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ARTICLE

Performance of Juvenile Cutthroat Trout Translocated as Embryos from Five Populations into a Common Habitat

Tessa C. Andrews[1]
Department of Ecology, Montana State University, Post Office Box 173460, Bozeman, Montana 59717, USA

Bradley B. Shepard*[2]
Montana Fish, Wildlife and Parks, Post Office Box 200701, Helena, Montana 59620, USA

Andrea R. Litt
Department of Ecology, Montana State University, Post Office Box 173460, Bozeman, Montana 59717, USA

Carter G. Kruse
Turner Enterprises, Inc., 901 Technology Boulevard, Bozeman, Montana 59718, USA

M. Lee Nelson
Montana Fish, Wildlife and Parks, 1420 East 6th Avenue, Helena, Montana 59620, USA

Patrick Clancey
Montana Fish, Wildlife and Parks, Post Office Box 1336, Ennis, Montana 59729, USA

Alexander V. Zale
U.S. Geological Survey, Montana Cooperative Fishery Research Unit, Montana State University, Post Office Box 173460, Bozeman, Montana 59717, USA

Mark L. Taper and Steven T. Kalinowski
Montana State University, Post Office Box 173460, Bozeman, Montana 59717, USA

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Abstract

The distributions of most native trout species in western North America have been severely reduced, and conservation of many of these species will require translocation into vacant habitats following removal of nonnative species. A critical question managers have is "Does it matter which donor sources are used for these translocations?" We present a case study that addressed this question for a large native trout translocation project in Montana. We introduced embryos from five source populations of Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi* to a large, fishless watershed in Montana following removal of nonnative fish with piscicides. Source populations providing embryos for translocations were three nearby (<120 km) wild populations, the state of Montana's captive Westslope Cutthroat Trout hatchery conservation population (initiated 32 years ago using fish from wild populations located >350 km from the translocation site), and a population in captivity for one generation comprised of individuals from the three wild populations used as single sources for this project, which were variably crossed (59% within populations and 41% between populations) to provide embryos. We

*Corresponding author: shepard.brad@gmail.com
[1]Present address: Department of Genetics, University of Georgia, C208A Davison Life Sciences Building, 120 East Green Street, Athens, Georgia 30602, USA.
[2]Present address: B. B. Shepard and Associates, 65 9th Street Island Drive, Livingston, Montana 59047, USA.
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used remote-site incubators at six different sites to introduce approximately 35,000 embryos from 400 genotyped parents. We later resampled and genotyped 1,450 of these individuals at age 1 and age 2. Juvenile survival for the more genetically diverse Montana Westslope Cutthroat Trout conservation population was twice as high as for other source populations, even though these other source populations were geographically closer to the translocation site than populations used to make the Montana Westslope Cutthroat Trout conservation population. Body weight for progeny from the two captive populations was higher than for progeny from wild source populations, and some differences were observed in body condition among source populations. Continued monitoring over several generations will be necessary to determine the eventual contributions of each source population and the relevance of these initial findings.

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The distributions of many inland native trout species in western North America have been severely reduced (Duff 1996; Rieman et al. 1997; Shepard et al. 1997, 2005; Thurow et al. 1997; Gresswell 2011; Muhlfeld et al. 2015), including the distribution of Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi*. Westslope Cutthroat Trout have been impacted significantly in the last 100 years by habitat loss, competition with nonnative species, and hybridization (Liknes and Graham 1988; Behnke 1992; Shepard et al. 1997, 2005). Nonintrogressed populations of Westslope Cutthroat Trout currently occupy only about 10% of their historical range in the United States (Shepard et al. 2005) and only 3% in the Missouri River drainage in Montana (Shepard et al. 1997). Despite these reductions, Westslope Cutthroat Trout are the most widely distributed subspecies of Cutthroat Trout *Oncorhynchus clarkii* and inhabit both sides of the Continental Divide in the USA and Canada (Behnke 1992; Shepard et al. 2005).

Translocations represent a potentially useful conservation tool for restoring native trout populations, including Westslope Cutthroat Trout populations (e.g., Harig et al. 2000; Harig and Fausch 2002; Al-Chokhachy et al. 2009; Dunham et al. 2011). One example of such a project is the Cherry Creek Cutthroat Trout Restoration Project, which involved introducing Westslope Cutthroat Trout embryos into suitable habitats within their historical range in southwestern Montana following the eradication of nonnative fish (Bramblett 1998; Shepard et al. 2005; Montana Department of Fish, Wildlife and Parks 2007). The purpose of this project was to create a genetically diverse Westslope Cutthroat Trout population in a secure refuge with enough high-quality habitat so that fish could move among different tributaries.

All managers considering translocation as a conservation tool must select an appropriate donor source population or populations for translocation (Griffith et al. 1989; Minkley 1995; Haight et al. 2000; George et al. 2009). Considerable discussion took place during the planning stages of the Cherry Creek Cutthroat Trout Restoration project concerning what populations should be used as sources for this translocation project. Managers faced a few challenges, including an extensive habitat to fill, a lack of nearby source populations, and small population sizes in regional populations of aboriginal Westslope Cutthroat Trout that could potentially be used as donor sources.

Genetic and species conservation theory suggest that the choice of source populations could affect project success (Stockwell et al. 1996, 2002; Case 2000). All Westslope Cutthroat Trout populations in the Missouri River basin in Montana are currently isolated from each other, and genetic differences among populations are often large, even among populations in relatively close proximity (Leary et al. 1987, 1988; Taylor et al. 2003; Young et al. 2004; Drinan et al. 2011). Such isolation may lead to local adaptation among populations. For example, Westslope Cutthroat Trout may adapt to local thermal regimes (Drinan et al. 2012) as water temperature strongly governs growth, development, reproductive cycles, migrations, and other life history traits important to the survival of trout (e.g., Xu et al. 2010).

But not all genetic differences among populations are adaptive. Wild populations of Westslope Cutthroat Trout have experienced genetic bottlenecks and are often isolated from gene flow by barriers to upstream movement, which creates conditions that promote inbreeding (Leary et al. 1988; Drinan et al. 2011). The effect of inbreeding is highly variable; some wild populations experience little (or no) reduction in fitness (e.g., Visscher et al. 2001), whereas others experience considerable reduction of fitness (e.g., Ralls et al. 1979; Lacy et al. 1996). The current lack of data on translocation projects limits our ability to learn from previous projects and apply that knowledge in the design and implementation of future projects (Oden et al. 2011; Vincenzi et al. 2012). This study presents initial results from an exemplary case study of a translocation project designed to conserve inland native trout, the largest Westslope Cutthroat Trout translocation project to date.

We evaluated the performance of juvenile Westslope Cutthroat Trout (hereafter, Cutthroat Trout) from five different donor source populations released at six different sites within Cherry Creek and its tributaries. Our specific objective was to determine whether juvenile survival, body weight, and body condition varied among individuals introduced from different donor sources. We also characterized the genetic variability in these donor populations. These results may inform fisheries managers considering future native trout translocations.

METHODS

Andrews et al. (2013) provided a detailed description of the study area and methods used to introduce Cutthroat Trout into

the study area. Here we provide a brief summary of that information and add details for methods not discussed by Andrews et al. (2013).

