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MANAGEMENT BRIEF

Juvenile Movement among Different Populations of Cutthroat Trout Introduced as Embryos to Vacant Habitat

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Abstract

Translocations are frequently used to increase the abundance and range of endangered fishes. One factor likely to affect the outcome of translocations is fish movement. We introduced embryos from five Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi* populations (both hatchery and wild) at five different locations within a fishless watershed. We then examined the movement of age-1 and age-2 fish and looked for differences in movement distance among source populations and among introduction sites; we also examined the interactions among age, population, and introduction site. At age 1, most individuals (90.9%) remained within 1,000 m their introduction sites. By age 2, the majority of individuals (58.3%) still remained within 1,000 m of their introduction site, but considerably more individuals had moved downstream, some more than 6,000 m from their introduction site. We observed a significant interaction between age and source population ($F_{4,\,1077} = 15.45$, $P < 0.0001$) as well as between age and introduction site ($F_{41,\,1077} = 11.39$, $P < 0.0008$), so we presented results in the context of these interactions. Within age-groups, we observed differences in movement behavior among source populations and among donor populations of Westslope Cutthroat Trout. We discuss these findings in light of previous research on juvenile salmonid movement.

Translocating fish is an important conservation strategy for many imperiled fish species. Translocations can create new populations by reestablishing fish in habitats that were historically occupied or by establishing new populations in historically fishless habitats (e.g., U.S. Fish and Wildlife Service 1998; Colorado Division of Wildlife 2004). Both of these types of translocations can increase the range and abundance of species at risk, which should decrease the risk of extinction (Griffith et al. 1989). In addition to creating new populations, fish managers

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use translocations to supplement existing populations. Introducing individuals into existing populations can reduce the effects of inbreeding and the demographic risk of extinction (e.g., Madsen et al. 1999; Pimm et al. 2006; Bouzat et al. 2009). Introducing individuals can also speed the recovery of populations following other management interventions, such as nonnative species removal or habitat restoration (e.g., Jones 2010).

Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi* exemplify an imperiled taxon that would benefit from translocations. Westslope Cutthroat Trout have been extirpated from much of their historical habitat (Shepard et al. 2005), and many of the remaining genetically pure populations are restricted to headwater streams where they are isolated from other trout populations by barriers that prevent upstream movement of fish. These barriers protect populations from hybridization with nonnative Rainbow Trout *O. mykiss* and from competition with nonnative Brook Trout *Salvelinus fontinalis*, but increase the risk of demographic stochasticity and inbreeding depression (Peterson et al. 2008; Fausch et al. 2009). Translocations of Westslope Cutthroat Trout could facilitate conservation by ameliorating the negative effects of inbreeding, simulating gene flow among isolated populations, and establishing additional populations (e.g., GCTRT 1998; Alves et al. 2004; CRCT Coordination Team 2006; Teuscher and Capurso 2007; MDFWP 2007; Gresswell 2011). However, before translocations are widely used as a Westslope Cutthroat Trout conservation tool, we need to know more about the factors affecting the success of these projects.

Data gathered from translocations of other Cutthroat Trout subspecies (Greenback Cutthroat Trout *O. clarkii stomias* and Rio Grande Cutthroat Trout *O. clarkii virginalis*) have helped identify factors that can influence the success of these conservation efforts. Habitat features like cold summer water temperature, narrow stream width, and a lack of deep pools has limited the success of previous Cutthroat Trout translocations (Harig and Fausch 2002), while translocation sites with at least 2 ha of habitat that previously supported reproducing trout populations have had the highest rates of success (Harig et al. 2000).

Movement following translocation is another factor likely to be important in Cutthroat Trout translocation projects. Stream-dwelling trout can exhibit extensive movement (e.g., Gowan and Fausch 1996; Hilderbrand and Kershner 2000; Schmetterling and Adams 2004; Gresswell and Hendricks 2007). Extensive downstream movement over a protective barrier could seriously compromise a Cutthroat Trout translocation because individuals moving past the barrier would be "lost" to the project, as would the genetic diversity they could add to the population. Stream-dwelling trout can also exhibit restricted movement, remaining within ~100-m home ranges (Clapp et al. 1990; Rodríguez 2002). If translocated fish remain in small home ranges near their introduction site, multiple introduction sites throughout a system—rather than a single introduction site—may be necessary to meet restoration goals.

The Cherry Creek project provided an opportunity to study trout movement in a translocation project. The goal of the Cherry Creek project was to create a genetically diverse Westslope Cutthroat Trout population in a secure refuge within the Madison River basin by translocating almost 35,000 embryos from multiple populations into habitat vacated after a series of piscicide treatments (Bramblett 1998). The translocated population is thriving and should soon be the largest genetically pure Westslope Cutthroat Trout population east of the Continental Divide in Montana (Lee Nelson, Montana, Fish, Wildlife, and Parks, personal communication).

Our goal for this study was to describe how translocated Westslope Cutthroat Trout in the Cherry Creek project moved. We looked for differences in movement between age-1 and age-2 individuals, among individuals from different source populations, and among individuals introduced to different locations in the study system.

METHODS

Study design.—The Cherry Creek project consisted of two phases. During the first phase, about 90 km of Cherry Creek that is isolated from downstream habitats by an 8-m-high waterfall was treated with the piscicides antimycin and rotenone to remove nonnative fish species. Historically, there were no fish above the waterfall. However, nonnative Brook Trout, Rainbow Trout, and Yellowstone Cutthroat Trout *O. clarkii bouvieri* occupied this habitat in the 20th century, most probably as a result of introductions to the watershed (P. Clancey, Montana Fish, Wildlife, and Parks, personal communication). During the second phase of the project, in which this study took place, we introduced Westslope Cutthroat Trout embryos and then examined the movement of juvenile fish.

