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[Article]

Quantification of the Vital Rates, Abundance, and Status of a Critical, Endemic Population of Bonneville Cutthroat Trout

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Abstract.—Most subspecies of cutthroat trout *Oncorhynchus clarkii* are imperiled or extinct due to the combined effects of habitat degradation and interactions with exotic species. To quantify abundance and vital rates and evaluate trends, we selected a large population of Bonneville cutthroat trout *O. clarkii utah* from the Logan River of northern Utah, a river characterized by high-quality and connected habitat. Over a 5-year period, we completed a comprehensive population assessment, including depletion-based abundance estimates and a mark–recapture study (1,050 tagged fish) of site fidelity, growth, and survival. Population density exceeded 1,500 cutthroat trout/km at high-elevation sites; this is substantially higher than most other reported densities of inland, stream-type cutthroat trout. Fish demonstrated extremely high rates of site fidelity on average (92%; SE = 6%), and growth rates were also high (up to 0.50 g/d; mean = 0.09 g/d). Cormack–Jolly–Seber survival rates (fish $\geq$ 100 mm) increased with age-class (group effect) and condition (individual covariate) and ranged from over 64% at high-elevation sites to approximately 30% at lower-elevation sites. Population growth rates (λ) appeared to be declining overall; however, 95% confidence intervals of λ frequently overlapped 1.0, indicating high variability that limited conclusions about future status. Both survival rate and fish density were consistently lower at sites where Bonneville cutthroat trout were sympatric with exotic brown trout *Salmo trutta*. The continuity, connectedness, and large size of this habitat fragment of the Logan River have clearly contributed to the persistence of this population. Our results provide important conservation and recovery benchmarks for identifying rangewide limiting factors of cutthroat trout. We recommend a precautionary approach to management of this endemic and important population; potential options include habitat protection or restoration and the removal of exotic brown trout.

Populations of native cutthroat trout *Oncorhynchus clarkii* were once distributed from the Columbia River to the Missouri River, across the Great Basin, and in southern parts of the northern Rocky Mountains. These populations have since declined or been extirpated from much of their historical range because of the combined effects of habitat fragmentation and degradation, disease, and hybridization and competition with nonnative salmonids (Behnke 1992; Dunham et al. 2002; Quist and Hubert 2004). Our understanding of the relative influence of these different threats in the overall decline, however, is limited by the overall paucity of even the most basic population and demographic data (e.g., Hilderbrand 2002) and in some cases by difficulties associated with studying small, fragmented populations (e.g., Novinger and Rahel 2003). In addition, when one or more of four demographic parameters (recruitment, survival or mortality, immigration, and emigration) is limiting, the cause of an observed change in abundance or distribution can be difficult to identify without long-term and exhaustive population and demographic data (e.g., Gowan and Fausch 1996; Ham and Pearsons 2000; Peterson et al. 2004). Nevertheless, identification and prioritization of conservation and management actions depend on accurate and precise population assessment (e.g., abundance and trend) and an ability to identify limiting factors and life stages (Williams et al. 2001; Morris and Doak 2002). Further, there is a need to proactively evaluate management options for populations that still have an opportunity for conservation (Allendorf et al. 1997; Hilderbrand 2002).

Despite the importance of accurate and precise population assessment, the estimation of intraannual and interannual population abundance and the quantification of key demographic factors (e.g., survival) are time consuming and often expensive (e.g., Hankin and Reeves 1988; Lebreton et al. 1992; Al-Chockhachy et al., in review). In addition, population assessment and trend analyses can be further limited by natural variability in fish distribution and abundance (Fausch et al. 2002; Young and Guenther-Gloss 2004), spatial and temporal variability in fish behavior (Zabel et al. 2005), and for many trout species, variable and large-scale fish movement (e.g., Hilderbrand and Kershner 2000a; Fausch et al. 2002; Colyer et al. 2005). Differences in fish behavior, whether natural or in response to sample methodology (e.g., Nordwall

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1999), can affect capture probability differentially among individuals or groups and thus can bias abundance and survival estimates (MacKenzie and Kendall 2002; Zabel et al. 2005). Movement, in the form of immigration or emigration, can also result in changes in abundance that can then be mistakenly attributed to changes in recruitment or survival (Gowan and Fausch 1996; Williams et al. 2001). Resulting estimates of apparent survival are often biased (typically low) because of emigration and low capture probability. This bias can be lessened, in part, with the use of individually marked animals and open-population maximum likelihood techniques (Fausch and Young 1995; Williams et al. 2001). These complexities point to the need for comprehensive and long-term population assessment studies, which include the ability to estimate key demographic parameters (e.g., growth, survival) for at least a subset of populations within the species or subspecies at risk.

The Bonneville cutthroat trout *Oncorhynchus clarkii utah*, endemic to the Bonneville River basin of Utah, Idaho, and Nevada, is currently protected under a multiagency conservation agreement (Hepworth et al. 1997; Lentsch et al. 1997). Bonneville cutthroat trout are threatened by the presence of exotic species, the negative effects of hybridization with rainbow trout *O. mykiss* (Weigel et al. 2003), and competition and predation with brook trout *Salvelinus fontinalis* (Griffith 1988; De Staso and Rahel 1994; Novinger 2000). Recently, potential for asymmetric competition with widely distributed brown trout *Salmo trutta* has also been demonstrated (McHugh and Budy 2005, 2006). The parasite that causes whirling disease, *Myxobolus cerebralis*, was first detected in Utah in 1991 and has since spread throughout the state; however, for Bonneville cutthroat trout, the effects of this parasite at the population level remain unknown (i.e., population declines have not been directly attributed to the effects of the parasite; Bartholomew and Reno 2002; de la Hoz Franco and Budy 2004). Habitat degradation and fragmentation has been widespread across the Bonneville cutthroat trout's range due to water diversion, overgrazing, and impoundments (e.g., Binns and Remmick 1994; Colyer et al. 2005). Like many subspecies of cutthroat trout, fluvial Bonneville cutthroat trout demonstrate the potential for long, seasonal migrations to and from spawning grounds; these movements have been restricted in many cases due to habitat alteration and fragmentation (Kershner et al. 1997; Colyer et al. 2005), thereby threatening their persistence. These factors likewise threaten many other cutthroat trout subspecies across western North America (Duff 1988; Kershner et al. 1997). Bonneville cutthroat trout now occupy only 33% of their historical range, but population size, population trends, and viability remain generally unknown.

