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Great Basin Redband Trout Genetic Status Assessment

Final Report

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Summary

Redband trout, a subspecies of *Oncorhynchus mykiss*, are found in the Columbia, Fraser, and Sacramento river systems as well as the Upper Klamath Lake Basin and the northern Great Basin in Oregon, California, and Nevada. The abundance of redband trout has declined across the subspecies range and many natural resource agencies are working to conserve redband trout. In 2007 the Oregon Department of Fish and Wildlife (ODFW) began a six year study to assess the abundance and distribution of redband trout in the northern drainages of the Great Basin in Oregon. As part of that study, genetic samples were collected from 23 redband trout populations across six species management units (SMUs – defined according to endorheic subbasin boundaries) in order to gain a better understanding of the level of genetic variation within and among redband trout populations and SMUs. Using a panel of 96 single nucleotide polymorphism (SNP) markers, we examined the level of genetic variation among SMUs and among populations within SMUs, the levels of genetic diversity within populations, and the level of introgression between native redband trout and introduced hatchery fish. We observed little temporal variation in allele frequencies within populations over the course of this study. Analyses of genetic variation among SMUs showed that Great Basin redband trout formed three distinct genetic groups: one group consisting of populations from the Goose Lake, Warner Lakes, and Chewaucan River SMUs; one group consisting of populations from the Fort Rock SMU; and one group consisting of populations in the Malheur Lakes SMU. Populations from the Catlow Valley SMU grouped with both the Malheur Lakes populations (Threemile and Home creeks) and the Fort Rock populations (Rock Creek). Despite historic and contemporary isolation among many populations, our data suggest that there has been recent gene flow among some populations of redband trout. Estimates of genetic diversity within SMUs and within populations ranged widely, with the greatest estimates observed in the Fort Rock SMU and the lowest estimates observed in two isolated populations in the Catlow Valley SMU. Despite extensive stocking efforts, coastal-origin hatchery fish have not replaced native redband trout in the northern Great Basin. The level of introgression between native redband trout and hatchery-origin fish varied among SMUs, among populations within SMUs, and among individuals within populations. Redband trout in the northern Great Basin represent a unique genetic legacy and data presented in this study will be useful for helping to design conservation plans for redband trout in this unique environment.

Introduction

Redband trout (*Oncorhynchus mykiss ssp.*) are a subspecies of rainbow trout that are generally found in the Columbia and Fraser river drainages east of the Cascade Mountain Range, the Upper Klamath Lake Basin, the upper Sacramento River Basin, and in several subbasins of the Great Basin. Although morphologic and genetic studies have demonstrated a strong degree of divergence between interior redband trout and coastal origin steelhead/rainbow trout (Behnke 1992; Currens et al. 2009; Blankenship et al. 2011; Pearse et al. 2011; Matala et al. 2014), classification of redband trout remains somewhat challenging and unresolved (Behnke 1992; Currens et al. 2009). Behnke (1992; 2002) identified three distinct redband subspecies corresponding to the Columbia, Sacramento, and upper Klamath river systems, but found that evolutionary relationships among redband trout from the Great Basin were more difficult to classify. Redband trout are found in a variety of different habitats including large lakes, large river systems, intermittent desert streams, and montane headwater tributaries (Behnke 1992; Behnke 2002; Schroeder and Hall 2007). Redband trout are able to persist in these diverse environments due a high degree of phenotypic plasticity that includes both resident and migratory life history types, varying age at maturity, and a broad thermal tolerance (Behnke 1992; Gamperl et al. 2002; Schroeder and Hall 2007; Meyer et al. 2010).

Although redband trout are widely distributed, they have presumably declined throughout their native range (Thurow et al. 1997; Thurow et al. 2007; Muhlfeld et al. 2015). Causes for these declines include competition and introgression with introduced coastal-origin rainbow trout, anthropogenic habitat alterations, and a changing climate (Knudsen et al. 2002; Thurow et al. 2007). Coastal-origin rainbow trout have been stocked extensively throughout the range of redband trout and varying levels of introgression between native redband trout and introduced rainbow trout have been observed in different watersheds (Small et al. 2007; Matala et al. 2008; Simmons et al. 2010; Kozfkay et al. 2011). The construction of migratory barriers such as irrigation diversions, dams, and culverts as well as land use activities such as timber harvest and grazing have also been linked to population declines and loss of genetic diversity in redband trout populations (Schroeder and Hall 2007; Neville et al. 2009; Weigel et al. 2013; Muhlfeld et al. 2015). Increasing water temperatures and changing hydrologic regimes associated with climate change are predicted to have negative impacts including habitat loss and reduced reproductive success on several western trout species including rainbow and redband trout

(Wenger et al. 2011). Currently redband trout are a species of conservation concern in all of the states in which they are found, and many state and federal natural resource agencies have developed management plans to help conserve redband trout.

The Great Basin is a large area of endorheic watersheds in Nevada, western Utah, southeastern Oregon, and a portion of eastern California. Historically many watersheds within the Great Basin contained large pluvial lakes and the remnants of some of these lakes still exist (Hubbs and Miller 1948; Minckley et al. 1986). The hydrology of the Great Basin has changed considerably over time as a result of geologic forces including volcanism and tectonism. Many subbasins that were formerly connected to one another or to basins that drained to the Pacific Ocean are now completely isolated (Hubbs and Miller 1948; Minckley et al. 1986). As a result of historic isolation and changing hydrology, many subbasins of the Great Basin contain unique assemblages of fishes. For example, unique species of suckers have evolved in the upper Sacramento River, Goose Lake, and Warner Lakes, despite historic connections between these different subbasins (Hubbs and Miller 1948; Minckley et al. 1986). There are six endorheic subbasins in southeastern Oregon that contain native redband trout: Fort Rock, Goose Lake, Chewaucan River, Malheur Lakes, Catlow Valley, and Warner Lakes (Hubbs and Miller 1948; Minckley et al. 1986; Behnke 1992; Behnke 2002). The upper Klamath system also contains redband trout and, despite the fact that it is currently connected to the Pacific Ocean, it is believed that the upper Klamath system was historically isolated and may have also had a connection to the Great Basin (Minckley et al. 1986).

Several previous studies have used genetic data to examine the evolutionary relationships among redband trout populations and assess the conservation status of various populations. Currens et al. (2009) used allozyme data to determine the evolutionary relationships among redband trout populations across the subspecies range in the United States. These authors found that redband trout could be divided into three major evolutionary groups corresponding to the Columbia River Basin, the Sacramento River Basin, and the upper Klamath Basin. In this analysis some populations from the Great Basin clustered with these three groups whereas other populations were intermediate to the three groups (Currens et al. 2009). Within the Great Basin, there appears to be a high degree of genetic divergence among the different subbasins (i.e., Fort Rock, Goose Lake, Malheur Lakes, etc.; Currens et al. 2009). At a local scale, previous genetic analyses have demonstrated that redband trout populations show a high degree of genetic

differentiation among subbasins and watersheds (Knudsen et al. 2002; Currens et al. 2009), as well as among populations within the same watershed (Small et al. 2007; Matala et al. 2008; Kozfkay et al. 2011). Genetic data have also been used to assess the threats to redband trout populations including the level of introgression between native redband trout and introduced rainbow trout (Matala et al. 2008; Kozfkay et al. 2011; Neville and Dunham 2011; Meyer et al. 2014) and the effects of habitat fragmentation and other disturbances on genetic variation and population status (Neville et al. 2009; Weigel et al. 2013).

Many natural resource agencies have developed monitoring plans for redband trout in response to population declines and increased conservation concern for the subspecies. In 2007 the Oregon Department of Fish and Wildlife (ODFW) began a six year study to assess the abundance and distribution of redband trout in northern Great Basin drainages in Oregon. This study assessed the status of 23 redband trout populations from six Species Management Units (SMUs - defined by endorheic basin boundaries) within the northern Great Basin: Fort Rock, Goose Lake, Warner Lakes, Chewaucan River, Catlow Valley, and Malheur Lakes (Figure 1). The study showed that redband trout were distributed throughout the six SMUs and that although the abundance of redband trout was highly variable both among populations and among SMUs, abundance was generally stable over the course of the study (Meeuwig and Clements 2014).

Genetic data have become increasingly valuable for monitoring species and populations of conservation concern (Schwartz et al. 2007). Genetic data can provide information on population abundance (Luikart et al. 2010), patterns of movement (Taylor et al. 2011), population viability (Osborne et al. 2010; Osborne et al. 2012), and genetic data are especially useful when traditional types of data are limited or difficult to collect. Furthermore, genetic data can provide important information for organizing populations into larger management and conservation groups (Ardren et al. 2011). Given the broad landscape that redband trout occupy in the northern Great Basin, the collection of genetic data was recognized as an important component for conservation planning. As a result, the U.S. Fish and Wildlife Service Abernathy Fish Technology Center Conservation Genetics Program worked with the ODFW Native Fish Investigations Program to conduct a genetic assessment of Great Basin redband trout populations that could inform the conservation planning efforts for redband trout in the State of Oregon. The three primary objectives of this study were:

1) Examine levels of genetic variation among redband trout populations from the northern Great Basin
2) Examine levels of genetic variation within redband trout populations in the northern Great Basin
3) Examine levels of introgression between native redband trout and coastal origin hatchery fish

Study Area and Sample Collection

This study examined native redband trout from across the northern Great Basin in Oregon. This included all six of the SMUs outlined above: Fort Rock, Goose Lake, Warner Lakes, Catlow Valley, Malheur Lakes, and Chewaucan River (Figure 1). ODFW designates 23 populations of redband trout within these six SMUs: three populations each in the Fort Rock, Warner Lakes, Chewaucan River, and Catlow Valley SMUs, five populations in the Goose Lake SMU, and six populations in the Malheur Lakes SMU (Figure 1; Table 1). Redband trout were collected from each population during electrofishing surveys conducted from 2007 to 2012 as part of the ODFW redband trout distribution and abundance status assessment (Meeuwig and Clements 2014). Redband trout were collected at multiple sites within each population and each population was sampled over the course of multiple years (Table 1). Varying numbers of fin clips were taken from redband trout in each population and preserved in 100% non-denatured ethanol.

Additional samples collected outside the ODFW sampling protocol were included in the analysis for purposes of comparison. The Goose Lake Basin extends south into northern California and redband trout populations exist in California tributaries to the lake (Gerstung 2007). We included samples from three Goose Lake populations in California: Cottonwood, Davis, and Lassen creeks. Since there was likely a historic connection between the upper Klamath system and the northern Great Basin (Minckley et al. 1986), we also included five representative redband trout populations from the upper Klamath Basin in our analysis: Moss Creek, an upper Klamath Lake tributary; Fort Creek, a Wood River tributary; Spring Creek, a Williamson River tributary; Rock Creek, a Sycan River tributary; and Fishhole Creek, a Sprague River tributary. Upper Klamath Basin collections were previously analyzed as part of a study conducted by Pearse et al. (2011). The Malheur River, a tributary to the Snake River system, also

had a historic connection to the northern Great Basin (Bisson and Bond 1971; Minckley et al. 1986). We included two redband trout populations from the Malheur River system, Little Malheur River and Blue Bucket Creek, in our analysis. Samples from the Malheur River were previously collected and analyzed for a study of redband trout in the Malheur River by DeHaan and Adams (2010). There is a long history of stocking coastal-origin rainbow trout in Oregon watersheds including the northern Great Basin (Kinunen and Moring 1978). We included samples from two commonly stocked strains of rainbow trout, Oak Springs and Cape Cod, in our analysis as representative coastal-origin hatchery populations.

Laboratory Methods and Preliminary Statistical Analysis

Genomic DNA was obtained from fin clips using DNeasy 96 Blood & Tissue Kits (QIAGEN Inc.) following the manufacturer's protocol. We selected a set of 96 single nucleotide polymorphism (SNP) markers for genetic analysis. Ten of these loci were chosen because they exhibited fixed allelic differences between *O. mykiss* and various subspecies of cutthroat trout (*O. clarki ssp.*; Pritchard et al. 2012). The remaining 86 loci were chosen because they were variable in preliminary screening efforts for Great Basin redband trout. A complete list of the loci used can be found in Appendix 1. All samples were pre-amplified at the 96 loci following the protocol detailed by Smith et al. (2011) to reduce genotyping failure and error rates. The resulting pre-amplified product was then diluted 1:20 with deionized water before further processing. The 96 SNP makers were processed using TaqMan® SNP Genotyping Assays (Life Technology, Inc.) on a Fluidigm® EP-1™ System with the 96.96 Dynamic Arrays following the manufacturer's protocol (Fluidigm Corporation). Multi-locus genotypes of each individual fish were visualized and scored using Fluidigm® SNP Genotyping Analysis software and were confirmed by two researchers.

One locus (known as both *SH10451-624* and *Omy104519-624*) was inadvertently run twice. Two loci (*Omy_crb-106* and *Omy_128996-481*) had excessive missing data and were removed from further analysis. This left us with ten loci for species ID analysis and 83 loci for population genetic analysis. Sixteen individuals that we genotyped failed to amplify at ten or more loci and were excluded from further analysis due to concerns with data quality. DNA was re-extracted from 270 samples for quality control analysis. These samples were then re-genotyped at the same set of SNP loci and genotypes were compared to determine our error rate.

The overall error rate was 2.57% and was largely due to samples that amplified the first run but not the second or vice versa. The call-to-call error rate (instances where we observed inconsistent genotypes between the original run and the second run) was 0.37%.

Each population was given a four letter code for statistical analysis. The first two letters of this code corresponded to the SMU the population was located in and the third and fourth letters corresponded to the population name. For example, FRBR corresponds to the Fort Rock Bridge Creek population. The complete list of four letter population codes can be found in Table 1.

Cutthroat trout frequently hybridize with *O. mykiss* when the two species occur sympatrically (Leary et al. 1995) and limited numbers of cutthroat trout have been stocked in the northern Great Basin. Ten of the loci we used for this study exhibited fixed allelic differences between *O. mykiss* and several subspecies of cutthroat trout (Pritchard et al. 2012) and we examined genotypes at these loci to determine if there was any evidence of hybridization between native redband trout and introduced cutthroat trout. No cutthroat trout alleles were detected at eight of the ten loci that differentiated *O. mykiss* and *O. clarki*. At the locus *Ocl_106419D*, we observed cutthroat trout alleles in 50 of 648 fish (approximately 7.7%) we analyzed in the Fort Rock Basin, but not in any other SMU. Thompson Valley Reservoir in the Fort Rock Basin was stocked with cutthroat trout 13 times from 1925 to 1991; however, fish in the reservoir do not have access to the rest of the Fort Rock Basin (S. Gunckel, ODFW, *personal communication*). Interestingly, Behnke (2007) observed that approximately 30% of the redband trout he examined from Buck Creek and 17% of the fish he examined from Bridge Creek (two Fort Rock tributaries) had basibranchial teeth; a trait often used to distinguish *O. mykiss* from *O. clarki* (Behnke 1992; Leary et al. 1996). These results provide further evidence that redband trout in the Fort Rock Basin retain some characteristics similar to cutthroat trout, as evidenced by the previous results of Behnke (2007). We also observed two cutthroat trout alleles at the locus *Ocl_98683D* in one fish from the West Goose population. Cutthroat trout were not stocked in the Goose Lake Basin in Oregon at any time. The presence of cutthroat trout alleles in a single individual from Goose Lake may represent a genotyping error or it may mean that this particular marker does not have fixed allelic differences between *O. clarki* and *O. mykiss* rangewide. The ten loci used for species ID analysis were excluded from further data analysis, but individuals

from Fort Rock and Goose Lake that had alleles associated with cutthroat trout in other watersheds were retained for analysis.

When the effective population size is low and only a small number of adults spawn each year, it's possible that there will be genetic variation among temporal samples collected from the same population (Ostergaard et al. 2003; DeHaan et al. 2011a). In order to determine if it was appropriate to combine temporal replicate samples, we used analysis of molecular variance (AMOVA; Excoffier et al. 1992) to determine the level of genetic variation among temporal replicates from the Great Basin populations (Malheur River, upper Klamath, and hatchery populations were excluded from this analysis). Samples from the same population were grouped according to their collection year and we conducted six separate AMOVAs, one for each SMU. For each analysis we determined the amount of genetic variation attributed to differences among populations within the SMU, differences among temporal replicate samples within populations, and differences among individuals within populations. We then conducted one additional AMOVA that included samples from all six SMUs and examined the level of variation among SMUs, among populations within SMUs (with all temporal replicates combined) and among individuals within populations. All AMOVAs were conducted using the program Arlequin v3.5.1.2 (Excoffier et al. 2005). The amount of variation among temporal replicates within a population ranged from 0.38% (Fort Rock) to 1.81% (Warner Lakes) and was much lower than the amount of variation we observed among populations within each SMU (range 3.42% to 41.43%; Table 2). Results of the AMOVA which included all populations from all SMUs indicated that 15.05% of the genetic variation could be attributed to differences among SMUs, 7.82% of the genetic variation could be attributed to differences among populations within SMUs, and 4.09% of the total genetic variation could be attributed to differences among individuals within populations.

We also conducted chi-squared contingency tests of allele frequency heterogeneity using the program GENEPOP v4.1 (Raymond and Rousset 1995) to determine if there were significant differences in allele frequencies between temporal replicate samples from Great Basin populations. Alpha values for contingency tests were adjusted for multiple comparisons using a Bonferroni adjustment (Rice 1989) based on the number of tests within each SMU. Overall, there were 102 comparisons among temporal replicates from the same population and 24 of these comparisons (23.5%) indicated a significant difference in allele frequencies among temporal

replicates from the same population (Table 3). Some of the significant tests were comparisons involving small samples sizes (i.e., 10 or fewer individuals sampled in a single year), which likely did not accurately represent the total variation in the population. Based on the fact that there were not significant allele frequency differences among the majority of the comparisons, as well as the results of the AMOVA that indicated that there was much more variation among populations than among temporal replicates from the same population, we chose to combine temporal replicates from the same population into a single population for all subsequent data analyses. Despite significant allele frequency differences among some temporal replicates, this should provide the most accurate representation of the total genetic variation in these populations (Waples 1989).

Once temporal replicates were pooled into a single population, we tested all populations in the dataset (Great Basin redband trout and other populations) for conformance to Hardy-Weinberg equilibrium (HWE) expectations and for evidence of linkage disequilibrium (LD) using GENEPOP. The purpose of these tests was to determine if collections were representative of a single, randomly mating population. Alpha values for HWE and LD tests were adjusted for multiple comparisons using a sequential Bonferroni adjustment (Rice 1989). Twenty of the 35 populations in our dataset did not deviate from HWE expectations at any loci (Table 1). The remaining 15 populations had between one and six loci that did not conform to HWE expectations (Table 1). The proportion of linked loci in each population ranged from 0.00 for several populations to 0.05 for Davis Creek in the Goose Lake SMU (Table 1). Results of HWE and LD tests suggested that the collections from each population appeared to be a random sample of individuals from that population.