Source populations.—Embryos introduced to the study site came from two hatchery and three wild-source populations. One of the hatchery populations was the state of Montana's captive Westslope Cutthroat Trout conservation population, which is reared at Washoe Park Hatchery in Anaconda, Montana. This population was founded in 1984 from populations of trout in the upper Flathead and Clark Fork river drainages. The population was infused with additional gametes from the Flathead River drainage about 20 years later (M. Sweeney, Montana Fish, Wildlife and Parks, personal communication). The other hatchery population was from a collaborative public–private Westslope Cutthroat Trout hatchery located on the Sun Ranch (44.965°N, 111.605°W) within the Madison River drainage. This population was founded in 2002 using individuals from the same three wild populations that donated embryos to this project (described below).

We introduced embryos from three wild-source populations—Ray, Muskrat, and White's creeks. All three of these creeks supported genetically pure Westslope Cutthroat Trout. The population from Ray Creek (46.411°N, 111.267°W) was estimated to have 2,000–3,000 age-1 and older individuals inhabiting over 8 km of stream when surveyed in 2007. This population was isolated from nonnative fish by a perched culvert (L. Nelson, Montana Fish, Wildlife and Parks, personal communication). The population from Muskrat Creek

(46.302°N, 112.032°W) was estimated to have 3,500–4,000 age-1 and older individuals inhabiting over 8 km of stream when surveyed in 2007 (L. Nelson, personal communication). This population may have been as small as 100 individuals before aggressive management began in 1997 (L. Nelson, personal communication). The population from White's Creek (46.618°N, 111.491°W) was estimated to have about 1,000 age-1 and older individuals inhabiting slightly more than 3 km of stream when surveyed in 2006. This population also decreased to about 100 individuals in the 1990s (Shepard et al. 2002). The populations in Muskrat and White's creeks required intensive restoration management in recent years, including the construction of human-made barriers, Brook Trout removal, and habitat restoration (Shepard et al. 2002; L. Nelson, personal communication).

Since hybridization is a constant threat to Cutthroat Trout populations, we screened all source populations for potential introgression with Rainbow Trout and Yellowstone Cutthroat Trout by genetically testing all source adults to ensure that no evidence of genetic introgression was present. In addition, all source populations were screened to ensure they were free of the following fish pathogens: *Renibacterium salmoninarum*, *Aeromonas salmonicida, Yersinia ruckeri*, *Myxobolus cerebralis*, infectious hematopoetic necrosis virus, infectious pancreatic necrosis virus, and viral hemorrhagic septicemia virus. We screened for these disease pathogens by sampling at least 60 fish from each source population or from a surrogate species in sympatry with the source population prior to transfer of embryos (Ken Staigmiller, Montana Fish, Wildlife and Parks, personal communication). All individuals collected for screening and for introduction to Cherry Creek were collected under permits issued by the state of Montana and in compliance with state policy regarding the transfer of fish among locations.

Embryo collection and introduction.—We collected embryos from source populations in 2007, 2008, and 2009. In the wild, we captured adult trout using a backpack electrofisher and confined them instream in flow-through containers until they were ready to spawn. After we spawned wild fish, we marked them by clipping their dorsal fins and then released them. This assured that wild fish were only spawned once for this project. We also collected a small pelvic fin clip from each spawning adult for genetic analysis.

At the Washoe Park Hatchery, we collected gametes from ripe adults once a week. Our goal was to introduce embryos from Washoe Park Hatchery into Cherry Creek at the same time as we introduced all wild embryos. Since we could not predict exactly when wild embryos would be at the eyed stage—and therefore ready for introduction—we collected embryos at the hatchery over the course of a month to maximize our chances of having embryos from Washoe Park Hatchery at the eyed stage at same time as the wild embryos.

At the Sun Ranch Hatchery, we attempted to spawn all ripe adults. We captured adults from the facility's holding pond with seine nets three times a week for the entire spawning season and spawned all ripe males and females that had not previously contributed gametes to the project. We held captured adults in mesh containers within the pond and released them from containers after completing embryo collection.

We followed the same spawning protocol for all fish contributing gametes to the project. We stripped each female of eggs and divided the eggs into groups, which were distributed among 1-L insulated bottles. The eggs in each bottle were fertilized with milt from a different male to produce a unique male × female cross. Next we used water to rinse away remaining milt and left the fertilized eggs (embryos) undisturbed for at least 30 min to water harden in a water–iodophor solution. Wild embryos were packed in coolers for transport to the hatchery at Sun Ranch, where they were incubated alongside embryos from the Sun Ranch Hatchery population. Embryos from the Washoe Park Hatchery population were incubated on site at that hatchery. We held all embryos in Heath tray incubators until the eyed stage and treated them with formalin every 3–7 d to prevent fungus growth. After the embryos had reached the eyed stage, we removed dead embryos, counted the number of survivors, and transported the surviving embryos to the study site in 1-L insulated bottles.

At the study site, we introduced embryos at the headwaters of the Cherry Creek basin in 2007 and then moved introduction sites down the basin in subsequent years (Figure 1). In 2007, we introduced embryos to the headwaters of Cherry Creek and Cherry Lake Creek. In 2008, we introduced embryos to two tributaries: an unnamed tributary of main-stem Cherry Creek and a tributary of Cherry Lake Creek called Pika Creek. In 2009, we again introduced embryos to two tributaries: Carpenter Creek and South Fork Cherry Creek.

The number of embryos introduced from each population varied depending on their availability (Table 1). Because embryos from Sun Ranch Hatchery were not available in 2009, only four populations were introduced that year. In 2007 and 2008, embryos from all source populations were introduced to all sites (Table 1). Embryos from a single male × female cross were introduced to the same incubator, with the exception of male × female crosses from Washoe Park Hatchery, which were sometimes divided among several incubators.

