.7 (10.9)	293.0 (5.0)	319.0 (-)	-
Duck Lake	77	106.8 (3.4)	178.9 (11.7)	249.0 (4.5)	285.8 (6.4)	-	-	-	-
Hard Creek Lake	47	133.3 (5.8)	162.3 (4.3)	227.1 (5.4)	255.3 (4.1)	264.0 (4.5)	-	-	-
Martin Lake	105	119.7 (4.0)	149.3 (3.4)	188.5 (8.8)	237.9 (6.5)	321.0 (19.0)	273.0 (-)	-	-
Rainbow Lake	85	109.7 (3.1)	173.3 (4.2)	200.1 (4.8)	218.6 (4.7)	219.4 (5.7)	246.0 (12.0)	248.0 (-)	-
Rapid Lake	60	115.1 (3.0)	169.7 (7.7)	250.4 (33.5)	311.7 (16.7)	325.3 (8.8)	-	-	-
Seafoam Lake #4	74	180.7 (2.3)	205.7 (8.2)	280.0 (5.8)	287.5 (4.8)	302.5 (2.5)	325.0 (-)	-	-
Snowslide Lake #1	63	111.8 (2.3)	151.9 (5.1)	208.7 (2.4)	220.2 (6.1)	-	-	-	-
Upper Hazard Lake	32	106.9 (2.9)	165.5 (7.8)	214.2 (7.6)	289.0 (-)	-	-	-	-
Streams									
Dry Creek	183	134.0 (3.5)	201.1 (3.8)	230.5 (7.7)	266.8 (5.4)	280.6 (7.6)	293.0 (6.6)	-	-
West Fork Rattlesnake Creek	155	127.7 (3.6)	171.8 (3.0)	219.5 (3.7)	239.4 (6.4)	263.0 (21.0)	280.0 (-)		

trofishing, suggesting that in these populations the catch from either gear type was representative of the population. One exception was at Martin Lake, where the corrected estimate was vastly different for gill net data than for data collected from a combination of gears. The difference in estimates at Martin Lake was likely related to the decrease in sample size at Martin Lake when only using the gill net data. Only 46% of the aged fish in Martin Lake were captured via gill net. In comparison, 89% of the aged fish in Seafoam Lake #4 were captured via gill net. Correcting age-length keys for selectivity had little impact on estimates of S for lakes because gill net capture efficiency varied little among length bins. However, even for the streams where capture efficiency varied substantially by size, S was little affected by accounting for capture efficiency. In some studies, uncorrected and corrected estimates of S have varied substantially, such as for smallmouth bass (*Micropterus dolomieu*), walleye (*Sander vitreus*), and northern pikeminnow (*Ptychocheilus oregonensis*) captured via a combination of gears (Beamesderfer and Rieman 1988), and for arctic char (*Salvelinus alpinus;* Jonsson et al. 2013) and lake trout (*Salvelinus namaycush;* Hansen et al. 1997) sampled with gill nets. Conversely, corrected estimates of S were similar to uncorrected estimates for mountain whitefish (*Prosopium williamsoni*) sampled via electrofishing (Meyer et al. 2009) and alligator gar (*Atractosteus spatula*) sampled via gill net (Schlechte et al. 2016). Regardless of the magnitude of bias in estimates of S, corrected estimates of population demographic parameters

TABLE 5. Comparison of parameter estimates from von Bertalanffy growth function (VBGF) models for various brook trout populations throughout Idaho, including the theoretical maximum average length that the population can achieve (L_∞), and the Brody growth coefficient (K). Studies followed by an * indicate that values from that study are an average. Locations are US state abbreviations, with the exception of Canadian provinces—ON (Ontario) and NL (Newfoundland and Labrador).