We selected a population of Bonneville cutthroat trout in the Logan River of northern Utah for quantification of abundance and vital rates, evaluation of trends, and identification of limiting factors that ultimately would aid in developing rangewide conservation and management strategies for this imperiled species. We chose this population based on its suspected large size and wide distribution, which allow for robust estimation of population statistics and vital rates, and because this population experiences threats common to native cutthroat trout across their historical range. To address the different factors that potentially threaten Bonneville cutthroat trout, our objectives were to (1) estimate distribution and abundance based on the long-term sites identified, (2) quantify survival, growth, and site fidelity and understand how those vital rates vary temporally and spatially, and (3) evaluate the population's relative status and trend. Our ultimate goal was to provide the necessary information to guide conservation and management of this unique population, as well as other populations of inland, stream-type cutthroat trout.

Methods

Overview of approach.—We initiated a large-scale, 5-year population assessment for Bonneville cutthroat trout in the Logan River in 2001; this effort included sampling fish at eight long-term index sites, encompassing more than 50 river kilometers (rkm). We also initiated a mark–recapture study in 2002 and tagged fish from 2002 to 2005. We used the combination of these methods to estimate distribution, abundance, site fidelity, growth, survival, and population trend for Bonneville cutthroat trout.

Study area.—The headwaters of the Logan River (2,600-m elevation) are located in the southeastern corner of Idaho in the Bear River Mountain Range (Figure 1), and the river runs into Utah and 64 rkm through Logan Canyon, ultimately draining into the terminal Great Salt Lake (Thoreson 1949). The climate ranges from cold snowy winters to hot, dry summers; the hydrograph is dominated by spring snowmelt floods (15.7 m^3/s) and base flow conditions of approximately 2.8 m^3/s. Average summer stream temperatures range from 9.2°C (high-elevation headwaters) to 12.1°C (midelevation main stem), and summer diel fluctuations are up to 9°C. Resident fish include endemic Bonneville cutthroat trout, brown trout, stocked rainbow trout, brook trout, mountain whitefish *Prosopium williamsoni*, and mottled sculpin *Cottus bairdii*. Logan River Bonneville cutthroat trout

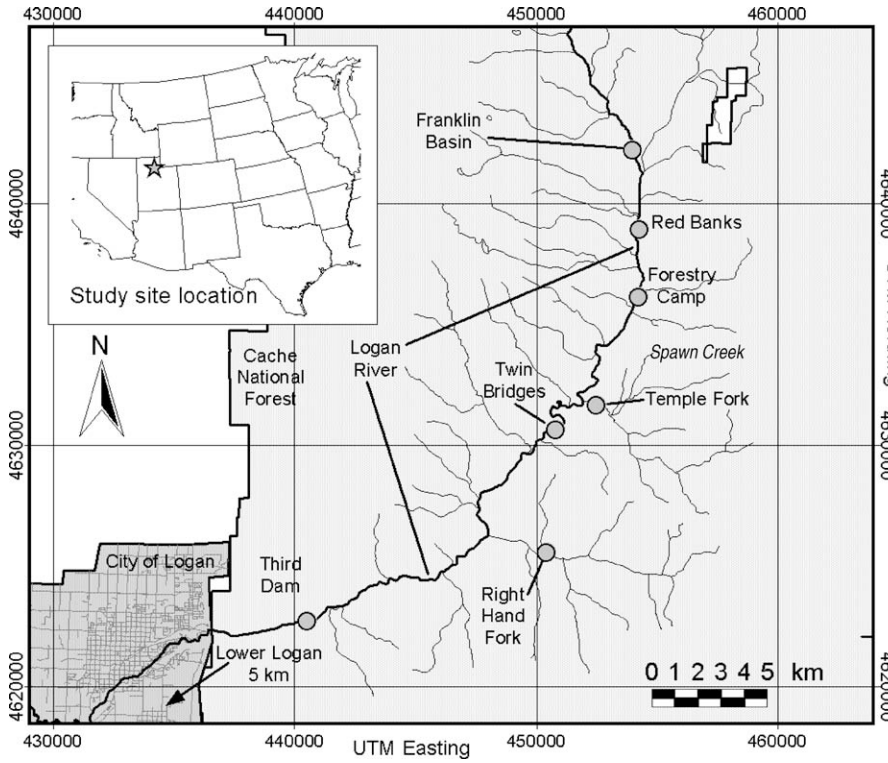

FIGURE 1.—Map of the Logan River drainage in northern Utah, where a unique population of Bonneville cutthroat trout was studied. Long-term index sites are labeled and marked with shaded circles.

spawn in tributaries in the spring (Bernard and Israelsen 1982).