Objective 1 - Examine Levels of Genetic Variation among Redband Trout Populations from the Northern Great Basin

The northern Great Basin has a complex hydrologic history which has played an important role in shaping genetic variation in fish species of the region. Tens of thousands of years ago, much of the northern Great Basin was part of a large system of lakes (Hubbs and Miller 1948). As the climate of the region alternated between glacial and arid periods, large lakes formed and then desiccated over the course of thousands of years (Hubbs and Miller 1948; Minckley et al. 1986). Individual subbasins that contained large pluvial lakes formed during this

period, and over time many of these large lakes were reduced to multiple smaller lakes (e.g., Warner Lakes, Malheur Lakes) or desiccated completely (e.g., Catlow Valley; Hubbs and Miller 1948; Minckley et al. 1986). Connections between various subbasins and between the Great Basin and the Pacific Ocean were formed and eliminated during this period as well. Examination of the historic and contemporary fish assemblages in the northern Great Basin has provided interesting clues into the hydrologic and evolutionary relationships among the different subbasins and among populations. The Goose Lake Basin has been periodically connected to the Pit River system (part of the upper Sacramento River) and the two subbasins share similar fish assemblages (Hubbs and Miller 1948; Minckley et al. 1986). Connections between the Goose Lake Subbasin and the Warner Lakes Subbasin and the Chewaucan River have also been suggested (Hubbs and Miller 1948; Minckley et al. 1986). Hydrologic connections between the Great Basin and the Pacific Ocean also existed during this time. Geologic and fossil evidence suggests a connection between the Fort Rock Subbasin and the adjacent Deschutes River Basin (Allison and Bond 1983), and connections between the Malheur Lakes Subbasin and the Snake and Columbia River systems have also been documented (Bisson and Bond 1971). Possible historic connections between the Upper Klamath Lake system and the northern Great Basin have also been suggested (Hubbs and Miller 1948; Minckley et al. 1986).

The widespread distribution of redband trout among Great Basin subbasins and the Columbia, Klamath, and Sacramento river systems has facilitated studies of redband trout evolutionary ecology. Behnke (1992; 2007) conducted extensive morphometric and meristic studies of redband trout rangewide and suggested that redband trout of the northern Great Basin all had affinities to the Columbia River system. The author noted the historic connection between the Goose Lake Basin and the Pit River system and suggested that Goose Lake redband trout were essentially Pit River origin fish. Behnke (1992; 2007) also suggested historic connections among the different subbasins including connections between the Catlow Valley and Malheur Lakes subbasins, connections between the Goose Lake, Warner Lakes, and Chewaucan subbasins, and possible connections between Fort Rock and the Upper Klamath Lake system. Currens et al. (2009) examined evolutionary relationships among redband trout based on genetic variation at allozyme loci. These authors suggested that redband trout in the northern Great Basin did not represent a single genetic lineage but that the northern Great Basin had been colonized by redband trout from multiple sources including the upper Sacramento/Pit River system, the

Columbia River system, and possibly the Upper Klamath Lake system (Currens et al. 2009). The authors concluded that the origins of some populations of redband trout such as those in the Fort Rock system were difficult to determine (Currens et al. 2009).

One caveat of previous redband trout studies is that they focused on evolutionary relationships at a broad, range-wide scale. Sampling from most Great Basin SMUs targeted one or two populations, but typically not all of the populations within an SMU. In order to effectively conserve and manage redband trout within the northern Great Basin, it's important that biologists have a clear understanding of the genetic relationships among all populations within the different SMUs. Previous studies suggest that there is not a consistent pattern of genetic variation among populations within SMUs; some SMUs can trace their origins to a single source (e.g., Goose Lake; Behnke 1992; 2007; Currens et al. 2009) whereas other SMUs likely represent colonization events by multiple genetic lineages (e.g., Malheur Lakes; Bisson and Bond 1971). Furthermore, connections among populations within SMUs and the potential for gene flow among populations has been highly influenced by changes in climate and hydrology over thousands of years as well as anthropogenic habitat alterations over the last century. Understanding how historical patterns of colonization along with contemporary patterns of gene flow influence genetic variation among populations will be important for evaluating current management unit boundaries as well as evaluating the level of connectivity and gene flow among spawning populations.

Methods

One aspect of SNP markers that distinguishes them from other classes of genetic markers is they are common in both coding and non-coding regions of the genome, providing researchers with the potential to analyze markers that may be subject to different selective forces (Morin et al. 2004). Whereas studies of population structure and conservation genetics have traditionally utilized neutral genetic markers, more recently the use of both neutral and non-neutral markers has been advocated to gain a more complete understanding of the total genetic variation that exists (Nei et al. 2010; Funk et al. 2012). Twelve of the SNP loci we used in this study were previously identified as candidate loci under selection for various climate variables in *O. mykiss* (Narum et al. 2010; Matala et al. 2014; see Appendix 1 for specific loci). We tested the set of loci used in our study for evidence of non-neutral markers using the methods described by Beaumont and Nichols (1996) implemented in the program LOSITAN (Antao et al. 2008).

Briefly, this method simulates expected F_{ST} values based on heterozygosity estimates for each locus and loci with F_{ST} values that fall above or below 99% confidence intervals (i.e., outliers) are considered candidate loci under selection. One downfall of this approach is that hierarchical population structure may lead to increased false positive results using these methods (Excoffier et al. 2009). Given the strong degree of population structure that exists among Great Basin redband collections, particularly among different SMUs (Currens et al. 2009; this study), we conducted these analyses for the entire dataset, and for each SMU independently. Given the extreme genetic divergence observed in the Catlow Valley SMU, we also analyzed Home and Threemile creeks separately. Although we did identify several loci that appeared to be candidate markers under selection (see below), we did not exclude any loci from population structure analysis due to inconsistent results among analyses. Results of population structure analyses based on a set of 74 putatively neutral markers are presented in Appendix 2.

We used the program FSTAT v2.9.3.2 to estimate the overall level of genetic variation (F_{ST}) among Great Basin redband trout populations only as well as the entire dataset, which included all Great Basin redband populations and all outgroups. We also estimated F_{ST} for each SMU individually and we then conducted permutation tests (1,000 permutations) in FSTAT to determine if there was a significant difference in F_{ST} estimates among the different SMUs. This method shuffles populations among the groups being compared (SMUs) while samples sizes remain the same. *P*-values for permutation tests represent the number of permutations that had a greater estimate of F_{ST} than the value observed based on the empirical data. We then estimated the level of genetic variation among all population pairs (i.e., pairwise F_{ST}), including outgroups.

In order to examine the genetic relationships among SMUs and among populations, we conducted multivariate analyses of allele frequencies using the *adegenet* package (Jombart 2008) for the R statistical environment (R development Core Team 2014). We first conducted a discriminant analysis of principal components (DAPC). DAPC is similar to principal components analysis (PCA) but unlike PCA, which maximizes the total variation in the dataset, DAPC maximizes the variation among different groups or clusters and minimizes variation within groups (Jombart et al. 2010). The DAPC analysis included only the Great Basin redband trout populations and not the outgroups. This was because the large number of individuals in the entire dataset made it difficult to interpret the graphs we produced when outgroups were included. We also conducted a correspondence analysis (CA) which focused only on the

variation among the different populations, but not on individuals within those populations. We conducted two separate CAs; one that included only the Great Basin redband trout populations and one that included all Great Basin redband trout populations and the various outgroups.

We constructed neighbor-joining (NJ) trees using the program PHYLIP v3.6 (Felsenstein 1993). We constructed two separate NJ trees; one that included only the Great Basin redband trout collections and one that included Great Basin redband trout populations and all of the outgroups. We first generated 1,000 replicates of each dataset using a bootstrap procedure and then estimated Cavalli-Sforza and Edwards' (1967) chord distances among populations for each dataset. Consensus NJ-trees were then constructed based on those chord distances.

Results

When we analyzed our entire redband trout dataset, we identified 27 loci that appeared to be F_{ST} outliers (Table 4). When we analyzed each SMU independently and when we split out Home and Threemile creeks into a separate analysis, we identified nine loci as F_{ST} outliers (Table 4). Six of the 27 loci identified as F_{ST} outliers when we analyzed the entire dataset were also identified as outliers in one or more of the individual SMU analyses (Table 4). Three of the nine loci identified as F_{ST} outliers when each SMU was analyzed separately were identified as outliers in more than one SMU (Table 4). Because we did not observe a consistent group of F_{ST} outliers across all analyses and populations, we chose to conduct all genetic population structure analyses using the entire 83 locus dataset. Analyses based on a reduced set of 74 presumably neutral loci (presented in Appendix 2) did not differ substantially from the complete 83 locus dataset.

The global F_{ST} estimate when all Great Basin redband trout populations and outgroups were included was 0.222 (95% C.I. = 0.201 to 0.240). When only Great Basin redband trout were included in the analysis, the global F_{ST} estimate was 0.212 (95% C.I. = 0.193 to 0.232). Estimates of F_{ST} for the individual SMUs were as follows: Catlow Valley F_{ST} = 0.418; Chewaucan River F_{ST} = 0.042; Fort Rock F_{ST} = 0.035; Goose Lake F_{ST} = 0.080; Malheur Lakes F_{ST} = 0.149; and Warner Lakes F_{ST} = 0.057. Permutation tests showed that F_{ST} was significantly greater in the Catlow Valley SMU compared to all other SMUs, but no other significant differences among SMUs were observed. Pairwise F_{ST} estimates ranged from 0.028 for the comparison between Silver Creek and Buck Creek in the Fort Rock SMU to 0.718 for the comparison between Spring Creek in the Klamath Basin and Home Creek in the Catlow Valley

SMU (Table 5). Estimates of F_{ST} among populations from different SMUs were relatively high; typically greater than 0.100 (Table 5). Pairwise estimates of F_{ST} between populations within the same SMU were much lower; however, there were exceptions (e.g., Malheur Lakes SMU; Table 5).

There were three main clusters of populations in the two multivariate analysis plots (DAPC and CA). One cluster consisted of populations from the Warner Lakes, Goose Lake, and Chewaucan River SMUs and there was a considerable degree of overlap among populations within this cluster (Figures 2 and 3). This cluster was separated from the other two clusters on the x-axis (first principal component) in both multivariate analyses. The second cluster consisted of populations from the Fort Rock SMU as well as the Rock Creek population from the Catlow Valley SMU (CVRC; Figures 2 and 3). The third cluster was separated from this cluster on the y-axis (second principal component) and consisted of populations from the Malheur Lakes SMU with the exception of the Malheur Lakes Silver Creek (MLSV) population (Figures 2 and 3). Silver Creek clustered intermediate to the Malheur Lakes and Fort Rock groups in the multivariate analyses. Home Creek (CVHC) and Threemile Creek (CV3M) clustered together and appeared most similar to the Malheur Lakes cluster, but there was little overlap between CVHC and CV3M and populations in the Malheur Lakes group (Figures 2 and 3). The CA plot that included all Great Basin populations and outgroups showed the same clustering pattern for Great Basin redband trout as the analyses without outgroups. The Upper Klamath Lake, Malheur River, and Cape Cod Hatchery populations grouped most closely to the Fort Rock populations and the Oak Springs Hatchery population was intermediate to the Fort Rock populations and the Goose-Warner-Chewaucan cluster (Figure 3).

Similar to the multivariate analyses, populations from the Warner Lakes, Goose Lake, and Chewaucan River SMUs grouped together on the NJ-tree and there was 100% bootstrap support for this branch on the tree (Figure 4). Populations generally grouped according to their SMUs with the exception of Honey Creek from the Warner Lakes SMU (WLHC) which grouped with populations from the Goose Lake SMU. However, bootstrap support for this branch was only slightly greater than 50% (Figure 4). Chewaucan River and Goose Lake were more similar to one another within this group and the remaining Warner Lakes populations (WLDC and WLTM) were more differentiated (Figure 4). All three Fort Rock populations grouped together and the Malheur Lakes populations split into two groups; one group from the southern Malheur

Lakes Subbasin (MLRD, MLMC, and MLBR) and one group from the northern Malheur Lakes Subbasin (MLEB, MLSR, and MLSV; Figure 4). The three Catlow Valley populations were split with Rock Creek clustering with the three Fort Rock populations and the other two populations (Home Creek [CVHC] and Threemile Creek [CV3M]) were most similar to the Malheur Lakes populations (Figure 4). These two populations were at the end of a relatively long branch on the NJ-tree, indicating a high degree of genetic divergence from other populations (Figure 4).

When the outgroups (hatchery fish, Upper Klamath Lake, and Malheur River) were added to the NJ-tree analysis, the genetic relationships among Great Basin redband populations was essentially the same as it was on the NJ-trees without outgroups (Figure 4). Four of the five Klamath populations formed their own group that was intermediate to the Goose-Warner-Chewaucan group and the other populations (Figure 4). The remaining Klamath population, Moss Creek (KLMC), grouped with the Fort Rock populations, but the relatively long branch length for this population suggested it was highly divergent. The Malheur River populations grouped intermediate to populations from the Fort Rock and Malheur Lakes SMUs (Figure 4). Similar to the Klamath populations, the two hatchery stocks, Oak Springs (OSH) and Cape Cod (CCH) grouped intermediate to the Goose-Warner-Chewaucan group and the other populations. In general, bootstrap support for the various outgroups was relatively low with the exception of the branches within the Klamath group, where populations consistently grouped together (Figure 4).

Discussion

Although studies of genetic population structure and evolutionary relationships have traditionally relied on neutral genetic markers, more recently the use of both adaptive and neutral genetic markers has been advocated (Nei et al. 2010; Funk et al. 2012). F_{ST} outlier tests did not identify a consistent group of loci under selection in this study. Instead we found that different loci were identified as outliers depending on which populations were being analyzed. Excoffier et al. (2009) demonstrated that underlying genetic population structure can have a strong influence on the results of F_{ST} outlier tests. We suspect that the results of F_{ST} outlier tests were heavily influenced by the high degree of genetic population structure among SMUs and among populations. Moreover, the models used to identify loci under selection may be too simplistic, and are thus expected to result in large numbers of false positive and false negative results (Nei et al. 2010). Only one of the loci we identified as an F_{ST} outlier (*Omy_stat3-272*) was also

identified as a candidate marker in previous studies of *O. mykiss* (Narum et al. 2010; Matala et al. 2014). Because results of these analyses were inconsistent in our study, we chose to focus on analysis of all 83 SNP loci. Results based on a subset of 74 putatively neutral markers are also presented in Appendix 2.

Previous studies proposed different scenarios for the evolutionary history of Great Basin redband trout (Behnke 1992; Behnke 2007; Currens et al. 2009). These studies provided important insights regarding the broad-scale patterns of evolution in Great Basin redband trout, but many spawning populations of redband trout were not included in these analyses. The extensive genetic sampling of redband trout populations for this study allowed us to further examine genetic relationships among Great Basin redband populations and to gain a better understanding of the relationships among populations within each of the different SMUs. We found that Great Basin redband trout generally formed three genetic groups which presumably reflect their origins from multiple sources. These three groups corresponded to: 1) the Goose, Warner, and Chewaucan SMUs; 2) the Malheur Lakes SMU; and 3) the Fort Rock SMU. Populations from the Catlow Valley showed genetic affinities to multiple groups. We discuss each of these three groups individually below.

Recent studies of redband trout populations have revealed varying patterns of genetic variation and gene flow among populations in different watersheds (Small et al. 2007; Neville et al. 2009; Kozfkay et al. 2011; Pearse et al. 2011; Matala et al. 2014). These studies demonstrate that the degree of genetic variation and genetic population structure is influenced by a number of factors including geographic scale, levels of hybridization/introgression, presence of barriers, and habitat type (Small et al. 2007; Neville et al. 2009; Kozfkay et al. 2011; Matala et al. 2014). The majority of these studies utilized microsatellite markers rather than SNPs (but see Matala et al. 2014) and direct comparisons to our study should be interpreted with this in mind. Our global F_{ST} estimates were generally greater than those reported in previous studies. This is not entirely surprising given the broad geographic range of our study and the fact that the different SMUs have been hydrologically isolated from one another for thousands of years (Hubbs and Miller 1948; Minckley et al. 1986). Even within SMUs, F_{ST} estimates among populations were often higher than values reported for redband trout in other watersheds. These data suggest that the level of gene flow among redband populations in the Great Basin is relatively low compared to redband trout in other parts of the subspecies range (e.g., Columbia River and Snake River

basins). Kozfkay et al. (2011) observed reduced gene flow among redband trout populations in desert habitats compared to montane habitats. The desert streams redband trout inhabit in the northern Great Basin are mostly isolated from one another and it is not surprising that levels of genetic variation among Great Basin redband trout populations were generally greater than those observed among populations in other watersheds. We discuss comparisons within individual SMUs and among specific populations below.

Goose Lake, Warner Lakes, and Chewaucan River SMUs

The first group of populations in the multivariate and NJ-tree analyses included populations in the Goose Lake, Warner Lakes, and Chewaucan River SMUs; which presumably reflects a common origin from Pit River redband trout. Goose Lake has had a historic hydrologic connection to the Pit River (as recently as the late 1800s) and similarities among the fish fauna in these two basins have been well documented (Hubbs and Miller 1948; Minckley et al. 1986; Behnke 1992). Currens et al. (2009) also noted the close genetic relationship among these three SMUs and suggested a Sacramento/Pit River origin. Although previous studies recognized the connection between the Goose Lake and Pit River systems, there was not as much information regarding the origins of redband trout in the Warner Lakes and Chewaucan River basins. Whereas some authors suggested these basins had long been isolated from each other, (Hubbs and Miller 1948; Minckley et al. 1986), others provided evidence of connections among them (Behnke 2007; Currens et al. 2009). The close genetic relationships we observed among these three SMUs as well as the genetic data presented by Currens et al. (2009) provide evidence of common ancestry among redband trout in these three SMUs, which can be traced to a connection between the Goose Lake system and the Pit River.

One interesting finding in our study was that Honey Creek in the Warner Basin appeared more genetically similar to the Goose Lake populations than it did to the other Warner Basin populations. Behkne (1992) also noted morphological similarities between redband trout in the Goose Lake system and Honey Creek. These data suggest that there may have been multiple instances of Goose Lake redband trout colonizing the Warner Lakes subbasin; once into the Crump Lake system (Deep and Twentymile creeks) and later into Honey Creek (a tributary to Hart Lake). Presumably Goose Lake redband trout colonized Honey Creek more recently given the greater degree of genetic similarity between those populations. It is important to note that a

large portion of Honey Creek could not be sampled (Meeuwig and Clements 2014) and our sample may only represent a portion of the total genetic variation present in this population.