We used instream remote-site incubators (RSIs) to plant eyed embryos at introduction sites. The RSIs are designed to consistently supply embryos with freshwater, while avoiding 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 while in the RSI. After swim-up, fry exited the incubators via an outflow tube, through which the water flowed into a 19-L (5 gal) bucket. After putting embryos in an RSI, we checked them every 2–3 d until the last fry was in the bucket. When we checked RSIs, we made sure they were still supplying embryos with freshwater and we counted and released any fry in the receiving bucket.

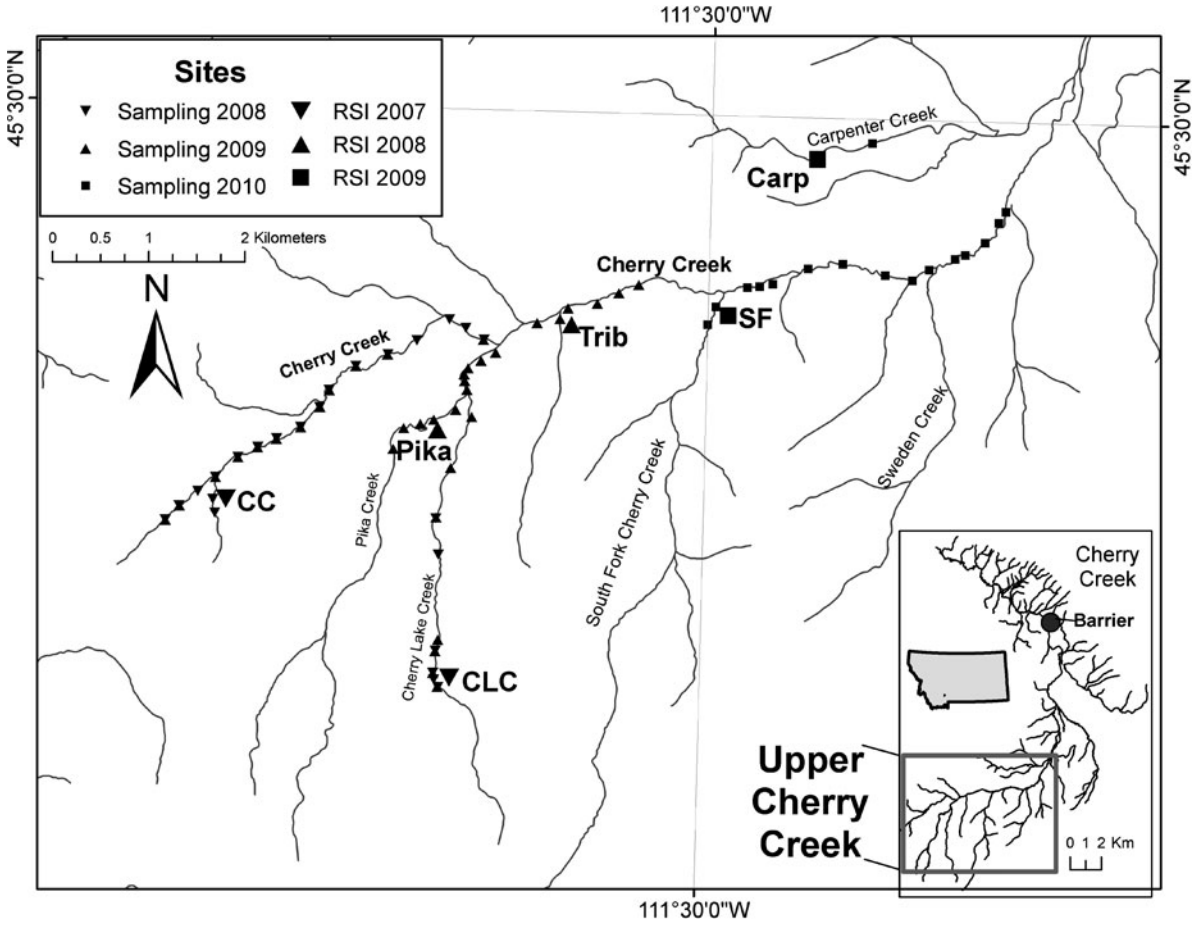

FIGURE 1. Upper Cherry Creek study area showing remote-site incubator (RSI) sites and Westslope Cutthroat Trout sampling sections (Sampling) by year. The symbols representing incubator sites are offset from the stream so they do not obscure symbols designating sampling sites. Several fish sampling sections were sampled in both 2008 and 2009 and they are shown as overlapping triangles that look like hourglasses. The inset map shows the entire Cherry Creek watershed including the 8-m-high waterfall that serves as a barrier to upstream movement, where Cherry Creek enters the Madison River, and the Cherry Creek's location within Montana. In this paper, we do not discuss fish introduced to Carpenter Creek because no movement data were available for this introduction site. CC = Cherry Creek, Pika = Pika Creek, CLC = Cherry Lake Creek, Trib = unnamed tributary, SF = South Fork, Carp = Carpenter Creek.

In all but one introduction location, we released fry in calm water immediately downstream from the RSIs. However, fry from the South Fork RSIs were released in two different locations: (1) just downstream from the RSIs in South Fork and (2) immediately upstream from the mouth of South Fork in mainstem Cherry Creek, 400 m from the RSIs. We released fish from all source populations at both of these release sites so that comparisons of movement among source populations would not be affected by the fact that we used two release locations for the South Fork introduction site.

TABLE 1. Number of Westslope Cutthroat Trout embryos introduced to each introduction site by source population.