Overall, the habitat quality is high, connectedness is intact, and anthropogenic effects are limited. However, some areas of the headwater and tributary areas are degraded, largely due to cattle grazing, and the lowermost section of the river is altered by three small impoundments and issues (channelization, run-off) associated with the city of Logan. First detected in the Logan River in 1999, *Myxobolus cerebralis* is now prevalent throughout the drainage at relatively high rates (de la Hoz Franco and Budy 2004; Budy et al. 2005). Although nonnative brown trout were introduced in the 1800s, Bonneville cutthroat trout and brown trout are allopatric within the system (de la Hoz Franco and Budy 2005; McHugh and Budy 2005). Angling pressure is moderate, and most angling (97%) is voluntary catch and release (Budy et al. 2003).

Sites.—The eight sites we selected for long-term study were distributed along the longitudinal gradient of the river and ranged in elevation and reach length as a function of size: (1) Franklin Basin (elevation = 2,023 m; 100-m reach), (2) Red Banks (elevation = 1,923 m; 200-m reach), (3) Forestry Camp (elevation = 1,855 m; 200-m reach), (4) Temple Fork (a tributary; elevation = 1,745 m; 100-m reach), (5) Twin Bridges (elevation = 1,691 m; 200-m reach), (6) Right Hand Fork (a tributary; elevation = 1,588 m; 100-m reach), (7) Third Dam (elevation = 1,509 m; 200-m reach), and (8) Lower Logan (elevation = 1,352 m; 200-m reach). In this system, Bonneville cutthroat trout are not limited in distribution by physiological restraints (e.g., water temperatures are suitable to optimal throughout the river); abiotic and biotic site characteristics are described in detail by de la Hoz Franco and Budy (2005) and McHugh and Budy (2005).

Fish sampling.—We sampled fish annually during base flows between late July and early August 2001–2005 and used a combination of electroshocking and mark–recapture techniques. For electroshocking surveys, crews placed block nets at the lower and upper end of each stream section. For smaller streams, we used a backpack-mounted electroshocking unit; for the larger main-stem surveys, we used a canoe-mounted electroshocking unit. Using size-frequency modes, a subsample of our scale-aged fish, data from a comprehensive size-at-age study of Logan River cutthroat trout (n = 306 fish; Fleener 1951), and our

TABLE 1.—The top-20 (most parsimonious) models of Cormack–Jolly–Seber survival (ϕ) for Logan River Bonneville cutthroat trout, based on program MARK output and information theoretic selection criteria. Site, time, and age were modeled as additive group effects; condition (cond) was an individual covariate (NP = number of parameters; AIC_c = corrected Akaike's information criterion; (.) = constant parameter).

Model	AIC_c	ΔAIC_c	AIC_c weight	Model likelihood	NP	Deviance
ϕ (cond, site, age), *p* (site, time)	1,574.29	0	0.37217	1	18	1,537.66
ϕ (time, cond, site, age), *p* (site, time)	1,574.61	0.32	0.31772	0.8537	21	1,531.75
ϕ (time, cond, site), *p* (site, time)	1,575.75	1.46	0.17969	0.4828	19	1,537.04
ϕ (site), *p* (site, time)	1,578.24	3.95	0.05161	0.1387	16	1,545.74
ϕ (site, age), *p* (site, time)	1,578.73	4.432	0.04058	0.109	19	1,540.02
ϕ (cond, site), *p* (site, time)	1,579.51	5.213	0.02746	0.0738	17	1,544.94
ϕ (cond, age), *p* (site, time)	1,583.71	9.41	0.00337	0.0091	13	1,557.37
ϕ (time, cond), *p* (site, time)	1,583.71	9.42	0.00336	0.009	13	1,557.37
ϕ (time), *p* (site, time)	1,584.64	10.34	0.00211	0.0057	13	1,558.30
ϕ (.), *p* (site, time)	1,585.82	11.53	0.00117	0.0031	11	1,563.58
ϕ (age), *p* (site, time)	1,588.21	13.92	0.00035	0.0009	14	1,559.82
ϕ (.), *p* (site, age, time)	1,588.98	14.68	0.00024	0.0006	14	1,560.59
ϕ (.), *p* (site, time), INT1diff[a]	1,589.92	15.62	0.00015	0.0004	13	1,563.58
Global (no cond)	1,595.09	20.80	0.00001	0	84	1,412.93
ϕ (.), *p* (time)	1,632.39	58.10	0	0	6	1,620.31
ϕ (.), *p* (age, time)	1,637.44	63.15	0	0	9	1,619.28
ϕ (.), *p* (site)	1,696.33	122.03	0	0	7	1,682.22
ϕ (.), *p* (site, age)	1,699.48	125.18	0	0	9	1,681.31
ϕ (.), *p* (.)	1,757.60	183.31	0	0	2	1,753.59
ϕ (.), *p* (age)	1,760.77	186.48	0	0	4	1,752.73

[a] INT1diff = estimates different recapture probabilities for each interval.

annual growth measurements from tagged fish, we grouped Bonneville cutthroat trout into three age-classes based on total length (TL): 100–149-mm fish were classified as age 1, 150–224-mm fish were classified as age 2, and 225-mm and larger fish were classified as age 3+. Because fish smaller than 100 mm are inefficiently captured by electrofishing in this river system, we only used fish 100 mm or longer. We marked Bonneville cutthroat trout (≥100 mm) at each site with color-coded, site-specific T-bar anchor tags each year (starting in 2002).

Population abundance and distribution.—We estimated population abundance using a three-pass, closed-model, generalized maximum likelihood removal estimator (White and Burnham 1999) for all fish at each site. We scaled up abundance to determine the total number of Bonneville cutthroat trout per linear kilometer and calculated 95% confidence intervals (CIs) for these estimates. For purposes of comparison, we also summarized available Bonneville cutthroat trout density data from other populations.

