Evaluating the success of a conservation reintroduction: The case of bull trout in the Wallowa River

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Abstract
Bull trout in the Wallowa River watershed were considered extirpated in the 1950s. In 1997, bull trout from the adjacent Imnaha River watershed were reintroduced into the Wallowa River watershed. We evaluated whether bull trout are currently present in the Wallowa River watershed and, if so, whether they appear to be the result of the 1997 reintroduction. From 2010 to 2018, we captured 181 *Salvelinus* spp. The majority (64.5%) of these individuals were bull trout. Bull trout in the Wallowa River watershed were more genetically similar to those from the Imnaha River watershed (pairwise $F_{ST} = 0.102$) than to the other populations we examined. They also exhibited genetic evidence of a recent bottleneck (observed heterozygosity was 0.598, significantly greater than expected). Modeled estimates of size (541–581 mm), survival (<0.0001–0.0015 probability) and age (14–22 years) for the reintroduced fish indicated the bull trout captured in the Wallowa River watershed were unlikely to be remnants from 1997. These results suggest the 1997 reintroduction has resulted in natural reproduction and recolonization of bull trout in the Wallowa River watershed. Whether the abundance and genetic diversity of these bull trout is sufficient to allow the population to persist over an ecological time period is unclear.

KEYWORDS
bull trout, conservation reintroduction, evaluation, genetics, recovery, threatened

1 INTRODUCTION

Translocations are a broad category of actions that are defined as the movement of a living organism from one area to another (IUCN, 1987). When their purpose is to conserve or recover imperiled species, they are considered conservation translocations (Minckley, 1995), which include conservation reintroduction efforts (henceforth reintroductions) (Seddon, 2010) or the movement of individuals of a species into a part of their native range where they no longer exist (IUCN, 2013). The goals of reintroduction programs can range widely but generally include repopulating previously occupied habitat and creating genetic reserves (see Schwartz & Martin, 2013). Approaches to reintroduction efforts also vary widely, with many efforts being opportunistic and relatively few, well planned and experimental examples (Seddon, Armstrong, & Maloney, 2007). Determining whether a reintroduction effort has been successful is not always straightforward and depends on establishing clear
objectives prior to initiating reintroduction efforts (Robert et al., 2015). While there is not a standard definition of a successful reintroduction (Robert et al., 2015), whether a reintroduced population is viable, self-sustaining and has an effective population size between 50 and 500 (see Rieman & Allendorf, 2001; Seddon, 2015) are often considerations in the evaluation of success. Nonetheless, both successful (e.g., DeHaan, Adams, Scheerer, & Bangs, 2016; Hayward, Adendorff, Moolman, Hayward, & Kerley, 2007; Snyder & Snyder, 2000) and failed (e.g., Bennett et al., 2013; Hardman, Moro, & Calver, 2016) reintroductions have been reported for a variety of animal species.

Globally, the abundance and distribution of many fish species are in decline and the conservation of these species is a significant concern (Helfman, 2007). In particular, fish species that rely on freshwater habitats are some of the most imperiled in the world and evidence suggests there has been a dramatic increase of at-risk or extinct taxa since 1989 (Jelks et al., 2008). In response to the deteriorating status of freshwater fishes globally, it is becoming common to consider translocations or reintroductions as tools for conserving imperiled fishes (Minckley, 1995) or restoring populations (Jachowski, Millspaugh, Angermeier, & Slotow, 2019; Shute, Rakes, & Shute, 2005). As with reintroductions involving many other taxon, most efforts to reintroduce imperiled fishes have not been adequately documented or monitored following implementation and it is often difficult to evaluate whether they were successful (Dunham, Gallo, Shively, Allen, & Goehring, 2011; Williams, Sada, & Williams, 1988). Despite this, evidence exists indicating some reintroduction efforts involving fish have succeeded while others have failed (Lyon et al., 2012; Reading, Clark, & Kellert, 2002).

Bull trout (Salvelinus confluentus) are char native to the northwest of North America (Haas & McPhail, 2001). They have experienced substantial declines throughout their range and are considered a threatened taxon (Gimenez, 1996; USFWS, 1999). Recovery actions for bull trout include ameliorating threats as well as restoring bull trout to habitats from which they have been extirpated (see Galloway, Muhlfeld, Guy, Downs, & Fredenberg, 2016; Mims et al., 2019). These actions have included a small number of reintroductions for which detailed documentation was uncommon and rigorous monitoring was rare (reviewed in Hayes & Banish, 2017). When some level of evaluation was possible, there are indications of both successful and failed reintroductions, although the definition of success varied by population. In general, successful examples are infrequent and the degree to which reintroductions can be used to reestablish self-sustaining populations remains unclear.