Project design and study area.—The study area included more than 60 km of upper Cherry Creek (45.467°N, 111.562°W) and its tributaries from Carpenter Creek upstream (Figure 1). The confluence of Carpenter Creek is located about 12 km upstream from an 8-m-high waterfall that prevents nonnative fishes from entering the 100-km project area (Bramblett 1998). Prior to the mid-20th century nonnative fishes had been introduced to Cherry Creek. We removed these fishes using the piscicides Antimycin A (Fintrol) and rotenone prior to the Cutthroat Trout translocation (Bramblett 1998). We introduced about 35,000 Cutthroat Trout embryos from five different source populations to two different sites during each of 3 years for a total of six distinct introduction sites (Figure 1). We chose these introduction sites to (1) spread fish throughout the watershed, (2) include sites with different temperature regimes (Table 1), and (3) enable selection of suitable habitat for remote-site incubators (RSIs; Andrews et al. 2013) to ensure embryo survival (e.g., rocky substrate to stabilize buckets and enough gradient to keep water consistently running through the incubators). The first two sites (Cherry Lake Creek and Cherry Creek) were the farthest upstream. Waterfalls near their confluence prevented upstream fish movement into stream reaches seeded by these first two introduction sites (Figure 1). We made additional introductions lower in the basin during each subsequent year.

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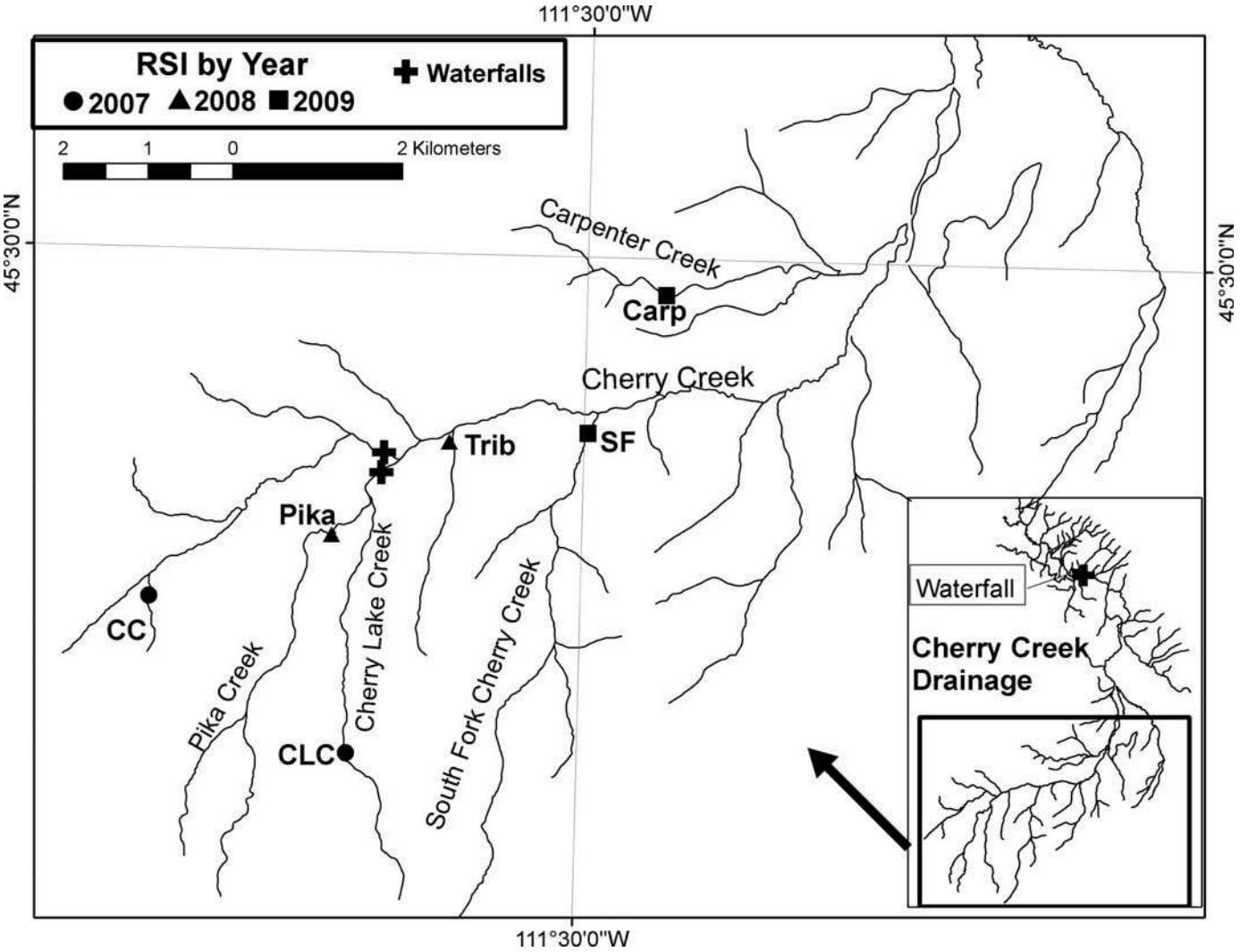

FIGURE 1. Upper Cherry Creek study area showing locations by year where Westslope Cutthroat Trout embryos were introduced in remote stream incubators (RSIs) during 2007 (solid circles), 2008 (triangles), and 2009 (squares) and waterfalls that prevented upstream fish movements. Abbreviations used to identify each RSI introduction site are shown in bold text adjacent to each site location. Inset map shows the Cherry Creek drainage with the lower large waterfall that was the lower boundary of the restoration project and the portion of the upper basin where this study occurred. CLC = Cherry Lake Creek, CC = Cherry Creek, Pika = Pika Creek, Trib = unnamed tributary, Carp = Carpenter Creek, SF = South Fork Cherry Creek.

TABLE 1. Average daily water temperature (°C) in July and August by year for streams that contain wild Westslope Cutthroat Trout source populations and for introduction sites within the Cherry Creek basin (ordered from coldest to warmest). We did not have water temperature data for every day of both months, so the number of days when temperatures were measured is shown for each monthly mean. Abbreviations in parentheses after stream names correspond to abbreviations used to identify the RSI sites.

Source and introduction sites	Year	Mean (SE), number of days	
		July	August
Wild source population creeks			
Ray Creek	2007	9.1 (0.12), 31	8.7 (0.11), 31
	2008	6.3 (0.16), 31	7.5 (0.10), 31
	2009	6.3 (0.12), 31	7.4 (0.12), 31
Muskrat Creek	2007	10.2 (0.14), 31	8.4 (0.19), 31
	2008	7.2 (0.18), 31	7.6 (0.14), 31
White's Creek	2006	8.7 (0.03), 31	8.6 (0.03), 31
	2008	8.3 (0.03), 31	8.5 (0.03), 31
	2009	7.9 (0.04), 31	8.3 (0.04), 31
Introduction sites			
Cherry Lake Creek (CLC)	2006	10.4 (0.21), 31	9.2 (0.25), 31
	2007	9.0 (0.38), 31	9.9 (0.09), 23
	2008	7.6 (0.26), 23	8.1 (0.18), 31
	2010	7.5 (0.36), 31	8.4 (0.28), 31
South Fork (SF)	2009	9.0 (0.23), 12	8.5 (0.16), 31
	2010	8.7 (0.14), 23	8.2 (0.19), 31
Unnamed tributary (Trib)	2008	10.7 (0.44), 3	8.6 (0.52), 7
Pika Creek (Pika)	2009	9.2 (0.23), 21	9.5 (0.23), 31
	2010	8.0 (0.32), 31	9.2 (0.24), 31
Carpenter Creek (Carp)	2009	11.6 (0.30), 11	10.8 (0.22), 31
	2010	12.0 (0.14), 22	10.6 (0.25), 31
Upper Cherry Creek (CC)	2008	12.1 (0.21), 22	11.3 (0.22), 31
	2009	13.4 (0.26), 22	12.2 (0.27), 31
	2010	13.6 (0.22), 31	11.7 (0.37), 31

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Water temperatures varied among the introduction sites and among streams occupied by source populations (Table 1). Water temperatures were recorded hourly (Onset Optic Stowaway, HOBO TempPro; www.onsetcomp.com) in all streams except an unnamed tributary that was one of the six introduction sites. Hourly data for the unnamed tributary were lost, but we recorded daily stream temperature during every visit to this site. We summarized average daily temperatures for the months of July and August to compare habitats.