Wild-source populations	Hatchery source populations	Cherry Creek	Cherry Lake Creek	Pika Creek	Unnamed tributary	South Fork	Total
Ray Creek		1,919	1,548	890	810	889	6,056
Muskrat Creek		2,790	2,655	1,583	1,621	1,891	10,540
White's Creek		351	664	409	565	322	2,311
	Sun Ranch	1,553	1,522	1,712	1,565		6,352
	Washoe Park	498	513	1,251	1,394	922	4,578
Total		7,111	6,902	5,845	5,955	4,024	29,837

Fish sampling and identification.—We sampled juvenile fish during August and September in 2008, 2009, and 2010 using backpack electrofishing crews consisting of two- to four-persons. We captured fish using Smith-Root BP-15, BP-12, and SR-24 backpack electrofishers operated at voltages in the range of 100–600 V, frequencies under 50 Hz, and pulse widths less than 2 μs to maximize the number of fish captured while minimizing injury to fish caused by the shock (Dwyer et al. 2001). We caught immobilized fish in dip nets and held them in buckets filled with stream water until they were completely recovered. We then anesthetized the fish, weighed them, measured length, and removed a small portion of the pelvic fin for genetic analysis.

We used a systematic sampling design with a nonrandom start to capture juvenile fish (Figure 1). We began sampling where RSIs had been located, rather than using a nonrandom start, because we expected the juvenile fish to be concentrated near introduction sites. We sampled 100-m sections every 300 m for about 600 m above and from 1 to 5 km below introduction sites (Figure 1). When fish became noticeably less abundant, we decreased our sampling frequency to sample one 100-m section per 500 m of stream. In some cases, such as in Cherry Lake Creek, sampled sections were more distant because we avoided stream sections where sampling was prohibitively difficult. In Cherry Lake Creek and the unnamed tributary, fish densities decreased substantially when we sampled more than 500 m from the RSI locations, so it was unnecessary to sample as far downstream. We continued downstream from an RSI location until few or no fish were found in consecutive sections. Our sampling protocol prioritized detecting downstream movement, so our observations may not have represented the extent of upstream movement. Because we did not sample continuously throughout the range of the translocated population but instead used a systematic sampling design, we did not sample all of the individuals that survived.

We concentrated our sampling effort to capture age-1 fish. In 2008, 2009, and 2010, we sampled the two introduction sites used the previous year. In 2009, we were also able to sample the two introduction sites used in 2007. Therefore, we were able to provide 1 year of data on age-2 individuals. In the process of sampling for age-1 fish in 2010, we captured some age-2 and age-3 fish. We excluded these fish from further analysis because we did not sample throughout their population range and therefore cannot provide a valid summary of their movement. We determined the age of a captured fish by determining its parents; this approach worked because we knew which parent pairs contributed each year. We introduced embryos in early summer and sampled juveniles in late summer and early fall, so captured individuals were approximately 14 months old (hereafter referred to as age-1 fish) or 26 months old (hereafter referred to as age-2 fish).

We used 12 microsatellite loci to genotype each captured individual and each adult that donated gametes using the laboratory protocols of Vu and Kalinowski (2009, see full list of loci in their Table 1). We assigned offspring to parent pairs by counting Mendelian exclusions (e.g., Muhlfeld et al. 2009). We accepted a parentage assignment if an offspring had two or fewer loci mismatched with only one parent pair. We excluded from further analysis any offspring that could not be matched to at least one parent pair with two or fewer mismatches. Consequently 77 offspring (5.3%) were excluded from further analysis. Another 92 offspring (6.3%) were excluded because they were assigned to two or more parent pairs.

Determining movement distance.—Hereafter, we use "movement distance" to refer to the distance between the location where a fish was released after fry emergence and the location where the fish was captured at age 1 or age 2. We used handheld GPS devices to record the location of each sampling section and location where we released fry. We recorded the locations of a captured individual as the lower bound of the 100-m sampling section in which it was captured. Therefore, our calculations of movement distance could overestimate downstream movement and underestimate upstream movement by up to 100 m. To determine movement distance, we computed stream distances between fry release sites, sampling sites, and a reference point using the national hydrography dataset plus hydrography layer (http://nhd.usgs.gov) and Network Analyst within ArcGIS version 9.3.1 (http://www.esri.com). We used negative numbers to designate downstream movement and positive numbers to designate upstream movement. Movement data were not available for individuals introduced to Carpenter Creek, so this creek was excluded from this study.

Statistical analysis.—We tested for associations between movement distance and three explanatory variables—age, source population, and introduction site—and examined interactions between these variables. We began by fitting a saturated ANOVA model with movement distance as the response variable. The three-way interaction among age, source population, and introduction site was not significantly associated with movement distance ($F_{4,\,1073} = 1.24$, $P = 0.29$), so we excluded it. We fit a final ANOVA model that included all of the two-way interactions and then completed post hoc analyses by examining interaction plots with mean movement distance and associated 95% confidence intervals. We used QQ-plots and plots of fitted versus residual values to check that the assumptions of normality and homogeneity of variance were met for our final ANOVA model. Because the movement data were skewed and the sample sizes differed substantially among groups in some cases, these assumptions of normality and homogeneity of variance were mildly violated. To ensure these violations did not affect the conclusions we drew, we used Kruskal–Wallis nonparametric ANOVA to confirm all relationships between movement distance and the three explanatory variables. In all cases, the results from the parametric and nonparametric analyses were equivalent, so we report only the more familiar parametric analyses in this paper. We used an alpha level of 0.05 for all statistical tests.

We released fry in the South Fork in two different locations, whereas at the other introduction sites we released fry in only

one location. Therefore, before comparing the movement distances among source populations and among introduction sites as described above, we looked more closely at movement distance in South Fork to see whether the location of fry release affected how far individuals moved. Mean movement distances of the individuals released at the two South Fork release sites (in South Fork and in Cherry Creek) were equivalent (Welch's two-sample $t = 0.73$, $P = 0.47$). Therefore, we pooled the movement distances of the two release sites in South Fork. We could not always determine the release location of captured individuals from Washoe Park Hatchery that were introduced to South Fork because fish from male × female crosses from Washoe Park Hatchery were sometimes split between more than one RSI. Therefore, we omitted 38 captured individuals from the Washoe Park Hatchery population that were introduced to South Fork from all analyses.