Pairwise F_{ST} estimates among populations within these three SMUs (Goose Lake, Warner Lakes, Chewaucan River) provide interesting information on patterns of movement and gene flow among populations. In the Goose Lake SMU, populations with a connection to the lake (e.g., Eastside [GLES], Lassen Creek [GLLC]) generally showed lower F_{ST} values than populations that are isolated from the lake by anthropogenic barriers, irrigation diversions, and intermittent stream sections (e.g., Cottonwood Creek [GLCW]). These data suggest that there has been recent gene flow among some populations within the Goose Lake SMU. Goose Lake periodically dries up and connections between many spawning streams and the lake are intermittent (Gerstung 2007; Tinniswood 2007). Small isolated salmonid populations typically show reduced levels of genetic diversity (Wofford et al. 2005; Neville et al. 2006; Neville et al. 2009) and may face an increased risk of extirpation. Periodic gene flow among populations in the Goose Lake SMU may help buffer small populations from any negative effects of low genetic diversity. In the Warner Lakes SMU, we observed lower pairwise F_{ST} between Twentymile and Deep creeks; the two populations connected to Crump Lake. Although irrigation diversions currently prevent redband trout in Twentymile Creek from accessing Crump Lake and Deep Creek (Gerstung 2007), in the recent past there was greater gene flow among these two populations compared to Honey Creek. The Chewaucan SMU also showed relatively low levels of F_{ST} compared to other SMUs suggesting that there has been some genetic exchange among populations in this SMU as well. Migratory fish have been observed in the Chewaucan River (Tinniswood 2007) and these migratory individuals facilitate genetic exchange among populations.

Malheur Lakes SMU

The Malheur Lakes formed another distinct cluster in our analyses. Several previous studies suggested that the fish fauna in the Malheur Lakes SMU was derived from the Columbia River and Snake River system (Hubbs and Miller 1948; Bisson and Bond 1971; Minckley et al. 1986). A hydrologic connection at the Malheur Gap existed between the Malheur Lakes and Malheur River basins during the late Pleistocene period (~9,000 years ago) and a more recent connection (~4,000 years ago) has also been suggested between the Silvies River and the headwaters of the John Day River based on similarities in the fish fauna between these two

basins (Bisson and Bond 1971). Samples from the Malheur Lakes SMU grouped with the two Malheur River collections we included as outgroups on the NJ-tree, providing further support for the common ancestry of redband trout in these two Basins (Behnke 2007; Currens et al. 2009). Multivariate analyses showed that Silver Creek clustered somewhat intermediate to the Malheur Lakes and the Fort Rock populations. This may be due to relatively high levels of introgression with coastal-origin hatchery fish in Silver Creek (see Objective 3 below); levels of introgression in Silver Creek were much higher than other Malheur Lakes populations and were more similar to levels observed in the Fort Rock populations. Although fish from the upper John Day River colonized the Silvies River during a period of headwater capture approximately 4,000 years ago (Bisson and Bond 1971), our Silvies River samples clustered closely with the other Malheur Lakes collections. Bisson and Bond (1971) found that cyprinids and catostomids from the central Silvies River had a high degree of morphological similarity to John Day River specimens but fish in the Silvies tributaries were more similar to other Malheur Lakes collections. Our collections of redband trout were collected in both the central Silvies River as well as the tributaries so it's not surprising that our collections appeared so similar to other Malheur Lakes populations.

The global and pairwise F_{ST} estimates for the Malheur Lakes SMU were greater than we observed for all other SMUs with the exception of Catlow Valley and suggest that there has been little contemporary geneflow among populations in the Malheur Lakes SMU. Historically all of the tributaries within the Malheur Lakes SMU were hydrologically connected to Malheur Lake, but connections among tributaries and the opportunity for genetic exchange were lost when the lake began to desiccate approximately 10,000 years ago (Hubbs and Miller 1948). During this period, Malheur Lake divided into two smaller lakes with Silver Creek draining into mostly isolated Harney Lake and all other populations draining into Malheur Lake. Eventually the connections between Malheur Lake and most tributaries including Riddle Creek, Silvies River, and the East Burns tributaries dried up or became intermittent, limiting opportunities for genetic exchange. Currently, only the Blitzen River and McCoy Creek still have a consistent hydrologic connection to the lake. Pairwise F_{ST} between these two populations (0.041) was much lower than all other estimates within the Malheur Lakes SMU and suggests that gene flow has occurred much more recently between these two populations.

Two of the Catlow Valley collections, Home Creek (CVHC) and Threemile Creek (CV3M), were highly divergent in all of our analyses, but they were most genetically similar to the Malheur Lakes collections. Catlow Lake, which formerly occupied the basin, did overflow into the Malheur Lakes subbasin historically and there was a connection between tributaries in the eastern Catlow Basin and the headwaters of the Blitzen River in the Malheur Lakes system (Hubbs and Miller 1948). Whereas pairwise F_{ST} estimates for these two populations (CVHC and CV3M) were all greater than 0.200, comparisons between these populations and the Blitzen River were both approximately 0.130. Our data, along with previous studies, suggest that redband trout originally colonized these two tributaries from the Blitzen River during the connection between the Catlow and Malheur Lakes subbasins (Behnke 1992; Behnke 2007; Currens et al. 2009). The current populations in Home and Threemile creeks are presumed to have very low abundance (Meeuwig and Clements 2014), have long been isolated from other populations and from each other, and have very little available habitat. These characteristics have presumably resulted in high rates of genetic drift in these two populations, which is evident in the extremely low levels of diversity we observed in both populations (see Objective 2 below) and the extremely high level of genetic differentiation these two populations showed. Sampling in these two populations was limited to a relatively small area (Meeuwig and Clements 2014) and it's possible that our samples did not capture the total genetic variation that exists in these two populations.

Fort Rock SMU

Populations in the Fort Rock SMU have proven difficult to classify in previous analyses. Historically there was a connection between the Fort Rock subbasin and the adjacent Deschutes River Basin (Allison and Bond 1983) and it's possible that redband trout colonized the Fort Rock subbasin from the Columbia River system via the Deschutes River. Alternatively, Behnke (2007) proposed that redband trout in the Fort Rock system originated in the upper Klamath system and a hydrologic connection between these two systems in the area of the Sycan Marsh has been suggested as well (Hubbs and Miller 1948; Minckley et al. 1986). Recent analyses suggest that Fort Rock redband trout have genetic similarities to populations in both the upper Klamath Lake system and the Deschutes River Basin (Currens et al. 2009; Pearse et al. 2011), and Currens et al. (2009) concluded that the evolutionary history of the Fort Rock populations was difficult to determine. Our multivariate and the NJ-tree analyses also suggested that the Fort Rock

populations had genetic similarities to both the Upper Klamath Lake and the Columbia River Basin providing additional evidence that Fort Rock redband trout may have evolutionary ties to both basins. Unfortunately, our study did not include any redband trout from the Deschutes River Basin, and the Malheur River (a tributary to the Snake River) was our only representative population from the Columbia River Basin. The Fort Rock populations did not cluster as closely to the Upper Klamath and Malheur River populations like we observed for the populations that originated from the Pit River system (Goose Lake, Warner Lakes, and Chewaucan River). This may reflect a longer divergence time between Fort Rock and the Klamath and Columbia basins, or it may be because the Fort Rock fish have mixed ancestry from these two different sources that were previously found to be highly divergent (Currens et al. 2009).

Previous studies found that redband trout in the Catlow Valley were most genetically similar to the Malheur Lakes Basin and specifically the Blitzen River (Behkne 1992, 2007; Currens et al. 2009); however, these studies did not include fish from Rock Creek in the Catlow Valley. We found that Rock Creek redband trout were most genetically similar to the Fort Rock populations. Early accounts suggested that there were no native salmonids in the Catlow Valley, only introduced populations (Hubbs and Miller 1948), but later studies provided strong evidence that Catlow Valley redband trout were indeed native (Behkne 1992; 2007). Introduced populations tend to show relatively low levels of genetic diversity (Mock et al. 2004; Stephen et al. 2005; Puckett et al. 2014), but gene diversity in Rock Creek was greater than the average we observed across all populations and Rock Creek had the highest estimate of contemporary N_e (see Objective 2 below), providing further evidence that Rock Creek is not an introduced population. All streams in the Catlow Valley were once connected to Catlow Lake, but the lake dried up approximately 10,000 years ago and Rock Creek has remained isolated (Hubbs and Miller 1948). Common ancestry between Rock Creek and the Fort Rock Basin seems unlikely given the large geographic distance separating these streams. It's possible that genetic similarity between the Fort Rock populations and Rock Creek is simply due to genetic drift in this long isolated population. Despite the fact that Rock Creek has a long history of isolation, redband trout were relatively abundant during recent surveys (Dambacher et al. 2009; Meeuwig and Clements 2014). Relatively high abundance and genetic diversity in Rock Creek suggest that it is a stronghold for redband trout in the Catlow Valley SMU and it may have unique conservation value.

The lowest pairwise F_{ST} estimates we observed were among populations in the Fort Rock Basin. All three Fort Rock tributaries drain into Paulina Marsh, but Behnke (1992) suggested that redband trout in the three Fort Rock tributaries have a long history of isolation. Our data suggest that there has been recent gene flow among these populations; the relatively low pairwise F_{ST} estimates were similar to those observed among connected populations such as Blitzen River and McCoy Creek and populations connected via Goose Lake. Isolated stream salmonid populations typically have low estimates of genetic diversity (Wofford et al. 2005; Neville et al. 2006; Neville et al. 2009), but we observed significantly higher levels of genetic diversity in the Fort Rock Basin compared to known isolated populations (e.g., Catlow Valley, Malheur Lakes; see Objective 1). Although habitat in the marsh may not currently be suitable for redband trout, higher water levels and better habitat quality in the recent past appear to have facilitated some genetic exchange among populations. Fort Rock populations did show greater levels of introgression with coastal-origin hatchery fish than most other populations (see Objective 3) and genetic similarity among populations could certainly be influenced by the presence of common hatchery-origin genes in these populations.

Objective 2 – Examine Levels of Genetic Variation within Redband Trout Populations from the Northern Great Basin

Estimates of genetic variation have become increasingly useful for monitoring populations and for developing effective conservation plans (Schwartz et al. 2007; Charlier et al. 2012; Osborne et al. 2012). Populations with low levels of genetic variation may have reduced fitness, may face a greater risk of extirpation, and may be unable to adapt to changing environmental conditions (Quattro and Vrijenhoek 1989; Saccheri et al. 1998; Reed and Frankham 2003; Allendorf and Luikart 2007). Monitoring genetic variation within populations over time can also help infer population trends (i.e., declining, stable, increasing), prioritize populations for conservation measures, and to evaluate the effects of management actions such as population supplementation or habitat improvement (Dowling et al. 2005; Osborne et al. 2012). Several metrics have been proposed for evaluating genetic variation within populations. For SNP datasets, estimates of heterozygosity provide an effective means of evaluating genetic variation within populations. Effective population size (N_e) represents the size of an ideal

population that has the same rate of genetic drift as the population being studied and represents another widely used metric for evaluating the level of genetic variation within populations.

Genetic variation within populations is influenced by historical and contemporary forces. Historic forces may include patterns of colonization (Costello et al. 2003) and geologic events such as flooding and glaciation (Bernatchez and Wilson 1998). Contemporary forces may include a species' life history (Whiteley et al. 2004; Neville et al. 2006), natural and anthropogenic disturbances (Jensen et al. 2005; Wahbe et al. 2005), and the construction of barriers that limit genetic exchange among populations (Wofford et al. 2005; Neville et al. 2009). An understanding of how these different forces affect genetic diversity within populations is important for biologists tasked with managing and conserving populations. Several previous studies have examined levels of genetic variation within populations of redband trout and the factors that influence this variation. Historic patterns of colonization, habitat type, habitat availability, the presence of anthropogenic barriers, climate patterns, and stocking of out of basin hatchery fish all appear to influence levels of genetic variation within redband trout populations (Small et al. 2007; Neville et al. 2009; Blankenship et al. 2011; Kozfkay et al. 2011; Matala et al. 2014). However, data on levels of genetic variation within redband trout populations in the northern Great Basin are currently limited. Given the unique ecological setting of these populations, along with increasing concern for the conservation of these populations, genetic data will be important for developing effective management plans.

Methods

We estimated the level of gene diversity (i.e., expected heterozygosity; Nei 1978) within each population using the program FSTAT v2.9.3.2 (Goudet 2001). We also used FSTAT to estimate the average gene diversity across all populations for each of the six SMUs. We then used permutation tests to compare gene diversity among each of the different SMUs. Permutation tests were conducted using FSTAT and based on 1,000 permutations of the dataset for each comparison. This method shuffles populations among the groups being compared (SMUs) while sample sizes remain the same. *P*-values for permutation tests represent the number of permutations that had a greater estimate of average gene diversity than the value observed based on the empirical data. Outgroups from the Malheur River, Upper Klamath Lake, and hatchery populations were excluded from permutation tests because they were located outside of the Great Basin. We also used FSTAT to estimate allelic richness (A_R) within each population

using rarefaction to correct for differences in sample size among populations (Petit et al. 1998). Estimates of allelic richness were based on a minimum sample size of 10 individuals.

We used the linkage disequilibrium method of Waples (2006) to estimate the contemporary effective population size (N_e) for each population. N_e was estimated using the program NeEstimator v2. 0 (Do et al. 2014) using a P_{crit} (minimum allele frequency) value of 0.02 as recommended by Waples and Do (2010). We estimated 95% confidence intervals for N_e estimates based on a jackknife procedure implemented in NeEstimator. For species such as redband trout that have overlapping generations, this method likely produces an estimate that lies somewhere between the effective number of breeders (N_b) that produced the sample and the true N_e (Luikart et al. 2010; Waples and Do 2010).

Results

Gene diversity ranged from approximately 0.150 in Threemile and Home creeks in the Catlow Valley SMU to approximately 0.400 for the three Fort Rock populations (Table 6; Figure 5). Among the different outgroups, gene diversity was lowest in the Fort Creek population (H_s = 0.148) from the upper Klamath Basin and greatest in the Blue Bucket Creek population in the Malheur River Basin (H_s = 0.405; Table 6, Figure 5). Mean estimates of gene diversity for each SMU were as follows: Catlow Valley H_s = 0.257, Chewaucan River H_s = 0.314, Fort Rock H_s = 0.397, Goose Lake H_s = 0.321, Malheur Lakes H_s = 0.318, Warner Lakes H_s = 0.362. The mean gene diversity across all Great Basin populations was 0.319. Permutation tests showed that the Fort Rock SMU had significantly greater levels of gene diversity than the Catlow Valley (P = 0.003), Goose Lake (P = 0.032), and Malheur Lakes (P = 0.035) SMUs, and the Warner Lakes SMU had significantly greater estimates of gene diversity than Catlow Valley (P = 0.014). All other comparisons were not significant (P>0.05; Table 7). Estimates of allelic richness were also lowest in Threemile and Home creeks ($A_R \approx 1.4$) and allelic richness was greatest in Buck Creek in the Fort Rock SMU (A_R = 1.98; Table 6, Figure 5).

Estimates of N_e ranged widely across the populations we analyzed (Table 6, Figure 5). N_e was lowest in the Davis Creek population in the Goose Lake SMU (N_e = 7.2) and greatest in the Rock Creek population in the Catlow Valley SMU (N_e = 551.0). The upper limit for 95% confidence intervals in three populations included infinity (Table 6, Figure 5).

Discussion

Estimates of genetic variation such as heterozygosity are a useful means for inferring population trends and viability. Populations with relatively low levels of genetic diversity may be declining or have undergone a bottleneck and may have an increased risk of extirpation (Quattro and Vrijenhoek 1989; Turner et al. 2007; Osborne et al. 2010). Although there are not minimum viable limits for gene diversity, comparisons among populations can help identify populations with reduced diversity that may face a greater risk of extirpation. For example, two of the three Catlow Valley populations (Home Creek and Threemile Creek) had estimates of gene diversity that were less than half of the average value across all Great Basin populations. Redband trout abundance in these two populations is presumably quite low (Meeuwig and Clements 2014) and both of these streams are isolated from other populations. Small, isolated populations with low genetic diversity such as Home and Threemile creeks may represent increased priorities for conservation measures aimed at stabilizing or increasing population size.

Estimates of N_e are closely related to the number of breeding adults in a population, and data on N_e is also useful for inferring population trends and viability (Schwartz et al. 2007). Similar to gene diversity, estimates of N_e ranged widely among populations in this study. Although minimum estimates for N_e have been suggested (e.g., the 50/500 rule; Franklin 1980), often it is more useful to focus on comparisons among populations or changes in N_e over time rather than whether or not a population meets a threshold minimum value. Populations with low N_e values such as Willow Creek in the Chewaucan River SMU or Davis Creek in the Goose Lake SMU (N_e = 12.5 and 7.2, respectively) presumably had very few spawning adults in recent years and likely face a greater risk of extirpation as a result. Although estimates of N_e are useful for conservation planning, there are important caveats to consider when interpreting these estimates. The method of estimating N_e we used for this study (based on linkage disequilibrium; Waples 2006) assumes that there is no overlap among generations within a population, which is certainly not the case for redband trout. As a result, our estimates are likely lower than the true N_e values for each population and fall between the true N_e and the effective number of breeders (N_b) that produced each sample (Luikart et al. 2010; Waples and Do 2010). Since all populations were sampled using the same rigorous protocol, any bias in our estimates due to increased linkage between cohorts should be consistent among populations. The linkage disequilibrium method we used to estimate N_e is much more precise when N_e (or N_b) is small (Waples 2006;

Palstra and Ruzzante 2008; Waples and Do 2010), and therefore point estimates for populations with low estimates of N_e such as Threemile Creek and Willow Creek (10.9 and 12.5, respectively) are much accurate than populations with relatively high estimates of N_e such as Rock Creek and Honey Creek (551.0 and 209.6, respectively).