Historically, a local population of bull trout existed in Wallowa Lake and a portion of the catchment upstream from the lake (henceforth Wallowa River watershed) (Figure 1) (Buchanan, Hanson, & Hooton, 1997). A dam constructed at the outlet of Wallowa Lake in the early 1900s effectively isolated bull trout in this population. During the 1930s and 1940s bull trout were intentionally removed from the Wallowa River watershed (Ratliff & Howell, 1992). Beginning in the 1950s, the population of bull trout in the Wallowa River watershed was considered to be extirpated (Buchanan et al., 1997). Brook trout (S. fontinalis), a non-native species known to compete (Warnock & Rasmussen, 2013) and hybridize (DeHaan, Schwabe, & Ardren, 2010) with bull trout, were also introduced into lakes at the headwaters of the Wallowa River. Brook trout established self-sustaining populations, dispersed downstream and eventually colonized the Wallowa River watershed (Buchanan et al., 1997).
Attempts have been made to reintroduce bull trout in the Wallowa River watershed. In the 1960s and 1970s, bull trout and dolly varden (S. malma) originating from Alaska were introduced into the watershed but these attempts were determined to be unsuccessful (see Buchanan et al., 1997). In 1997, 600 bull trout, ranging from 70 to 380 mm in fork length and originating from the adjacent Imnaha River watershed, were salvaged from the Wallowa Valley Improvement Canal and translocated to the Wallowa River watershed (see Shively et al., 2007). This conservation action combined both a reestablishment and salvage effort. As with many reintroductions (see Seddon et al., 2007), the 1997 reintroduction was opportunistic in nature, not rigorously planned and criteria for success were not explicitly defined. The outcome was not well monitored but initial surveys suggested the effort was not successful (Shively et al., 2007). As a result, status assessments continued to consider bull trout as extirpated from the Wallowa River watershed (ODFW, 2005; USFWS, 2002). It was, thus, somewhat unexpected when several putative bull trout were observed in the watershed in 2010 (see Doyle, 2013). Whether char in the Wallowa River watershed were bull trout or brook trout and whether they were a remnant of the native Wallowa River population or originated from the 1997 reintroduction effort was not known.

The goal of this study was to evaluate whether the opportunistic reintroduction of bull trout into the Wallowa River watershed in 1997 was successful. Although we were not directly involved during its implementation, the circumstances allowed for an evaluation of the reintroduction several generations after bull trout were translocated. The objectives of the study were to determine (1) whether and to what extent char in the Wallowa River watershed were bull trout and (2) whether individuals identified as bull trout in the Wallowa River watershed likely originated from populations in the Imnaha River watershed. Given the extensive history of hatchery releases of nonnative char into the Wallowa River watershed, we predicted a priori that the char in the Wallowa River watershed would include hybrids with bull trout. We examined genotypes at 12 taxon-diagnostic SNP loci to determine whether there was introgression between nonnative char and bull trout and the frequency of hybridization. We also analyzed 16 microsatellite loci to inform whether bull trout in the Wallowa River watershed are likely progeny of the opportunistic reintroduction from the Wallowa Valley Improvement Canal in 1997 or progeny of the indigenous population. Due to the belief that bull trout were extirpated from the Wallowa River watershed, we predicted a priori that bull trout in the upper Wallowa River would be genetically most similar to bull trout from the Imnaha River watershed and not to those from the Grande Ronde River watershed. We tested this prediction by comparing the genetic characteristics of bull trout in the Wallowa River watershed to the genetic characteristics of nine, relatively proximate bull trout populations.

2 | MATERIALS AND METHODS

2.1 | Study area and sample collection

Our study area included Wallowa Lake and a portion of the catchment upstream of the lake (Wallowa River watershed) (Figure 1). Char in this area have unconstrained access to Wallowa Lake, approximately 900 m of the Wallowa River upstream of the lake, 900 m of the East Fork Wallowa River, 1.0 km of the West Fork Wallowa River and 480 m of BC Creek. Waterfalls in each of the tributaries were barriers to the upstream movement of fish. During this study, the tailrace of the Wallowa Falls Hydroelectric Project also provided approximately 300 m of accessible habitat. In recent years, the majority of char in the study area appear to have spawned in the East Fork Wallowa River (Doyle, 2020).

Char (bull trout, brook trout and their hybrids) were captured from the study area from 2010 to 2013 and 2016 to 2018. From 2010 to 2013, collections were to provide a genetic characterization of any char that appeared to be bull trout. Based on their morphology, captured char believed to be brook trout (see Popowich, Venturelli, Stelfox, & Taylor, 2011) were excluded from the sample. From 2016 to 2018, collections were designed to provide an unbiased estimate of the proportion of char that were bull trout. Thus, all captured char were included in the sample. Char were captured by electrofishing wadeable sections of the study area or by angling and using tangle nets in the lake. Captured char were anesthetized using buffered, tricaine methane sulfonate at a concentration of 50 mg/L. For captured char, we recorded collection location and fork length (FL, measured to the nearest mm) and collected approximately 4 mm² of fin tissue for genetic analysis (see DeHaan & Bernall, 2013).