Source populations.—Managers used five populations as Cutthroat Trout sources. These included three wild populations located east of the Continental Divide, crosses within and between these wild populations that spent one generation in captivity, and the state of Montana's Westslope Cutthroat Trout conservation hatchery population. The three wild source populations originated from Ray, Muskrat, and White's creeks in the Missouri River drainage (<120 km from Cherry Creek). These were the nearest nonhybridized populations east of the Continental Divide in Montana that could provide enough embryos without unduly affecting the populations. Average July and August water temperatures of the three wild source streams ranged from 6.3°C to 9.1°C (Table 1). We screened all wild sources for genetic purity and disease pathogens (Andrews et al. 2013).

Captive sources were from Montana's Washoe Park Hatchery (hereafter, WPH) and a brood pond located at the Sun Ranch (hereafter, SR) within the Madison River basin. Washoe Park Hatchery houses Montana's Westslope Cutthroat Trout conservation brood, which was originally created in 1983–1984 by mixing 14 wild populations (~6,400 fish) from west of the Continental Divide (>350 km from Cherry Creek). The WPH brood has been periodically infused with wild gametes and is operated to limit hatchery selection. We initially designed our study to test only first-generation captivity effects and not the effect of within- versus between-population crosses. However, the SR brood consisted of first-generation adults raised from embryos obtained from three wild sources (Ray, Muskrat and White's creeks), and these adults were crossed to create the embryos used for the Cherry Creek translocation project. We used post hoc genetic back-assignment to determine

TABLE 2. Count of Westslope Cutthroat Trout parental crosses by year from Sun Ranch brood by stream of origin based on genetic back-assignment. Embryos from Sun Ranch were only introduced in 2007 and 2008.

	Year spawned	
Mating pairs by stream origin	2007	2008
Ray × Ray	9	2
Ray × Muskrat	2	7
Ray × White's	2	
Muskrat × Muskrat	1	4
Total pairs	14	13

the parental sources of the translocated embryos (Table 2) but were not able to evaluate the influence on juvenile performance of within- versus between-population crosses from the SR brood.

Embryo collection, incubation, and introduction.—We collected embryos by artificially spawning adults from each population from 2007 to 2009 (Table 3). We captured adults from wild populations using a backpack electrofisher. At SR we captured adults from the brood pond with seines. Adults collected from streams and the SR pond were confined in enclosures on-site until they were ready to spawn. Because ambient water temperatures regulated the timing of spawning, the collection of gametes followed a predictable pattern with SR fish maturing earliest each season, followed by the three wild sources (Tables 1, 2). Water temperatures in WPH were regulated to ripen adult fish and incubate embryos so that embryos from WPH were ready for introduction at the same time as were embryos from wild sources and SR.

A single female's eggs were generally split into two nearly equal lots, and each lot was fertilized with milt from a different male. Eggs from a few females were fertilized by one, three, or four males. After spawning, we clipped each adult's dorsal fin as a mark to ensure each wild fish contributed gametes only once. We also collected pelvic fin tissue for genetic analysis to identify each parental pair to back-assign juveniles to their parental pair. We followed the same spawning procedure for all fish contributing gametes to Cherry Creek (Andrews et al. 2013).

Newly fertilized eggs (embryos) from the wild were moved to the SR facility where they were incubated to the eyed stage in vertical incubators (Heath Trays) before being moved to RSIs located at introduction sites within the Cherry Creek drainage (Andrews et al. 2013). The RSIs supply embryos with fresh water and avoid sedimentation problems associated with buried incubators and have been used previously to successfully introduce other species of salmonid embryos (e.g., Donaghy and Verspoor 2000; Kaeding and Boltz 2004; Al-Chokhachy et al. 2009). Hatched fry absorbed the yolk sac in the RSI, and after swim-up, they exited the incubators through an outflow water tube that flowed into a 19-L (5 gal) bucket. Fry were then counted and released into slow-moving water.

The number of embryos from each source varied annually depending on the availability of ripe adults (Table 3). No embryos were available from SR in 2009. Otherwise, embryos from all source populations were introduced to all sites (Table 3). Embryos from each female were generally split between the two sites used for introductions during each year. Embryos from different sources reached the eyed stage at different times, so embryos were introduced over a 4- to 6-week period each summer (Table 3). Washoe Park Hatchery provided embryos for almost every introduction day, except during 2007 when they were only available earlier in the summer (Table 3). In both 2008 and 2009, WPH embryos were cooled to slow development in order to ensure their availability for introduction at the same time as embryos from other populations.

Juvenile sampling.—We sampled juvenile Cutthroat Trout in Cherry Creek by backpack electrofishing (two to four person crews) during the late summers of 2008, 2009, and 2010 to estimate their survival, body weight, and body condition. Each year we sampled near the two sites into which we had introduced embryos the previous year to capture age-1 individuals (i.e., we sampled near the two 2007 introduction sites in 2008). In 2009, we also sampled near the two 2007 introduction sites to capture age-2 fish. At each introduction site, we began sampling at the location of the RSIs and attempted to sample throughout the reach occupied by introduced fish. We used a systematic sampling design with a nonrandom start. We sampled 100-m sections every 300 m for about 0.6 km above and 1.5 km below RSI sites. At that point, we decreased our sampling frequency to sample one 100-m section per 500 m of stream. We continued sampling downstream from the RSI sites until few or no fish were found in several sequential sections. We weighed (g), measured TL (mm), and removed a small portion of the pelvic or anal fin of each fish for subsequent genetic analysis before releasing the fish within 100 m of its capture location.

Genetic analysis and parentage assignment.—We genotyped 400 adults that donated gametes to the Cherry Creek restoration project and 1,455 juvenile fish captured in Cherry Creek. We used genetic markers to identify the parents—and thereby the source population—of juveniles. We extracted genomic DNA using Qiagen DNeasy Blood and Tissue Kits (Qiagen, Valencia, California). We genotyped 12 microsatellite loci (Vu and Kalinowski 2009) and scored genotypes using Genemapper version 3.7 (Applied Biosystems, Carlsbad, California). All captured juveniles were assigned to parent pairs using the Mendelian exclusion method (e.g., Araki et al. 2007; Muhlfeld et al. 2009). Assigning juveniles to a parent pair also confirmed the age of the juvenile because different parent pairs were used each year.

Back-assignment of salmonid progeny to parents has been done in the past, but these studies did not have the advantage

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TABLE 3. Summary of Westslope Cutthroat Trout embryo introductions into the upper Cherry Creek basin by year, introduction site (abbreviations for sites), donor source, number of parental pairs, mean TL (mm), number of embryos introduced into remote stream incubators, number of fry released at each site, and range of dates when eyed eggs were introduced. The total numbers of fry released each year (in bold italics) were computed by summing the numbers counted leaving each remote stream incubator.

