[Article]

Persistence of Colorado River Cutthroat Trout Populations in Isolated Headwater Streams of Wyoming

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Abstract.—For populations of cutthroat trout *Oncorhynchus clarkii*, isolation in headwater streams may provide protection from invasion by nonnative species but also may enhance a population's vulnerability to extirpation. We assessed the risk of extirpation for eight Colorado River cutthroat trout *O. clarkii pleuriticus* populations isolated above water diversion structures in the North Fork Little Snake River drainage, Wyoming. The populations had been isolated for 25–44 years, occupied headwater streams that ranged from 850 to 6,100 m in length, and had adult populations that were estimated to range from 12 to 506 fish. Adult population sizes were compared with published occurrence models to identify populations that may be at risk of extirpation. One population had experienced an 11% annual rate of decline in abundance over the past 29 years, but there was no evidence of declines among the other populations. There was evidence of recruitment failure for age-1 fish in two of the smaller populations. Abundance estimates and published logistic regression models consistently identified the largest tributary in the drainage as being the most likely to support a Colorado River cutthroat trout population in the future and the smallest tributary as being the least likely to support a population in the future. The analyses indicated that isolated populations may persist for decades, but small effective population sizes can make populations vulnerable to eventual loss of genetic variability and to extirpation.

Inland cutthroat trout *Oncorhynchus clarkii* have experienced declines in distribution and abundance due to habitat fragmentation, habitat degradation, and interactions with nonnative species (e.g., Behnke 1992; Hitt et al. 2003; Peterson et al. 2004a). Most genetically pure populations of cutthroat trout are now confined to high-elevation streams that are isolated by natural or anthropogenic barriers (Thompson and Rahel 1996; Kruse et al. 2000; Shepard et al. 2005). Although barriers provide protection from invasion by nonnative species, isolation has its own risks (Peterson et al. 2008; Fausch et al. 2009). When immigration is blocked by barriers, isolated populations may be vulnerable to extinction because of stochastic demographic or environmental events (Rieman et al. 1991; Hilderbrand 2003). Isolation also results in reduced gene flow and genetic variation, increasing the risk of inbreeding depression and reducing evolutionary potential (Allendorf and Ryman 2002).

Strategies for conserving native cutthroat trout call for securing and enhancing individual populations (e.g., CRCT Coordination Team 2006). Genetically pure cutthroat trout are given special consideration in rangewide conservation strategies; thus, most popula-

tions of conservation concern are isolated in high-elevation streams (Hirsch et al. 2006; May et al. 2006). As a result, there is considerable interest in identifying factors that influence the persistence of such populations (Harig et al. 2000; Hilderbrand and Kershner 2000; Hilderbrand 2003; Peterson et al. 2008).

Genetic variation is often cited as an important determinant of population viability (Allendorf and Ryman 2002; Pritchard et al. 2007). Low genetic variation can lead to reduced capacity for adaptation or, in the case of inbreeding, the expression of deleterious alleles. The amount of genetic variation in a population is related to its effective population size (N_e), or the number of reproducing individuals under idealized conditions of no sexual selection, random mating, equal sex ratios, and equal reproductive probability among adults (Rieman and Allendorf 2001). These idealized conditions rarely occur in nature, so N_e is typically a fraction of the actual population size (N). Empirical estimates of N_e/N ratios for isolated salmonid populations have been reported to range from 0.2 to 0.5 (Palm et al. 2003; Jensen et al. 2005).

Low genetic variability, demographic stochasticity, or harsh environmental conditions can synergistically cause a population to decline over time. Once a population is small enough that declines cause genetic bottlenecking, reduced fitness due to genetic factors can lead to further declines. The combined effects of low genetic variation, environmental stressors, and catastrophic events are hypothesized to lead to negative

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population growth rates, a phenomenon that has been described as an "extinction vortex" (Gilpin and Soulé 1986; Rieman et al. 1991). For isolated cutthroat trout populations, demographic support from nearby populations is not available and negative population growth is a sign that a population may not persist (Peterson et al. 2008).

Trout populations vary considerably in abundance from year to year (Dauwalter et al. 2009). Variations in reproduction and recruitment are often linked to increased extirpation risk (Hilderbrand 2003; Coleman and Fausch 2007b). At low population sizes, variable abundance may cause the population to fall below extinction thresholds or experience genetic bottlenecking (Vucetich et al. 1997; Kalinowski and Waples 2002).

The quantity and quality of available habitat can affect the carrying capacity of isolated trout populations and the likelihood of extirpation (Rieman and McIntyre 1995; Morita and Yamamoto 2002). For example, cold water temperatures can decrease growth and survival of age-0 cutthroat trout (Coleman and Fausch 2007a, 2007b) and can reduce the probability of persistence for translocated cutthroat trout populations (Harig and Fausch 2002). Strong relationships between cutthroat trout abundance and amount of available habitat in streams have been identified (Kruse et al. 2001; Young et al. 2005).