2.2 | Laboratory analysis

DNA was extracted from all tissue samples using Qiagen DNeasy 96 blood and tissue extraction kits (Qiagen Inc., Valencia, CA). All individuals were genotyped at 12 SNP loci following the protocols outlined in DeHaan, Pascal, and Seeb (2014) that showed fixed differences among multiple Salvelinus spp. for initial species identification. Genotypes of Wallowa River watershed bull trout were compared with genotypes from known bull trout and
brook trout for species identification. Any individuals identified as bull trout × brook trout hybrids or brook trout were excluded from further analysis. All remaining individuals were then genotyped at a suite of 16 microsatellite loci following protocols identified in DeHaan and Bernall (2013). These 16 loci have previously been screened, utilized to assess bull trout population structure, and applied to conservation and management decisions (DeHaan, Bernall, DosSantos, Lockard, & Ardren, 2011; Meeuwig, Guy, Kalinowski, & Fredenberg, 2010).

3 | STATISTICAL ANALYSIS

3.1 | Hybridization

To evaluate hybridization between char species in the Wallowa River watershed, we calculated a hybrid index for each individual (see Anderson & Thompson, 2002). The hybrid index was based on nine SNP loci that provided adequate resolution to distinguish between bull trout and brook trout specifically. The hybrid index was calculated as the number of brook trout alleles divided by the total number of alleles for a given individual. This value ranged from 0.0 (100% bull trout) to 1.0 (100% brook trout). Samples with a hybrid index score >0.0 but <1.0 were characterized as hybrids. We calculated the proportion of bull trout, brook trout and hybrids in the sample. We then estimated values for the population by calculating the Bayesian (uninformed prior) credible intervals (95%) around the observed sample proportions.

3.2 | Population genetic characteristics

To determine genetic similarities among populations, we compared the Wallowa River watershed population to populations from the geographically proximate Grande Ronde River and Imnaha River watersheds (Figure 2). Bull trout from these watersheds had been previously

![Figure 2](https://example.com/figure2.png)
genotyped at the same 16 loci that were used in this study and were considered distinct populations (Ardren et al., 2011; Hudson, Bingham, Whitesel, & Hawkins, 2013). To provide information from a population that was likely to be relatively distinct, we also included bull trout collected from the North Fork Asotin Creek population (Figure 2). The spawning area in North Fork Asotin Creek is separated from those in the Grande Ronde River and Imnaha River watersheds by approximately 176 and 197 river km, respectively. All bull trout collected from the Wallowa River watershed between 2010 and 2013 were pooled into a single population for genetic analysis.

To screen the Wallowa River watershed dataset for individual bull trout with matching genotypes, we used the program CERVUS v3.0 (Kalinowski, Taper, & Marshall, 2007; Marshall, Slate, Kruuk, & Pemberton, 1998). Samples with matching genotypes at all loci were presumed to be from the same individual and only one sample was included in subsequent analysis. Each population was tested for conformance to Hardy–Weinberg equilibrium (HWE) expectations using the program GENEPOP v4.1 (Raymond & Rousset, 1995). We also tested each population for evidence of linkage disequilibrium (LD). Alpha values for HWE and LD tests were adjusted for multiple comparisons using a sequential Bonferroni adjustment (Rice, 1989). For each population, we estimated the mean number of alleles per locus, allelic richness (corrected for differences in sample size among populations), expected heterozygosity and observed heterozygosity. All measures of genetic diversity were estimated using the program GDA (Lewis & Zaykin, 2001) with the exception of allelic richness, which was estimated using the program HP-Rare v June 6, 2006 (Kalinowski, 2005).

To test for evidence of a recent (within the past 0.2–4.0 generations) genetic bottleneck, we used the program BOTTLENECK v1.2.02 (Piry, Luikart, & Cornuet, 1999). This program tests for an excess of heterozygotes relative to the frequency of alleles in a population (Cornuet & Luikart, 1996) under the assumption of mutation-drift equilibrium. We assumed a two-phased model of mutation with 90% stepwise mutations and 10% variance in non-stepwise mutations. We assessed significance of a genetic bottleneck using a one-sided Wilcoxon test for heterozygosity excess.

We used a variety of methods to examine the relationship among bull trout populations and to infer the possible origins of bull trout from the Wallowa River watershed. We first conducted a principal components analysis (PCA) of allele frequencies using the adegenet package (Jombart, 2008) for the R statistical environment (R Development Core Team, 2014). We then used the program GENEPOP to estimate the level of genetic variation among each population pair (pairwise $F_{ST}$). Subsequently, we used the program PHYLIP v3.6 (Felsenstein, 1993) to construct a consensus neighbor-joining tree. We generated 1000 replicate datasets using a bootstrap procedure then estimated chord distances (Cavalli-Sforza & Edwards, 1967) among collection locations and used these values to construct a consensus neighbor-joining tree.