Waterbody	Location	Number of populations	$L\infty$ (mm)	K	Reference
		Lakes			
Anderson Lake	ID	1	231	0.60	This study
Black Lake	ID	1	263	0.76	This study
Disappointment Lake	ID	1	375	0.28	This study
Duck Lake	ID	1	398	0.34	This study
Hard Creek Lake	ID	1	349	0.26	This study
Martin Lake	ID	1	475	0.15	This study
Rainbow Lake	ID	1	251	0.49	This study
Rapid Lake	ID	1	490	0.23	This study
Seafoam Lake #4	ID	1	367	0.30	This study
Snowslide Lake #1	ID	1	293	0.33	This study
Convict Creek Basin Lakes	CA	8	217	0.62	Hall 1991*
Boreal Lakes	NL	17	368	0.44	van Zyll de Jong et al. 2018*
Owhi Lake	WA	1	510	0.31	Taylor et al. 2020*
		Streams			
Dry Creek	ID	1	315	0.46	This study
West Fork Rattlesnake Creek	ID	1	330	0.28	This study
Cold Brook	NH	1	616	0.05	Hoover 1939
Lake Superior tributaries	ON	8	550	0.05	Robillard et al. 2011*
Lawrence Creek	WI	1	373	0.38	Mcfadden 1961
Milk River Drainage Creeks	MT	2	375	0.24	Domrose 1960*
Pennsylvania streams	PA	7	429	0.11	Wydoski 1966*
Pigeon River	MI	1	310	0.34	Cooper 1952

TABLE 6. Estimates of model parameters, residual deviance, and degrees of freedom (df) from selectivity models estimated using the total length of brook trout sampled via experimental gill nets in lakes throughout central Idaho (2015 to 2016). See Table 2 for a description of the specific parameters included in each model. A dash (-) indicates that the given model did not estimate that parameter.

Model	Parameter 1	Parameter 2	Parameter 3	Parameter 4	Parameter 5	Deviance	df
Log-normal	92.19	26.79	-	-	-	300.21	73
Normal location	88.82	50.87	-	-	-	412.98	73
Normal scale	102.30	26.09	-	-	-	431.91	73
Bimodal	102.31	26.09	7.24	–2.47	0.99	431.92	70

should be used whenever possible because, as mentioned above, even small changes to demographic parameters can have substantial impacts on population models (Power 2007).

Based on estimates of RCD, recruitment was stable in all brook trout populations in the current study. Although this is the first study to formally estimate RCD for brook trout populations, the data necessary to calculate RCD can be found in numerous brook trout studies (e.g., Domrose 1960, Warner 1970, Frenette and Dodson 1984, Toetz et al. 1991). Such data indicate that stable recruitment was also common in other introduced brook trout populations (e.g., Domrose 1960, RCD = 0.95, Toetz et al. 1991, RCD = 0.97) as well as native populations (e.g., Warner 1970,

TABLE 7. Overall selectivity (S_1) by length bin for brook trout sampled via experimental gill nets (mesh panels of 10.0-, 12.5-, 18.5-, 25.0-, 33.0-, and 38.0-mm bar mesh) in various lakes throughout Idaho (2015 to 2016). Also included is overall selectivity by length bin for brook trout sampled via experimental gill nets, fyke nets, angling, and boat electrofishing in Martin Lake and Seafoam Lake (2017), and brook trout sampled via backpack electrofishing in Dry Creek and West Fork Rattlesnake Creek, Idaho (2016 to 2017).

Length bin (mm)	(S_1)
Alpine Lakes	
80–99	0.49
100–119	0.76
120–139	0.79
140–159	0.76
160–179	0.76
180–199	0.80
200–219	0.85
220–239	0.90
240–259	0.95
260–279	0.99
280–299	1.00
300–319	0.99
320–339	0.95
340–359	0.88
360–379	0.80
Martin Lake	
80–159	0.14
160–229	0.36
230–249	0.44
250–359	0.67
Seafoam Lake #4	
80–269	0.12
270–329	0.11
Dry Creek	
100–139	0.25
140–179	0.47
180–189	0.64
190–199	0.55
200–209	0.33
210–219	0.56
220–229	0.93
230–249	0.46
250–259	0.85
260–269	0.78
270–279	0.38
280–289	1.00
290–349	0.78
West Fork Rattlesnake Creek	
100–119	0.40
120–149	0.55
150–159	0.24
160–169	0.90
170–179	0.89
180–189	0.46
190–209	0.67
210–219	0.75
220–289	0.50