Although theoretical studies have advanced the understanding of factors that contribute to population persistence, few studies have documented the extirpation of isolated salmonid populations. Morita and Yamamoto (2002) developed a logistic regression model to predict the occurrence of whitespotted char *Salvelinus leucomaenis* populations upstream of dams on the island of Hokkaido, Japan. The authors assumed that whitespotted char populations had become extirpated in stream segments where snorkeling and electrofishing failed to detect the species. They identified watershed area, stream gradient, and time since isolation as important predictors of population occurrence. Harig and Fausch (2002) examined 27 naturally and anthropogenically isolated streams that were historically either fishless or treated with a piscicide and then stocked with cutthroat trout. Six of these streams failed to support cutthroat trout populations 3–31 years after initial stocking, and logistic regression modeling indicated that populations tended to fail in streams that (1) lacked pool habitat, (2) had cold summer water temperatures, or (3) were affected by both factors. The models by Morita and Yamamoto (2002) and Harig and Fausch (2002) were developed to predict probabilities of occurrence and reestablishment, respectively, of isolated populations of different salmonid species, but they may provide insight into factors that influence cutthroat trout persistence.

We studied populations of Colorado River cutthroat trout *O. clarkii pleuriticus* that had been isolated in headwater streams for 25–44 years. Our first objective was to assess the status of these populations based on adult abundance, trends in abundance over time, age structure, and available habitat. Our second objective was to compare our estimates of abundance with published models that predict population occurrence in isolated habitats. Because the study streams supported isolated Colorado River cutthroat trout populations, the modeled probabilities of persistence for these streams should be high (i.e., >0.5). The outputs were used as relative measures of the likelihood of streams to support populations in the future. By comparing the outputs of these models with the abundance estimates (assuming that abundance is positively related to persistence), we identified populations that were most (or least) vulnerable to extirpation.

Methods

We examined eight populations of Colorado River cutthroat trout in first- and second-order streams in the upper North Fork Little Snake River (NFLSR) drainage in the Sierra Madre of south-central Wyoming (Figure 1). Populations in Ted Creek and the main-stem NFLSR had been isolated since water collection structures were built in the mid-1960s. During the 1980s, structures were built on the West Branch, which is the largest tributary of NFLSR, as well as on Standard, Rabbit, Harrison, Deadman, and Third creeks. Although introgression with introduced rainbow trout *O. mykiss* and Yellowstone cutthroat trout *O. clarkii bouvieri* has taken place in the downstream portion of the drainage, fish upstream from the diversion structures were known to be genetically pure Colorado River cutthroat trout (Wyoming Game and Fish Department, unpublished data). To protect these populations, the Wyoming Game and Fish Department closed the isolated streams to fishing in 1984.

To estimate fish abundance and distribution, Colorado River cutthroat trout were systematically sampled in 50-m reaches with a backpack electrofishing unit. Trout were sampled in every other 50-m reach in all streams but the West Branch, where every fourth reach was sampled because of this tributary's long length. The first sampled reach was randomly selected from the four (West Branch) or two (all other streams) reaches closest to the diversions. Third Creek, Deadman Creek, and the NFLSR were sampled between June 15 and August 31, 2007. Ted Creek, Harrison Creek, Rabbit Creek, Standard Creek, and the West Branch were sampled between July 1 and October 10,
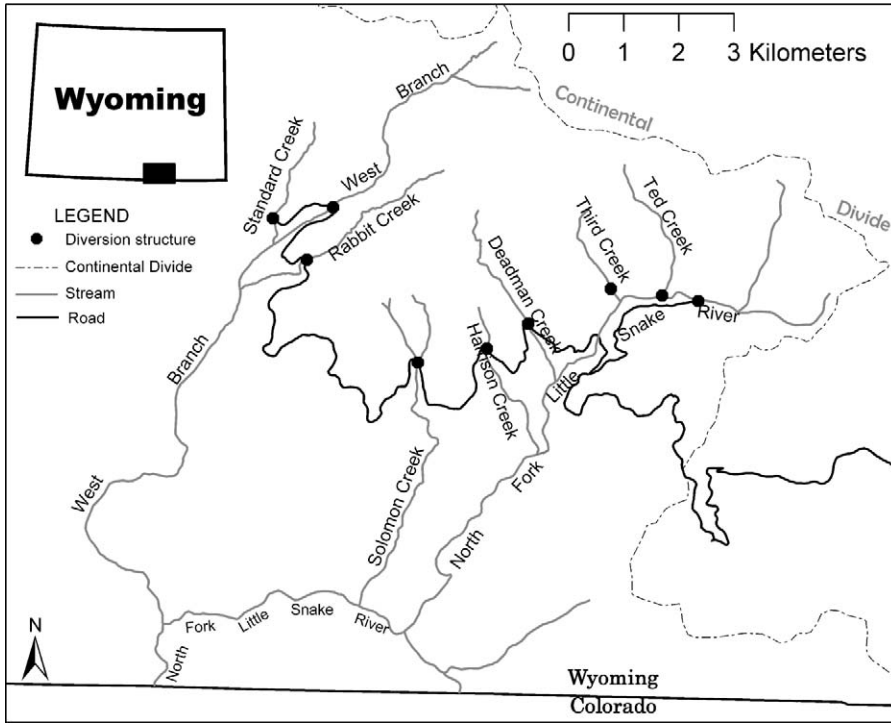
FIGURE 1.—The upper North Fork Little Snake River (NFLSR) drainage, Wyoming. Water diversions were built near the intersections of the streams and the "Pipeline Road," which is depicted by the solid black line. Colorado River cutthroat trout upstream of the diversion structures had been isolated for 25 years (West Branch and Standard, Rabbit, Harrison, Deadman, and Third creeks) or 44 years (Ted Creek and NFLSR). No fish had ever been observed in the isolated forks of Solomon Creek. Inset shows location of the study area in southern Wyoming.