Year	Site (abbreviation)	Donor	Number of pairs	Mean TL of females	Number of embryos	Number of fry released	Date range
2007	Cherry Lake Creek (CLC)	Muskrat	11	219	2,655		Jul 12–16
		Ray	12	197	1,548		Jul 16–24
		Sun Ranch	7	406	1,522		Jun 19–28
		Washoe	21[a]		568		Jun 22–Jul 10
		White's	5	194	664		Jul 10–17
		Total	***35***		***6,957***	***5,231***	
2007	Cherry Creek (CC)	Muskrat	11	219	2,790		Jul 12–16
		Ray	13	195	1,919		Jul 16–24
		Sun Ranch	7	406	1,553		Jun 19–28
		Washoe	21[a]		553		Jun 22–Jul 10
		White's	3	192	351		Jul 10–17
		Total	***34***		***7,166***	***5,476***	
2008	Pika Creek (Pika)	Muskrat	13	204	1,583		Jul 19–28
		Ray	11	198	890		Jul 14–Aug 7
		Sun Ranch	7	397	1,712		Jul 4
		Washoe	18	273	1,251		Jul 6–28
		White's	4	184	409		Jul 4–19
		Total	***53***		***5,845***	***4,385***	
2008	Unnamed tributary (Trib)	Muskrat	14	202	1,621		Jul 19–28
		Ray	12	200	810		Jul 14–Aug 7
		Sun Ranch	6	397	1,565		Jul 4
		Washoe	20	274	1,394		Jul 6–28
		White's	5	180	565		Jul 4–24
		Total	***57***		***5,955***	***4,746***	
2009	South Fork Cherry Creek (SF)	Muskrat	10	207	1,891		Jul 19–21
		Ray	10	195	889		Jul 26–Aug 4
		Washoe	6	258	922		Jul 19–Aug 4
		White's	4	187	322		Jul 21
		Total	***30***		***4,024***	***2,837***	
2009	Carpenter Creek (Carp)	Muskrat	14	202	2,113		Jul 19–21
		Ray	10	195	1,022		Jul 26–Aug 4
		Washoe	6	280	792		Jul 19–Aug 4
		White's	4	190	314		Jul 21
		Total	***34***		***4,241***	***2,850***	

[a] Embryos from 21 parent pairs were mixed and introduced into both Cherry Creek and Cherry Lake Creek.

of having DNA samples of all adults that contributed to the population (Stevens et al. 1993; Leung et al. 1994; Hudy et al. 2010; Vollestad et al. 2012; Kanno et al. 2014). Here, we successfully assigned 87.9% (n = 1,279) of the juveniles to a single parent pair. Including missing data for a locus as a mismatch, any juveniles that could not be matched to at least one parent pair with 10 or more loci (out of 12) were excluded from analysis. This resulted in the removal of 5.8% of our sample, or 84 individuals (with 34 of these being removed due to incomplete genotypes). Some juveniles were assigned to more than one parent pair with an equal number of two or fewer mismatches. In these cases, we accepted the assignment to each parent pair and fractionally allocated the juveniles to parent pairs for the analysis of survival data. For example, if a juvenile was assigned to two parent pairs, we would assign 0.5 juvenile to each parent pair. Ninety-two individuals (6.3%)

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were assigned to two or more parent pairs. These individuals were excluded from analyses on body weight and condition because they could not be assigned to a single parent pair. The unit of analysis for body weight and condition models was the individual; to include individuals that were assigned with equal confidence to more than one parent pair, we would have to include these individuals once for each parent pair, which would violate the model assumption of independence of errors. We were able to retain these individuals for our analysis of survival rates because the unit of analysis was the parent pair rather than individual juveniles.

We also examined genetic variation in each of our source populations using several estimators. We calculated average expected heterozygosity (Nei 1978). We estimated F_{ST}, which is a measure of population differentiation (Frankham et al. 2003), with Weir and Cockerham's (1984) estimator using Genepop (available at http://kimura.univmontp2.fr/~rousset/Genepop.htm). We also calculated allelic richness using HP-Rare, a program that accounts for differences in sample size (Kalinowski 2005; available at http://www.montana.edu/kalinowski/Software/HPRare.htm).

Estimating relative survival, weight at age, and body condition.—In estimating the survival rate for each parent pair, we applied a continuity correction recommended for binomial proportions by Agresti and Coull (1998). This correction allowed us to deal with zeros in our data, which were common. We applied this correction by calculating survival rate for each parent pair as

$$\frac{X_s}{n_s}\left(\frac{n_s}{n_s+z^2}\right)+\frac{1}{2}\left(\frac{z^2}{n_s+z^2}\right),$$

where X_s = number of age-1 or age-2 juveniles captured that were assigned to a parent pair and introduction site s, n_s = number of embryos introduced from that parent pair in introduction site s, and z = upper critical value of the normal distribution, or 1.9599 when alpha = 0.05.

We then calculated relative survival as a ratio of the survival rate for a parent pair (calculated as described above) divided by the median survival rate—calculated with the same continuity correction—of all WPH parent pairs introduced to the same introduction site in the same year. We refer to this ratio of relative survival as "survival ratio." When we refer to "survival rate," we are indicating the percent survival for a single population.

We calculated a survival ratio because we could not assume that capture efforts and efficiencies were equal across introduction sites due to variation in habitat features and variation in sampling crews across years. We considered WPH was an appropriate baseline because our sample design ensured that embryos from this population were introduced at all sites and across a wider timeframe each year (Table 3) than the embryos from the other sources.

We examined differences in weight and body condition at the level of the individual, rather than at the level of the parent pair, to investigate individual variation. We collected these data by weighing (g) and measuring (mm) juveniles captured during late summer sampling.

We calculated Fulton's condition factor K as weight (g) $\times 10^5$ /TL^3 (mm) for each individual and evaluated these estimated condition factors by age-class for age-1 and age-2 individuals. The assumption of cubic growth made by the Fulton-type condition factor was verified because the slope of a simple linear regression of log(weight) versus log(length) of captured fish was near 3.0 (2008: 95% CI of slope = 3.02–3.10, n = 500; 2009: 95% CI of slope = 2.98–3.03, n = 795; Pope and Kruse 2007). Fulton's condition factor estimator was used rather than relative weight (W_r) because we were comparing relative conditions of individual fish among donor sources within each of the two age-classes that had relatively narrow length ranges and comprised mostly fish smaller than recommended for use with published standard weight (W_s) equations.

Statistical analysis of survival, weight, and body condition.—We used linear mixed models to compare the relative performance of source populations using estimated survival ratio, weight, and body condition of first-generation juveniles as the response variables (Table 4). We applied a log transformation to each of these response variables. In addition to testing for an association between performance metrics and the source population, the statistical models we used controlled for the structure of our data and potential confounding variables. All models included donor source population, introduction site, and the interaction between donor source population and introduction site as fixed, categorical effects (Table 4). Linear mixed models can control for a lack of independence caused by clustering or repeated sampling (Gelman and Hill 2007). In our study design, RSIs were nested within introduction sites, and two different parent pairs could share a common female. We accounted for this hierarchical structure by including random effects in our models (Gelman and Hill 2007; Table 4). We also included year as a categorical, random effect in models of the performance of age-1 individuals to account for variation in the response variable attributable to year (Gelman and Hill 2007; Table 4). We used SAS to complete all statistical analyses (SAS Institute 2011) and R to create graphs (R Development Core Team 2008).

For each response variable, we considered age-1 and age-2 individuals separately. Two differences existed between models for age 1 and age 2: the numbers of introduction sites that were included and whether year was included as a random effect. Models for age-1 juveniles included six introduction sites, whereas models for age-2 juveniles included two introduction sites. All fish that were age 2 at capture were introduced during the same year, precluding the need to include introduction year as a random effect in the models for age-2 juveniles (Table 4).