3.3 Growth, survival, and age

To explore whether the population of bull trout currently in the Wallowa River watershed is likely a remnant of the 1997 reintroduction, we evaluated fish size and age as well as expected growth and survival. Migratory bull trout in the Wallowa River watershed were likely adfluvial. Fortunately, the growth and age characteristics of fluvial and adfluvial populations of bull trout can be similar (see Al-Chokhachy, Doyle, & Lamperth, 2019; Erhardt & Scarnecchia, 2016; Harris, Newlon, Howell, Koch, & Haeseker, 2018; McCubbins, Hansen, DosSantos, & Dux, 2016). Thus, to make these evaluations, we used relatively recent and robust information from populations that migrate to large rivers or reservoirs. To estimate the minimum growth of bull trout, we derived the following Equation (1) from the information presented in Harris et al. (2018):

\[
FL_d = (-0.126 \times FL_y) + 81.64
\]

where $FL_d$ is the yearly change in fork length and $FL_y$ is the fork length in a given year. We initiated this exercise using the minimum FL of bull trout reintroduced in 1997 (70 mm) and estimated the FL of these fish from 1998 to 2013. To estimate what the growth rate would have been if the bull trout collected from 2010 to 2013 were the shortest fish reintroduced in 1997, we used the following Equation (2):

\[
EGR = (FL_c - 70)/CY - 1997
\]

where $EGR$ is the estimated growth rate (mm/yr), $FL_c$ is the fork length (mm) at collection and $CY$ is the collection year. To estimate the yearly probability of bull trout surviving, we derived the following Equation (3) from the information presented in Al-Chokhachy and Budy (2008) and the assumption that bull trout in the Wallowa River watershed would exhibit a Type III survivorship curve (reviewed in Sinclair, 1989):
where $S_y$ is the probability of surviving for a given year and FL is the estimated fork length in that given year. Since fish that survived a given year would also be expected to have grown during that year, we used calculations of growth (described previously) to adjust the anticipated FL of fish and recalculate the probability of survival for each subsequent year. In Equation (3), the probability of survival is positively related to fish length and, mathematically, could exceed 1.00. Since no mortality is unlikely, we assumed the probability of bull trout surviving for a given year would not exceed 0.667 (see Howell, Colvin, Sankovich, Buchanan, & Hemmingsen, 2016). These calculations were done for the minimum and maximum fork lengths (70 and 380 mm) of bull trout reintroduced into the Wallowa River watershed. We estimated the overall probability of bull trout surviving from 1997 to 2013 using the following Equation (4):

$$S = \prod_{t=1998}^{2013} S_t$$

where $S$ is the probability of survival from 1997 to 2013 and $S_t$ is the probability of survival for a given year. To evaluate their age in 2010–2013, bull trout reintroduced in 1997 were assumed to range in age from 1 (fish with a FL of 70 mm; Zymonas & McMahon, 2009) to 6 (fish with a FL of 380 mm; Al-Chokhachy & Budy, 2008) years old upon their reintroduction.

For all statistical comparisons or assessments, significance was assigned when $p < 0.05$.

4 | RESULTS

4.1 | Sample collection

From 2010 to 2013, tissue was collected from 119 *Salvelinus* spp. Two char were captured from Wallowa Lake and 117 char were captured in the tributaries upstream of the lake (107 from the East Fork Wallowa River, one from the West Fork Wallowa River, and nine from the tailrace). The FL of unique bull trout that were measured ($N = 74$) ranged from 41 to 550 mm with the majority of individuals ≤250 mm. Genotypes consistent with bull trout × brook trout hybrids were observed in 34 of the 119 fish, which were excluded from the population analysis. We also identified three pairs of bull trout individuals that had matching genotypes at all loci, indicating the same fish had been sampled twice. We retained only one individual from each pair for the population analysis. As a result, 82 individual bull trout from the 2010 to 2013 collection were included in the population analysis. From 2016 to 2018, fin tissue was collected from 62 char in the tributaries (58 from the East Fork Wallowa River, one from BC Creek, and three from the tailrace) and included in the hybridization analysis. The FL of unique bull trout that were measured ($N = 40$) ranged from 23 to 600 mm with the majority of individuals ≤150 mm.

4.2 | Hybridization

For the 62 char collected in the Wallowa River watershed from 2016 to 2018 the hybrid index for the collection ranged from 0.0 to 1.0. Bull trout, brook trout and bull trout × brook trout hybrids represented 40, 12, and 10 individuals, respectively. The corresponding proportion of the sample that represented bull trout, brook trout and bull trout × brook trout hybrids was 0.65, 0.19, and 0.16, respectively. The hybrids included three F1 hybrids, five bull trout backcrosses and two brook trout backcrosses. The proportion of the population estimated to be bull trout, brook trout and bull trout × brook trout hybrids ranged from 0.520 to 0.753, 0.115 to 0.309, and 0.091 to 0.265, respectively.