The degree of isolation among populations (as a result of both historic and contemporary forces) appears to influence genetic variation within Great Basin redband trout populations. Isolated populations typically show reduced levels of genetic diversity compared to populations that exchange migrants at some rate (Morita et al. 2009; Neville et al. 2009; DeHaan et al. 2011b) and isolated redband trout populations in the Great Basin also show reduced levels of genetic diversity. For example in the Catlow Valley, hydrologic connections among populations have dried up over thousands of years (Hubbs and Miller 1948) and populations have become isolated and have low genetic diversity as a result. Alternatively in the Warner Lakes and Malheur Lakes SMUs, populations that have hydrologic connections to large lakes (and presumably to other populations) had somewhat higher levels of gene diversity and N_e than populations isolated more recently by irrigation structures or other barriers (e.g., Twentymile Creek in the Warner Lakes SMU). Great Basin redband trout have been isolated from populations in other watersheds (e.g., Columbia River, Snake River) for thousands of years, and as a result genetic diversity is likely lower in Great Basin populations than other areas across the species range. Estimates of genetic diversity we observed in the two Malheur River populations were greater than those observed for most Great Basin populations. Although the Malheur River is currently isolated above a series of dams, this occurred only within the past century and prior to that time, anadromous *O. mykiss* facilitated genetic exchange between the Malheur River Basin and other Snake River populations.

Recently, several studies have explored how landscape features such as stream gradient, stream temperature, and barriers influence genetic diversity in salmonid populations (Neville et al. 2006; Olsen et al. 2011; Ozerov et al. 2012). These studies have provided valuable insight for management and conservation of native salmonids and such data could also be useful for Great Basin redband trout. In the future we intend to combine landscape and habitat data collected during ODFW redband abundance surveys with genetic data described in this study to gain a better understanding of how different factors affect genetic diversity in Great Basin redband trout populations.

Objective 3 - Examine Levels of Introgression between Native Redband Trout and Coastal Origin Hatchery Fish

Hybridization between native and introduced individuals has become a substantial threat to the persistence of many species and populations of fishes (Allendorf et al. 2001). Many fishes face both inter- and intra-specific hybridization threats, often resulting from extensive releases of hatchery origin individuals. Hybridization and introgression between native fish and introduced hatchery fish often results in offspring with reduced fitness in the native population due to the loss of locally adapted genotypes (Araki et al. 2007b; McClelland and Naish 2007; Fraser et al. 2010). Intra-specific hybridization with introduced hatchery rainbow trout (typically coastal-origin strains) has been recognized as a major threat to the persistence of native redband trout throughout their range (Thurow et al. 2007; Muhlfeld et al. 2015). Introgression of coastal-origin rainbow trout genes into native redband trout populations presumably results in the loss of genes that allow redband trout to persist in their unique habitats. Previously, genetic markers have proven useful for examining the degree of introgression between native redband trout populations and introduced hatchery rainbow trout (Small et al. 2007; Matala et al. 2008; Simmons et al. 2010; Kozfkay et al. 2011; Neville and Dunham 2011). These studies found that although large numbers of hatchery rainbow trout have been stocked into redband trout habitat, genetically pure redband trout still persist in many watersheds, and the degree of introgression between redband trout and hatchery-origin rainbow trout is variable among watersheds and tributaries. Information on the level of introgression between native redband trout and introduced hatchery origin rainbow trout is essential for understanding the threats that local populations face and for prioritizing populations for conservation.

Coastal-origin hatchery fish have been stocked extensively in Oregon watersheds that contain native redband trout populations. Stocking of hatchery-origin rainbow trout into Great Basin streams persisted until the mid to late 1990s when stocking was ceased due to concerns for native redband trout stocks and low angler harvest of hatchery stocks. Most hatchery strains of rainbow trout propagated in Oregon originated from coastal watersheds in California (Kinunen and Moring 1978; Behnke 1992) and as a result, hatchery-origin fish are highly phenotypically and genetically divergent from native redband trout. Based on morphological and meristic characteristics, Behnke (1992) observed varying degrees of introgression in native redband populations in the northern Great Basin, but noted that in general, many populations retained

characteristics indicative of native redband trout. Currens et al. (2009) used allozyme markers to document introgression of coastal-origin rainbow trout genes in redband populations in the northern Great Basin. These authors documented introgression in the Blitzen River in the Malheur Lakes SMU but not in any of the other SMUs; however sampling in that study targeted populations presumed to be free of hatchery influence based on stocking records.

In many cases, levels of hybridization and introgression can be determined using genetic markers that exhibit fixed allelic differences among the two species or lineages believed to be interbreeding. When hybridization occurs between two lineages of the same species, markers with fixed differences often do not exist and analyses of hybridization and introgression rely on allele frequency differences between the two lineages. This has been the case for many salmonids (including redband trout) where biologists are interested to know if there has been introgression between native fish and introduced hatchery-origin individuals (Hansen et al. 2001; Kozfkay et al. 2011; Neville and Dunham 2011). Often times 'pure' native populations that have not been supplemented with hatchery-origin fish do not exist, and defining allele frequencies of 'pure' wild populations can be difficult. Analyses of both simulated (Vaha and Primmer 2006; Sanz et al. 2009) and empirical (Small et al. 2007; Matala et al. 2008; Kozfkay et al. 2011; Neville and Dunham 2011) datasets have utilized Bayesian clustering methods employed in the program STRUCTURE (Pritchard et al. 2000) to address this issue. Simulated datasets have demonstrated that increased genetic variation among lineages and increased numbers of genetic markers result in an increased ability to identify introgressed populations and individuals with mixed ancestry (Vaha and Primmer 2006; Sanz et al. 2009). Updated information on levels of introgression in Great Basin redband trout populations from this study will be important for determining the effects of previous hatchery stocking on redband trout populations and for better quantifying the threats that individual populations face.

Methods

There is a high level of genetic divergence between coastal-origin rainbow trout/steelhead and interior redband trout (Currens et al. 2009; Blankenship et al. 2011; Matala et al. 2014), and many of the SNP markers that we used in this study have previously been used to examine those differences (Matala et al. 2014). We included collections from two hatchery strains widely stocked in Oregon in our study: Cape Cod Hatchery (CCH) and Oak Springs Hatchery (OSH). These hatchery strains were not supplemented with redband trout at any point

and we presumed them to be 'pure' hatchery fish. Based on stocking records, it appears that nearly all of the populations in our study were supplemented with coastal-origin hatchery fish at some point (ODFW, *unpublished data*); therefore we did not have a representative sample of a 'pure' redband trout population from the northern Great Basin. Riddle Creek (MLRD), a tributary in the Malheur Lakes SMU, was only stocked twice and is isolated from other populations; therefore we assumed this population should have very little influence from hatchery populations. Preliminary data analysis showed that there was indeed a high degree of divergence between Riddle Creek and the two hatchery strains (pairwise estimates of F_{ST} were 0.415 between CCH and MLRD and 0.387 between OSH and MLRD) and preliminary STRUCTURE analysis indicated that there was very little shared ancestry between these two hatchery strains and Riddle Creek.

Based on studies of simulated data, previous studies of redband trout, and our preliminary results that showed little shared ancestry between hatchery strains and native redband trout, we felt confident that we could use STRUCTURE to examine the degree of introgression between native redband trout of the Northern Great Basin and coastal-origin hatchery fish. STRUCTURE uses Bayesian clustering methods to partition individuals into *K* populations (specified by the user) based on conformance to Hardy-Weinberg and linkage equilibrium expectations. Similar to previous studies, we set the number of populations (*K*) for STRUCTURE analysis to two and then had the program determine the proportion of each individual's genome attributed to each cluster (i.e., Q-value). Based on our preliminary analysis, we predicted that the two clusters would correspond to hatchery-origin fish (Q-value of approximately 1.0) and native redband trout (Q-value of approximately 0.0), and individuals with mixed ancestry would have some proportional membership in each cluster. We initially ran STRUCTURE with all of the native redband trout collections and the hatchery collections in a single analysis but this method produced inconsistent results among replicate analyses, presumably due to the extreme genetic divergence among the different SMUs (see Objective 1 above). Because of this, we conducted a separate STRUCTURE analysis for each of the six SMUs. Each analysis contained the two hatchery strains and all populations within the SMU. Each analysis consisted of 20 replicate runs with 100,000 burn-in iterations followed by 100,000 data collection iterations. We used the admixed ancestry model with an initial alpha value of 1.0 and the correlated allele frequency model with an initial lambda value of 1.0.

We used the program CLUMPP (Jakobsson and Rosenberg 2007) to determine the consensus individual and population level Q-values across the 20 replicate runs for each STRUCTURE analysis as well as the level of similarity among runs. We used the *'FullSearch'* algorithm in CLUMPP to compute the similarity coefficient *H'* and to determine the consensus Q-values across all 20 replicate runs. We used the program DISTRUCT (Rosenberg 2004) to produce graphical outputs for each STRUCTURE analysis.

Initial results suggested that the Rock Creek population in the Catlow Valley SMU (CVRC) was almost entirely hatchery origin (Figure 6). The other Catlow Valley populations, Threemile and Home creeks, showed remarkably high genetic divergence from Rock Creek (see Objective 1 above) and we suspected that when we forced STRUCTURE to group samples into two genetic clusters, Rock Creek was grouped with hatchery fish because of the high level of divergence between this population and the other Catlow Valley populations. Furthermore, stocking records indicated that Rock Creek was supplemented relatively few times, which makes the possibility that hatchery fish completely replaced the native population in Rock Creek unlikely. Therefore, we conducted a separate STRUCTURE analysis that only included Rock Creek and the two hatchery stocks.

Results

Mean Q-values for the two hatchery collections across the different runs were 0.962 for both CCH and OSH (Table 8). *H'* values were greater than 0.99 for all STRUCTURE analyses indicating a high degree of consensus among our replicate runs for each SMU. Population level Q-values for Great Basin redband trout collections ranged from 0.001(indicative of essentially pure redband populations) in Threemile and Home creeks in the Catlow Valley SMU to 0.590 in Silver Creek in the Fort Rock SMU (Table 8).

Patterns of individual Q-values varied considerably among SMUs, among populations within SMUs, and among individuals within populations (Figure 6). After we separated Rock Creek from the other Catlow Valley populations, we observed virtually no evidence of introgression between coastal-origin hatchery fish and native redband trout in any of the Catlow Valley populations (Figure 6). Populations in the Warner Lakes SMU also showed very little introgression from hatchery fish (Table 8; Figure 6), however, there were a few Warner Lakes individuals that had slightly higher levels of introgression (Figure 6). The Goose Lake and Malheur Lakes SMUs also showed very low levels of introgression between redband trout and

hatchery-origin fish; however, there were populations with greater Q-values than others within these SMUs. In Goose Lake, most individuals appeared to have very little genetic material from hatchery-origin fish but there were a few individuals in Davis Creek and West Goose that had a high proportion of hatchery-origin genes (Figure 6). In the Malheur Lakes SMU most individuals showed very low levels of introgression, except for fish in Silver Creek which appeared to have a greater hatchery influence (Figure 6). There appeared to be a greater degree of introgression in the Chewaucan River and Fort Rock SMUs, where nearly all individuals had some influence from coastal-origin hatchery fish in their genome (Figure 6). Within these SMUs, there was still a difference in the level of introgression among different populations (e.g., Silver Creek in the Fort Rock SMU) and among individuals within populations (Figure 6).

Discussion

Stocking of coastal-origin hatchery fish into redband trout habitat and subsequent introgression represents a major threat to the persistence of redband trout across the subspecies range (Thurow et al. 2007; Muhlfeld et al. 2015). Our results showed that there has been introgression of hatchery-origin rainbow trout genes into native redband trout populations in the Northern Great Basin, and that the degree of introgression is highly variable among SMUs, populations, and individuals. In some populations such as those in the Warner Lakes SMU, introgression was only detected at low levels (population Q-values ranged from 0.045 to 0.080), suggesting that introgression between redband trout and hatchery-origin fish has not been very prevalent. In other populations such as those in the Chewaucan River SMU, introgression seems to be much more prevalent (population Q-values ranged from 0.105 to 0.340) and likely represents a more serious conservation concern. Clearly these data show that redband trout conservation and management plans would be most effective if they approached the threat of introgression between native fish and hatchery-origin fish on a population by population basis.

In general, we did not observe the replacement of native redband trout genes with genetic material largely descended from hatchery-origin rainbow trout. These results are similar to several previous studies which showed that in many cases, coastal-origin hatchery fish do not replace native redband trout when the two lineages occur sympatrically (Small et al. 2007; Matala et al. 2008; Simmons et al. 2010; Kozfkay et al. 2011; Neville and Dunham 2011). Out-of-basin hatchery-origin fish often have reduced fitness, presumably due to a lack of adaption to local habitat conditions in the novel environment (Araki et al. 2007a). Redband trout in the Great

Basin have adapted to a unique environment characterized by very little precipitation, extreme temperatures, and intermittent habitat (Behnke 1992; Schroeder and Hall 2007). Given the high level of genetic divergence between coastal and interior lineages of *O. mykiss* and the differences in the native habitats these two lineages occupy, it is not surprising that coastal-origin hatchery fish have reduced fitness in redband trout habitat. In a study of introgression between redband trout and hatchery-origin rainbow trout in desert and montane habitats in the Snake River Basin, Kozfkay et al. (2011) found that redband trout populations in desert environments had lower levels of introgression than populations in montane environments. Additional factors influencing the level of introgression between native redband trout and hatchery-origin fish may also include the intensity of past stocking and proximity to stocking locations (Small et al. 2007). In the future we hope to explore the relationship between specific habitat variables such as temperature, elevation, precipitation, etc. and the level of introgression in native redband populations.

Our analyses of introgression showed some interesting similarities and differences to previous studies. In the Malheur Lakes SMU for example, Behnke (1992; 2007) observed generally low levels of introgression based on morphometric and meristic data and described a mostly pure population in Smyth Creek, a tributary to Riddle Creek; results that were similar to what we observed based on genetic data. Both our data and the Behnke studies (1992; 2007) observed the greatest level of hybridization in the Malheur Lakes Basin in Silver Creek, a population that has been heavily supplemented in the past. Conversely, Behnke (1992; 2007) noted some hybrid influence in populations in the Warner Lakes and Goose Lake basins, whereas we found relatively low levels of introgression in these populations. The morphometric and meristic analyses conducted by Behnke (1992; 2007) were based on analysis of fish collected in the late 1960s and early 1970s when hatchery-origin rainbow trout were still being stocked in the northern Great Basin. The fact that contemporary samples from areas previously believed to be introgressed such as the Warner Lakes showed little evidence of admixture in our study may be a sign that once hatchery stocking of Great Basin streams ceased, locally adapted native redband trout persisted and coastal-origin hatchery fish did not. Currens et al. (2009) found little evidence of hatchery introgression in Great Basin redband trout based on genetic markers, even in watersheds where we documented low to moderate levels of introgression (e.g., Fort Rock SMU). Currens et al. (2009) intentionally avoided sampling areas believed to contain non-native hatchery fish and greater levels of introgression documented in our study reflect a

broader sampling of populations, many of which were intensively stocked with hatchery-origin rainbow trout (ODFW, *unpublished data*).

There are a number of important points to consider when interpreting these data. Most importantly, hatchery-origin rainbow trout have not been stocked into streams in the study area since the 1990s, therefore none of these fish, regardless of Q-values, represent hatchery-origin fish or first generation (F1) hybrids. Assuming the maximum spawning age is five years for Great Basin redband trout (Behnke 2002; Tinniswood 2007), the fish we sampled are at least two to three generations removed from any hatchery stocking. Rather, individuals with moderate to high Q-values represent fish with mixed ancestry between native redband trout and hatchery-origin fish due to past hybridization events. Presumably greater individual Q-values represent fish descended from more recent hybridization events. Vaha and Primmer (2006) found that in populations where hybridization has occurred across a span of several generations, the proportion of hybrids or individuals with mixed ancestry will likely be underestimated. Previous studies have also suggested that when Bayesian methods are used, even 'pure' individuals may have Q-values consistent with low levels of introgression (e.g., ≤ 0.1; Sanz et al. 2009; Kozfkay et al. 2011; Neville and Dunham 2011) due to shared evolutionary history and common alleles. Based on these data, Q-values we present should not necessarily be viewed as definitive measures of introgression, but rather as a means to compare the relative level of introgression among populations. For example, the two hatchery stocks we analyzed had mean Q-values of 0.962, indicating that even pure hatchery fish have some genetic similarity to native redband trout.

In the Fort Rock SMU, all three populations showed evidence of introgression. Bridge Creek was only stocked with hatchery-origin fish three times, but it had a population Q-value of 0.201 suggesting a moderate level of introgression. When Bridge Creek was run in a separate STRUCTURE analysis with only the two hatchery strains, the level of introgression was much lower (average Q-value approximately 0.029). These results highlight the fact that when STRUCTURE is forced to group individuals into a pre-defined number of clusters or populations that is not an accurate biological representation of the dataset, shared alleles among the clusters may cause genetically differentiated groups to appear more similar than they actually are. In this case, genetic similarities between Bridge Creek and Silver Creek, which had been stocked 50 times and had a much higher degree of shared ancestry to the two hatchery strains, presumably

caused Bridge Creek to appear genetically more similar to the hatchery fish. These results provide additional evidence that Q-values should not be viewed as definitive estimates of introgression, but rather represent a relative measure of the degree of introgression that can be compared among populations.

Conclusions

Redband trout populations have declined across the subspecies range and face numerous threats to population persistence (Thurow et al. 2007; Muhlfeld et al. 2015). Despite the fact that many natural resources agencies have been working to evaluate the status of redband trout, data gaps still exist that limit the ability of biologists and managers to develop effective conservation plans. Status assessments for redband trout can be difficult due to the subspecies broad geographic range, the remoteness of many populations, limited access to stream habitats on private lands, and relatively small population sizes. Genetic data presented in this study provide an additional and complementary means of assessing redband trout population status. Data on levels of genetic diversity and effective population size can be used to infer trends in population abundance (Schwartz et al. 2007; Osborne et al. 2012) and provide a more complete picture of population status when considered in the context of recent population assessments (e.g., Thurow et al. 2007; Dambacher et al. 2009; Meeuwig and Clements 2014). For example, Home and Threemile creeks in the Catlow Valley SMU had relatively low abundance (Meeuwig and Clements 2014) and also had low genetic diversity, suggesting that these small isolated populations likely face an increased risk of extirpation. Large portions of some populations such as Willow Creek in the Chewaucan River SMU or Honey Creek in the Warner Lakes SMU could not be sampled (Meeuwig and Clements 2014) and estimates of genetic diversity provide an alternative means of examining population status. The Fort Rock SMU had lower abundance estimates than most other SMUs in recent surveys (Dambacher et al. 2009; Meeuwig and Clements 2014), but had the highest estimates of genetic diversity, suggesting that despite lower abundance, populations in the Fort Rock SMU do not face threats from inbreeding and low effective size.