TABLE 4. Descriptions of linear mixed models by response variable.

Age-group	Unit of analysis	*N*	Fixed explanatory variables (number of levels)	Random explanatory variables	Hierarchical structure
			Log survival ratio		
Age 1	Lot	186	Population (4) Introduction site (6) Population × Introduction site	Introduction year RSI	RSI nested within introduction site Subject = female[a]
Age 2	Lot	67	Population (4) Introduction site (2) Population × Introduction site	RSI	RSI nested within introduction site Subject = female[a]
			Log weight at age (g)		
Age 1	Individual	701	Population (5) Introduction site (5) Population × Introduction site Stream width Dispersal distance	Introduction year RSI	RSI nested within introduction site Subject = female[a] Parent pair nested within female
Age 2	Individual	270	Population (5) Introduction site (2) Population × Introduction site Dispersal distance	RSI	RSI nested within introduction site Subject = female[a] Parent pair nested within female
			Log Fulton's condition factor *K*		
Age 1	Individual	912	Population (5) Introduction site (6) Population × Introduction site	Introduction year RSI	RSI nested within introduction site Subject = female[a] Parent pair nested within female
Age 2	Individual	270	Population (5) Introduction site (2) Population × Introduction site	RSI	RSI nested within introduction site Subject = female[a] Parent pair nested within female

[a] Embryos from a single female are not independent. Including female as a subject effect accounts for this lack of independence in our models by adjusting the covariance structure.

We used a two-step analysis. We began by fitting a full linear mixed model that included an interaction between introduction site and source population for each response variable because juvenile performance could vary among source populations at one introduction site, but all source populations could perform similarly at another. In this case, an interaction between introduction site and source population would be significant because the patterns of the response variable among source populations varied across introduction sites. When a significant interaction existed (i.e., P-value < 0.05), we did not interpret the main effects of source population because this is not meaningful when an interaction between source population and introduction site is present (Ramsey and Schafer 1997). Instead, we compared the performance of source pouplations within a single site using Tukey's honestly significant difference (HSD) tests, also called the Tukey–Kramer method, a single-step multiple comparisons procedure.

For models without a significant interaction (i.e., P-value > 0.05), we proceeded to the second step of analysis, i.e., fitting a "reduced" model that excluded the interaction to test for a main effect of source population on performance. For all models, we back-transformed estimates to compute median values and associated 95% CIs and presented these data in graphs. We tested for differences among source populations using Tukey's HSD tests. Familywise error rate for multiple comparisons was alpha = 0.05.

Interpretation of results from our modeling of survival ratio required one additional step. Since WPH was used as the baseline population in our calculation of survival ratio, we did not include WPH as a level of the "population" variable in our models (Table 4). Therefore, the estimates

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of main effects of population produced by the regression models of survival of age-1 and age-2 fish do not take into account differences in survival rate between WPH and other populations. To make comparisons in survival between WPH and other populations, we plotted median survival ratio estimates and 95% CIs produced by the models. Estimated survival ratios equal to one indicate that individuals from that population survived at the same rate as individuals from WPH. If the upper confidence limit of the survival ratio of population "A" is below one then it is legitimate to conclude that population A survives significantly less well than that from the WPH. If the lower confidence limit of the survival ratio of population "A" is above one, it is legitimate to conclude that population "A" survives significantly better than that from the WPH.

Weight models included additional explanatory variables to account for potential effects of density on growth (Table 4). Individuals in our study site varied in the degree to which they dispersed (Andrews et al. 2013). Because this was a fishless habitat, dispersing individuals were likely to encounter habitats with fewer individuals (i.e., lower densities) and therefore less competition for resources than more sedentary individuals. Fish that moved farther downstream may also have benefited from warmer, more productive habitat. Therefore, their weights may have been influenced by dispersal distance. We calculated dispersal distance as the stream distance in meters between the location where fry were released (i.e., introduction site) and their capture location at age 1 or age 2. Dispersal distance did not take into account the direction of dispersal (i.e., upstream or downstream), but the vast majority of individuals dispersed downstream (Andrews et al. 2013). We also included stream width at capture location as a proxy for available habitat in the model for weight at age 1. We did not include stream width in the analysis of the model for weight at age 2 because stream width and dispersal distance were significantly correlated at age 2 ($r = 0.62$, $t_{248} = 12.26$, $P < 0.0001$) and would therefore create a redundancy in the model. Stream width and dispersal distance were not significantly correlated at age 1 ($r = -0.028$, $t_{706} = -0.75$, $P = 0.455$). Dispersal distance data were unavailable for one of the six introduction sites (Carpenter Creek) because sampling locations were not recorded, so the analysis of weight at age 1 included data from only five introduction sites.

RESULTS

Genetic Analyses

Allelic richness and average heterozygosity were highest in adult Cutthroat Trout from the WPH population and lowest in adults from White's Creek (Table 5). The value for F_{ST} was 0.27, indicating substantial genetic differentiation among source populations. Across populations, 76.8% ($N = 215$ of 280) of the parent pairs that donated gametes contributed to the age-1 and age-2 juveniles we captured.

Relative Survival

We did not detect an interaction between introduction site and source population, meaning the patterns of median survival ratio of age-1 individuals among populations were the same at all introduction sites ($F_{13,\ 66} = 1.35$, $P = 0.2084$). After removing the interaction, the median survival ratio did not vary by source population ($F_{3,\ 66} = 0.90$, $P = 0.4466$). Recall that this estimate does not take into account differences between WPH fish and other populations since the WPH population was used as the baseline population in our calculation of survival ratio. Plots of estimated medians from the linear regression model allowed us to make these comparisons (Figure 2). The other four populations that contributed embryos to this system had survival ratios of around 0.5 with upper confidence limits below one, indicating they had significantly lower survival than WPH fish (Figure 2).

For age-2 juveniles, we did not detect differences in the patterns of relative survival among populations at both introduction sites ($F_{3,\ 21} = 0.48$, $P = 0.7022$). After removing the interaction between introduction site and source population, we did not detect differences in relative survival across source populations ($F_{3,\ 21} = 0.65$, $P = 0.5946$; Figure 3). As at age 1, the estimates of the survival ratio for age-2 individuals from Muskrat Creek, Ray Creek, White's Creek, and SR had upper confidence limits well below one, indicating age-2 individuals from these sources

TABLE 5. Results of molecular analyses and parentage assignment of Westslope Cutthroat Trout, by source population.

Variable	Muskrat Creek	Ray Creek	White's Creek	Sun Ranch	Washoe Park Hatchery
Average allelic richness[a]	4.91	2.91	2.17	5.00	17.27
Expected heterozygosity[a]	0.59	0.33	0.28	0.55	0.80
Number of parent pairs identified for sampled juveniles	61	48	23	17	65
Proportion of parent pairs contributing to sample	0.84	0.71	0.92	0.68	0.74

[a] Values are calculated for all adults that contributed gametes, rather than just those identified as parents of sampled juveniles.

