Partial Migration in Steelhead (*Oncorhynchus mykiss*): Identifying Factors That Influence Migratory Behavior and Population Connectivity Across a Watershed

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Authorization to Submit Thesis

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Abstract

Partial migration describes a population that includes both resident and migratory individuals. For steelhead (*Oncorhynchus mykiss*), variation in the relative costs and benefits of an ocean migration can have consequences for the decision to migrate and its effect on individual lifetime fitness. Understanding the factors that influence migratory decisions, and how they may shift in the face of global change, is important for conserving these threatened species. The objectives of this study were to determine biotic and abiotic factors influencing juvenile *O. mykiss* life-history decisions in a partially migratory population, as well as how migration barriers alter these migratory behaviors and influence population connectivity. Using a combination of movement, genetic, and maternal origin analysis, our results illustrate the temporal and spatial variability of *O. mykiss* migratory behaviors in a degraded and fragmented watershed.

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Chapter 1: Variability of Life-History Expression in *Oncorhynchus mykiss*: Causes of Partial Migration

Abstract

Partial migration describes a population that includes both resident and migratory individuals. For steelhead (*Oncorhynchus mykiss*), variation in the relative costs and benefits of an ocean migration can have consequences for the decision to migrate and its effect on individual lifetime fitness. While genotypes can play a role in determining the occurrence of migration, juvenile steelhead migratory behavior is highly plastic in response to environmental conditions experienced in freshwater rearing habitat. Human-induced changes have decreased the variation in life-history strategies and shifted relative phenotypic proportions in partially migratory populations of the family Salmonidae, resulting in decreased long-term viability. Understanding the factors that influence migratory decisions in these populations is important for preserving these species. The objective of this study was to determine biotic and abiotic factors influencing juvenile *O. mykiss* life-history trajectories in a partially migratory population. In a watershed of the Clearwater River, Idaho, I tagged approximately 1600 juvenile steelhead during three summer growing seasons from 2011-2013 and estimated apparent survival probabilities using mark-recapture modeling. I then monitored downstream movements during the subsequent outmigration periods using in-stream PIT arrays. Multi-strata mark-recapture models were used to evaluate biotic and abiotic influences on steelhead migration tendencies. I hypothesized that relatively high interspecific densities and low apparent survival rates would result in an increased proportion of outmigrating individuals. Results, based on 202 outmigrating individuals, showed that interspecific density, modeled apparent survival probability, and body-size played important roles in shaping *O. mykiss* life-history expression. Additionally, I observed interannual variation in predictors of life-history expression that was related to weather: two relatively warm years (2012 and 2013) had larger outmigrants, and the relatively cool year (2011) had small outmigrants. Results of this study illustrate the spatial and temporal variability in outmigration strategies of juvenile *O. mykiss*. Understanding the factors influencing migratory behavior is important for improving our quantification of life cycle demographics and our conservation strategies for threatened populations.

Introduction

Individuals from a diverse array of animal taxa undertake annual long-distance movements, which are frequently synchronized with their conspecifics over space and time. The synchronization and apparent homogeneity of vertebrate animals undertaking migration emphasizes the general rules governing migratory processes. However, the selective pressures that favor long-distance migration may vary among populations, or even among individuals within a single populations. Ecologists generally agree that populations become fixed when selection favors opportunities for increased resource acquisition and growth opportunity (Nordeng 1983), avoidance of physiological stress (Alonso et al. 2009), and predator avoidance (Corkeron and Connor 1999). Despite costs of migration may include increases in energy expenditure (Leonard and McCormick 1999), disease risk (Altizer et al. 2011), and predation risk (Wood 1987), migratory behavior must have substantial benefits for it to persist in so many species.

However, in some populations, the variation or instability in the costs and benefits of migration may result in the expression of migratory individuals while some individuals may delay, or completely forgo migration. The disruptive selection, by which a single migratory phenotype is not consistently favored, results in the coexistence of at least two distinguishable phenotypes and is commonly referred to as partial migration (Lundberg 1988, Jonsson and Jonsson 1993). Partial migration is exhibited across a diverse group of organisms, including fish (Nordeng 1983, Jonsson 1985, Kerr et al. 2009), birds (Lundberg 1988, Alonso et al. 2000), mammals (Craig and Herman 1997, Cagnacci et al. 2011), crustaceans (Hartnoll et al. 2007), and amphibians (Grayson and Wilbur 2009). While genetics likely plays a role in determining the decision to migrate at the individual scale (Pulido et al. 1996, Narum et al. 2004), previous research has shown differing migratory strategies among progeny of the same parentage (Pascual et al. 2001). This suggests that at least some individuals from partially migratory populations are able to express either strategy.