Genetic data presented in this study also provide important information that wasn't available from previous population assessments. Introductions of coastal-origin hatchery fish represent a significant threat to native redband trout populations (Thurow et al. 2007), but little

information was available regarding the level of introgression in Great Basin redband trout populations. Data presented in this study will help to determine which populations have been impacted by previous hatchery supplementation and how different biotic and abiotic factors (e.g., available habitat, stream temperature, population size, etc.) influence the degree of introgression between hatchery fish and native redband. Clearly some populations such as Silver Creek in the Fort Rock SMU and Silver Creek in the Malheur Lakes SMU have had greater levels of introgression and may face a greater risk. Connectivity among populations is important for the long term persistence of many salmonid species including redband trout (Northcote 1997); unfortunately there was little information available on the level of connectivity and gene flow among most Great Basin populations. Although many populations in our study were assumed to be isolated (Behnke 1992; 2007), our data showed that there has been recent gene flow among some populations. Genetic exchange among populations will no doubt be important for the persistence of Great Basin redband trout populations, and ongoing efforts to restore connectivity in areas such as the Warner Lakes Basin should help facilitate genetic exchange. Considered altogether, the genetic data in this study will provide a complimentary means of assessing the status of Great Basin redband trout populations and help to prioritize populations for conservation actions such as barrier removal (Weigel et al. 2013) and habitat improvement (Bayley and Li 2008).

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Tables and Figures

Table 1. Population codes, numbers of redband trout collected each year, and results of Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium tests (LD) for northern Great Basin redband trout populations and outgroups. HWE represents the number of loci that did not conform to HWE expectations over the total number of variable loci and LD represents the number of locus pairs that showed evidence of linkage over the total number of locus pairs analyzed.

Sub Basin	Population	Population Code	Collection Year									Total number samples	HWE	LD
			2000	2004	2006	2007	2008	2009	2010	2011	2012			
Catlow Valley	Threemile Creek	CV3M						13		10		23	1/34	2/595
Catlow Valley	Home Creek	CVHC						9		10	10	29	0/36	0/701
Catlow Valley	Rock Creek	CVRC						10	25	10	28	73	0/34	2/3401
Chewaucan River	Chewaucan River	CRCR						42	48	46	189	325	2/85	6/3570
Chewaucan River	Crooked Creek	CRCC									122	122	2/85	9/3570
Chewaucan River	Willow Creek	CRWC						10			19	29	0/63	2/2244
Fort Rock	Bridge Creek	FRBR						45	47	30	93	215	6/85	7/3570
Fort Rock	Buck Creek	FRBK						47	43	54	127	271	4/85	16/3570
Fort Rock	Silver Creek	FRSV						38	36	20	68	162	4/85	2/3570
Goose Lake	Cottonwood Creek	GLCW		47								47	1/71	7/2555
Goose Lake	Davis Creek	GLDV		56								56	4/81	19/3486
Goose Lake	Drews Creek	GLDW						10	14	20	10	54	0/82	1/3403
Goose Lake	Dry Creek	GLDY				10		27		10		47	0/81	0/3321
Goose Lake	Eastside	GLES						10	42	20	20	92	0/83	1/3486
Goose Lake	Lassen Creek	GLLC						46				46	0/79	0/3317
Goose Lake	Thomas-Bauers Creek	GLTB						10	16	20	38	84	0/83	0/3486
Goose Lake	West Goose	GLWG						10	38	10	10	68	0/82	2/3485
Malheur Lakes	Blitzen River	MLBR						22	9	36	40	107	1/85	0/3570
Malheur Lakes	East Burns	MLEB								34	20	54	2/83	0/3403
Malheur Lakes	McCoy Creek	MLMC								31	40	71	0/83	0/3568
Malheur Lakes	Riddle Creek	MLRD							10	27	30	67	2/80	0/3319
Malheur Lakes	Silvies River	MLSR						9	22	38	60	129	0/85	0/3570

Sub Basin	Population	Population Code	Collection Year									Total number samples	HWE	LD
			2000	2004	2006	2007	2008	2009	2010	2011	2012			
Malheur Lakes	Silver Creek	MLSV						10		46		56	1/85	0/3570
Warner Lakes	Deep Creek	WLDC				30		17	31		70	148	0/84	0/3569
Warner Lakes	Honey Creek	MLHC						10	38	18	29	95	0/82	0/3570
Warner Lakes	Twentymile Creek	WLTM				20		10	31	20	20	101	3/84	1/3486
Malheur River	Little Malheur River	MRLM					45					45	0/47	0/1376
Malheur River	Blue Bucket Creek	MRBB					48					48	0/73	0/2921
Upper Klamath Lake	Moss Creek	KLMC				24						24	1/56	0/1651
Upper Klamath Lake	Fishhole Creek	KLFH	24									24	1/79	0/3317
Upper Klamath Lake	Rock Creek	KLRC	24									24	0/48	0/1476
Upper Klamath Lake	Spring Creek	KLSC				24						24	0/84	1/3486
Upper Klamath Lake	Fort Creek	KLFC				24						24	0/82	0/3481
Oak Springs Hatchery Stock		OSH			48							48	0/77	1/3303
Cape Cod Hatchery Stock		CCH						46				46	0/79	2/3081

Table 2. Analysis of Molecular Variance (AMOVA) results summary. AMOVA was conducted for each SMU to determine the percent of the total variation attributed to differences among temporal replicate samples from the same population.

Description	Number of Groups	Among Groups	Among Populations (Temp Reps) w/in Groups	Among Individuals w/in Populations
All populations grouped by SMU	6	15.05%	7.82%	4.09%
Catlow Valley - pops split by temporal replicate	3	41.43%	0.92%	0.39%
Chewaucan River - pops split by temporal replicate	3	3.76%	0.65%	5.71%
Fort Rock- pops split by temporal replicate	3	3.42%	0.38%	5.64%
Goose Lake - pops split by temporal replicate	8	7.22%	1.46%	2.78%
Malheur Lakes - pops split by temporal replicate	6	14.26%	1.33%	4.45%
Warner Lakes - pops split by temporal replicate	3	5.22%	1.81%	4.07%

Table 3. Temporal replicate samples from the same population that showed significant differences in allele frequencies from one another.

SMU	Population	Year 1	Year 2
Chewaucan	Chewaucan River	2009	2010
Chewaucan	Chewaucan River	2010	2011
Chewaucan	Chewaucan River	2010	2012
Chewaucan	Willow Creek	2009	2012
Catlow	Home Creek	2009	2011
Catlow	Home Creek	2009	2012
Fort Rock	Buck Creek	2010	2011
Fort Rock	Buck Creek	2011	2012
Fort Rock	Bridge Creek	2010	2011
Goose Lake	Eastside Goose	2009	2012
Goose Lake	West Goose	2009	2010
Malheur Lakes	East Burns	2011	2012
Malheur Lakes	Silvies River	2009	2010
Malheur Lakes	Silvies River	2009	2011
Malheur Lakes	Silvies River	2009	2012
Malheur Lakes	Silver Creek	2009	2011
Warner Lakes	Deep Creek	2007	2010
Warner Lakes	Deep Creek	2007	2012
Warner Lakes	Twentymile Creek	2007	2010
Warner Lakes	Twentymile Creek	2007	2011
Warner Lakes	Twentymile Creek	2007	2012
Warner Lakes	Twentymile Creek	2010	2011
Warner Lakes	Twentymile Creek	2010	2012
Warner Lakes	Twentymile Creek	2011	2012

Table 4. List of loci identified as putative markers under selection based on F_{ST} outlier tests. The first column gives locus names and subsequent columns show which SMU the locus was identified as an F_{ST} outlier in.

Locus	All Populations Analyzed Together	Chewaucan River	Fort Rock	Goose Lake	Malheur Lakes	Warner Lakes	Catlow Valley (All Populations)	Catlow Valley (Home and 3Mile)
OMGH1PROM1SNP1	X							
OMS00006	X				X			
OMS00039								X
OMS00053					X		X	
OMS00078		X						
OMS00090	X							
Omy_101832195	X							
Omy_114587480								X
Omy_9707773	X							
Omy_cd59206	X							
Omy_g1282	X						X	
Omy_mapK3103	X						X	
Omy_NaKATPa350	X							
Omy_nramp146	X	X					X	
Omy_Ots249227	X							
Omy_oxct85	X							
Omy_rbm4b203	X						X	
Omy_redd1410	X		X				X	X
Omy_stat3273*								X
Omy_vatf406	X							
SH10728569	X							
SH109525403								X
SH11282082	X							

*This locus was previously identified as a candidate marker under selection (Narum et al. 2010; Matala et al. 2014).

Table 5. Pairwise estimates of genetic variation (F_{ST}) among all population pairs. Population code definitions are given in Table 1.

	Catlow			Chewaucan			Fort Rock			Goose Lake							
	CV3M	CVHC	CVRC	CRCC	CRCR	CRWC	FRBK	FRBR	FRSV	GLCW	GLDV	GLDW	GLDY	GLES	GLLC	GLTB	GLWG
CVHC	0.191																
CVRC	0.421	0.429															
CRCC	0.404	0.428	0.230														
CRCR	0.472	0.492	0.316	0.036													
CRWC	0.610	0.628	0.401	0.083	0.050												
FRBK	0.345	0.356	0.096	0.137	0.199	0.254											
FRBR	0.324	0.330	0.064	0.149	0.227	0.286	0.030										
FRSV	0.362	0.384	0.121	0.149	0.203	0.262	0.028	0.055									
GLCW	0.563	0.584	0.340	0.153	0.168	0.230	0.205	0.241	0.206								
GLDV	0.480	0.502	0.310	0.110	0.110	0.174	0.180	0.206	0.173	0.126							
GLDW	0.480	0.510	0.289	0.093	0.102	0.162	0.150	0.191	0.153	0.106	0.089						
GLDY	0.492	0.523	0.320	0.110	0.108	0.164	0.174	0.211	0.169	0.120	0.068	0.046					
GLES	0.447	0.473	0.280	0.089	0.111	0.152	0.168	0.198	0.170	0.067	0.092	0.062	0.076				
GLLC	0.474	0.506	0.262	0.107	0.121	0.181	0.136	0.182	0.139	0.079	0.089	0.042	0.053	0.047			
GLTB	0.531	0.556	0.359	0.116	0.101	0.153	0.228	0.256	0.224	0.126	0.097	0.056	0.061	0.081	0.075		
GLWG	0.467	0.496	0.272	0.083	0.083	0.139	0.149	0.180	0.132	0.138	0.075	0.061	0.074	0.086	0.073	0.083	
MLBR	0.134	0.137	0.213	0.260	0.344	0.394	0.187	0.162	0.211	0.385	0.310	0.313	0.324	0.309	0.307	0.375	0.306
MLEB	0.255	0.269	0.197	0.238	0.322	0.395	0.170	0.148	0.199	0.361	0.298	0.297	0.316	0.288	0.289	0.373	0.285
MLMC	0.204	0.215	0.237	0.288	0.371	0.433	0.218	0.192	0.242	0.418	0.340	0.345	0.349	0.339	0.330	0.401	0.342
MLRD	0.346	0.345	0.290	0.323	0.390	0.493	0.264	0.236	0.296	0.479	0.382	0.404	0.425	0.392	0.407	0.451	0.388
MLSR	0.284	0.254	0.269	0.316	0.385	0.434	0.231	0.212	0.253	0.426	0.363	0.367	0.375	0.360	0.358	0.428	0.360
MLSV	0.309	0.312	0.151	0.250	0.333	0.401	0.145	0.121	0.162	0.360	0.292	0.292	0.294	0.286	0.270	0.357	0.284
WLDC	0.395	0.419	0.231	0.090	0.135	0.173	0.124	0.151	0.132	0.150	0.082	0.101	0.100	0.094	0.086	0.127	0.090
WLHC	0.469	0.488	0.290	0.108	0.132	0.160	0.159	0.204	0.174	0.092	0.084	0.068	0.074	0.049	0.055	0.096	0.101
WLTM	0.408	0.444	0.222	0.079	0.114	0.168	0.100	0.136	0.104	0.126	0.096	0.073	0.078	0.078	0.056	0.113	0.073
KLFC	0.700	0.714	0.425	0.308	0.345	0.489	0.214	0.263	0.215	0.408	0.361	0.343	0.341	0.344	0.344	0.412	0.342
KLFH	0.568	0.593	0.291	0.228	0.277	0.386	0.112	0.163	0.101	0.308	0.255	0.231	0.248	0.256	0.236	0.320	0.231
KLMC	0.600	0.628	0.321	0.341	0.395	0.522	0.232	0.229	0.248	0.474	0.376	0.412	0.388	0.407	0.366	0.471	0.369
KLRC	0.493	0.517	0.200	0.157	0.206	0.312	0.073	0.087	0.060	0.247	0.184	0.186	0.188	0.196	0.185	0.259	0.167
KLSC	0.701	0.718	0.420	0.311	0.348	0.494	0.215	0.261	0.213	0.417	0.366	0.349	0.344	0.356	0.350	0.414	0.344
MRBB	0.341	0.366	0.103	0.169	0.252	0.325	0.064	0.048	0.079	0.266	0.221	0.208	0.227	0.219	0.189	0.284	0.197
MRLM	0.354	0.386	0.126	0.228	0.326	0.403	0.107	0.076	0.139	0.338	0.291	0.284	0.297	0.280	0.254	0.358	0.277
CCH	0.492	0.500	0.245	0.230	0.276	0.353	0.124	0.169	0.127	0.312	0.241	0.236	0.250	0.267	0.223	0.315	0.226
OSH	0.464	0.481	0.259	0.201	0.236	0.311	0.142	0.177	0.108	0.256	0.189	0.194	0.217	0.211	0.195	0.273	0.166

Table 5. *Continued*

	Malheur Lakes						Warner Lakes			Klamath					Malheur River		Hatchery
	MLBR	MLEB	MLMC	MLRD	MLSR	MLSV	WLDC	WLHC	WLTM	KLFC	KLFH	KLMC	KLRC	KLSC	MRBB	MRLM	CCH
CV3M																	
CVHC																	
CVRC																	
CRCC																	
CRCR																	
CRWC																	
FRBK																	
FRBR																	
FRSV																	
GLCW																	
GLDV																	
GLDW																	
GLDY																	
GLES																	
GLLC																	
GLTB																	
GLWG																	
MLBR																	
MLEB	0.112																
MLMC	0.041	0.135															
MLRD	0.164	0.197	0.196														
MLSR	0.137	0.120	0.141	0.219													
MLSV	0.138	0.126	0.156	0.233	0.172												
WLDC	0.252	0.240	0.276	0.319	0.304	0.228											
WLHC	0.319	0.306	0.342	0.405	0.363	0.305	0.067										
WLTM	0.268	0.245	0.294	0.348	0.314	0.231	0.041	0.068									
KLFC	0.439	0.461	0.486	0.588	0.459	0.417	0.290	0.330	0.253								
KLFH	0.334	0.338	0.378	0.469	0.359	0.298	0.207	0.250	0.169	0.177							
KLMC	0.367	0.381	0.393	0.493	0.388	0.333	0.303	0.388	0.299	0.516	0.383						
KLRC	0.276	0.262	0.314	0.400	0.310	0.211	0.153	0.203	0.122	0.162	0.080	0.306					
KLSC	0.441	0.468	0.484	0.590	0.469	0.426	0.293	0.339	0.256	0.032	0.190	0.492	0.176				
MRBB	0.170	0.148	0.185	0.266	0.210	0.143	0.152	0.224	0.148	0.327	0.198	0.234	0.131	0.321			
MRLM	0.171	0.162	0.182	0.285	0.219	0.155	0.210	0.284	0.216	0.397	0.282	0.275	0.200	0.392	0.042		
CCH	0.296	0.297	0.326	0.415	0.362	0.240	0.180	0.249	0.181	0.376	0.198	0.335	0.179	0.365	0.174	0.263	
OSH	0.281	0.278	0.316	0.387	0.305	0.237	0.177	0.211	0.162	0.356	0.192	0.349	0.166	0.370	0.193	0.279	0.193

Table 6. Estimates of genetic diversity for Great Basin redband trout populations and outgroups. Population code definitions are given in Table 1. Estimates include gene diversity, allelic richness, effective population size (N_e) based on linkage disequilibrium, and the associated 95% confidence intervals.

Population Code	Gene Diversity (Hs)	Allelic Richness	N_e	95% C.I.
CV3M	0.154	1.396	10.9	7.1-17.4
CVHC	0.148	1.410	46.1	25.7-130.6
CVRC	0.331	1.893	551	222.8-Infinity
CRCC	0.355	1.954	38.8	35.2-42.9
CRCR	0.307	1.919	99.3	88.8-111.3
CRWC	0.227	1.744	12.5	10.4-15.2
FRBK	0.401	1.981	219.9	179.5-276.6
FRBR	0.398	1.973	80.8	68.7-95.8
FRSV	0.391	1.973	297	214.1-460.5
GLCW	0.288	1.785	34.3	27.0-44.9
GLDV	0.331	1.912	7.2	6.4-8.1
GLDW	0.326	1.910	127.3	88.0-215.2
GLDY	0.330	1.913	57	44.9-75.5
GLES	0.334	1.927	100.5	81.7-127.6
GLLC	0.353	1.919	118.4	80.0-211.3
GLTB	0.285	1.811	217	143.2-410.6
GLWG	0.329	1.913	40.6	34.9-47.8
MLBR	0.342	1.906	130.4	103.4-171.5
MLEB	0.330	1.917	31.7	27.2-37.2
MLMC	0.321	1.887	111.3	85.4-154.4
MLRD	0.243	1.825	190.1	123.1-378.8
MLSR	0.309	1.903	71.7	62.2-83.3
MLSV	0.369	1.968	41.9	35.5-50.3
WLDC	0.375	1.951	168.3	137.5-212.4
WLHC	0.330	1.896	209.6	149.9-332.0
WLTM	0.375	1.931	73.7	62.5-88.1
KLFC	0.148	1.530	14.4	10.2-21.2
KLFH	0.282	1.840	21.6	16.7-29.1
KLMC	0.237	1.661	9.7	7.7-12.2
KLRC	0.348	1.927	249.1	85.9-Infinity
KLSC	0.148	1.542	51.6	27.4-196.6
MRBB	0.405	1.971	98.8	70.8-154.8
MRLM	0.360	1.918	454.9	171.8-Infinity
CCH	0.338	1.875	133.4	84.1-285.7
OSH	0.335	1.896	285.3	137.7-13104.5

Table 7. *P*-values for permutation tests (1,000 permutations) for differences in gene diversity among SMUs. Values in bold represent significant differences.

	Catlow Valley	Chewaucan River	Fort Rock	Goose Lake	Malheur Lakes
Chewaucan River	0.202				
Fort Rock	**0.003**	0.070			
Goose Lake	0.089	0.880	**0.032**		
Malheur Lakes	0.113	0.935	**0.035**	0.952	
Warner Lakes	**0.014**	0.281	0.464	0.288	0.281

Table 8. Population level Q-values from STRUCTURE analysis when *K* (the number of genetic clusters) was set to two. Q-values of approximately 1.0 represent costal origin hatchery fish and values of 0.0 represent genetically pure redband trout. Values are based on 20 replicate STRUCTURE runs for each SMU.