We also omitted one individual from Ray Creek that was captured in the unnamed tributary. It was the only individual from Ray Creek captured in the unnamed tributary, which meant that the ANOVA model could not reasonably compare the Ray Creek population to other source populations in the unnamed tributary.

RESULTS

We captured and determined the population of origin of 836 age-1 Westslope Cutthroat Trout from five introduction locations and 269 age-2 individuals from two introduction locations. At age 1, most individuals (90.9%) remained within 1,000 m of their introduction sites (Table 2), but a few individuals were captured farther than 4,000 m downstream from their introduction site (Figure 2). By age 2, the majority of individuals (58.3%) still remained within 1,000 m of their introduction site, but considerably more individuals had moved downstream, some more than 6,000 m from their introduction site (Table 2; Figure 3).

We examined associations between movement distance and three explanatory variables: age, source population, and introduction site. Two of the three two-way interactions among these variables were significant. Therefore, results are presented in the context of the interactions among variables. The pattern of differences in movement distance among source populations varied between age-1 and age-2 fish ($F_{4,\,1077} = 15.45$, $P < 0.0001$; Figure 4A), as did the pattern of differences in movement distance among introduction sites ($F_{41,\,1077} = 11.39$, $P < 0.0008$; Figure 4B). The pattern of differences in movement distance among source populations did not vary among introduction sites ($F_{13,\,1077} = 1.44$, $P = 0.13$).

Though there were statistically significant interactions between age and introduction site and between age and source population, some patterns of movement distance were consistent across ages. Among source populations, individuals from Washoe Park Hatchery and White's Creek remained much closer to the RSI locations (represented by 0 on the *y*-axis in Figure 4A) than individuals from other populations at both age 1 and age 2 (Figure 4A). For example, the mean movement distance of age-1 individuals from Washoe Park Hatchery was 18 m (SD = 221) downstream, while the mean movement distance of age-1 individuals from Ray Creek was 778 m (SD = 873) downstream (Figure 4A). As another example, in most populations individuals moved farther downstream at age 2, but individuals from White's Creek were actually closer to the RSI locations at age 2 than at age 1 (Figure 4A).

Among introduction sites, individuals moved farthest downstream in Cherry Creek and moved the least in Cherry Lake Creek (Figure 4B) at both age 1 and age 2. At age 1, the mean movement distance in Cherry Creek was 862 m (SD = 866) downstream, while the mean movement distance in Cherry Lake Creek was 4 m (SD = 249) *upstream*. By age 2, the mean movement distances were 2,161 m (SD = 1,851) downstream in Cherry Creek and 835 m (SD = 1,603) downstream in Cherry Lake Creek.

DISCUSSION

In this study, we observed that the movement exhibited by translocated Westslope Cutthroat Trout varied by source population, introduction site, and age. Overall, age-1 individuals exhibited relatively restricted movement, but there were differences among introduction sites and among source populations. Among introduction sites, downstream movement farther than 1,000 m from introduction sites was uncommon at all sites except one (Cherry Creek). Among source populations, individuals from two populations (White's Creek and Washoe Park Hatchery) remained closer, on average, to their introduction sites than individuals from other populations. By age 2, movement was more extensive; more juveniles ventured farther than 1,000 m from their introduction site. Differences in movement between introduction sites and source populations also persisted at age 2.

TABLE 2. Summary of Westslope Cutthroat Trout movement, by age. For calculations of mean distance moved, negative values were used to represent downstream movement and positive values were used to represent upstream movement.

Age-group	Percent moved downstream	Percent within 1,000 m of introduction	Mean distance (m) (SD)	Farthest distance upstream (m)	Farthest distance downstream (m)
Age 1	82.1	90.9	−402 (658)	510	4,207
Age 2	84.8	58.3	−1,530 (1,857)	345	6,185
Both ages	82.7	82.9	−676 (1,183)	510	6,185