Site fidelity and growth.—From the total number of tagged fish that were recaptured by electroshocking or angling (i.e., telephone returns) at a given site, we quantified site fidelity as the percentage of fish that had originally been tagged at the site of recapture. Site fidelity was calculated on an annual basis (i.e., where the interval between tagging and recapture was 1 year). We also documented long-range movement (>0.5 km) of fish recaptured at sites other than the original site of tagging. We used measurements of weight and length for individually tagged and recaptured fish to estimate annual growth rate (change in size divided by the number of days between the two measures of size; g/d) for each age-class, site, and year.

Survival.—Based on our tagging data, we calculated Cormack–Jolly–Seber (CJS) survival rates from individual encounter histories for all tagged fish. We estimated survival (ϕ) and recapture probability (p_s) using a CJS model based on maximum likelihood estimation procedures in program MARK (White and Burnham 1999). We excluded known unnatural mortalities (sampling) and fish that emigrated and grouped Bonneville cutthroat trout by site and age-group at initial capture. Based on age and growth data, we developed a stage-structured survival modeling framework whereby age-1 and age-2 fish grew (moved) into the next stage each time iteration (1 year), and fish in the last age-group remained in that group. We included fish condition at the time of tagging as an individual covariate in the model analysis, where condition was calculated as Fulton's condition factor *K*. We considered a set of a priori candidate models based on biological hypotheses of factors affecting survival and ranked models according to Akaike's information criteria (AIC; Table 1; Burnham and Anderson 2002). We first estimated the best model for p_s by varying the recapture structure (i.e., the global parameter index matrix and then eight reduced versions with a constant survival structure [*S*(.)]) and combinations of group effects on p_s for fish age, site, and time (year; Franklin et al. 2004). Using

the best p_s model, we then fit the remaining models allowing survival to vary as a function of all combinations of group (age, site, and time) effects and Fulton's K as an individual covariate.

Trend.—We estimated population trend based on population estimates from our 5 years of depletion sampling (2001–2005), via linear regression of log-transformed annual changes in population growth rate (λ) as a function of time step (Morris and Doak 2002). Values of λ are reported here with 95% CIs. We also calculated an overall λ for the entire Logan River population based on pooled abundance estimates across sites. A λ-value greater than 1 indicates positive population trend, a value equal to 1 indicates no change in population growth rate, and a value less than 1 indicates that the population is declining. However, given the short time series available, we cannot completely rule out a population increase or decrease in cases when the 95% CIs overlap 1.0. In our analyses, fish losses due to sampling for parasite and diet analyses (de la Hoz Franco and Budy 2004, 2005) and due to sampling-related mortality (i.e., electroshocking or other stressors) were accounted for such that final λ-values represented the observed trend at each site in the absence of these minor fish losses.

Results

Population Distribution and Abundance

Population abundance of Bonneville cutthroat trout was highest at upper-elevation sites (>1,850 m) and lowest at mid-elevation sites (<1,750 m) that contained brown trout. Bonneville cutthroat trout were absent from two sites containing brown trout (Right Hand Fork and Lower Logan) and occupied six sites in allopatry (Figure 2). Density of Bonneville cutthroat trout was as high as 2,051 fish/km (95% CI = 2,021–2,092) at Red Banks in 2002 and was lowest at Third Dam in 2001, which had the lowermost elevation (1,509 m) and distribution of Bonneville cutthroat trout (density = 53 fish/km; 95% CI = 51–66). Depletion-based capture probabilities (p_N) were quite high at all sites: highest at Twin Bridges (0.685; SE = 0.039) and lowest at Temple Fork (0.563; SE = 0.057), where we experienced chronic sampling problems associated with the activities of beavers *Castor canadensis*. Over the course of the study, 1,054 Bonneville cutthroat trout were tagged and 315 were recaptured; percentage of recaptured fish was as high as 58% (Red Banks site).

Site Fidelity and Growth

Site fidelity was consistently high both across years and sites; average fidelity was 92% (SE = 6%) and as high as 100% (Figure 3). In addition, 49 fish were recaptured twice at their initial tagging sites, and 14 fish were recaptured three times at their initial tagging sites. Only 10 tagged fish were recaptured at locations other than their original tagging sites, and they had moved from 0.63 to 34 km (mean = 8.4 km). The longest distance moved (34 km) was by a fish moving downstream; this individual was tagged on 8 August 2005 at Franklin Basin and recaptured on 26 October 2005 at Third Dam.

Overall, growth of tagged Bonneville cutthroat trout was relatively high but varied differentially by age-group and site (Figure 4). Average growth rates were greatest for age-1 fish and lowest for age-3+ fish at upper-elevation sites. When averaged across sites, growth rates were greatest for age-1 fish (but sample size was low) and were lowest for age-3+ fish. The smallest fish tagged was 118 mm (August 2002); that fish, which was subsequently recaptured each year (2003–2005), ultimately reached 228 mm (279 g).

Survival

We used 1,054 marked fish (≥100 mm) in our analysis of survival (N) and show the results from the top-20 models (Table 1). The recapture probability model ($p_s\{N[.]\}$) exhibiting the lowest change in corrected AIC (ΔAIC_c) included additive site and time group effects. We used this recapture (p_s) framework for all subsequent models used to estimate survival. The top-ranking model based on ΔAIC_c included additive group effects of site and age-class on survival and included condition as an individual covariate. However, the top-three models were within two ΔAIC_c units of one another and together accounted for 87% of the Akaike weights. As such, the three top models explained a large portion of the variation (number of parameters = 18–21), and all three models were plausible. In addition, recapture probabilities were generally high (overall average $p_s = 0.46$ for the top model), and 95% CIs for survival parameters never overlapped zero for any of the top-three models.