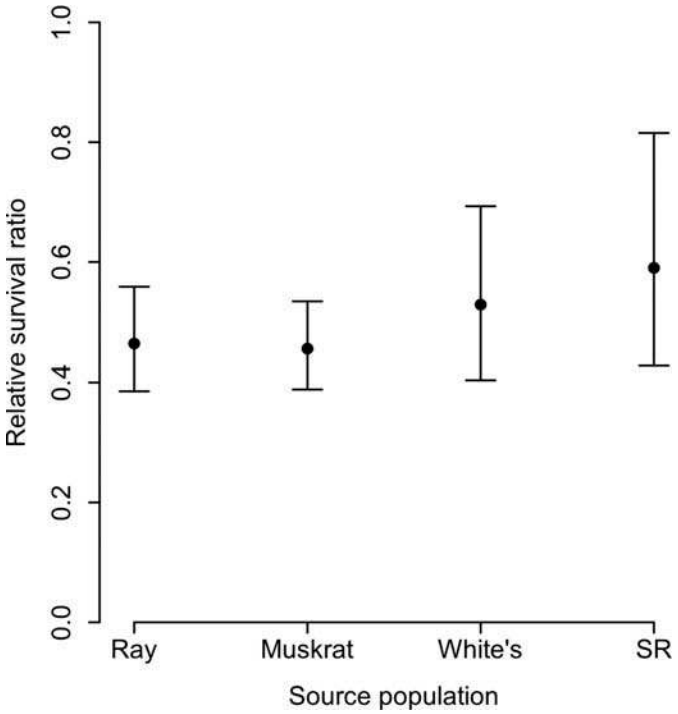

FIGURE 2. Estimated median survival ratio of Westslope Cutthroat Trout and associated 95% CIs by source population at age 1. Each estimate of survival ratio is a ratio of the survival of the population listed on the *x*-axis divided by the survival of Washoe Park Hatchery in that introduction site. SR = Sun Ranch, WPH = Washoe Park Hatchery.

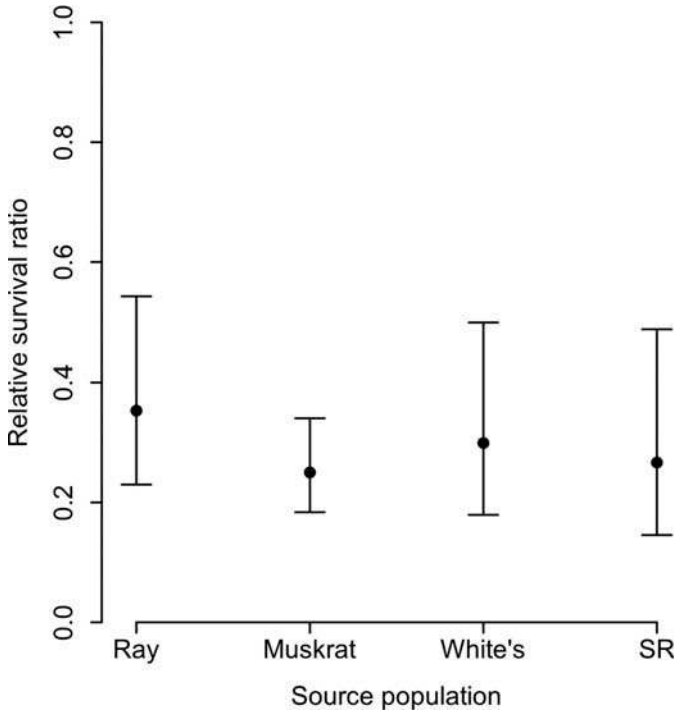

FIGURE 3. Estimated median survival ratio of Westslope Cutthroat Trout and associated 95% CIs by source population at age 2. Each estimate of survival ratio is a ratio of the survival of the population listed on the *x*-axis divided by the survival of Washoe Park Hatchery in that introduction site. SR = Sun Ranch, WPH = Washoe Park Hatchery.

had significantly lower survival than age-2 individuals from the WPH (Figure 3).

Weight at Age

Weights of fish at age 1 and age 2 were strongly correlated with dispersal distance (age 1: $r = 0.54$, $t_{825} = 18.66$, $P < 0.0001$; age 2: $r = 0.61$, $t_{278} = 12.80$, $P < 0.0001$), so dispersal distance was included as a variable in models estimating weights at age (Table 4). At age 1, we did not detect an interaction between introduction site and source population, meaning the patterns of median weight estimates of age-1 individuals among populations were the same at all introduction sites ($F_{13,\ 600} = 1.31$, $P = 0.2038$). We found significant differences existed in median weights of age-1 individuals among populations, after excluding the interaction between source population and introduction site ($F_{4,\ 607} = 28.25$, $P < 0.0001$; Figure 4). Using the Tukey–Kramer HSD test for multiple comparisons, we found that fish from SR were significantly heavier than fish from Muskrat Creek ($t_{607} = 9.10$, $P < 0.0001$), Ray Creek ($t_{607} = 6.71$, $P < 0.0001$), White's Creek ($t_{607} = 7.19$, $P < 0.0001$), and WPH ($t_{607} = 3.60$, $P = 0.0032$). We also found that fish from WPH were significantly heavier than fish from Muskrat Creek ($t_{607} = 5.83$, $P < 0.0001$), Ray Creek ($t_{607} = 3.97$, $P = 0.0008$), and White's Creek ($t_{607} = 5.14$, $P < 0.0001$). There were no other significant differences (Figure 4).

At age 2, we detected an interaction between source population and introduction site ($F_{4,\ 220} = 2.51$, $P = 0.0432$; Figure 5). We therefore compared populations within the two introduction sites. Individuals from SR were heavier at age 2 than individuals from Muskrat Creek ($t_{220} = 5.41$, $P < 0.0001$), Ray Creek ($t_{220} = 4.98$, $P < 0.0001$), and White's Creek ($t_{220} = 4.38$, $P = 0.0008$) in the cooler introduction site (Cherry Lake Creek), but there were no other differences among populations within this site and no significant differences among any populations in the warmer introduction site (Cherry Creek).

Body Condition

We did not detect an interaction between introduction site and source populations at age 1, meaning the patterns of median body condition estimates among populations were the same at all introduction sites ($F_{17,\ 793} = 1.03$, $P = 0.4263$). Excluding the interaction, the median condition of age-1 individuals differed among populations ($F_{4,\ 802} = 3.42$, $P = 0.0088$). Tukey–Kramer HSD tests showed that individuals from WPH were in significantly better condition than individuals from one of the wild populations, Muskrat Creek, ($t_{802} = 3.56$ $P = 0.0035$), but there were no other significant differences among populations (Figure 6).

For age-2 individuals, a significant interaction existed between introduction site and source population ($F_{4,\ 221} =$

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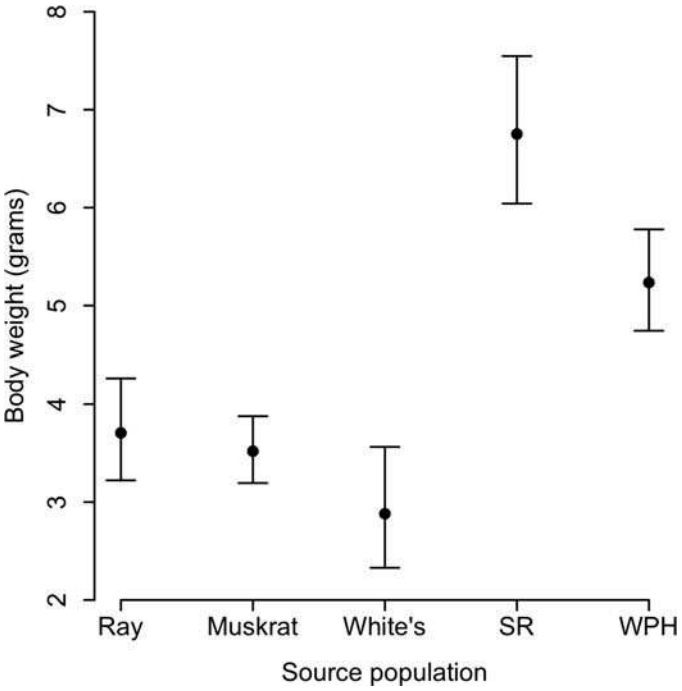

FIGURE 4. Estimated median weight (g) of Westslope Cutthroat Trout and associated 95% CIs at age 1 by source population. Introduction sites are arranged from coldest to warmest. SR = Sun Ranch, WPH = Washoe Park Hatchery.