2008. We assumed that fish were absent upstream from headwaters (typically characterized by subterranean flow) or at locations where no fish were captured in two consecutive reaches and where spot electrofishing and visual surveys failed to detect Colorado River cutthroat trout. Tributaries of each creek were also sampled if Colorado River cutthroat trout were found, with the exception of two NFLSR tributaries (Dale and Happy creeks), which contain low numbers of fish (Oberholtzer 1987) but were not sampled due to time constraints. Total lengths (TLs) of all collected fish were measured to the nearest millimeter.

To estimate adult abundances, we assumed that fish greater than or equal to 125 mm TL were adults. This length threshold was selected based on length-frequency analysis and was similar to other studies of cutthroat trout populations inhabiting high-elevation streams (Quinlan 1980; Downs et al. 1997; Young and Guenther-Gloss 2004; Coleman and Fausch 2007b). Population estimates were generated using a two-stage sampling design (Young and Guenther-Gloss 2004; Young et al. 2005). In the first stage, a block net was

placed at the upstream end of the sampled reach and fish were counted by using single-pass electrofishing. In the second stage, block nets were placed at both the downstream and upstream ends of approximately every fourth sampled reach and depletion electrofishing was conducted. A minimum of three electrofishing passes were conducted except in one reach of Deadman Creek, where only two passes were conducted because sampling was suspended due to an electrical storm. Abundance estimates were calculated using Huggins' (1991) closed-capture model in program MARK (White and Burnham 1999). For reaches sampled in multiple electrofishing passes, the number of fish captured in the first electrofishing pass was divided by the depletion estimate for that reach, yielding an estimate of capture efficiency on the first electrofishing pass ($\hat{c}_1$). We averaged $\hat{c}_1$ over all streams and years because (1) there was a limited number of $\hat{c}_1$ estimates (range = 2–7) in each stream, (2) $\hat{c}_1$ was not significantly related to stream width ($r = -0.078$, $P = 0.678$; see Kruse et al. 1998; Young and Guenther-Gloss 2004), and (3) average capture efficiencies ($\bar{c}_1$)

were the same for each year (2007 $\bar{c}_1 = 0.77$, SE = 0.0426; 2008 $\bar{c}_1 = 0.77$, SE = 0.0501). The inverse of $\bar{c}_1$ was multiplied by single-pass fish counts from the first stage to obtain reach-scale abundance estimates, which were then extrapolated to the entire stream (Hankin and Reeves 1988). To compute bootstrap 95% confidence intervals (CIs) for stream abundance estimates, we used the Statistical Analysis System (version 9.1; SAS Institute, Cary, North Carolina) to resample reach-scale abundance estimates 1,000 times for each stream, extrapolate the resampled estimates to the entire stream, and compute the 2.5th and 97.5th percentiles of resampled estimates.

The number of 125-mm TL or longer fish was considered an index of the number of breeding adults and, thus, an estimate of maximum N_e. We also used an N_e/N ratio of 0.5 to compute an estimate of N_e. This ratio is at the upper end of the range of empirically estimated N_e/N ratios for isolated salmonid populations (Palm et al. 2003; Jensen et al. 2005) and was selected to provide what we considered to be optimistic estimates of N_e.

Removal-based abundance estimates may be negatively biased compared with other methods (Riley and Fausch 1992; Peterson et al. 2004b; Rosenberger and Dunham 2005). To assess this bias, mark–recapture population estimates were conducted on a subset of sampled reaches. Block nets were placed at the upper and lower ends of a sampled reach. Fish were collected from the reach in a single electrofishing pass, marked by clipping a portion of the pelvic fin, and then redistributed throughout the sampled reach. Block nets were left in place overnight, depletion electrofishing was conducted the next day (within 16–20 h), and fish collected in all passes were used to compute mark–recapture estimates (Chapman 1951). Mark–recapture estimates were conducted in 9 of the 33 reaches for which depletion estimates were made. The relationship of removal estimates to mark–recapture estimates was assessed through linear regression with the intercept forced through the origin. The slope of the regression line was used to adjust estimates of adult population size (N), N_e, and CIs.