For our assessment, we used survival estimates from the second-best model ($N_{\text{time,cond,site,age}}$, $p_{\text{site,time}}$), because this model provided estimates of average survival rate across sites and time and was as plausible as the first model. Based on our selected model, survival estimates were consistently highest at the three uppermost-elevation sites (high of 77.2% at Red Banks; Figure 5) and consistently lowest at the mid- and low-elevation main-stem sites and Temple Fork (low of 33.7% at Twin Bridges). In addition, overall (across sites) survival consistently increased with age-group; the largest fish demonstrated an average annual

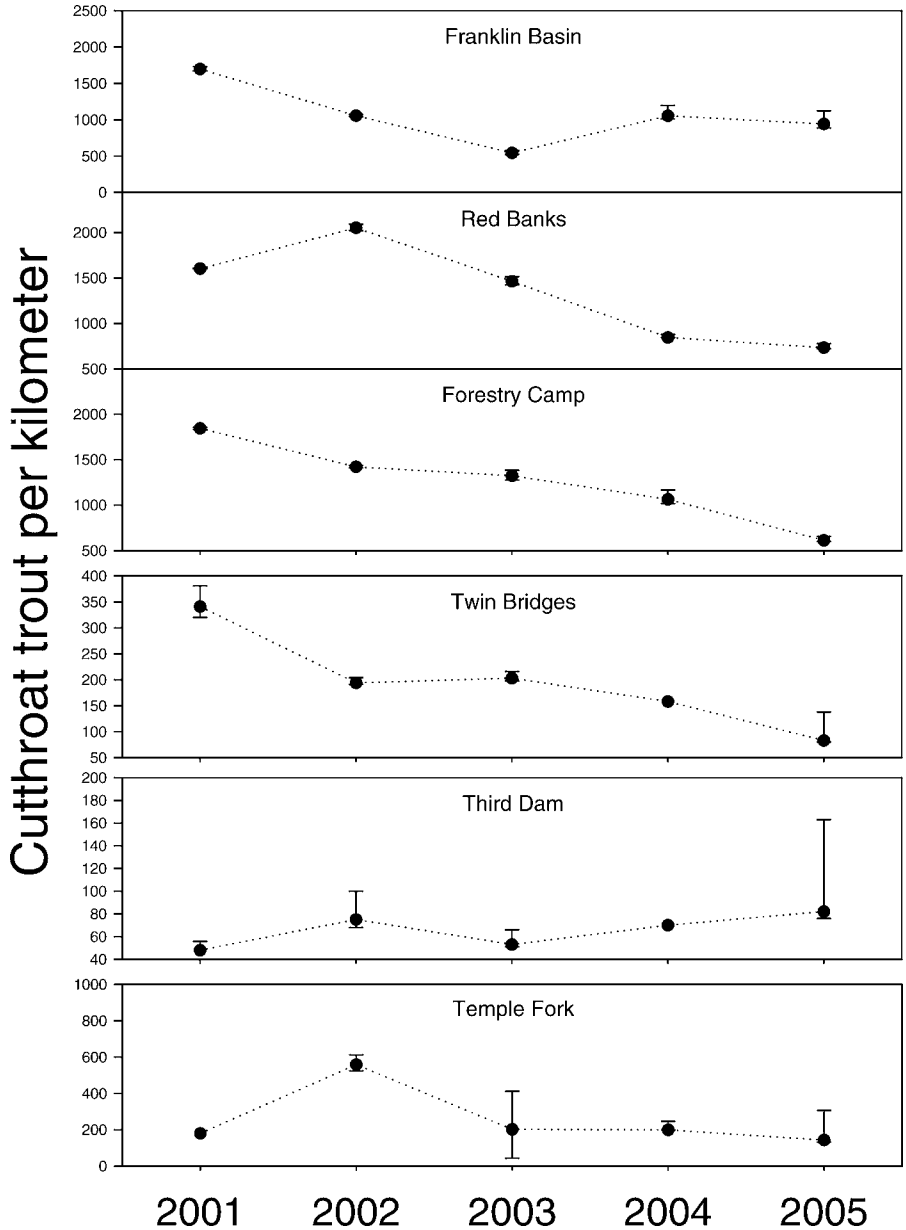

FIGURE 2.—Population abundance estimates (fish/km; ±95% CI) for Bonneville cutthroat trout at six sites on the Logan River, Utah, based on the maximum likelihood removal method in Program MARK. Note the large changes in *y*-axis scales.

survival rate of 54% (SE = 8%), whereas small fish had a 41% average survival rate (SE = 10%; Figure 6).

We also observed a strong relationship between increasing survival and individual fish condition (Fulton's *K*; Figure 7):

$$\text{logit}(\phi) = -0.609 + \left(0.106 \times \frac{\text{cond} - \text{cond}_{\text{avg}}}{\text{SD}}\right)$$

where cond is Fulton's *K*, cond_{avg} and SD_{cond} are the respective standardized average condition and standard deviation values from the CJS MARK model, and logit(ϕ) is transformed back to survival as $N = e^{\text{logit}(N)}/[1 + e^{\text{logit}(N)}]$. This relationship was nearly linear over the range of condition values we observed (maximum $K = 6.5$), but it necessarily plateaus at a theoretical maximum survival of 1.0.