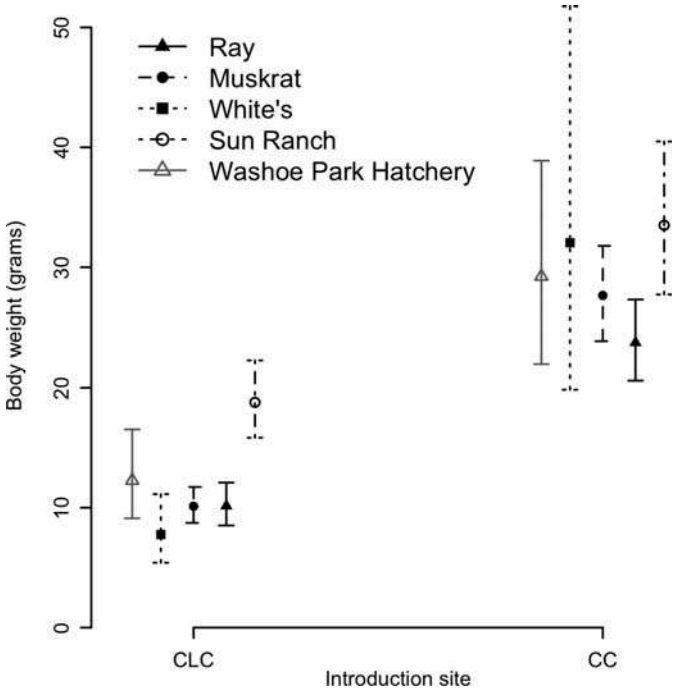

FIGURE 5. Estimated median weight (g) of Westslope Cutthroat Trout and associated 95% CIs at age 2 by source population. Introduction sites are arranged from coldest to warmest. CLC = Cherry Lake Creek, CC = Cherry Creek.

2.47, $P = 0.0455$; Figure 7). Tukey–Kramer HSD tests showed that age-2 individuals from the Muskrat Creek population were in better condition than individuals from the Ray Creek population ($t_{221} = 3.78$, $P = 0.0077$) in the warmer of the two introduction sites (Cherry Creek) but not in the cooler site (Cherry Lake Creek). There were no other significant differences among populations within Cherry Creek or among populations within Cherry Lake Creek (Figure 7).

DISCUSSION

We monitored progeny from five different source populations of Westslope Cutthroat Trout introduced at six different locations in a fishless habitat. Survival of first-generation age-1 and age-2 juveniles from the captive brood at WPH was about twice as high as survival rates of juveniles from the other source populations, and this difference increased slightly from age 1 to age 2 (Figures 2, 3). Genetic diversity is often associated with increased fitness among individuals, or, conversely, loss of genetic diversity is often associated with low fitness among individuals (e.g., Hedrick and Kalinowski 2000). The WPH population had a higher level of heterozygosity and more unique alleles than the wild populations of Cutthroat Trout introduced into the Cherry Creek basin (Table 5). This high level of genetic diversity in the WPH donor adults could have allowed for higher survival and growth of some of their progeny. The wild populations used in this study are known to have gone through population bottlenecks (Andrews et al. 2013), and, like many populations of Cutthroat Trout in the Missouri River watershed, have relatively low levels of genetic diversity (Drinan et al. 2011). In contrast, the WPH population was created by combining 14 populations of Cutthroat Trout from the Clark Fork River watershed in the Columbia River basin.

A second potential explanation for the higher survival of WPH fish is that progeny from captive populations at WPH had higher median weights at age 1 than did individuals from the wild populations (Figure 4), and this increased body size may have conferred a survival advantage. If greater size lent a competitive advantage to the Cutthroat Trout in this system, we would have expected to see that individuals from SR have even better survival than individuals from WPH because age-1 individuals from SR were significantly heavier than individuals from any other population, including those from WPH (Figure 4). This was not the case; survival of individuals from SR was similar to the wild populations, and significantly lower than survival of WPH individuals (Figure 2).

A related explanation is that in 2007 embryos from WPH were introduced earlier in the season than individuals from the wild populations, potentially providing a survival advantage by allowing more time to gain weight prior to winter. However, individuals from SR were also introduced earlier

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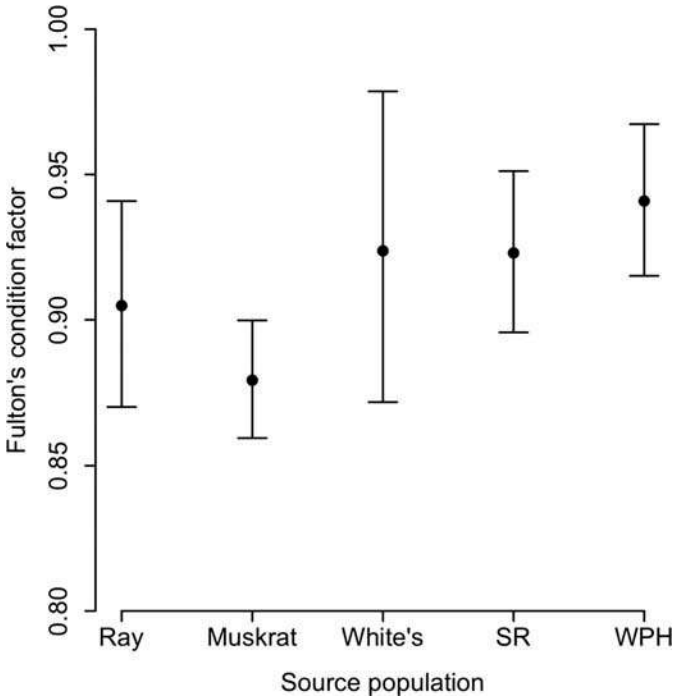

FIGURE 6. Estimated median Fulton's condition factor *K* of Westslope Cutthroat Trout and associated 95% CIs by source population at age 1. Introduction sites are arranged from coldest to warmest. SR = Sun Ranch, WPH = Washoe Park Hatchery.