A combination of historical and new data was used to assess trends in abundance over time. Historical abundance data for Colorado River cutthroat trout were available from long-term monitoring sites for all study streams except Rabbit Creek (Wyoming Game and Fish Department, unpublished data). These data consisted of removal-based abundance estimates for fish of at least 25 mm TL in approximately 100-m-long reaches sampled at irregular time intervals from 1978 to 2006. To add to this data set, we obtained similar abundance estimates at these sites in 2007 for Deadman

Creek; in 2008 for the West Branch, Ted Creek, Harrison Creek, and Standard Creek; and in both years for the NFLSR and Third Creek. In six of the streams, only one site had been sampled more than once. In Ted Creek, two sites had been sampled repeatedly, so trends at both sites were evaluated. We calculated population growth rate (λ) and 90% CIs by performing linear regression analyses of log-transformed changes in abundance over time (Morris and Doak 2002). To generate an estimate of λ, abundance estimates had to be available from at least three sampling occasions. A λ value less than 1 indicates that a population is declining over time, a λ of 1 indicates a self-replacing population, and a λ greater than 1 indicates that the population is increasing. At sites where the 90% CIs around λ included 1, declines or increases could not be detected with certainty (Budy et al. 2007).

Temporal variation for each population was expressed as the coefficient of variation ($100 \times$ SD/mean) in abundance among years (Dauwalter et al. 2009). To evaluate recruitment success, fish were placed into three age categories based on TL. Fish that were 80 mm TL or less were defined as juveniles (age 1), fish between 81 and 125 mm TL were categorized as subadults (age 2), and fish 125 mm TL or longer were classified as adults (age 3 and older; Young and Guenther-Gloss 2004). To calculate the proportion of fish in each length category within a population, the number of captured fish from each length category (including fish captured in all electrofishing passes) was divided by the total number of fish captured from that population. Age-0 Colorado River cutthroat trout (<43 mm TL) had yet to emerge at the time of sampling in most streams, so age-0 fish were not included in the length-structure analysis. We used the criterion of Young and Guenther-Gloss (2004), which states that fish in each of the juvenile, subadult, and adult length categories must constitute at least 5% of the total population to indicate successful recruitment.

Probability of fish occurrence was calculated based on the models of Harig and Fausch (2002) and Morita and Yamamoto (2002). Harig and Fausch (2002) developed the following model to predict the absence of fish in streams that received translocated cutthroat trout:

$$p_a = \frac{\exp(11.454 - 0.891t - 1.451w - 0.017d)}{1 + \exp(11.454 - 0.891t - 1.451w - 0.017d)},$$

where p_a = probability of fish being absent from a stream, t = mean July water temperature (°C), w = mean bank-full pool width (m), and d = number of deep pools. A pool was considered deep if residual depth (RD) was 30 cm or more. Harig and Fausch

TABLE 1.—Available stream lengths, estimates of Colorado River cutthroat trout adult abundance ($\hat{N}_{adult}$; ≥ 125 mm total length), and adult abundance adjusted for the negative bias of removal estimates ($\hat{N}_{adj}$) in isolated headwater streams of Wyoming (NFLSR = North Fork Little Snake River). Ninety-five percent confidence intervals are shown in parentheses.

Stream	Available stream length (m)	$\hat{N}_{adult}$	$\hat{N}_{adj}$ ($\hat{N}_{adult} \times 1.243$)
West Branch	6,100	506 (451–559)	628 (560–694)
NFLSR	3,200	275 (243–310)	342 (302–385)
Rabbit Creek	1,950	109 (79–149)	136 (98–185)
Deadman Creek	2,800	106 (86–127)	132 (106–158)
Ted Creek	1,950	83 (67–105)	104 (84–131)
Standard Creek	1,050	51 (41–73)	64 (51–91)
Third Creek	1,250	17 (9–27)	22 (11–34)
Harrison Creek	850	12 (6–21)	15 (8–26)

(2002) also developed a model predicting occurrence of cutthroat trout based on watershed area above a barrier:

$$p_a = \frac{\exp(0.251 - 0.123a)}{1 + \exp(0.251 - 0.123a)},$$

where p_a = probability of fish being absent from a stream and a = watershed area (km^2). Morita and Yamamoto (2002) used the presence (number of sites = 35) and absence (number of sites = 17) of whitespotted char in dammed streams to develop the following model:

$$p = \frac{\exp(5.668 + 1.404g - 2.389i + 2.071a)}{1 + \exp(5.668 + 1.404g - 2.389i + 2.071a)},$$

where p = probability of fish occurring, $g = \log_e$(percent stream gradient), $i = \log_e$(time period of isolation in years), and $a = \log_e$(watershed area [km^2] above the barrier).