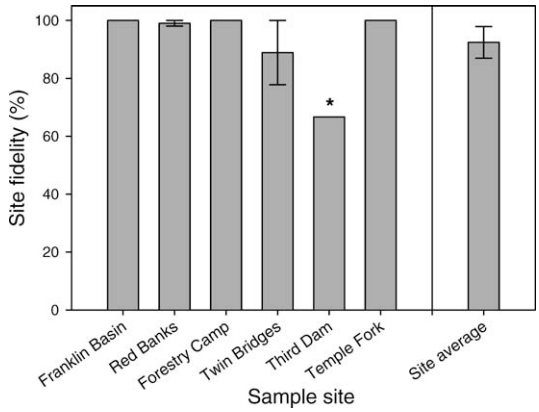

FIGURE 3.—Side fidelity (3-year average; ±SE) expressed as the percentage of tagged, recaptured Bonneville cutthroat trout that had originally been tagged at the site of recapture in the Logan River, Utah. The rightmost bar indicates the composite average across all sites; asterisk indicates that data were available from only 1 year (i.e., no variance). For Franklin Basin, Twin Bridges, and Temple Fork, SE = 0.

Trend

Population growth rates of Bonneville cutthroat trout demonstrated an increasing trend at the Third Dam site, and stable λ-values were estimated at two sites, Franklin Basin (headwater site) and Temple Fork (tributary site; Table 2). Conversely, population growth rates at Red Banks, Forestry Camp, and Twin Bridges were all less than 1.0, indicating a negative population trend over our 5-year study. However, we observed

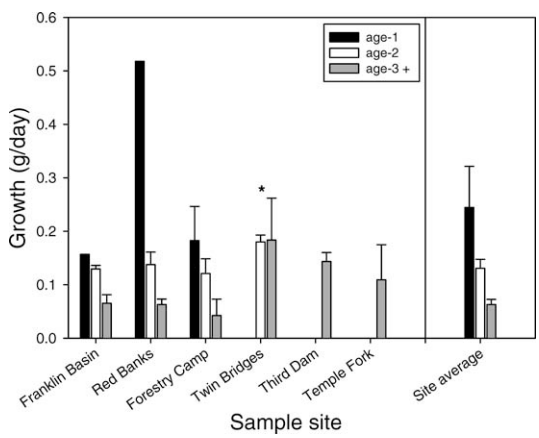

FIGURE 4.—Growth rates (g/d; ±SE) for three age-classes (where available) of tagged, recaptured Bonneville cutthroat trout at six sites on the Logan River, Utah, 2002–2005. The rightmost bars indicate the composite average across all sites. The asterisk represents data that was excluded from analysis because the fish was recaptured after only 15 d and demonstrated improbable negative growth (−1.6 g/d).

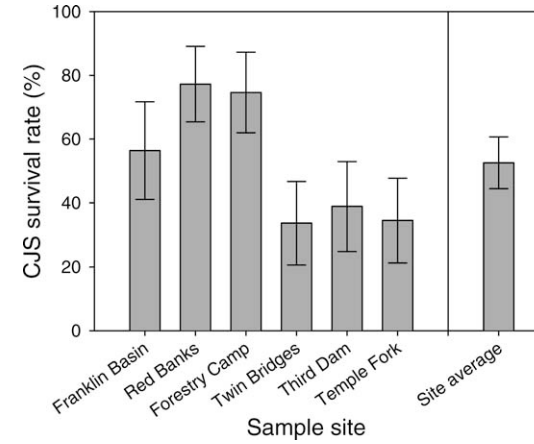

FIGURE 5.—Mean (±SE; across years) Cormack–Jolly–Seber (CJS) survival rates of Bonneville cutthroat trout at six sites on the Logan River, Utah, 2002–2005. The rightmost bar indicates the composite average across all sites.

wide 95% CIs for site-specific estimates of λ at five of the six sites, indicating that we cannot make conclusions about increasing or decreasing population trends with great certainty at this time. Nevertheless, the λ estimated for the entire Logan River population based on pooled site abundance estimates was 0.86 (95% CI = 0.77–0.95), indicating an apparent overall decline.

Discussion

We chose this population of Bonneville cutthroat trout for study because of its presumed large size and the relatively high-quality condition of its habitat; both components have become a rarity among many populations of Bonneville cutthroat trout and cutthroat

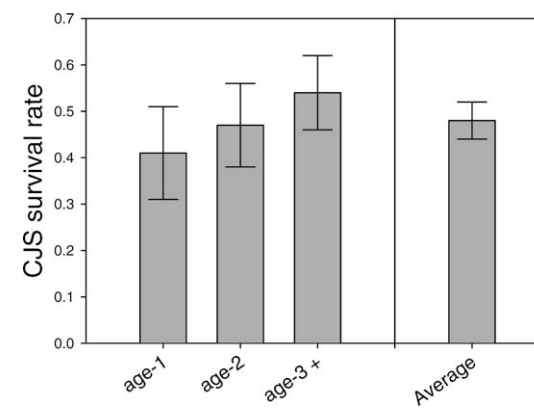

FIGURE 6.—Mean (±SE; across sites) composite Cormack–Jolly–Seber (CJS) survival rates of three age-groups of Bonneville cutthroat trout from the Logan River, Utah. The rightmost bar indicates the composite average across all age-groups.