4.3 | Population genetic characteristics

Bull trout from North Fork Catherine Creek deviated from HWE expectations at *Sco218* and *Sco106*, Big Sheep Creek deviated from HWE expectations at the locus *Sco220* and upper Imnaha River deviated from HWE expectations at the locus *Sco109*, all due to a deficiency of heterozygotes. Bull trout from the Wallowa River watershed deviated from HWE expectations at five loci, *Sco109, Sco218, Sco107, Sco216*, and *Smm22*, all due to an excess of heterozygotes. We observed the following number of locus pairs that showed evidence of LD after Bonferroni adjustment: North Fork Asotin Creek, five of 105; Lostine River, one of 105; South Fork Wenaha River, three of 91; North Fork Catherine Creek, one of 91; Big Sheep Creek, 13 of 91; Lick Creek, four of 105; McCully Creek, four of 105; upper Imnaha River, six of 91; Wallowa River, 38 of 91. The only evidence of a genetic bottleneck was from a significant Wilcoxon test for heterozygosity excess in the Wallowa River watershed ($p < 0.05$; Table 1).

There were nine alleles (out of 189 total across all populations) found in the Wallowa River watershed that were present in populations from the Imnaha River watershed but not from the Grande Ronde River.
There were no alleles in the Wallowa River watershed that were present in populations from the Grande Ronde River watershed but not from populations in the Imnaha River watershed. Three private alleles were observed only in the Wallowa River watershed. Estimates of genetic diversity varied moderately among the populations we surveyed and the Wallowa River watershed sample had relatively low estimates of diversity (Table 1). Allelic richness was lowest in the Wallowa River watershed ($A_R = 4.29$) and greatest in the South Fork Wenaha River ($A_R = 6.33$) (Table 1).

The first variance component of the PCA separated the Wallowa River watershed and Big Sheep Creek from all other populations in the analysis (Figure 3). The second variance component separated the Wallowa River watershed from Big Sheep Creek (Figure 3). The remaining bull trout populations clustered together with moderate separation among them. Pairwise $F_{ST}$ estimates ranged from 0.071 between South Fork Wenaha River and North Fork Asotin Creek to 0.244 between Big Sheep Creek and Lostine River (Table 2). Pairwise $F_{ST}$ estimates showed the Wallowa River watershed was most similar to Big Sheep Creek ($F_{ST} = 0.102$) and most different from the Lostine River ($F_{ST} = 0.222$) and North Fork Catherine Creek ($F_{ST} = 0.240$). In the neighbor-joining tree analysis, the Wallowa River watershed population clustered with the Big Sheep Creek population with 100% bootstrap support, other populations from the Imnaha River clustered together, and populations from the Grande Ronde River clustered together (Figure 4). The branches on the tree were relatively long indicating a high degree of divergence among populations.

### Table 1 Genetic diversity of the nine bull trout populations evaluated in this study

| Population                   | Watershed                  | $N$ | $A$  | $A_R$ | Private alleles | $H_{exp}$ | $H_{obs}$ | Wilcoxon |
|------------------------------|----------------------------|-----|------|-------|-----------------|-----------|-----------|----------|
| Wallowa River watershed      | Grande Ronde River         | 82  | 4.81 | 4.29  | 3               | 0.565     | 0.598     | S        |
| Lostine River                | Grande Ronde River         | 23  | 4.38 | 4.30  | 3               | 0.511     | 0.512     | NS       |
| South Fork Wenaha River      | Grande Ronde River         | 28  | 6.75 | 6.33  | 15              | 0.630     | 0.674     | NS       |
| North Fork Catherine Creek   | Grande Ronde River         | 25  | 5.13 | 5.01  | 8               | 0.520     | 0.490     | NS       |
| Big Sheep Creek              | Imnaha River               | 63  | 6.19 | 5.18  | 0               | 0.567     | 0.570     | NS       |
| Lick Creek                   | Imnaha River               | 23  | 6.19 | 6.11  | 2               | 0.653     | 0.679     | NS       |
| McCully Creek                | Imnaha River               | 78  | 6.25 | 5.28  | 1               | 0.589     | 0.575     | NS       |
| Imnaha River                 | Imnaha River               | 76  | 7.75 | 6.26  | 11              | 0.635     | 0.600     | NS       |
| North Fork Asotin Creek      | Asotin Creek               | 29  | 6.31 | 5.83  | 11              | 0.596     | 0.584     | NS       |

Note: Fish are characterized by collection locations (population, watershed), number of fish analyzed ($N$), mean number of alleles per locus ($A$), allelic richness ($A_R$), private alleles, expected heterozygosity ($H_{exp}$), observed heterozygosity ($H_{obs}$), and results of a one-sided Wilcoxon test (Wilcoxon) where, relative to the frequency of alleles in a population, $S$ indicates a significant excess and NS indicates no significant excess.
4.4 Growth, survival, and age

From 2010 to 2013, 74 unique bull trout were collected and measured. The shortest bull trout reintroduced in 1997 would have been expected to grow to FLs near 548, 560, 571, and 581 mm in 2010, 2011, 2012, and 2013, respectively. Bull trout collected between 2010 and 2013 had a median FL of 121 mm (range 41–550 mm). If these fish had a length of 70 mm in 1997, then their median growth rate was 3.2–3.9 mm/yr (range –1.8–34.6). The probability a 70 and 380 mm bull trout would survive from 1997 to 2013 was estimated to be <0.0001 and 0.0015, respectively. If bull trout captured from 2010 to 2013 were remnants from the 1997 reintroduction, we estimated they would have been 14–22 years old.