We measured a suite of habitat variables in each study stream for use in the models by Harig and Fausch (2002) and Morita and Yamamoto (2002). Water temperatures (°C) were measured using thermographs (Onset Computer Corporation, Bourne, Massachusetts) set to record at 15-min intervals. Two thermographs were placed in each stream except Harrison Creek, which received only one thermograph due to its short length. Thermographs were placed between 677 and 2,763 m apart within the study streams in habitats intended to represent the range of conditions within each stream (i.e., one in a low-gradient meadow and one in a steep-gradient riffle). For analysis, mean July water temperatures were averaged from thermographs within a stream and for the years 2007 and 2008 to provide an overall index of the different temperature regimes among streams. We conducted pool measurements, pool counts, and gradient measurements in sampled (electrofished) reaches. Pool wetted width (m) was measured at the upstream end, middle, and downstream end of pools with RDs of 20 cm or more.

Wetted widths were converted to bank-full widths by multiplying the wetted width measurements by 1.5 (Young et al. 2005); bank-full width estimates were then averaged for each stream. Counts of deep pools (RD $\geq$ 30 cm) from sampled reaches were extrapolated to the entire stream. Watershed area (km^2) above the diversions was computed using the Spatial Analyst toolbox in ArcMap (version 9.3; Environmental Systems Research Institute, Redlands, California). Channel slope (percent gradient of sampled reaches) was measured using a clinometer and was averaged for each stream. Isolation period was calculated as 2008 minus the first year of diversion construction (1964 for NFLSR and Ted Creek, 1983 for all other streams). We also evaluated an isolation period of 100 years in the Morita and Yamamoto (2002) model to assess persistence of Colorado River cutthroat trout populations into the future.

To identify streams that were consistently predicted to support (or not support) Colorado River cutthroat trout populations, the streams were ranked by decreasing probability of occurrence according to each logistic model and decreasing adult population size. Concurrence of outputs with adult population size was assessed by computing Spearman's rank correlation coefficients (ρ) using STATISTIX (version 7.0; Analytical Software, Tallahassee, Florida).

Results

Estimated abundances of adult Colorado River cutthroat trout based on depletion methods varied widely, ranging from 12 to 506 fish among the eight streams (Table 1). Six of the eight populations contained 50 adults or more, but only the West Branch had more than 500 adults. The regression ($r^2 = 0.986$, $P < 0.0001$) of mark–recapture abundance estimates versus depletion estimates indicated that on average, mark–recapture estimates were 1.243 times greater than depletion estimates. Adjusted population estimates yielded adult abundances ranging from 15 fish

TABLE 2.—Population growth rates (λ) and 90% confidence intervals (CIs) for Colorado River cutthroat trout monitoring sites on isolated streams in the upper North Fork Little Snake River (NFLSR) drainage. Time period of monitoring, number of years in which abundance was estimated, and coefficient of variation (CV) in abundance over time are also presented. Because of insufficient data, λ could not be estimated for Rabbit Creek.

Stream	λ	90% CI	Time period	Number of years with data	CV (%)
NFLSR	1.03	0.92–1.16	1978–2008	9	31
Third Creek	0.97	0.80–1.17	1979–2008	7	46
Ted Creek (site 1)	0.91	0.76–1.09	1978–2008	7	84
Ted Creek (site 2)	0.89	0.83–0.96	1979–2008	6	82
Deadman Creek	0.97	0.83–1.13	1984–2007	6	27
Standard Creek	1.01	0.79–1.30	1986–2008	4	53
West Branch	1.05	0.87–1.27	1986–2008	4	67
Harrison Creek	0.95	0.25–3.35	1976–2008	3	65

(Harrison Creek) to 628 fish (West Branch). Using these adjusted abundance estimates, the calculated N_e ranged from 8 fish in Harrison Creek to 314 fish in the West Branch.

Among the eight sites for which we had data to calculate λ values, only one site on Ted Creek had a statistically significant population trend—an 11% annual rate of decline ($\lambda = 0.89$, 90% CI = 0.83–0.97; Table 2). The other site on Ted Creek had the second-lowest λ value at 0.91, but the decline was not statistically significant (90% CI = 0.76–1.09). The extent of temporal variation within each population (expressed as the coefficient of variation) ranged from 27% to 84% (Table 2). Juvenile fish comprised 0% and 2% of the catches in Harrison Creek and Standard
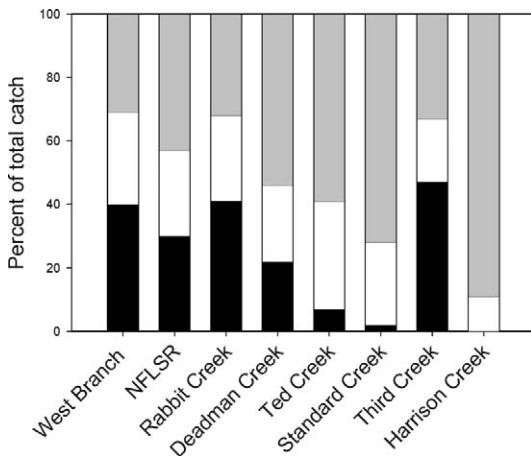

FIGURE 2.—Percentages of all Colorado River cutthroat trout captured in each study stream that were juvenile (black bars), subadult (white bars), and adult (gray bars). The total number captured was 338 fish in the West Branch, 256 fish in the North Fork Little Snake River (NFLSR), 135 fish in Rabbit Creek, 86 fish in Deadman Creek, 59 fish in Ted Creek, 42 fish in Standard Creek, 30 fish in Third Creek, and 9 fish in Harrison Creek.