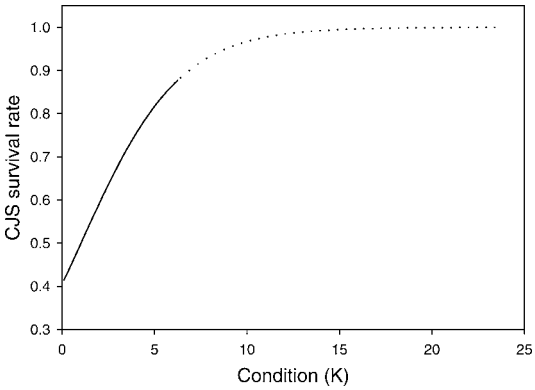

FIGURE 7.—Modeled relationship between condition (Fulton's K) and Cormack–Jolly–Seber (CJS) survival rate for Bonneville cutthroat trout that were tagged and recaptured in the Logan River, Utah, 2002–2005. The solid line represents the observed range of K-values (maximum $K = 6.5$); the dashed line represents the plateau towards a theoretical maximum survival of 1.0.

TABLE 2.—Population growth rates (λ; 95% CIs) for Bonneville cutthroat trout at six sites on the Logan River, Utah, based on three-pass depletion abundance estimates during 2001–2005.

Site	λ	95% CI
Franklin Basin	1.02	0.60–1.73
Red Banks	0.90	0.67–1.22
Forestry Camp	0.81	0.69–0.96
Twin Bridges	0.77	0.57–1.06
Third Dam	1.21	0.86–1.72
Temple Fork	1.01	0.58–1.75
Pooled estimate	0.86	0.77–0.95

trout in general (Behnke 1992). The Logan River remains largely connected across 43 rkm including the three primary tributaries. Accordingly, we observed much higher densities of 100-mm and larger Bonneville cutthroat trout at certain sites in this system than have been observed in other such populations and other subspecies of cutthroat trout (Table 3). Densities of Bonneville cutthroat trout in the Logan River averaged 694 fish/km across our sites and years, while densities of this subspecies in northern (129 fish/km) and southern (228 fish/km) Utah as well as Wyoming (128 fish/km) are much lower. Logan River Bonneville cutthroat trout densities are as much as 25 times the densities of Colorado River cutthroat trout *O. clarkii pleuriticus* in similar, albeit slightly smaller-sized, streams (Horan et al. 2000). The Logan River drainage provides a diversity of habitat types within close proximity that provide adequate food and cover and are suitable for different life stages (Fausch and Young 1995; Young 1995; Dunham et al. 1997; Hilderbrand 2003). Thus, the continuous and connected nature of Logan River habitat and large size of the remaining habitat area are important for maintaining a large population of cutthroat trout.

In addition to high population densities, we also observed relatively high annual growth and survival rates overall, especially at upper-elevation sites. At upper-elevation main-stem sites, fish grew as much as 0.5 g/d and annual survival rates of adult fish were as high as 75%. In contrast, observed survival rates at sites where exotic brown trout were present (Twin Bridges, Third Dam, and Temple Fork) were nearly half those observed at sites where brown trout were absent or occurred in extremely low abundance (Franklin Basin, Red Banks, and Forestry Camp). This pattern is similar to that reported by Peterson et al. (2004), who found survival rates of juvenile and age-1 Colorado River cutthroat trout increased from 23% to 42% when exotic, sympatric brook trout were reduced in density. We also observed higher survival rates for older age-classes and an increase in individual survival with condition. The relation between survival and condition makes biological sense, in that individuals that are heavier per unit length must have either a high

TABLE 3.—Summary of existing quantitative data (means and ranges) on Bonneville cutthroat trout density (fish/km), by management unit (MU) and state. Fish were captured via electrofishing (EF); N is the number of times the reach was sampled.

Location	Years	Method	N	Reach		Density (fish/km)	Source
				Length (m)	Width (m)		
Logan River and tributaries, Utah	2001–2005	3-pass EF	6	167 (100–200)	9.7 (7.5–13.7)	694 (66–1,339)	This study
North Bonneville MU, Utah	1996–2004	2-pass EF	20	177 (66–745)	3.4 (2.7–4.3)	129 (24–350)	Cowley 1997a, 1997b; Budy et al. 2005; Thompson 2003
North Bonneville MU, Wyoming	1999–2001	2- and 3-pass EF	6	100	5.2 (2.0–10.3)	128 (50–302)	Schrank et al. 2003; Cowley 2001
South Bonneville MU, Utah	1994–2005	1-pass EF[a]	16	161	2.0 (1.0–3.3)	228 (118–546)	Hepworth 1997

[a] Includes age-1 and older fish that were observed but not captured during a single electrofishing pass.

intrinsic growth potential or greater access to food resources; both factors typically lead to increased survival and often to increased fitness (Williams et al. 2001).

There are several sampling issues that must be considered when evaluating the population assessment and vital rates reported here. First, survival rates at the Temple Fork site are probably affected by the transitory nature of fish using this tributary reach and by changes in site habitat (which affect sampling efficiency), due to extensive but variable beaver activity. Survival rates at this site averaged 34% (SE = 13%) across years, an estimate we believe is negatively biased. Spawn Creek, a tributary stream that flows into Temple Fork (Figure 1), has been demonstrated to be one of the primary spawning areas for Bonneville cutthroat trout in the upper Logan River; Bernard and Israelsen (1982) documented a distinct spawning migration to and from the main-stem Logan River through the Temple Fork site and into Spawn Creek. As such, many fish collected at Temple Fork were probably not residents; this premise is supported by both the low recapture probability and the relatively high movement rate at this site, factors that can bias survival estimates (Williams et al. 2001; Fausch et al. 2002; Franklin et al. 2004).