**TABLE 2** Pairwise $F_{ST}$ estimates of genetic variation among bull trout populations evaluated in this study

| Population                  | North Fork Asotin Creek | Lostine River | South Fork Wenaha River | North Fork Catherine Creek | Big Sheep Creek | Lick Creek | McCully Creek | Imnaha River |
|-----------------------------|-------------------------|---------------|-------------------------|---------------------------|----------------|------------|--------------|--------------|
| Lostine River               | 0.170                   |               |                         |                           |                |            |              |              |
| South Fork Wenaha River     | 0.071                   | 0.152         |                         |                           |                |            |              |              |
| North Fork Catherine Creek | 0.166                   | 0.199         | 0.138                   |                           |                |            |              |              |
| Big Sheep Creek             | 0.168                   | 0.244         | 0.140                   | 0.229                     |                |            |              |              |
| Lick Creek                  | 0.097                   | 0.159         | 0.092                   | 0.135                     | 0.113          |            |              |              |
| McCully Creek               | 0.107                   | 0.180         | 0.093                   | 0.153                     | 0.128          | 0.083      | 0.104        |              |
| Imnaha River                | 0.105                   | 0.154         | 0.074                   | 0.173                     | 0.137          | 0.086      | 0.157        | 0.127        |
| Wallowa River watershed     | 0.165                   | 0.222         | 0.134                   | 0.240                     | 0.102          | 0.132      | 0.157        | 0.127        |

**FIGURE 4** Consensus neighbor-joining tree for bull trout populations from the Wallowa River watershed bull trout, populations from the Grande Ronde River and Imnaha River watersheds, and the North Fork Asotin Creek population. The analysis was based on Cavalli-Sforza and Edwards’ chord distance. Values at the nodes represent the number of bootstrap replicates out of 1000 that exhibited the displayed topology.
5 | DISCUSSION

Bull trout are no longer extirpated from the Wallowa River watershed. Although native bull trout ceased to exist in the watershed after the 1950s (Buchanan et al., 1997), char were known to persist in the watershed, presumably from historic introductions of brook trout (ODFW, 2005). Our evaluation suggested the majority of char in the area of the Wallowa River watershed we sampled were bull trout. To our knowledge, this is the first report documenting a conservation reintroduction of bull trout resulting in the reestablishment of a population in an area from which it had become extirpated. In addition, this conservation reintroduction consisted of a single translocation event of a relatively small number of fish. There have been limited reports of other bull trout reintroductions that also indicated some degree of success (Middle Fork Willamette River and McKenzie River, Oregon, USA; see Hayes & Banish, 2017). In contrast to the Wallowa River watershed reintroduction, these efforts involved multiple years of translocations, relatively large numbers of fish and may have benefited from the removal of factors preventing immigration of bull trout from adjacent areas (Zymonas, 2011). When limiting factors are removed, there is evidence bull trout can reestablish if habitat is accessible (e.g., Brenkman, Peters, Tabor, Geffre, & Sutton, 2019). Reestablishments have generally appeared to benefit from anthropogenic assistance (e.g., Buktenica, Hering, Girdner, Mahoney, & Rosenlund, 2013). In contrast, for most areas where bull trout populations have become extirpated, recolonization has not occurred either after human intervention (e.g., Rode & Dean, 2004) or naturally (e.g., Allen et al., 2016). For many of the reasons associated with their extirpation (e.g., habitat loss and fragmentation) (see Brignon, Peterson, Dunham, Schaller, & Schreck, 2018; Dunham et al., 2011), bull trout may have difficulty recolonizing areas naturally (Dunham, Taylor, & Allendorf, 2014). Although bull trout now exist in the Wallowa River watershed, they remain isolated from other bull trout populations, are sympatric with brook trout and show relatively low levels of genetic diversity compared with neighboring populations (see Ardren et al., 2011). How long bull trout will persist in the Wallowa River watershed is unclear.