Creek, respectively (Figure 2). In Ted Creek, 7% of the 59 captured fish were juveniles. In other streams, the juvenile, subadult, and adult length-classes comprised at least 11% of the total number of fish captured.

All logistic regression models predicted that the West Branch was the stream most likely to retain Colorado River cutthroat trout—a result that was consistent with the relatively high abundance of fish in that stream (Table 3). Also consistent with population estimates were the low rankings for Harrison Creek based on each model. According to the Morita and Yamamoto (2002) model, small differences in predicted persistence became large differences when the isolation period was increased to 100 years. For example, the probability of containing fish in 2008 was 0.901 for Ted Creek and 0.912 for Rabbit Creek, but when the 100-year isolation period was used, the predicted probability decreased to 0.586 for Ted Creek and 0.275 for Rabbit Creek. The Morita and Yamamoto (2002) model predicted higher probabilities of fish occurrence than did either of the Harig and Fausch (2002) models. The Harig and Fausch (2002) model predictions based on watershed area were highly correlated ($\rho = 0.929$, $P = 0.002$; Table 4) with our estimates of adult population size, but model predictions based on pool habitat and July water temperature did not have significant correlations with our population estimates ($\rho = 0.381$, $P = 0.327$). Probability of persistence based on Morita and Yamamoto's (2002) model had a nearly significant correlation with adult population size ($\rho = 0.667$, $P = 0.070$), and the correlation increased slightly when we increased the isolation period to 100 years ($\rho = 0.691$, $P = 0.058$).

Discussion

Despite small population sizes, eight populations of Colorado River cutthroat trout persisted in anthropogenically isolated streams in the upper NFLSR drainage for 25–44 years. Except for Ted Creek,

TABLE 3.—Input variables and resulting probabilities of occurrence for Colorado River cutthroat trout populations in isolated streams of the upper North Fork Little Snake River (NFLSR) drainage. Streams are listed in order of decreasing adult abundance from left to right. Bold numbers in parentheses are the ranks of the streams in terms of the probability of fish occurrence (i.e., 1 = highest probability, 8 = lowest probability) for each model. For the Morita and Yamamoto (2002) model, isolation period (years) was computed as 2008 − 1964 for NFLSR and Ted Creek and 2008 − 1983 for the other study streams. This model was also run with an isolation period of 100 years for all streams.

Variable	West Branch	NFLSR	Rabbit Creek	Deadman Creek	Ted Creek	Standard Creek	Third Creek	Harrison Creek
Morita and Yamamoto (2002) model								
Isolation period (years as of 2008)	25	44	25	25	44	25	25	25
Mean gradient (%)	6.33	5.07	4.15	7.67	7.33	7.73	10.46	8.56
Watershed area (km^2)	9.14	7.73	3.13	5.06	4.03	2.75	2.28	1.36
Probability of fish occurrence (2008)	0.994 (**1**)	0.959 (**3**)	0.912 (**6**)	0.985 (**2**)	0.901 (**7**)	0.950 (**5**)	0.952 (**4**)	0.835 (**8**)
Probability of fish occurrence (100 years)	0.863 (**1**)	0.765 (**2**)	0.275 (**7**)	0.708 (**3**)	0.586 (**4**)	0.410 (**6**)	0.418 (**5**)	0.156 (**8**)
Harig and Fausch (2002) model								
Mean July temperature (°C)	8.80	8.80	8.58	8.90	9.26	10.00	11.05	9.69
Mean pool bank-full width (m)	2.31	2.34	2.46	2.25	2.29	2.30	1.53	2.12
Number of deep pools	193	62	25	64	57	23	12	17
Probability of fish occurrence (temperature and pools)[a]	0.953 (**1**)	0.698 (**4**)	0.543 (**8**)	0.697 (**5**)	0.746 (**3**)	0.767 (**2**)	0.692 (**6**)	0.634 (**7**)
Probability of fish occurrence (watershed area)[a]	0.705 (**1**)	0.668 (**2**)	0.534 (**5**)	0.592 (**3**)	0.561 (**4**)	0.522 (**6**)	0.507 (**7**)	0.479 (**8**)

[a] To make the model outputs more comparable, we converted the Harig and Fausch (2002) model output from probability of fish absence to probability of persistence (probability of persistence = 1 − probability of absence).