SMU	Population Name	Population Code	Q
Hatchery Stock	Cape Cod Hatchery	CCH	0.962
Hatchery Stock	Oak Springs Hatchery	OSH	0.962
Catlow Valley	Threemile Creek	CV3M	0.001
Catlow Valley	Home Creek	CVHC	0.001
Catlow Valley	Rock Creek	CVRC	0.009
Chewaucan River	Crooked Creek	CRCC	0.340
Chewaucan River	Chewaucan River	CRCR	0.233
Chewaucan River	Willow Creek	CRWC	0.105
Fort Rock	Buck Creek	FRBK	0.393
Fort Rock	Bridge Creek	FRBR	0.201
Fort Rock	Silver Creek	FRSV	0.590
Goose Lake	Cottonwood Creek	GLCW	0.018
Goose Lake	Davis Creek	GLDV	0.182
Goose Lake	Drews Creek	GLDW	0.066
Goose Lake	Dry Creek	GLDY	0.051
Goose Lake	Eastside Goose	GLES	0.030
Goose Lake	Lassen Creek	GLLC	0.058
Goose Lake	Thomas-Bauers Creek	GLTB	0.009
Goose Lake	West Goose	GLWG	0.183
Malheur Lakes	Blitzen River	MLBR	0.098
Malheur Lakes	East Burns	MLEB	0.165
Malheur Lakes	McCoy Creek	MLMC	0.062
Malheur Lakes	Riddle Creek	MLRD	0.036
Malheur Lakes	Silvies River	MLSR	0.096
Malheur Lakes	Silver Creek	MLSV	0.394
Warner Lakes	Deep Creek	WLDC	0.074
Warner Lakes	Honey Creek	WLHC	0.045
Warner Lakes	Twentymile Creek	WLTM	0.080

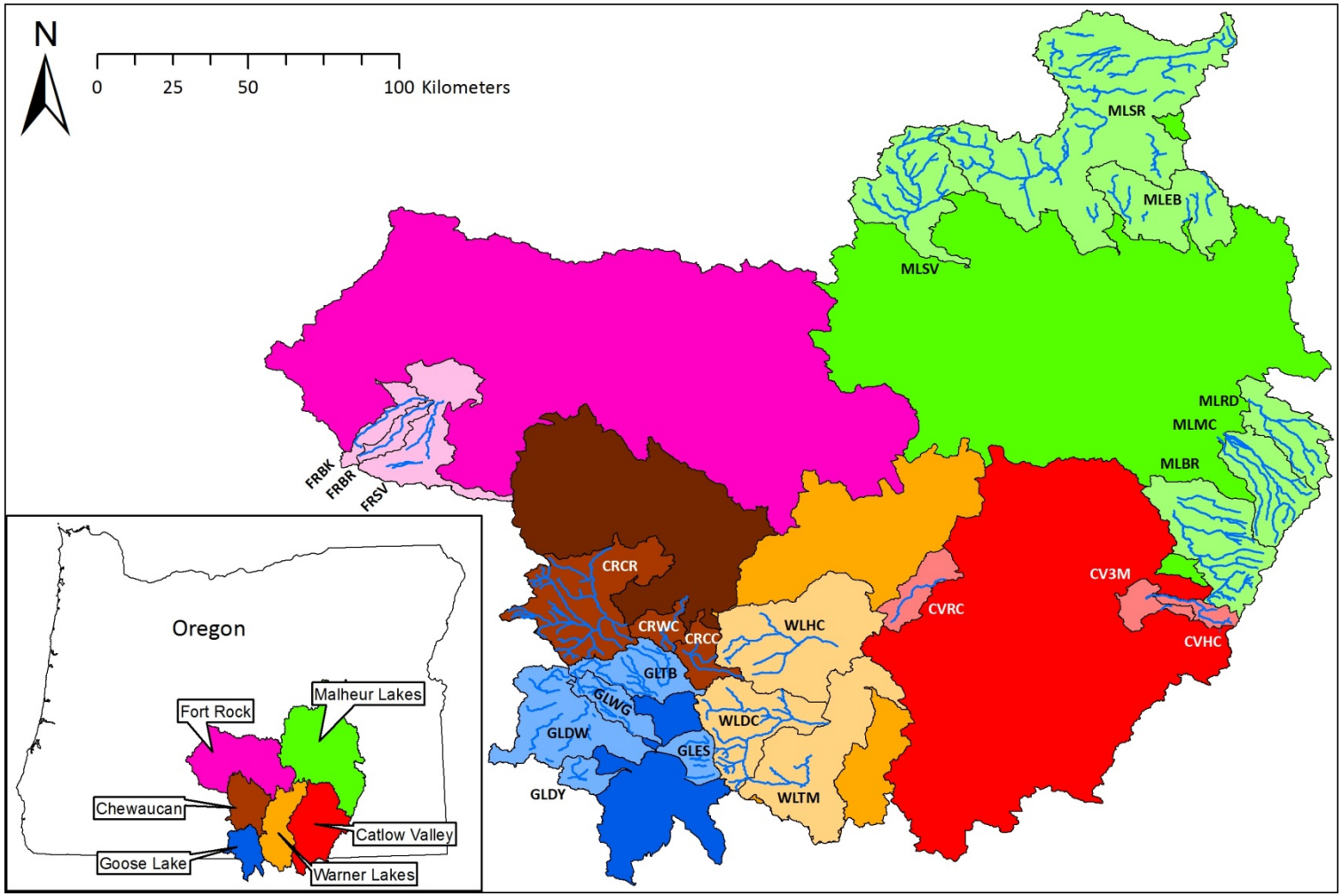

Figure 1. Redband trout were collected from 23 populations in six species management units (SMUs) in the northern Great Basin in Oregon. Population codes on the map correspond to population codes in Table 1. Stream segments that were sampled are shown within each population.

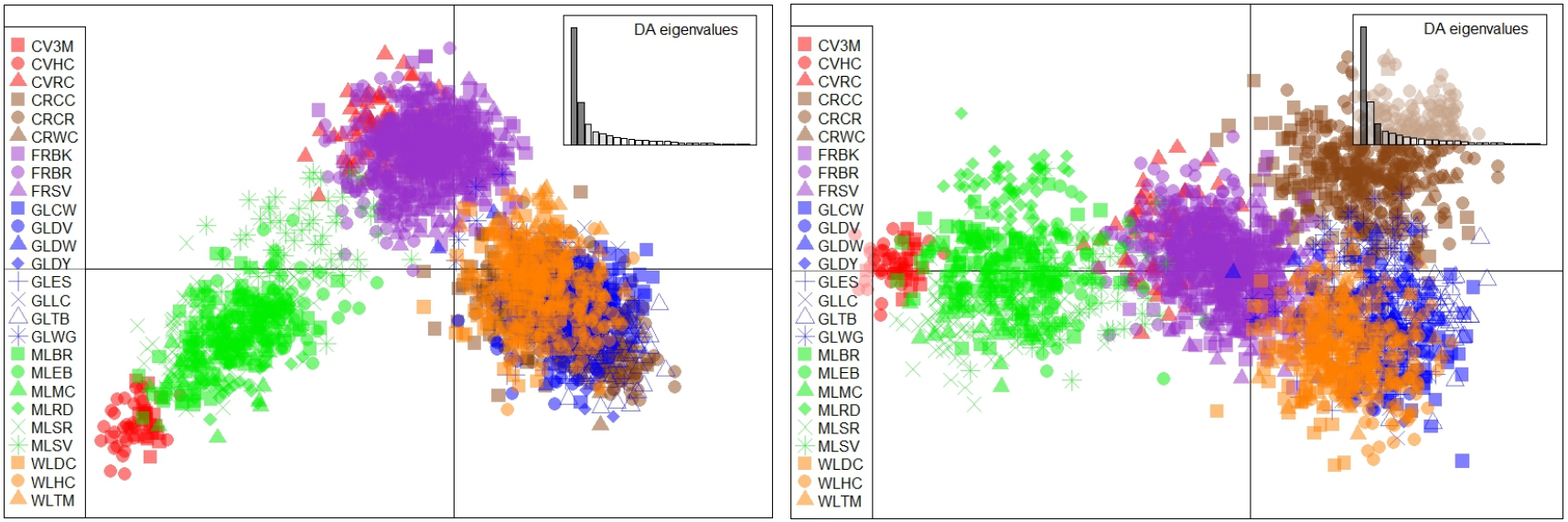

Figure 2. Plots of the first three variance components of the DAPC for Great Basin redband trout. The plot on the left represents variance components 1 (x-axis) vs. 2 (y-axis) and the plot on the right represents variance components 1 (x-axis) vs. 3 (y-axis). Each point on the plots represents an individual fish in the analysis. Different colors represent the different SMUs and different shapes correspond to the different populations within each SMU. Population codes are given in Table 1.

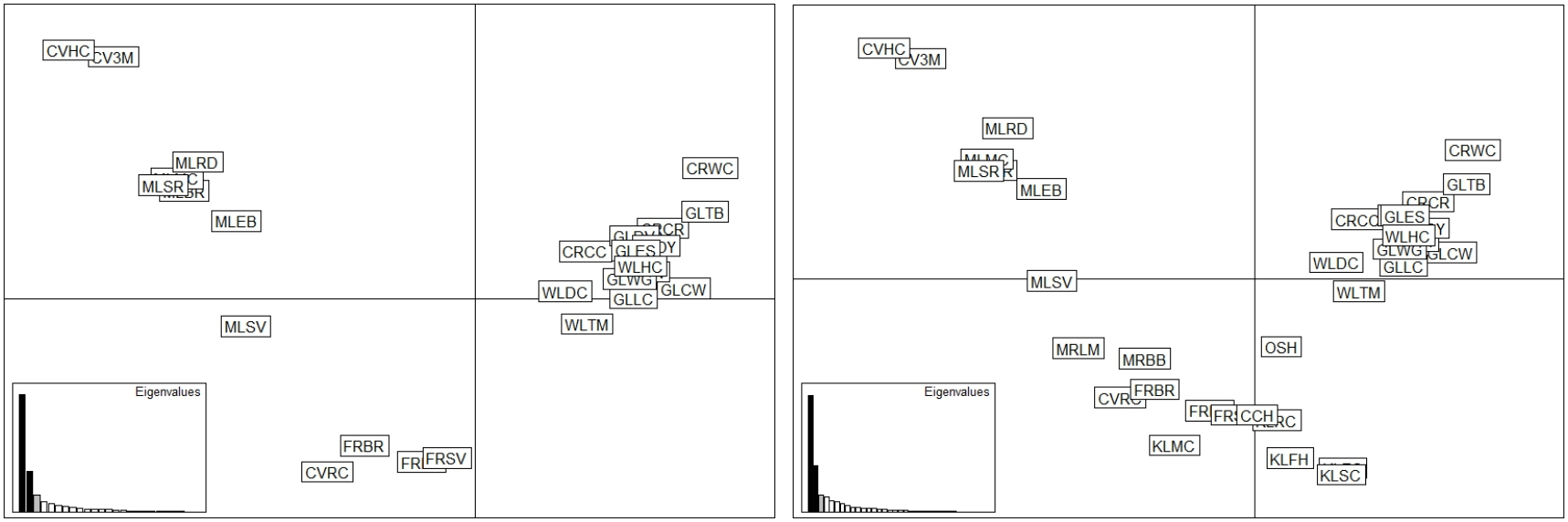

Figure 3. Plot of the first two variance components of correspondence analysis (CA) for Great Basin redband trout populations. The plot on the left represents Great Basin redband trout only and the plot on the right represents Great Basin redband trout and outgroups from Upper Klamath Lake, Malheur River, and two hatchery stocks. Population labels correspond to population codes given in Table 1.

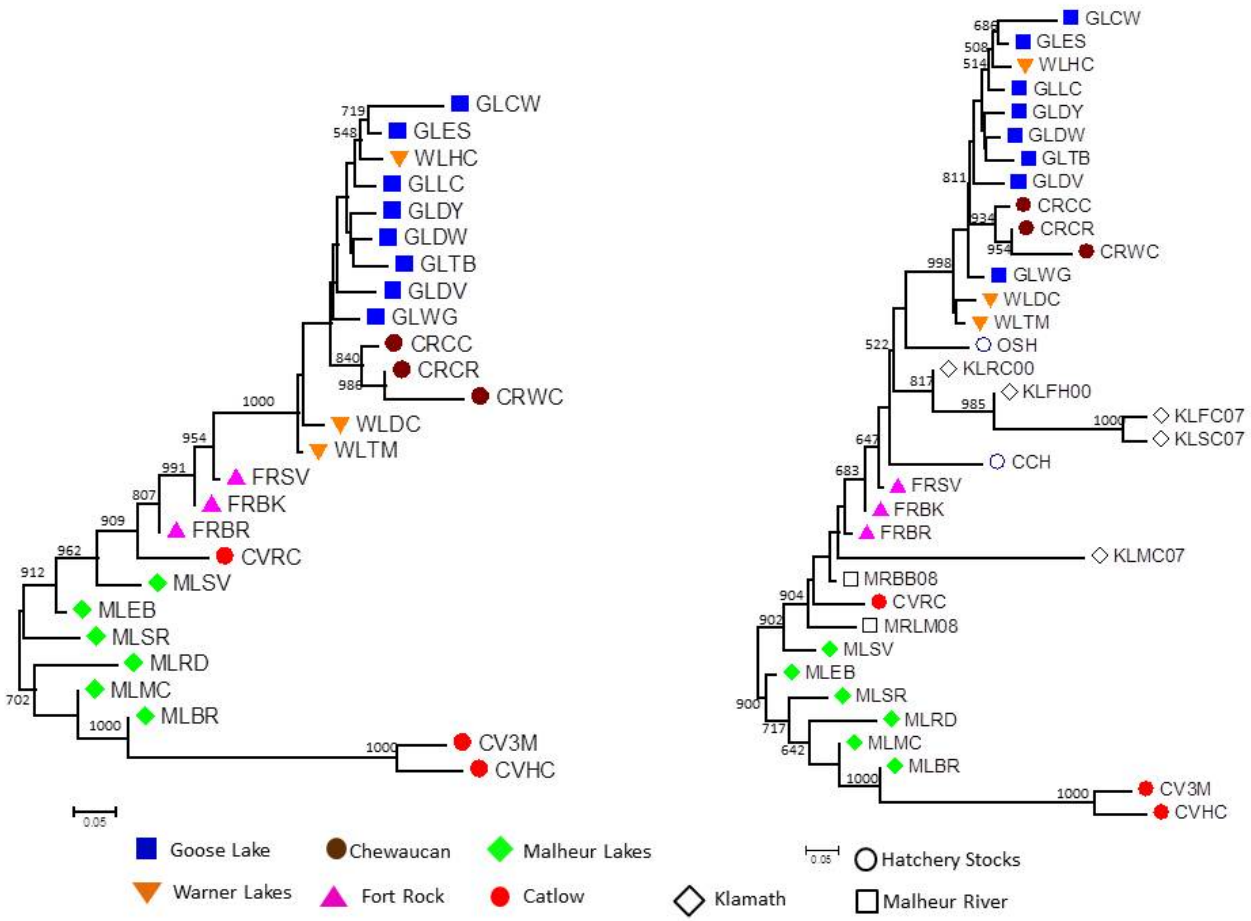

Figure 4. Great Basin redband trout consensus NJ-trees based on Cavalli-Sforza and Edward's (1967) chord distance. The tree on the left represents only the Great Basin redband trout populations and the tree on the right represents Great Basin redband trout plus outgroups. Population codes are listed in Table 1 and shapes correspond to the different SMUs. Values at the nodes represent the number of bootstrap replicates (out of 1,000) that showed the displayed topology. Only bootstrap values greater than 500 are shown.

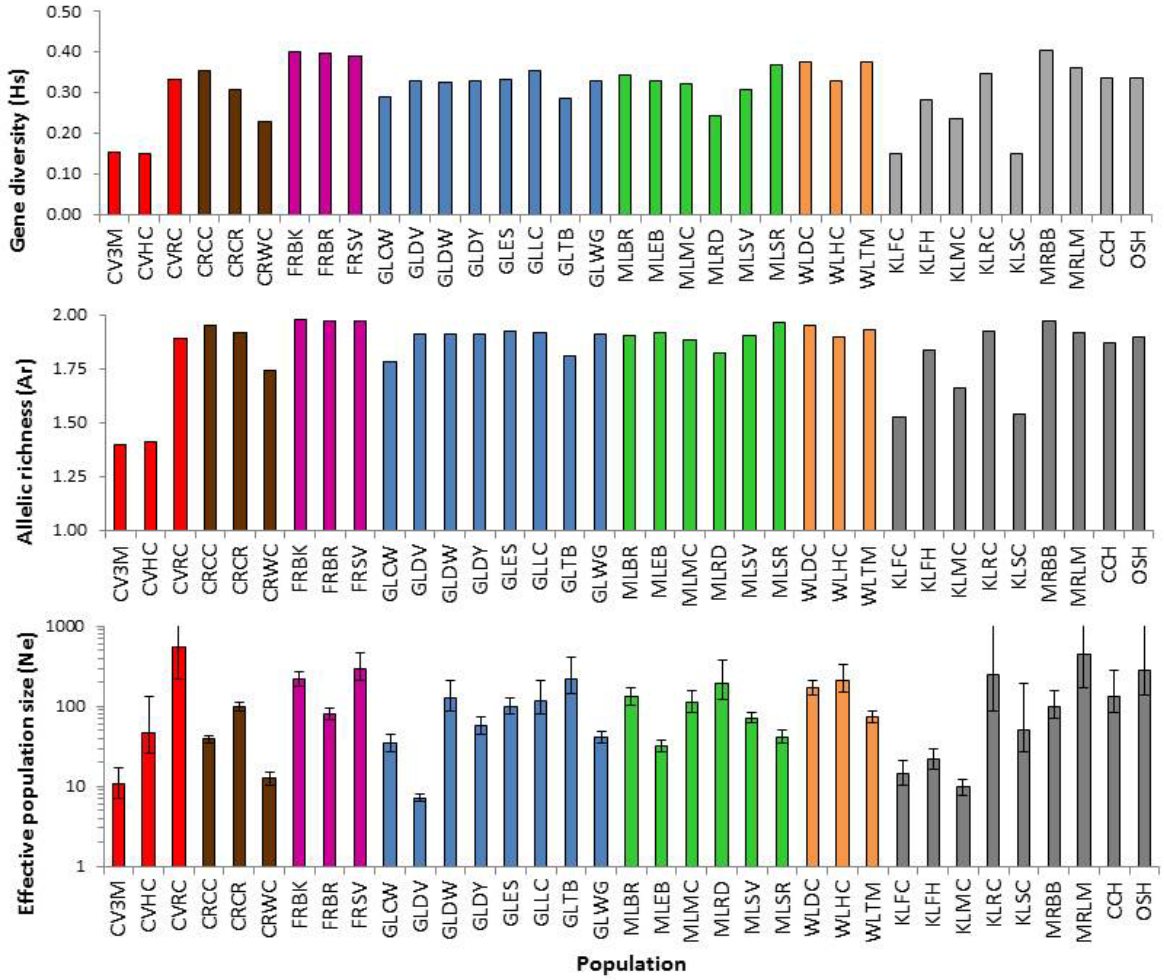

Figure 5. Estimates of genetic diversity in Great Basin redband trout populations and outgroups. The top panel represents estimates of gene diversity, the middle panel represents estimates of allelic richness, and the lower panel represents estimates of effective population size and 95% confidence intervals. Note the logarithmic scale on the y-axis on the bottom panel. Population codes on the x-axis correspond to population names in Table 1 and Figure 1.