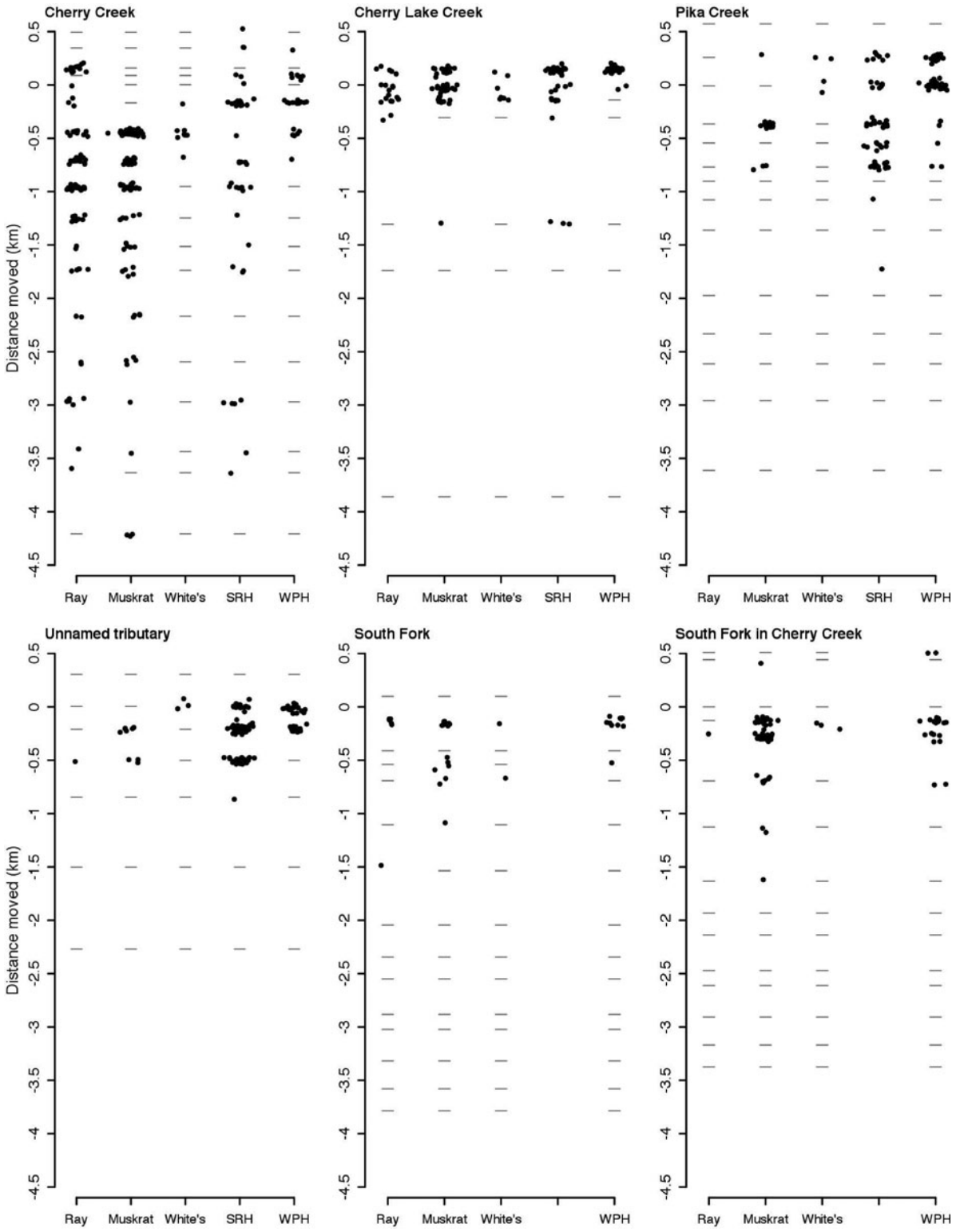

FIGURE 2. Sampling design and Westslope Cutthroat Trout captured at age 1 ($n = 836$) by introduction site and source population. Note the substantial difference in fish densities near the RSI locations (represented by 0) versus those more than 1 km downstream. Each line represents a section sampled in which no fish from that source population–introduction site combination were captured. Each dot represents a captured fish. Dots have been jittered horizontally and vertically to avoid overlap, but overlap still occurs in the particularly densely populated areas near the RSI sites. Distance moved equals distance between hatching location and location of capture at age 1. Negative values for movement distance represent downstream movement; positive values represent upstream movement. Each panel represents one introduction site, except South Fork and South Fork in Cherry Creek. At the South Fork introduction site, hatched fry were released in one of two locations: at the introduction site in South Fork and in Cherry Creek immediately upstream from the mouth of South Fork. Individuals from Sun Ranch Hatchery were not introduced to South Fork and so do not appear in these two panels of the graph. SRH = Sun Ranch Hatchery, WPH = Washoe Park Hatchery.