historical data provided no evidence that these populations are declining. Such persistence is remarkable for Harrison and Third creeks, where the adult populations (adjusted for electrofishing capture efficiency) were estimated to be 15 and 22 fish, respectively. There have been few studies of anthropogenically isolated trout populations where demographic trends could be assessed without the confounding effects of stocked fish. Nineteen (70%) of the translocated cutthroat trout populations that Harig and Fausch (2002) studied persisted with fewer than 500 fish of age 1 or older, but most of these

TABLE 4.—Spearman's rank correlation coefficients (ρ) and related P-values between Colorado River cutthroat trout adult population size and probability of occurrence according to published logistic regression models. Probability of occurrence based on the Morita and Yamamoto (2002) model was computed using the isolation period isolated as of 2008 as well as an increased isolation period of 100 years. Probability of occurrence was also computed using the Harig and Fausch (2002) models based on water temperature and pool habitat or based on watershed area only (see Methods).

Model	ρ	P
Morita and Yamamoto (2002		
Isolation to 2008	0.667	0.070
Isolation for 100 years	0.691	0.058
Harig and Fausch (2002)		
Temperature and pools	0.381	0.327
Watershed area	0.929	0.002

populations were stocked repeatedly. Coleman and Fausch (2007b) identified and studied isolated cutthroat trout populations that were self-sustaining for at least 20 years and had estimated adult population sizes of 6–530 fish. Morita and Yokota (2002) reported that small, isolated populations of whitespotted char had persisted in isolation for approximately 30 years. However, when Morita and Yokota (2002) modeled the probability of persistence after 100 years, population viability decreased dramatically. It appears that the longer a population is isolated, the more likely it will experience loss of genetic variability, inbreeding, and catastrophic events.

Local adaptations to isolation—particularly demographic rate shifts and selection against emigration—may enhance viability of fish populations above movement barriers (Letcher et al. 2007). However, in order for a population to persist, the rate of adaptive genetic evolution would need to outpace the rate at which genetic variation is lost due to drift or emigration; this situation is unlikely in small populations. Long-term persistence of trout populations, especially with respect to evolutionary potential, has been hypothesized to require abundances of 500–5,000 fish (Allendorf et al. 1997; Hilderbrand and Kershner 2000; Frankham 2005). Our estimates of N_e (half of the adult population) for the eight study streams were well below these abundance thresholds. The West Branch, which was the longest of the study streams at 6.1 km, had an estimated

N_e well below 500 fish. Hilderbrand and Kershner (2000) estimated that at least eight linear kilometers of stream were required to support cutthroat trout populations with N_e values of 500 or greater. Additionally, because fish abundances tend to increase with stream size, larger streams would be expected to support populations with more genetic variation. Genetic variation measured in microsatellite DNA has been positively related to population size and the amount of habitat occupied by Lahontan cutthroat trout *O. clarkii henshawi* (Neville et al. 2006). However, in another study using microsatellite DNA to assess populations of Rio Grande cutthroat trout *O. clarkii virginalis*, genetic variability was not related to population size or the amount of habitat (Pritchard et al. 2007). While more research is needed to elucidate the relationships between population size, habitat size, and genetic diversity, empirical studies consistently indicate that isolation leads to reduced genetic variation in cutthroat trout populations (Wofford et al. 2005; Cegelski et al. 2006; Neville et al. 2006; Pritchard et al. 2007).

Abundance estimates generated by depletion electrofishing were lower than mark–recapture estimates by an average of 24.3%. Other studies of salmonids have reported depletion electrofishing estimates to be 21–22% (Bohlin and Sundström 1977), 15% (Peterson and Cederholm 1984), 60–116% (Peterson et al. 2004b), and 29–63% (Rosenberger and Dunham 2005) less than mark–recapture estimates. The negative bias in depletion-based estimates may result from variation in capture efficiency among electrofishing passes (Riley and Fausch 1992; Peterson et al. 2004b). However, we used a depletion estimator that allows for variable capture efficiency among passes. A second explanation for the differences between depletion and mark–recapture estimates is that some marked fish moved out of sampled reaches before they could be recaptured. On average, 74% (range = 20–100%) of the fish we marked were recaptured in multiple electrofishing passes, suggesting that some marked fish either escaped sampled reaches by swimming past block nets or perished between the marking and recapture periods. In studies that have assessed fish movements past block nets set overnight, Rosenberger and Dunham (2005) found that fish escaped 45% of sampled reaches and Temple and Pearsons (2006) found that fish escaped 75% of sampled reaches. The movements of marked fish out of sampled reaches would violate the assumption of a closed system and would cause an upward bias in mark–recapture estimates. In any case, adjusting depletion estimates based on mark–recapture did not change the number of study populations that were smaller than the recommended minimum of 500 fish.