Second, electroshocking and handling during depletion and tagging sampling could have induced or intensified movement and decreased recapture rates (Nordwall 1999). Further, the harmful effects of electroshocking are well documented; in some studies, injuries have occurred in up to 98% of sampled fish (reviewed in Snyder 2003). Because all sites received the same degree of effort (i.e., electroshocking time and handling), we cannot determine whether electroshocking increased movement. However, we believe electroshocking had minimal impacts in our study because (1) density of fish encountered during our sampling was extremely high, (2) recapture probability of marked fish for survival analyses was consistently high (averaging 50% but as high as 88%), (3) many tagged fish were recaptured more than once (some up to three times) and thus survived one or more electroshocking experiences, and (4) recapture probabilities based on independent depletion estimation techniques were consistently high. In addition, Snyder's (2003) review documented that over 90% of the fish injured during electroshocking survive and that long-term survival is seldom significantly affected. Nevertheless, the potential effects of handling on survival rate estimation and population assessment cannot be ignored (Krebs 1999; Williams et al. 2001).

Although our purpose was not to track individual fish (e.g., via telemetry methods), we did tag and recapture over 1,050 Bonneville cutthroat trout (some were recaptures) across the more than 30 rkm that constitute their current home range in the Logan River (Hilderbrand and Kershner 2000b). Recapture probabilities were high (46% on average); overall, we observed extremely high site fidelity as measured here (but see Fausch et al. 2002). In addition, consistent with other studies of trout movement, fish recaptured at sites other than their original site of tagging did move long distances (up to 34 km). Although Hilderbrand and Kershner (2000b) documented maximum seasonal movements of 5.2 rkm for resident Bonneville cutthroat trout in the Logan River, Colyer et al. (2005) recently reported maximum movements of 86 rkm for large fluvial Bonneville cutthroat trout in the nearby Bear River system. These were fish that migrated back and forth from the main stem to the tributaries to spawn, which suggests that the large-sized, highly migratory fluvial form disappeared from many Bonneville cutthroat trout populations because of habitat fragmentation.

The connectivity among different habitat types that remain in the Logan River system is important for allowing access to suitable spawning and rearing grounds while providing adequate main-stem habitat for adult growth and survival. In addition to maintaining the high densities of Bonneville cutthroat trout we observed, this connectivity is important for maintaining the degree of exchange among subpopulations. Exchange will be especially important if the populations are in synchrony, a pattern that could occur in response to a large-scale environmental factor (e.g., regional drought; Hilderbrand 2003; Isaak et al. 2003). The Logan River and surrounding areas experienced a prolonged drought cycle extending from 1999 to 2004 (U.S. Geological Survey [USGS], unpublished data). Local subpopulations would probably experience synchronous declines in abundance in response to drought (Isaak et al. 2003), potentially resulting in widespread declines across a large geographic area. These considerations emphasize the management importance of maintaining connectivity and, in turn, maintaining opportunities for recolonization among remaining populations of cutthroat trout (Allendorf et al. 1997; Ham and Pearsons 2000).

Finally, despite the relatively high densities of Bonneville cutthroat trout, we also observed declining ($\lambda < 1$) population growth rates at three of the six sites and an overall λ-value of 0.86 (95% CI = 0.77–0.95). However, we also observed wide 95% CIs, overlapping 1.0 at five of the six sites where Bonneville cutthroat trout occur (i.e., when CIs overlap 1.0, we cannot be certain of the true direction of the population trend; Ham and Pearsons 2000; Morris and Doak 2002).

Natural environmental stochasticity and the relatively short time series available to date (5 years) contribute to these wide CIs. Most estimates of trend will increase in certainty as the time series becomes longer, and the trend estimates we reported should be reevaluated after more years of data accumulate. However, count-based population viability analyses are also sensitive to additional factors. For instance, nonstationarity, density dependence, and Allee effects are all population-level processes that influence viability and trend, yet can be difficult to capture and model for many imperiled populations (Morris and Doak 2002; Franklin et al. 2004). The uncertainties associated with estimating trend illustrate the need for establishing comprehensive monitoring and evaluation programs that include the consistent collection of long-term data and the ability to estimate vital rates, at least for a subset of populations within an imperiled species (Al-Chokhachy 2006). In addition, the inherent uncertainties associated with estimating trend in general and the wide variation in population growth rates we observed emphasize the need for a cautious interpretation of these trend results and conservative management decisions regarding the acceptable level of harvest, habitat degradation, or other anthropogenic impacts (Caswell 2000; Young and Guenther-Gloss 2004; Legault 2005).

Management Implications

We provide some of the first robust estimates of density, growth, survival, and population trend for an imperiled subspecies of cutthroat trout based on field measurements and mark–recapture techniques. These viability measures are critical for identifying limiting factors, evaluating management options, and identifying conservation priorities. The conservation and management of an imperiled endemic subspecies require managers to evaluate and protect populations that have declined in abundance and distribution and also to assess populations for which conservation options remain. These viable populations offer an important opportunity to create benchmarks (e.g., life-stage-specific survival rates) for recovery and identify limiting factors.

The Logan River contains one of the largest remaining populations of Bonneville cutthroat trout; the densities observed here are some of the highest reported densities of inland stream-type cutthroat trout. Survival and growth rates were also relatively high. These are all components of population persistence. Clearly, the remaining continuity and connectedness of habitat fragments in the Logan River and their large size have contributed to the persistence of this population. Nevertheless, abundance now appears to be declining at some sites, and survival and abundance were lower at sites where Bonneville cutthroat trout were sympatric with exotic brown trout than at sites of allopatry. As such, to ensure the long-term viability of this important population, we recommend that proactive management measures be considered, such as exotic brown trout removal and habitat restoration and protection.

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