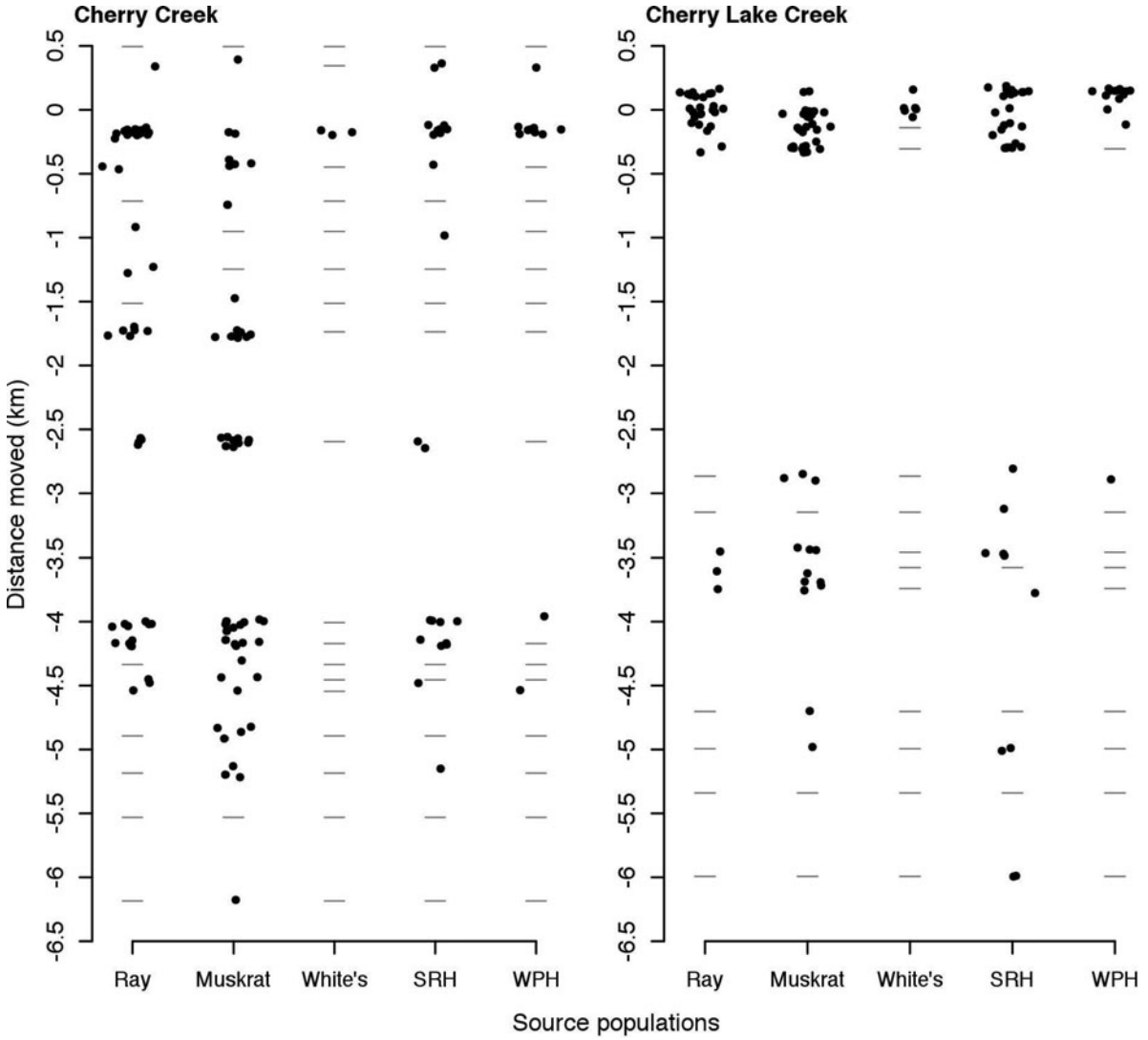

FIGURE 3. Sampling design and Westslope Cutthroat Trout captured at age 2 (n = 269) by introduction site and source population. Each line represents a section sampled in which no fish from that source population–introduction site combination were captured. Each dot represents a captured fish. Dots have been jittered horizontally and vertically to avoid overlap but overlap still occurs in the particularly densely populated areas near the RSI sites. Distance moved equals distance between hatching location and location of capture at age 2. Negative values for movement distance represent downstream movement; positive values represent upstream movement. Each panel represents one introduction site. SRH = Sun Ranch Hatchery, WPH = Washoe Park Hatchery.

Movement after translocation could affect the success of current and future projects so it is useful to consider what may have led to the differences in movement we observed in this study. We will do so in the context of previous research on juvenile trout movement. This study was *not* designed to determine what caused the observed differences, so the potential explanations described below should be considered as hypotheses that need to be tested in future research on juvenile trout movement after translocation.

Variation in movement distance among introduction sites could have been caused by density-dependent competition. Density-dependent survival has been observed for juveniles of many salmonid species, and downstream displacement of less-dominant individuals appears to be a common response to density-dependent competition (e.g., Chapman 1966; Crisp 1993; Bujold et al. 2004; Westley et al. 2008). We observed that habitats nearest the introduction sites held the highest abundances of age-1 fish and that fish abundances declined precipitously as we moved away from the introduction sites (Figure 2), which suggests that density-dependent factors have regulated how individuals moved from introduction sites. Fish moved farthest downstream from the Cherry Creek introduction site, where the greatest number of embryos were released (Table 1), further supporting this hypothesis. Differences in