The scarcity of historical data, coupled with historically low population sizes and naturally high variation in trout abundances, limited our ability to detect possible declines in populations among our study streams. The data set we used to calculate λ consisted of three to nine sampling occasions for each population. Ten sampling occasions is the recommended minimum for making population risk assessments based on patterns in abundance over time (Morris and Doak 2002; Lotts et al. 2004). However, such limited historical abundance data are not unusual among cutthroat trout monitoring programs. The Colorado River cutthroat trout conservation strategy recommends that population monitoring be conducted at least once every 5 years (CRCT Coordination Team 2006). We used historical abundance data from Colorado River cutthroat trout monitoring sites that were sampled, on average, once every 5 years. The low power associated with infrequent estimates of abundance will make it difficult to detect statistically significant trends, so additional indicators of extirpation risk should be considered in conservation strategies for fishes such as cutthroat trout within headwater stream systems (Maxwell and Jennings 2005).

Population estimates and published occurrence models indicated that the West Branch was the stream most likely to support a population of Colorado River cutthroat trout in the future, and Harrison Creek was least likely to support a population in the future. The tenuous status of the Harrison Creek population was further indicated by the lack of age-1 fish in that stream. There was less agreement between models and adult abundance estimates for streams with intermediate rankings. For example, Rabbit Creek had the third-highest abundance of the eight study streams but was ranked fifth to eighth by the models in terms of the probability of occurrence. Because trout populations vary in abundance from year to year, it is possible that we sampled Rabbit Creek during a year with unusually high abundance. It is also possible that habitat characteristics not accounted for in the Harig and Fausch (2002) models or the Morita and Yamamoto (2002) model may allow Rabbit Creek to support a larger population than the models predicted.

Rabbit Creek had the lowest mean July temperature among all eight study streams but had relatively high Colorado River cutthroat trout abundance. Interestingly, the two streams with the highest abundances, the NFLSR and West Branch, were also relatively cold compared with the other study streams. This apparent paradox could indicate that water temperatures in streams in the upper NFLSR are above the minimum required for consistent recruitment and growth of young cutthroat trout. July water temperatures across all streams in the upper NFLSR (average = 9.89°C)

were considerably higher than those in streams that failed to support the translocated cutthroat trout populations (average = 7.05°C) studied by Harig and Fausch (2002). Coleman and Fausch (2007b) reported slow growth and low recruitment of age-0 cutthroat trout in high-elevation streams with summer water temperatures below 8.5°C. Once minimum temperature requirements are satisfied, other stream habitat characteristics could become factors limiting cutthroat trout abundance in headwater stream systems.

The Harig and Fausch (2002) model based on watershed area was highly correlated with estimates of adult population size in our eight study streams. The Morita and Yamamoto (2002) model also uses watershed area as a predictor of fish occurrence; thus, it was not surprising that the outputs of their model were also correlated with our adult population estimates. Watershed area is an index of the amount of habitat available to isolated populations, and available habitat is an important determinant of trout abundance (Horan et al. 2000; Kruse et al. 2001; Young et al. 2005). Although trout abundance can be expected to increase with stream length, watershed area, or other measures of available habitat, the exact function of this relationship probably varies among regions, species, or even subspecies (Young et al. 2005). Differences in life histories between white-spotted char and Colorado River cutthroat trout or differences between the climate of the Rocky Mountains and the island of Hokkaido in Japan preclude strict application of the Morita and Yamamoto (2002) model to isolated cutthroat trout streams in the western United States. Harig and Fausch (2002) examined the persistence of newly established cutthroat trout populations, some of which disappeared over time because of unsuitable habitat, particularly cold water temperatures. Therefore, the models of Harig and Fausch (2002) may tend to underpredict the probability of persistence for naturally occurring cutthroat trout populations since native populations may be more adapted to local habitat conditions and occur in streams with sufficiently warm water temperatures.

This study highlights the remarkable ability of isolated populations of cutthroat trout to persist at low abundances for decades, but it also indicates that long-term persistence of smaller populations is unlikely. Extremely low population sizes, such as those observed in Harrison and Third creeks, indicate the vulnerability of some isolated populations to stochastic events and inbreeding depression. Translocating fish from larger populations (e.g., the West Branch) to smaller populations may temporarily increase genetic diversity and resilience to stochastic events (Hilderbrand 2002; Yamamoto et al. 2006). Translocated fish

can be lost from target populations by moving downstream over barriers (Schmetterling et al. 2002; Novinger and Rahel 2003), so the efficacy of a translocation program should be monitored. A longer-term strategy would be to reconnect isolated headwater streams to facilitate gene flow, but in the NFLSR drainage this strategy could lead to hybridization between pure Colorado River cutthroat trout populations and the introgressed cutthroat trout populations that occur downstream from the current barriers. An option would be to move barriers downstream to below the junctions of currently isolated streams to increase population sizes and available habitat, but this option would require successful removal of nonnative and introgressed fish downstream to the new barrier locations. Removal of fishes from long stream reaches, construction of effective and persistent barriers, and prevention of future illegal introductions possess associated risks and substantial costs. These kinds of cutthroat trout restoration projects should reconnect the most stream habitat possible but should also reconnect small streams that contain the most vulnerable populations.

Acknowledgments

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