Bull trout currently in the Wallowa River watershed likely originated from a reintroduction in 1997. Bull trout typically exhibit an isolation by distance relationship whereby geographically proximate populations from the same watersheds exhibit a greater degree of genetic similarity than populations from different watersheds (Costello, Down, Pollard, Pacas, & Taylor, 2003; DeHaan et al., 2011). Given this, we would expect that, historically, bull trout in the Wallowa River watershed were more genetically similar to bull trout populations from the Grande Ronde River than to those from the Imnaha River. The PCA, pairwise $F_{ST}$ estimates, and the neighbor-joining tree analyses all suggested bull trout we collected from the Wallowa River watershed were more genetically similar to populations from the Imnaha River watershed than to those from the Grande Ronde River watershed. Specifically, bull trout in the Wallowa River watershed were most similar to those from Big Sheep Creek. Bull trout in the Wallowa River watershed were also less similar to those from Grande Ronde River populations than to the relatively distant population from Asotin Creek. Thus, the most likely explanation for the genetic pattern we observed is that bull trout currently in the Wallowa River watershed share an ancestry with those from the Imnaha River watershed. Alternatively, the indigenous population may have been undetected rather than extirpated, and the source of the fish we characterized. In this case, the data would suggest the indigenous population is more closely related to those from an adjacent watershed than from the watershed in which it exists. It is also possible that the current population is progeny of indigenous and reintroduced fish. It is impossible to fully test these hypotheses without genetic samples from the historic Wallowa River watershed population and the translocated fish. However, given the data presented herein and our knowledge of bull trout population structure, it is reasonable to suggest the most plausible hypothesis is bull trout currently in the Wallowa River watershed originated from the 1997 reintroduction.

Estimates of genetic variation within the bull trout population from the Wallowa River watershed were consistent with a recent reintroduction. Bull trout in this investigation had a relatively low level of genetic diversity, several loci that deviated from HWE expectations, a high proportion of loci that showed evidence of LD and they exhibited evidence of a genetic bottleneck. The bottleneck test we used was capable of detecting a relatively recent genetic bottleneck (within the past 0.2–4.0 generations; Cornuet & Luikart, 1996). Assuming a 5-year generation interval for bull trout (Maxell, 1999), this suggests bull trout in the Wallowa River watershed experienced a bottleneck that occurred between 1990 and 2009. Many introduced populations show a similar pattern of low diversity coupled with a recent genetic bottleneck (Mock, Latch, & Rhodes, 2004; Williams, Serfass, Cogan, & Rhodes, 2002). Fish from Big Sheep Creek were the likely source for the majority of fish in the Wallowa Valley Improvement Canal, the waterbody from which bull trout were captured for translocation in 1997 (Buchanan et al., 1997). Bull trout in the Wallowa River watershed exhibited a substantial level of differentiation and reduced genetic diversity from those in Big Sheep Creek after approximately three
generations. Introduced populations often experience high levels of genetic drift and show significant genetic divergence from their source population within only a few generations (Fitzsimmons, Buskirk, & Smith, 1997; Wright et al., 2014). In addition, bull trout from populations in the Imnaha River watershed other than Big Sheep Creek (e.g., Little Sheep Creek) are able to enter the Wallowa Valley Improvement Canal. The recent bottleneck and patterns of genetic diversity that we detected are consistent with the hypothesis that relatively few bull trout, some possibly from the same family group, reintroduced to the Wallowa River watershed in 1997 were responsible for founding the current population.

Interestingly, we observed alleles that were unique to the Wallowa River watershed. This might be expected in the case of a small, historically isolated population. These alleles may have been at low frequency in the donor population and were either lost due to genetic drift or were not sampled in the collections used for this study. Alternatively, char may have existed in the Wallowa River watershed at low levels, gone undetected and not been extirpated when the 1997 reintroduction occurred. If this were the case, the current population could represent an admixture of some combination of the indigenous bull trout, dolly varden and bull trout from stocking efforts, including the most recent reintroduction. If indigenous bull trout persist, they have been isolated for almost 100 years by the dam at the outlet of Wallowa Lake. Each of these scenarios could also be consistent with the observation of unique alleles.

Bull trout in the Wallowa River watershed are likely to be the result of successful spawning and natural production. A proportion of the bull trout we collected were shorter than 70 mm, the length of the smallest introduced fish in 1997. It is unlikely that the growth rate for some of the reintroduced fish would have been negative for 13 years (see Al-Chokhachy & Buddy, 2008), a requirement to reach the sizes we observed. In addition, given their length, some of the small fish we observed were likely <3 years old (Howell et al., 2016). This suggests they originated from spawning around 2009. Finally, there is typically a positive, curvilinear relationship between the size of bull trout and their probability of survival (see Al-Chokhachy et al., 2019; Harris et al., 2018; Howell et al., 2016). Given this, for the reintroduced bull trout, we estimated relatively large fish could have experienced negligible mortality, but it is improbable that relatively small fish would have survived from 1997 to 2010. Furthermore, if large bull trout did survive during this period and were the same fish reintroduced in 1997, their estimated ages would have been up to 19 years old, which would have been possible but uncommon (see Bahr & Shrimpton, 2004; Howell et al., 2016). Growth and size can vary between bull trout populations and life history expressions (McPhail & Baxter, 1996). However, taken as a whole, the information from our study suggests bull trout in the Wallowa River watershed are unlikely to be remnants from the reintroduction in 1997.