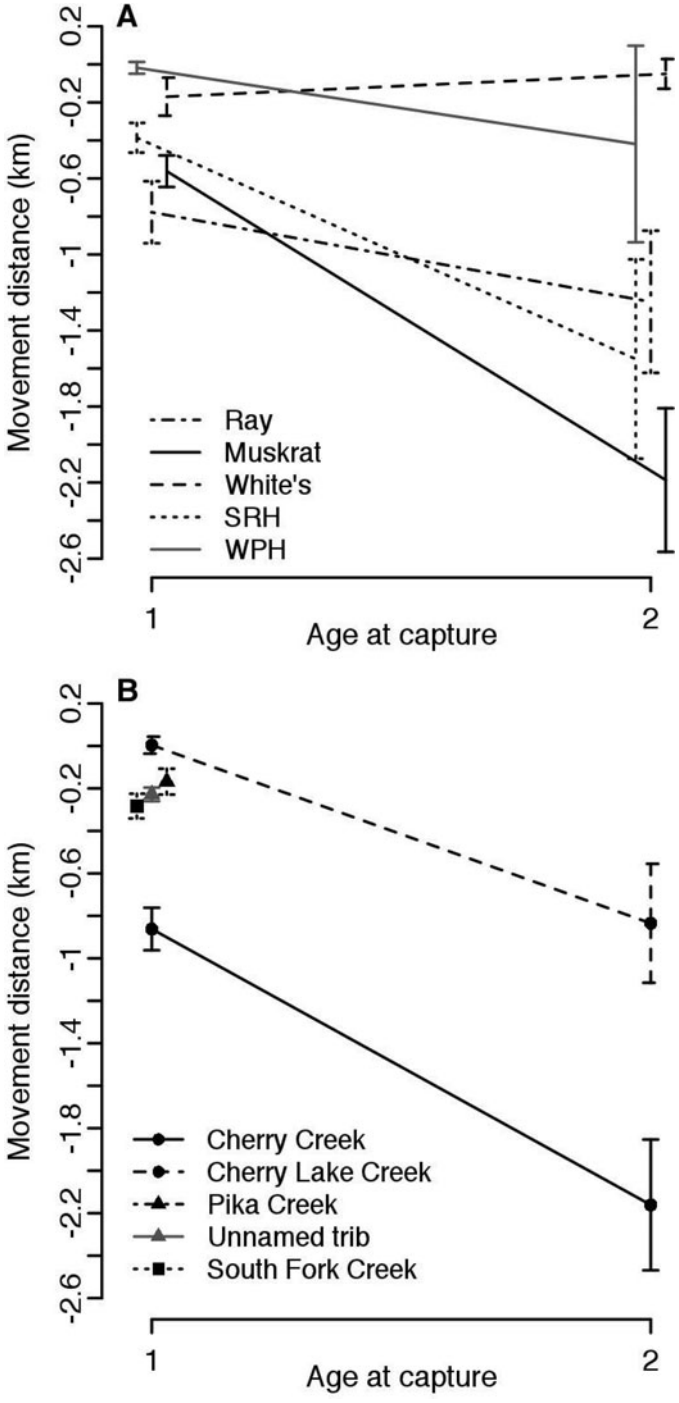

FIGURE 4. Mean movement distances of Westslope Cutthroat Trout and associated 95% confidence intervals by (**A**) source population and age at capture and (**B**) introduction site and age at capture. Zero on the *y*-axis represents the RSI location. Negative values for movement distance represent downstream movement; positive values represent upstream movement. Symbol shape in panel B represents the year of introduction: circles represent data for sites where RSIs were deployed in 2007, triangles represent data for sites in 2008, and the square represents data for the site in 2009. Data for age-2 fish are only available for sites where RSIs were deployed in 2007.

movement among introduction sites also persisted at age 2 (Figure 4), which is consistent with a pattern of density-dependent movement because as fish grow they require more space (e.g., Chapman 1966; Chapman and Bjornn 1969). Future research should test the hypothesis that movement after translocation is affected by density-dependent competition.

Habitat conditions at introduction sites may also have contributed to the differences in movement we observed among sites. Fish may be moving to find more ideal habitats, either during the summer (e.g., Kahler et al. 2001; Gowan and Fausch 2002) or during fall and early winter to find better overwinter habitats (e.g., Bjornn 1971; Cunjak and Power 1986). We did not systematically collect habitat data in this study, but future research should test the hypothesis that fish move to find suitable habitat after translocation.

Variation in movement distance among source populations could be caused by heritable variation in the tendency to move. Early life movement patterns exhibited by individuals native to lake inlet versus lake outlet streams and from populations above versus below waterfalls are heritable (e.g., Northcote 1962; Bowler 1975; Kaya 1989; Van Offelen et al. 1993) and selection for sedentary habits can occur very rapidly (Pearse et al. 2009).

All wild source populations used for this study occupied relatively short headwater reaches, but the three source streams were different. It is plausible that selection against downstream movement in White's Creek contributed to the differences we observed between individuals descended from the wild populations. White's Creek (whose progeny moved only short distances) has infrequent and intermittent surface flows in its lower reaches due to large valley-bottom alluvium, irrigation withdrawals, and mining impacts (L. Nelson, personal communication). Muskrat and Ray creeks (whose progeny moved farther downstream than progeny from White's Creek) both have perennial flows that connect them to downstream habitats, and isolation of these populations probably occurred much later than for the White's Creek population (L. Nelson, personal communication). Given that many of the wild Cutthroat Trout populations that are potential source populations for translocations are sequestered above barriers to upstream movement (Shepard et al. 2005) and adaptation to barriers can occur rapidly (Pearse et al. 2009), future work should test the hypothesis that sequestered populations of Westslope Cutthroat Trout evolve to exhibit more restricted movement.

Differences in movement among source populations could also result from the fact that some individuals were descended from wild populations and others were descended from populations raised in captivity. Salmonids from hatchery populations can move differently than wild fish (e.g., Bjornn and Mallet 1964; Richards and Cernera 1989; Bettinger and Bettoli 2002; Baird et al. 2006). Young hatchery-origin salmonids can also grow more quickly and behave more aggressively than

individuals from wild populations (Rhodes and Quinn 1999; Tatara and Berejikian 2012). This could lead to hatchery-origin fish outcompeting wild fish, which could lead to wild fish moving farther than hatchery fish (Nakano 1995; Hughes 2000; Hansen and Closs 2009). In a companion study in the Cherry Creek system, we observed that individuals descended from the hatchery populations (Washoe Park and Sun Ranch Hatchery) indeed grew more quickly than individuals descended from the wild populations (Andrews 2012). However, the outcomes of the Cherry Creek project do not support a simple relationship between origin (hatchery versus wild) and movement because individuals from the two hatchery populations moved very differently (Figure 4) despite growth rate similarities. Using hatchery populations for translocations is not only convenient, it also avoids affecting existing wild populations. Thus, future studies should test the hypotheses that individuals from hatchery populations outgrow and outcompete individuals from wild populations, and that this leads to differences in movement.

Considering how juvenile trout can move after introduction will better prepare managers to carry out and evaluate the success of translocation projects. For example, if the Cherry Creek system had less than 4 km of available habitat above a protective barrier, the project would have lost a number of individuals to downstream movement over the barrier as early as age 2. In that case, maintaining a genetically diverse reproducing population might have required recurring translocations. As another example, if the project had used only individuals from the state of Montana's Westslope Cutthroat Trout hatchery population (Washoe Park Hatchery), we might have observed limited downstream movement. In that case, it would have taken more time or more introductions throughout the system to meet the conservation goal of establishing a reproducing population throughout the Cherry Creek drainage. Finally, if we had measured the success of the project by sampling only age-1 individuals, we would have concluded that individuals remained close to introduction sites, creating discrete populations with limited ranges and limiting the potential for mating between individuals introduced to different sites. In reality, individuals exhibited much more extensive movement by age 2, mitigating these concerns.

As is true for all management projects, the outcomes we observed in the Cherry Creek project were affected by our unique project design. It would be imprudent to infer that the same patterns will be observed in translocations with different designs. For instance, we introduced embryos to a fishless system, which meant that age-1 individuals rarely (if ever) had to compete with adult fish for resources. Introducing embryos to an occupied habitat could result in more extensive movement if native adults outcompete the smaller introduced juveniles for resources (Nakano 1995; Hughes 2000; Hansen and Closs 2009). As studies of the outcomes of trout translocations accumulate, fisheries managers will be better able to predict the factors that will affect the success of their unique conservation project.

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