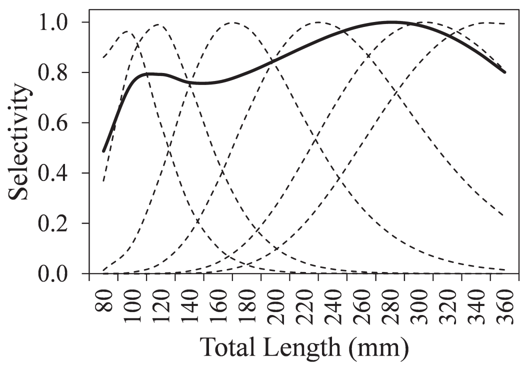

Figure 3. Selectivity curves by 20-mm length bins for brook trout sampled using experimental gill nets throughout Idaho during 2015 and 2016. The solid line represents the overall selectivity of the entire gill net and the dotted lines represent the selectivity of each mesh size (10.0-, 12.5-, 18.5-, 25.0-, 33.0-, and 38.0-mm bar mesh, from left to right).

RCD = 0.95, Frenette and Dodson 1984, RCD = 0.87). In the current study, the similar stability in recruitment between streams (mean RCD = 0.96) and lakes (mean RCD = 0.84) is surprising given that environmental conditions are typically more variable during spawning and over winter in streams than in lakes. For example, stream flows can be highly variable across years during fall spawning and over winter, while winter icing impacts (i.e., frazil ice, or shelf ice collapse) also exhibit interannual variation in streams (Brown et al. 2011), whereas alpine lakes generally do not experience any of these effects. However, the similarity we observed in RCD between streams and lakes could be due in part to the fact that estimates of RCD can be biased, for various reasons (e.g., sampling methodology or mortality varying among age classes; Quist 2007). Additionally, the estimates of RCD in streams could be further biased due to the low sample size of streams (n = 2) in the current study.

Results of this study provide estimates of vital rates for stream and alpine lake populations of brook trout in western North America that have heretofore been sparse outside their native range. Moreover, it is the first study to report gill net size selectivity curves for brook trout. While vital rates in Idaho were highly variable among populations,

TABLE 8. Comparison of sex ratios for various brook trout populations throughout Idaho. For waterbodies, WF is West Fork. Also included are the sample size (*n*), and 95% confidence intervals (95% CI).

Waterbody	*n*	% male	95% CI
Lakes			
Anderson Lake	56	33.9	21.5 – 46.3
Black Lake	70	55.7	44.1 – 67.3
Disappointment Lake	59	59.3	46.8 – 71.8
Duck Lake	50	62.0	48.5 – 75.5
Hard Creek Lake	46	50.0	35.6 – 64.4
Martin Lake	73	50.6	39.1 – 62.1
Rainbow Lake	71	49.3	37.7 – 60.9
Rapid Lake	29	58.6	40.7 – 76.5
Seafoam Lake # 4	52	57.7	44.3 – 71.1
Snowslide Lake #1	42	45.2	30.1 – 60.3
Upper Hazzard Lake	12	75.0	50.5 – 99.5
Streams			
Dry Creek	204	51.5	44.6 – 58.4
West Fork Rattlesnake Creek	202	43.6	36.8 – 50.4

they were generally similar to the ranges observed in their native distribution. Considering the threat that brook trout often pose to native salmonids in western North America, and the variability observed in vital rates across their distribution, reliable demographics data are important to inform and predict outcomes of management strategies to suppress or eradicate brook trout populations. For example, Schill et al. (2017) was forced to use brook trout demographics data from a Midwestern stream (i.e., McFadden 1961) when modeling the effects of various brook trout eradication strategies for Rocky Mountain streams because such information for western populations were lacking. Based on available information, Schill et al. (2017) assumed that brook trout survival was substantially lower in streams than in alpine lakes in western waters, whereas our results suggest their survival is similar between such environments. Given the effect that even small changes to demographics data can have on population models (Power 2007), more accurate assumptions on population vital rates (when site-specific information is lacking) would result in more reliable model output, ultimately improving management strategies directed at controlling undesirable nonnative fish populations.

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