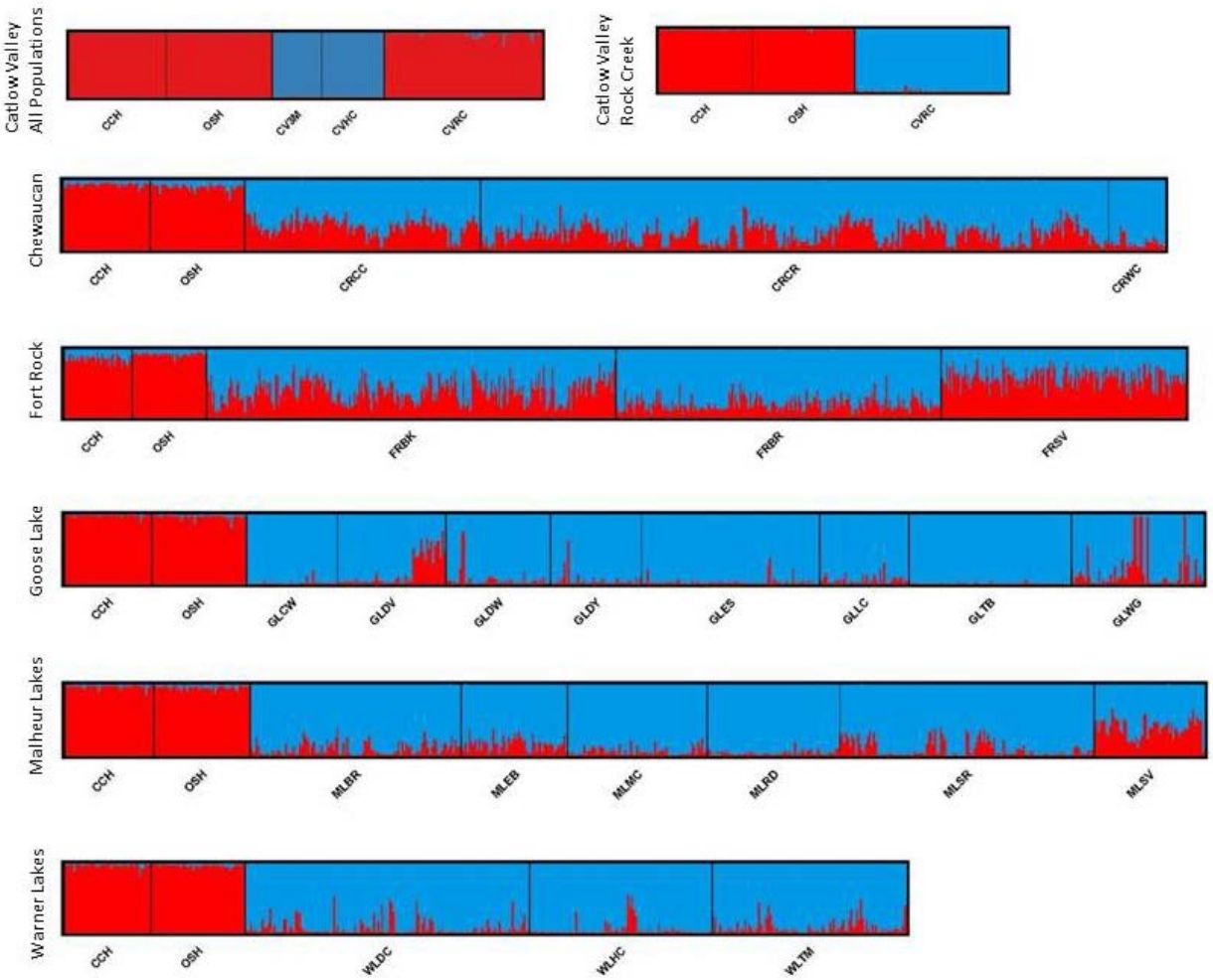

Figure 6. Results of STRUCTURE analysis when *K* (the number of genetic clusters) was set to two. Each vertical bar on the graphs represents an individual in the analysis and the shading pattern corresponds to that individual's membership in each genetic cluster. Black vertical bars separate different populations and population codes are given below each graph.

Appendix 1. List of SNP loci used in this study.

Marker Name	Forward Primer	Reverse Primer	VIC - Probe	FAM - Probe	Source
M09AAE.082	CTATGTGCAGTGCCCTTCTCA	GGCTTACAAGTATGCATGACTAGCT	AGGTTGTTTTACAAATTTAA	AGGTTGTTTTACACATTTAA	Young et al. unpubl.
Ocl 101704D	GTGTGGTCAGCGGTGAGA	CTAGTGGAGGAGATCAAGAGAAGGA	ACCCCGCCTCATCAT	ACCCCGCCTCACCAT	Pritchard et al. 2012
Ocl 102267D	TGGTAGAGCATGGTGCTTACAAC	CCGCTAGCACAAGTTACTTTTTCC	TTCGTACTGATCCCCC	TCGTACTGGTCCCCC	Pritchard et al. 2012
Ocl 102414D	TGTGCACACAGTGTAGCTCTACTA	ACTCAGGTGTGTAACTAAGATTGCATTT	TGTCCATTACTGTCATACAT	TCCATTACTGCCATACAT	Pritchard et al. 2012
Ocl 102505D	GTTCTGTTACTCTAAGCTCTGCCA	GCATCTTTTTGCTACCATGTCAGTT	ATAGCCTCAGAAGTATCT	TAGCCTCAGAGGTATCT	Pritchard et al. 2012
Ocl 106419D	TCCGTCAGCCGTGTGATT	GGCAATACGGAGCTCTATGCT	CCAGCAAATGCC	CCAGCGAATGCC	Pritchard et al. 2012
Ocl 106479D	GCCGTTTGGGAGCTTTGTC	CAAACACTACATGGATGCATCGAAA	TCCGAACTCTGACTTTCGTGCTA	TCCGAACTCTGACTTCCGTGCTA	Pritchard et al. 2012
Ocl 106747D	CAGCACCAAAGGGAGGTACT	TGCTCCTGCCTGCAAGAC	TAGGTTTTCAGAAGAATTAA	TAGGTTTTCAGAATAATTAA	Pritchard et al. 2012
Ocl 96127D	AGTGGTAATCAGTGAATGTGTTGCT	GGCTGCCTACCACTTAGGG	AGGCCTTGGTAGAGATA	AGGCCTTGGTAGAGCTA	Pritchard et al. 2012
Ocl 98409D	GTCGAAGCACGCCAATGAG	TGACTACATAATTCTACTCTGTGATGAAAGA	AGCATCAGCTTTACTGCGTA	AGCATCAGCTTTCCTGCGTA	Pritchard et al. 2012
Ocl 98683D	CCACCTGCTGGAGGATACG	CACCTCAGCTTTCATTAGAGCACTA	ATCCCCGTCCCCAGCAA	ATCCCTGTCCCCAGCAA	Pritchard et al. 2012
OMGH1PROM1-SNP1	TCAAACTGCATTTGATGGAAACAAACAT	AGGACAATTCTAAGTGACCTCAAACTG	TAGTGTTCACTGACTTCA	TAGTGTACACTGACTTCA	Carlos Garza
OMS00002	TTTGATTTGATTTGTATCTGCTTCTT	CCAACATGCCTCACACAAAA	TGTTTTGCAGCGCTC	TGTTTGGCAGCGCT	Castano Sanchez et al. 2009
OMS00006	TCCACGTAGGACATAGTTTGAGCTA	TGTGGTGTCATGTTTGCCCTAC	CACTTACAAATACAAAATT	CTTACAAATGCAAAATT	Castano Sanchez et al. 2009
OMS00039	GTCAGTACTGTGTGTGTCTGTGT	CCATCTACATTGTCAGCAGTGTGA	CAGAGACACGTACGCACA	AGACACGCACGCACA	Castano Sanchez et al. 2009
OMS00053	GGAGCCAGGTCAAGGTGATC	GGATGTCTGGTGTGGCTGTAAA	TGTGTGATTGATACATATAAAT	TGTGATTGATACGTATAAAT	Castano Sanchez et al. 2009
OMS00058	GTGACATTTGGAGCCACTGC	GCTAGGAGACAGAGGGTGAAAG	CAACACTTTGTACCCCTC	CACTTTGCACCCCTC	Castano Sanchez et al. 2009
OMS00064	GTGGATATGTAGTTCGATGGAACAGT	TTTACAACAATCTTCTTTTAATAAAAATATAGCCACTTAT	CAGGCAACATTTTATATAACTA	CAGGCAACATTTTATCTAACTA	Castano Sanchez et al. 2009
OMS00070	CGTTCCTGCGGGACAGT	GTTTCTCTCACGTCCACAGATCT	CAAAATACGGAAATGCAG	AAATACGGGAATGCAG	Castano Sanchez et al. 2009
OMS00072	GTGGGAGAGCTCGTCTATGG	ACAACAGGTCATTGGATGTGATCAG	TAGAAGGTCCATGTATCTC	AAGGTCCATGCATCTC	Castano Sanchez et al. 2009
OMS00077	AATACCATCTTGAGCTCATTAGTAATTATTCAA	CCAGACTTTACACACTCTTGACTGA	TTCCGGTGGTGAAGTT	CCGGTGCTGAAGTT	Castano Sanchez et al. 2009
OMS00078	GAGGGAAGCAGCCATAAACAGAATA	GTCTCACTATGGTCCATATCTGTGTAGA	TTCACATGCATAAGAGTG	TCACATGCATGAGAGTG	Castano Sanchez et al. 2009
OMS00079	GTAACATTATGAATCTATCAGTTTCCCTAGCT	ACCTGCAACGTTAGAGCTGTTTATT	CTACTTTTCACAGTAACACAG	CTACTTTTCACAGTGACACAG	Castano Sanchez et al. 2009
OMS00089	GCACCATTTGAATAAAAAATCTGCTTTGT	GCAACCCAATTCAATATTAAGCACATGAT	ATGAATCCCAAATAAGAAC	AATCCCAAACAAGAAC	Castano Sanchez et al. 2009
OMS00090	AGGGCACAACACCACTCTAAATT	TCGAAAAGCAACATCTGTCTCAGT	ACAACCACACAAGATT	AACCACGCAAGATT	Castano Sanchez et al. 2009
OMS00105	ACATTTGAAGTCAGTATGGGTGTTGAG	GAACCTCACCACAGTACTAAATGCA	CTGCTATTCAAATTGCT	CTGCTATTCACATTGCT	Castano Sanchez et al. 2009

Marker Name	Forward Primer	Reverse Primer	VIC - Probe	FAM - Probe	Source
OMS00106	CGTGTAGCATTCTTGAGGAAGCTT	TTTCCAACAGATGCCAGAATCCT	TCTGATGGAAACTTTC	TGATGGCAACTTTC	Castano Sanchez et al. 2009
OMS00118	GCTTATTTAGAGTGCATGCCAGATG	TGGAACCAATGGGACAGTCCTA	AATGTGCACACCCCGC	AATGTGCACCCCCCGC	Castano Sanchez et al. 2009
OMS00120	GGCAGAAGAGGAGAGAGATATGATTG	CCTCAAATACCTCTGACATTGAAGGTT	TCGCCCACTAAAAC	CGCCCACCAAAAC	Castano Sanchez et al. 2009
OMS00121	GGAAGGAGGTCCAGTGTGAGT	AAAATATGCAACACCACTAAAACTGGAAAA	ACAGCGTGATAAATT	CAGCGTGGTAAATT	Castano Sanchez et al. 2009
OMS00133	GACCACTTCACTCATTCCTCCTTTT	TCCGGTTTACACACTTCATGCA	CGCCTCCATCTTTGTGGT	CGCCTCCATCTCTGTGGT	Castano Sanchez et al. 2009
OMS00175	TTGCGATATGGGACTGTATACATTTATTCC	ACTACCTCCAGTTAAAATAGTGTGGGAAA	CATCACTAGTTCAAATACAA	CATCACTAGTTCAGATACAA	Castano Sanchez et al. 2009
OMS00179	GTCATAACAAAATCAGGGCTTTCCAA	TGGGAGATTTGGGCTGCTTTAAA	TGCCTCTTCTCTTTTCTCAT	CCTCTTCTCTTGTCTCAT	Castano Sanchez et al. 2009
OMS00180	GCGCCGAATGGCATTAGG	CACATTGCTGTCGTTTAGTTTGACT	CTAAAAGTGCATTAAGCC	CTAAAAGTGCCTTAAGCC	Castano Sanchez et al. 2009
Omy_101832-195	TGGCTCTGGACCTGTTGAGA	CGTCACAGCTATTTTAGGCGTAGT	TGTAGTCTTTCAGAGTAGTATG	TAGTCTTTCAGAGGAGTATG	Abadia-Cardoso et al. 2011
Omy_104519-624*	CGTGTGAGTTTGCGGTAAAGAC	TGACGAGTCCGTCTTATCATCCT	CAGCAGGATACATCCGACT	AGCAGGATACGTCCGACT	Abadia-Cardoso et al. 2011
Omy_107806-34	TCTTTGTCCATGCACATTGATATT	AGCACATTTAGTTAGCAGTGATGGA	ATTGGATGTCAGTGTCATT	ATTGGATGTCAATGTCATT	Abadia-Cardoso et al. 2011
Omy_108007-193	GTGAATACCACCCAGGCTTGT	GTCCCTTCCCCAGTTTCACTTAATT	ATGTTTTCTCCCTACTTAAC	TTTTCTCCCCACTTAAC	Abadia-Cardoso et al. 2011
Omy_110201-359	GGTAAGGCCTGTCTGACTATTTTGA	AGAGGTCAATGGATGCCAGTTT	TTTGGCTATTGAAATTATACATT	TTGGCTATTGAAATTCTACATT	Abadia-Cardoso et al. 2011
Omy_114315-438	CCTCACCGATCTAGTCAACTTCATC	AGGAGGCTGAGGGAGATTCTAG	TTATGGGCTTAAGGGTC	TTATGGGCTTACGGGTC	Abadia-Cardoso et al. 2011
Omy_114587-480	CAGATTACGTTATTACGTTTGGGAAATTTTTAAGT	GTGAAAGAGTGGGAAATATAATTATAAGGTCAGA	CCTGTCCAAAATTGT	CCTGTCCACAATTGT	Abadia-Cardoso et al. 2011
Omy_128996-481	CTCATCCACACTGTACAGTACAAGT	CATGCCTTCGTCTCATCAATAACAC	CTTGTGGTTGAGGTTTG	TTGTGGTTGCGGTTTG	Abadia-Cardoso et al. 2011
Omy_130524-160	CGAAGGTAGCGATTGGTCGTT	TGTCTGTTCTGCTGTGTGCTT	ATGGCTTGATCCTCA	ATGGCTTCATCCTCA	Abadia-Cardoso et al. 2011
Omy_97077-73	GTGTAAACAAAATGACTCTGGGATTCAG	AGAAGTGGCAATGGTGTGAAGTAT	TGGTGCAATAGAAATA	CATGGTGCAATAGTAATA	Abadia-Cardoso et al. 2011
Omy_aldB-165	GGGTTAGGTGGATTTGAAGGAGTAA	AGGAAGGTGATGCCTGAGAGA	ATGCTAAAATGAACTCCCCACCA	CTAAAATGAACTCGCCACCA	CRITFC Shawn Narum
Omy_anp-17	GGTAATGCCACATGCGGTAAATT	GGCGAAATCTGAAAATGTGCTGTTA	CTCTCATTGGTATAGTAACC	CTCATTGGTATATTAACC	CRITFC - Nate Campbell
Omy_arp-630	CTGCACAACTTGTTTCCTGCTATT	ACCAAGTGTCCCTGTAAGCC	CCGCTCCGTCTGCT	CCGCTCTGTCTGCT	CRITFC Shawn Narum
Omy_bcAKala-380rd	TTGCTCTCTTCTGGTTGCCTTA	CTTCAGGAGAAAGCGCTACTGT	CATACCCATCCTATGTCAG	CATACTCATCCTATGTCAG	CRITFC - Nate Campbell
Omy_cd59-206	CGATTGGCCCAGATGTTTCCAT	GCTCCGTTGCATAGGTGACT	CAACAATCGAAGGTAAAT	CAACAATCAAAGGTAAAT	WSU - J. DeKoning
Omy_colla1-525	CCTCGGCGTGACAACCT	CCCAGAGAATGGTGCGATTAGG	CTGTTGGGAGAAGAG	TGTTGGGAAAAGAG	WSU - J. DeKoning
Omy_COX1-221	CACTGAACTGTAAGCCATTGTGATT	GCAACATGGGAATGATTCATAAATGCA	CGGTAAGACCATTAAAA	CGGTAAGACCATTTAAA	Campbell et al. 2009
Omy_crb-106	GCTCAAAAAGATTCTGCCAAATTCACA	ATTACAATGAAAGTACTTGAGTGTTTATGCAAA	TTGCAATGCGTCTTT	TTGCAATGAGTCTTT	Young et al. unpubl.
Omy_g12-82	GATCAATTCGATCGCTCATGAAACTT	CTTCTCTCGTTCTCATTGTGTCTCA	CAAACTCTCAGGATTAG	AAACTCTCGGGATTAG	WSU - J. DeKoning
Omy_gluR-79	GACTGTCTATAGCTATTCTTCTCAAACTGT	AGAAACTACCATTGTGATTAACAGATAGAAAATACAT	CAAGTATTTTGCGTAGGAAT	CAAGTATTTTGCATAGGAAT	CRITFC Shawn Narum
Omy_hsc715-80	CCGGTCTACCCTATAGCTGTTG	AGTCAGTCAATTAGTGGTTTGAAATACTATCA	AACTGTATTTGGGAAAAT	ATAAACTGTATTTGTGAAAAT	Young et al. unpubl.
Omy_Il-1b_.028	ACTGTCTGGCTAGAGCACATTG	ATCTTCTACCACCGCACTGTTTTAA	CTGAGGCAACTTTTGT	TGAGGCAGCTTTTGT	Young & McGlauflin unpubl.