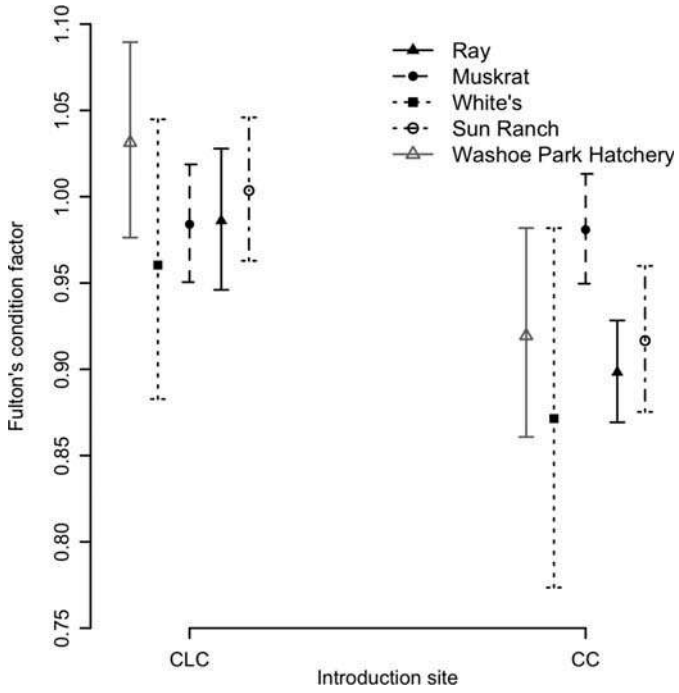

FIGURE 7. Estimated median Fulton's condition factor *K* of Westslope Cutthroat Trout and associated 95% CIs across source populations and introduction sites at age 2. Introduction sites are arranged from coldest to warmest. CLC = Cherry Lake Creek, CC = Cherry Creek.

than individuals from other populations in 2007, and they did not enjoy the same survival advantage. Our age-2 analysis only included individuals introduced in 2007 and so might provide a clearer picture of the effect of early introduction of WPH embryos. We saw the same patterns at age 2, but it was more extreme. The SR and the wild populations have significantly lower survival than WPH fish (Figure 3), again suggesting that the early introduction is an insufficient explanation for the high survival of WPH, as SR individuals were also introduced early in the season in (Table 3).

The higher estimated median weights at age 1 for captive populations (SR and WPH) might have been related to greater initial weights of the fry due to the larger sizes of their female parents. The mean lengths of SR females that provided eggs were 406 mm in 2007 and 397 mm in 2008, whereas the range of mean lengths of female egg donors from the three wild populations was 184 to 219 mm and mean lengths of WPH donor females were between 250 and 300 mm (Table 3). Many studies have observed a positive relationship between size of a female salmonid and the size of her eggs (e.g., Beacham and Murray 1985, 1990; Einum and Fleming 1999; Quinn et al. 2004, 2011; Beacham 2010), but a few studies found no relationships (e.g., Scott 1962). Beacham and Murray (1990) found a direct relationship between egg weight and fry weight. Some studies found that larger egg size translated to increased growth or survival (e.g., Burton et al. 2013), but in other studies it did not (e.g., Barnes et al. 2000; Lobon-Cervia 2000). Another possible reason for greater median weights of age-1 progeny from SR is that SR embryos were introduced 2 to 3 weeks earlier than embryos from the three wild donor sources and would have had more days to put on weight during their first year. We did not measure eggs or fry that left the RSIs because we had limited numbers of gametes for introduction and we were concerned about potential handling mortality.

In summary, the larger body weight at age 1 and age 2 of individuals from captive populations (SR and WPH) compared with wild populations may have been influenced by the mother's size and, in some cases, by earlier introduction of embryos into the study site. However, differences in body size, mother's size, and timing of introduction are insufficient to explain observed differences in survival rate.

Considerations for Selecting Donor Sources in Translocation Projects

Reproductive success is the ultimate measure of translocation outcomes and will therefore be the most reliable metric for evaluating the long-term success of this or any other translocation project (Anderson et al. 2014). It is feasible that maternal effects and phenotypic plasticity contributed to the juvenile outcomes we observed. In subsequent generations, the

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performance of fish descended from different source populations may differ after reproduction occurs in the wild and as fish densities reach carrying capacity and intraspecific competition becomes more intense (Vincenzi et al. 2010; Parra et al. 2011). We caution that more research is needed both over a longer time period (evaluating second- and third-generation individuals) and across a variety of recipient translocation habitats to apply these results more broadly. A few long-term studies of native trout translocations have been conducted (Vincenzi et al. 2012), but we found none that evaulated the translocation of embryos from different donor sources.

There are trade-offs between using captive-origin versus wild-origin sources as donors for translocations. Some advantages of bringing wild sources into captivity are to (1) produce more and larger offspring (e.g., Primack 2014), (2) increase genetic diversity by using many different donor sources (e.g., Van Doornik et al. 2011), and (3) provide a stable and easily accessible source for translocation (Frankham et al. 2003). Some disadvantages are: (1) captive selection may occur rapidly such that progeny may lose genetic variability and be less fit in a wild setting (e.g., Frankham et al. 2003; Heath et al. 2003), (2) the expense of maintaining a captive population, and (3) the need for stringent biocontrols to prevent transmission of diseases or parasites into the captive population. Advantages of using wild-origin donors are to (1) preserve the unique genetic legacy of each wild population (e.g., Allendorf and Leary 1988) and (2) take advantage of potential adaptation to local or regional conditions (i.e., nearest neighbor). The disadvantages are: (1) lower genetic diversity (i.e., genetic load: Frankham et al. 2003), (2) potential demographic impacts of removing adults or gametes from a small population, and (3) limited numbers of fish or embryos can be translocated in any one year due to small population sizes.

Another consideration in translocation projects is whether to mix sources by introducing individuals from multiple populations. Using multiple sources may allow for the introduction of a greater number of individuals, thereby avoiding a genetic bottleneck or low genetic diversity in translocated populations when compared with source populations (Stockwell et al. 1996). Additionally, if a single donor source lacks genetic variation, mixing populations can act like a "genetic rescue" (Edmands 2007). Genetic rescue results from added genetic variation, which allows selection to act to eliminate deleterious alleles that may have become fixed in a population as a result of genetic drift. There have been multiple examples of populations rebounding following the introduction of new individuals (e.g., Madsen et al 1999; Hogg et al. 2006). Additional evidence for the value of mixing genetically distinct lineages comes from studies of invasive species that reveal high within-population genetic variation resulting from intraspecific mixing of source populations (e.g., Neville and Bernatchez 2013; Roy et al. 2015).

However, mixed-source populations may also have lower fitness than pure populations. Interbreeding among distinct populations can lead to outbreeding depression or reduced fitness due to disruption of interactions among genes or interactions between genes and the environment that have evolved within a single population (Edmands 2007). For example, hybrid second-generation progeny had lower fitness than pure strain progeny of Slimy Sculpin *Cottus cognatus* at nine reintroduction sites in Minnesota (Huff et al. 2011). Frankham et al. (2011) have developed a decision tree to help determine the probability of outbreeding depression in different scenarios. It indicates that the probability of outbreeding depression is low for populations that do not have fixed chromosome differences, have been isolated for less than 500 years, and occupy similar environments (Frankham et al. 2011) .

Though the Cherry Creek translocation project used multiple donor sources, this study did not evaluate the effect of mixing donor sources. Additional studies in this system need to sample and genotype individuals from subsequent generations to evaluate the effect of mixing sources. According to the decision tree (Frankham et al. 2011), there is some risk of outbreeding depression in crosses among individuals from the donor sources we used. Westslope Cutthroat Trout populations do not have fixed chromosomal differences, but the populations used to create the WPH population (from the Clark Fork River drainage) and the wild populations introduced to Cherry Creek (from the Missouri River drainage) have likely been separated for more than 500 years and show high genetic differentiation (Drinan et al. 2011). The wild populations within the Missouri River drainage were likely connected by gene flow prior to human intervention as recently as 150 years ago, but there is some evidence of temperature differences among these natal streams (Table 2) and of local adaptation to the thermal regime in these populations (Drinan et al. 2012), potentially indicating that these populations do not occupy similar environments.

As suggested by Houde et al. (2011), the relative risks of inbreeding and outbreeding depression must be weighed on a case-by-case basis. Our results should not be inferred directly to other scenarios. In order to maximize the biological benefits of translocations as a conservation tool, we suggest that outcomes of existing projects be monitored and results published to provide insight for future projects (Pullin and Knight 2001; Sheller et al. 2006; Terhune et al. 2010; Anderson et al. 2014).

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