Whether the reintroduction of bull trout into the Wallowa River watershed represents a success is not completely clear. The definition of reintroduction success is a subject of considerable debate (see Haskins, 2015; Robert et al., 2015) and criteria are often poorly defined (Godefroid et al., 2011). Given bull trout are no longer absent from in the Wallowa River watershed, are spawning successfully and reproducing naturally, there are certainly components of a successful reintroduction. However, the long-term fate of the population is dubious and relatively few generations have elapsed since the single reintroduction effort. The genetic diversity of the population was relatively low, exhibiting fewer than 4.5 alleles/locus and (along with the Lostine River population) the lowest allelic richness of the nine populations we evaluated. Allelic richness of the population was also below the mean reported for most bull trout populations and within the range of relatively isolated or vulnerable populations (Ardren et al., 2011; Kovach et al., 2015; Meeuwis et al., 2010). Of the different diversity measures we examined, allelic richness is the most sensitive to population declines (Allendorf & Luikart, 2007) and is often used to monitor population status (Schwartz, Luikart, & Waples, 2007). This population also remains isolated upstream of the Wallowa Lake dam and isolated populations may be prone to increased risk of extinction (Allendorf & Luikart, 2007). In addition, char in the Wallowa River watershed currently include bull trout, brook trout and hybrids. Hybridization and competition with brook trout can represent a substantial risk to many bull trout populations (Kanda, Leary, & Allendorf, 2002; Rieman, Peterson, & Myers, 2006; Williams et al., 1988). Furthermore, although a robust assessment has not been conducted, the size of the bull trout population in the Wallowa River watershed is likely low. Redd surveys of all available habitat within the East Fork Wallowa River have been performed annually since 2017. Total redd counts during this timeframe have ranged from 3 to 11 (Doyle, 2020). Finally, the Wallowa River watershed now appears to contain an out-of-basin population of bull trout that, if they are able to emigrate from the watershed, could pose a genetic risk (e.g., outbreeding depression) to other Grande Ronde River bull trout populations. While an out-of-basin source population may not have been optimal, at the time this reintroduction occurred, biologists had limited knowledge of bull trout population structure. For species where robust source populations are scarce, it is not uncommon for reintroduction efforts to consider those
that show similar ecological characteristics or from adjacent areas (see IUCN, 2013; Soorae, 2011).

The 1997 reintroduction of bull trout into the Wallowa River watershed was opportunistic in nature. Opportunistic reintroductions in general, and for freshwater fishes in particular, have been relatively common (Seddon et al., 2007). For a variety of reasons (e.g., resources) these efforts are often poorly planned and not evaluated. When evaluations are conducted, they are frequently associated with constraints and limitations. The 1997 reintroduction of bull trout into the Wallowa River watershed is encumbered by some of these limitations. For example, this reintroduction lacked explicit and predefined criteria to evaluate success, systematic monitoring of demographic characteristics, and the collection of tissue samples from the translocated individuals to allow genetic characterization of the source fish. Nevertheless, while data in this study may not allow the success of this reintroduction effort to be fully evaluated, they do allow for a relatively rare assessment of a reintroduction, multiple generations after a translocation. In addition, the data provide a useful basis for monitoring efforts that could be used to evaluate the long-term viability of this population in particular and are useful for informing future reintroduction efforts in general. The limitations to and difficulty in making a definitive claim about whether the reintroduction of bull trout into the Wallowa River watershed was successful emphasize the need and value of clearly defining success prior to a reintroduction (Ewen, Soorae, & Canessa, 2014). This evaluation also underscores the importance of a systematic approach to reintroductions and maximizing the value of assessments (IUCN, 2013). To the extent the reintroduction we evaluated was a success, this does not imply that bull trout reintroductions will be useful and appropriate in all cases. The 1997 reintroduction of bull trout into the Wallowa River watershed may have benefited from specific circumstances (see Galloway et al., 2016), such as the ability of bull trout to express an adfluvial life history form in the presence of adequate prey. It is also noteworthy that reintroduced bull trout in the Wallowa River watershed were able to persist and reproduce for several generations despite being sympatric with brook trout and lake trout (Salvelinus namaycush) as well as lacking connectivity from other bull trout populations.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

(In alphabetical order) Patrick W. DeHaan and Timothy A. Whitesel were responsible for the conceptualization and design of the study. Jeremiah Doyle, Paul M. Sankovich and Timothy A. Whitesel were responsible for the acquisition of the data. Brice A. Adams, Patrick W. DeHaan, Timothy A. Whitesel were responsible for data analysis. Brice A. Adams, Jeremiah Doyle, Patrick W. DeHaan, Paul M. Sankovich and Timothy A. Whitesel were responsible for interpretation of the analysis and writing of the manuscript.

ETHICS STATEMENT

This research was conducted in accordance with the guidelines, terms and conditions put forth in multiple permits from the U.S. Fish & Wildlife Service and the Oregon Department of Fish & Wildlife.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are stored by the U.S. government and under the OPEN Government Data Act, are available from the corresponding author, Timothy A. Whitesel, upon request.

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