Marker Name	Forward Primer	Reverse Primer	VIC - Probe	FAM - Probe	Source
Omy_mapK3-103	GAAGTCATTACTGGTCAGTGGTCAA	GCACAAAACATGAGGAAAGTTGAGA	AATTATTAAGCCTATTTTTTT	ATTATTAAGCCTAATTTTTT	CRITFC Shawn Narum
Omy_metA-161	CGCATGCACCAGTTGTAAGAAAG	AGTGCCACCAGCGATAAGAAAA	CAAGTAAGTGGTTATATTCT	CAAGTAAGTGGTTCTATTCT	CRITFC Shawn Narum
Omy_NaKATPa3-50	GTTGAGCGTGTTATGGGAAAAGAG	TTGCATCGGCTTTCTGAAAACC	CACTCTGTTTCCTTTCTTT	TCTGTTTCCGTTCTTT	Campbell et al. 2009
Omy_ndk-152	AAGAATTGAGGGATAAAAACAAAATAATATATAAACATGA	CAAACCTACATTCATTAAAGTCCAGTTTTGT	CACCCACTTTCAAAAC	ACCCACTCTCAAAAC	CRITFC Shawn Narum
Omy_nkef-241	AGTGTCATTGATGTCGGCCTATTTT	AAACGAATGTCCACCTCAGATGTT	CTTCTGTATCATTTTTG	TCTTCTGTATAATTTTTG	CRITFC Shawn Narum
Omy_nramp-146	TGAGAGTGCACATTGTATTGTTAACCTTT	CACATCCCTACTGACAAAACACTGA	CGTGTGTTGGTGTTTT	CGTGTGTTGATGTTTT	Campbell et al. 2009
Omy_Ogo4-212	TCCTCTCTCCCATTCAATCACTAATGA	AGACAGTAACAAAGCCTCAAACTTGA	CATTTGATGAGACATCTT	ATTTGATGAGGCATCTT	CRITFC Shawn Narum
Omy_Ots249-227	CCCCTAGATTAAACCTGTCCAGTCT	CTATCTATCTATCTATCTATCTATCTATCTATCTATCTACTTACTGAGA	CCCTCTGAGAACTAC	CCTCTGAAAACTAC	Campbell et al. 2009
Omy_oxct-85	CGTCACTGAAACATTACTGTAACATCCA	CATCATCACGCTGTTGGTTTCTTAA	CATCGCTTATTTATGC	CATCGCTAATTTATGC	WSU - J. DeKoning
Omy_p53-262	CCCCAACATCCAGTATACAGTTTCA	CCCAAATTGGCAATTTTAATAGGATTCAGA	CAAGTAGTATGGAGCTCTAT	AAGTAGTATGGTGCTCTAT	CRITFC Shawn Narum
Omy_rbm4b-203	CTGAAATTTGATGAATGGAAGCTGCA	CGTATTCAAGTCGATATACAGTCACGAT	CACGTTATTATGAAAAGGATGT	ACGTTATTATGAAAAAGGATGT	CRITFC - Nate Campbell
Omy_redd1-410	GTACTCCCACTAACATACAGTAGACTCA	GGCACCATTGTGTTTTAGGATGTAG	AAAATATCCTGCAAGGAAT	AATATCCTGCAAGAAAT	CRITFC - Nate Campbell
Omy_srp09-37	TAGTTGTATTAACTCTTCTTTGAGTCTAGA	TCATTCCAGCTCCGTTCTCTTC	TTGTGCTATTGACGCCACAG	TTGTGCTATTGACACCACAG	CRITFC - Nate Campbell
Omy_sSOD-1	GCCGGACCCCACTTCAA	CAGACTAACCGAACAGCATCAGT	CCACAACAAGACCC	CCACAACCAGACCC	WSU - Thorgaard
Omy_stat3-273	CAGACCTCCTCTATCTCCCTATGAG	ACCTCCTTTAAATTGTGCCCAAGAA	TTTTCCAGACTCCAGTTTG	TTTTCCAGACTCAGTTTG	WSU - J. DeKoning
Omy_txnip-343	CCTTCAAACTAACGCATCATAGACATG	GGTCACTTGGCTAATCCCCTTAT	CCAACTGAAGAGATCTG	CAACTGAAGGGATCTG	CRITFC - Nate Campbell
Omy_u09-53.469	ACAGCCTGAGCGTTTGCA	GGAAACTGGGAGAGATCAAAGGA	TTGCAGCCCTTATTGTG	TTGCAGCCCTTGTTGTG	Young et al. unpubl.
Omy_vatf-406	TTGCTTCATTTTGTCATAACCTTGGG	TGCATGCTCTGACAAATGTTACACT	TTGCAGATGACTATCCACA	TGCAGATGACTGTCCACA	CRITFC - Nate Campbell
OMY1011SNP	GAGGCTGGTTTGGGATTCACT	CGCCAAACACTAACTCTCTGTCT	CTTTACCTCGAAGACAAT	ACTTTACCTCTAAGACAAT	Pascal and Hansen unpubl.
SH100974-386	ACATGCAAATTAAGTGTTTGTTTTTAAAAATCGAA	CGACTTCATCCTTTTCATGTAGTGAGT	CACAGTATTATCAAGATTTT	CAGTATTATCGAGATTTT	Abadia-Cardoso et al. 2011
SH104519-624*	CGTGTGAGTTTGCGGTAAAGAC	TGACGAGTCCGTCTTATCATCCT	CAGCAGGATACATCCGACT	AGCAGGATACGTCCGACT	Abadia-Cardoso et al. 2011
SH105075-162	GGAGAAGGACAAGGACATTGGTAAT	AAAGCAGACCACACCATACTTCTC	CTTTCTCTCCTACTTTCC	CTTTCTCTCCTCCTTTCC	Abadia-Cardoso et al. 2011
SH105105-448	CAATTTGCAAGCAGGGAAAGGTTAT	GTGATGGGCTGCAATTGCTT	AAGGAGAATGCATAATC	TGAAAGGAGAATACATAATC	Abadia-Cardoso et al. 2011
SH105385-406	ACCTACCCTCACCTGAACTTCA	CGCTCTTCTGGGCGTATCG	CTTGGAACCATTGCTAC	TTGGAACCGTTGCTAC	Abadia-Cardoso et al. 2011
SH105714-265	CCACTCAGTGCAAGCATGGA	GCTTTCAATCCTTGGCTCCAATATC	CTGTTGTTTGAGGTTCAG	TGTTGTTTGAGATTCAG	Abadia-Cardoso et al. 2011
SH107285-69	GCCCTTGTGACAATGCACTGTTATA	AGGTCTAGACAGTGTGCCATTTG	ATACGTTACTTTTGACCTTGT	ACGTTACTTTTCACCTTGT	Abadia-Cardoso et al. 2011
SH109243-222	ATGTGCACCTCTTAAATTGTAAGTAAAATGT	ACCCTATATTCAGTGGCAAGATTGC	TGTTCATTAAATTGACTTTTT	TTCATTAAATGGACTTTTT	Abadia-Cardoso et al. 2011
SH109525-403	CCTCATTCTCATTGGTGAGTTGTCT	TGTAAGATCTGACCACATGAGTATAACCA	CCTACACCTCTTTTTTCCACA	CCTACACCTCTTTTCTCCACA	Abadia-Cardoso et al. 2011
SH110078-294	GCAGTAAATCAGCAGAGACCTACA	CCTTAAGCTCAGATTTAAACGATCAAAACA	TGTCTACGGATGACTTC	TCTACGGACGACTTC	Abadia-Cardoso et al. 2011
SH110689-148	GTGTGTGGCAGAGAACTAACTGAT	GGTTAAGACATTAACATAACACTGGACTCT	CAAATGAACACATTATTTATC	ATGAACACATGATTTATC	Abadia-Cardoso et al. 2011

Marker Name	Forward Primer	Reverse Primer	VIC - Probe	FAM - Probe	Source
SH112208-328	GTCAACAGTTGGACGTAGATGCT	CCTTCAGCTTGATCACCTCATAGG	CTGACAGTGATT**A**TTTTGT	TGACAGTGATT**G**TTTTGT	Abadia-Cardoso et al. 2011
SH112301-202	GTAAACCCTGCCCACATAATTAGGT	CTGAGACACTGCTCCAAGGT	AATGCGAAG**A**CAAACT	AATGCGAAG**C**CAAACT	Abadia-Cardoso et al. 2011
SH112820-82	CCTTTCCTTTTGCATTTCCTCTACTTATTTATTT	AAATGAACTCACGTTGACCTCTGA	CGCCGC**C**AAGTTA	CGCCGC**T**AAGTTA	Abadia-Cardoso et al. 2011
SH117259-96	CAAGGGAAGAGCTCTGAGATGAG	GGGATCAGTGGCAGGTAGAG	CGTCATGCC**A**TCATGT	CGTCATGCC**G**TCATGT	Abadia-Cardoso et al. 2011
SH117370-400	TGCAAACACAGAGGAAAGGGATTT	GGCTTATTTGTTCCGTACTTGCATT	CAACTCCAA**T**GAATTAA	AACTCCAA**C**GAATTAA	Abadia-Cardoso et al. 2011
SH118654-91	CAGCGTAGACCGTTTCCTCATTAT	GCGCCGATGAGCAGCTT	TCAGCTTGTC**T**TGCCGC	CAGCTTGTC**C**TGCCGC	Abadia-Cardoso et al. 2011
SH127645-308	ACACTGATATTAACATGGCACAAGTCA	CAGGGCCGGTCGTAGATTTT	AAGTTTGTTACA**T**ATTTTG	TTTGTTACA**A**ATTTTG	Abadia-Cardoso et al. 2011
SH95318-147	CGTGTTCTATTTGAAGGCTGTTAAAGG	TCCTGAACTTAAACCTGCCGTTTT	TTGGTTCTG**G**ATATTAT	CTTGGTTCTG**A**ATATTAT	Abadia-Cardoso et al. 2011
SH97954-618	GCTCTGCTTCCTCGGCAAATA	CACAATTGGTTTTTGCACAAAAGTAAAGTATT	CAACGCTTACC**G**GTGTGT	CAACGCTTACC**A**GTGTGT	Abadia-Cardoso et al. 2011
SH98188-405	CACAGTTGCAAGGTAGAGGCTTATA	GCTGAAAGATTAATCCCAGACTGTAGATT	CTCTCATAAGTCT**A**TCCTCC	CTCATAAGTCT**G**TCCTCC	Abadia-Cardoso et al. 2011

Locus names in bold were identified as candidate markers under selection in previous studies

*This locus was unknowingly run twice under two different names

Appendix 2. Genetic population structure analyses based on a subset of 74 putatively neutral SNPs.

Table A2.1 Estimates of genetic variation (F_{ST}) among different population groupings based on 74 putatively neutral SNPs.

Population grouping	$\boldsymbol{F_{ST}}$ **estimate**
All populations including outgroups	0.217
Great Basin redband trout only	0.207
Catlow Valley	0.383
Chewaucan River	0.039
Fort Rock	0.036
Goose Lake	0.079
Malheur Lakes	0.136
Warner Lakes	0.056

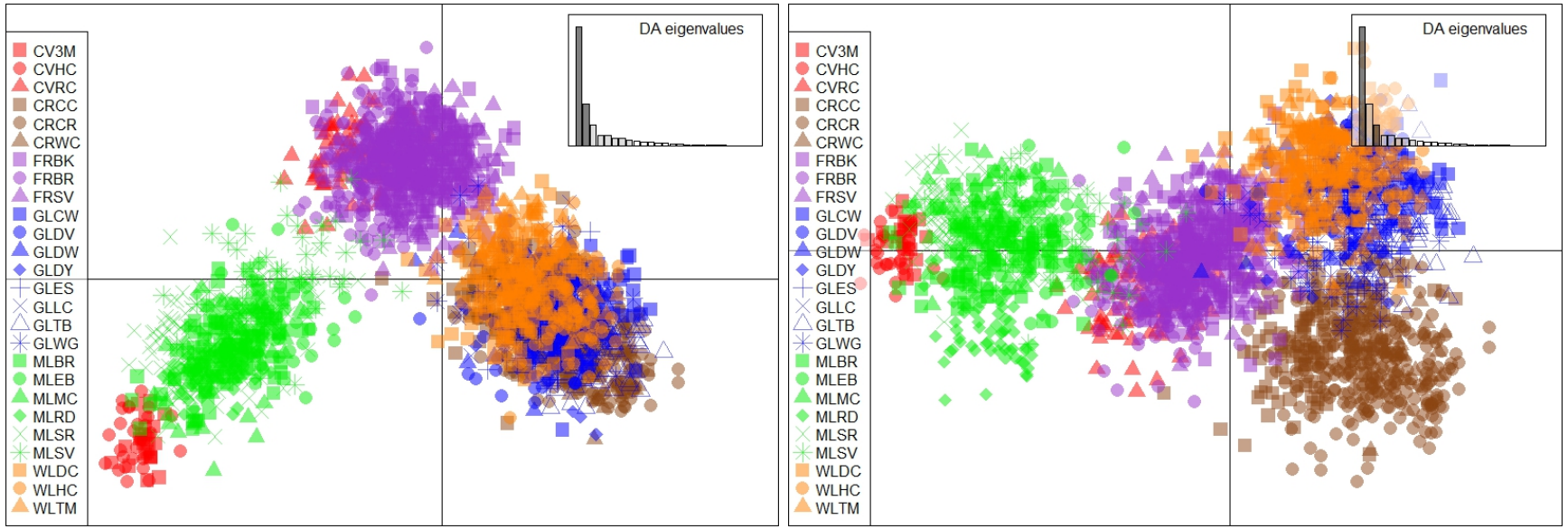

Figure A2.1 Plots of the first three variance components of the DAPC for Great Basin redband trout. The plot on the left represents variance components 1 (x-axis) vs. 2 (y-axis) and the plot on the right represents variance components 1 (x-axis) vs. 3 (y-axis). Each point on the plots represents an individual fish in the analysis. Different colors represent the different SMUs and different shapes correspond to the different populations within each SMU. Population codes are given in Table 1.

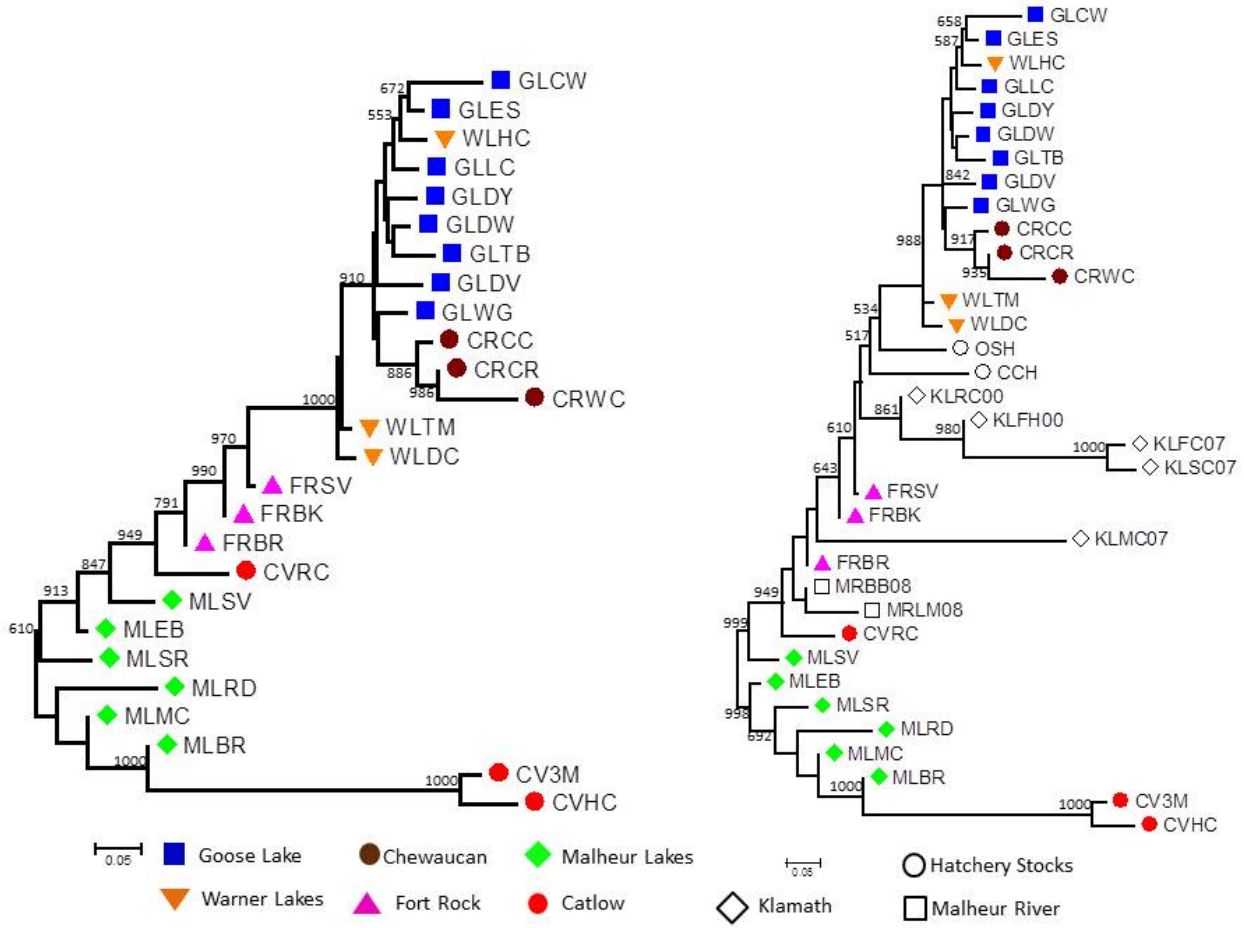

Figure A2.2 Great Basin redband trout consensus NJ-trees based on Cavalli-Sforza and Edward's (1967) chord distance. The tree on the left represents only the Great Basin redband trout populations and the tree on the right represents Great Basin redband trout plus outgroups. Population codes are listed in Table 1 and shapes correspond to the different SMUs. Values at the nodes represent the number of bootstrap replicates (out of 1,000) that showed the displayed topology. Only bootstrap values greater than 500 are shown.

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