One of the most studied examples of partial migration occurs among *Oncorhynchus mykiss* and several other fishes of the family Salmonidae (*Oncorhynchus*, *Salmo*, *Salvelinus* spp.). Within partially migratory populations of *O. mykiss*, ocean-going individuals, commonly referred to as steelhead, typically spend 1-4 years in freshwater as juveniles (Quinn 2011) before migrating to the ocean and ultimately returning to freshwater to spawn (anadromy). Conversely, individuals from the same population may complete their entire life-cycle in freshwater (residency). Populations of *O. mykiss* can vary from entirely resident landlocked populations (Nielsen and Sage 2001) to completely anadromous populations (Berejikian et al. 2013). More commonly, partial migration occurs, although the proportion of either migratory phenotype can be highly variable between populations (Quinn and Meyers

2004, Soggard et al. 2012, Berejikian et al. 2014) and over time (Bjornn 1978, Savvaitova et al. 2002).

Concerns over declining population abundance of *O. mykiss* and other salmonids (Finney et al. 2000, McClure et al. 2003) has focused attention on the causes and consequences of partial migration and the environmental conditions that influence migratory decisions (Gross 1991, Satterthwaite et al. 2010, Benjamin et al. 2013). Anthropogenic impacts, in the form of barrier construction (Morita et al. 2000, Pearse et al. 2009), harvest (Savvaitova et al. 2002, Thériault et al. 2008), and climate change (Satterthwaite et al. 2010, Benjamin et al. 2013, Sloat and Reeves 2014), can cause dramatic shifts in the relative prevalence of anadromy and residency. Large-scale changes in productivity or species assemblages can also alter migratory behavior. Reduction in life-history diversity associated with environmental change can have negative consequences for salmonid populations, as life-history diversity can buffer populations from changing conditions and increase viability (Greene et al. 2010, Schindler et al. 2010, Moore et al. 2014). Thus, identifying drivers of *O. mykiss* life-history trajectories and how they affect population dynamics is critical for future conservation of the species (McPhee et al. 2007).

O. mykiss life-history expression is thought to be a product of genotype, individual condition, and external environmental conditions (Kendall et al. 2015). While some studies have shown reproductive isolation between sympatric resident and anadromous individuals within populations (Zimmerman and Reeves 2000, Narum et al. 2004), many have demonstrated the ability for each parental phenotype to produce offspring that exhibit the alternate strategy (Thrower and Joyce 2004, Hayes et al. 2012, Courter et al. 2013). Moreover, *O. mykiss*, are more likely to migrate when prey availability declines (Keeley et al.

2001, Benjamin et al. 2013), lipid content declines (McMillan et al. 2012, Sloat and Reeves 2014), growth efficiency declines (Morinville and Rasmusen 2003), and migration is female-biased (McMillan et al. 2007, Rundio et al. 2012). However, previous research has shown opposite trends in predictors of life-history selection in partially migratory *O. mykiss* populations (reviewed by Kendall et al. 2015), such as temperature (Sogard et al. 2012, Doctor et al. 2014), growth (Beakes et al. 2010, Sloat and Reeves 2014), body size (Berejikian et al. 2014), and intraspecific competition (Bjornn et al. 1978, Olsson et al. 2006). The myriad of competing hypotheses suggests there are hierarchical factors driving migratory decisions in *O. mykiss* and to understand which factors are operating at any temporal-spatial combination requires comprehensive analysis.

The objective of this study was to identify the abiotic and biotic factors that influence migratory decisions of a partially migratory population of natural origin *O. mykiss* across a watershed in the Clearwater River, ID. From 2011-2013 we captured and tagged approximately 1600 yearling *O. mykiss* and modeled apparent survival and outmigration probability of individuals using Pollock's Robust Design (Pollock 1982, Kendal et al. 1995, 1997) and multi-state live recapture (Hestbeck et al. 1991, Brownie et al. 1993) mark-recapture models. I considered individual factors, site-specific effects, and temperature, in modeling the outmigration of any individual. At the individual level, I hypothesized that survival probability would exert a negative effect on migration tendencies, where sites with high survival would exhibit decreased probabilities for outmigration. Between sites, I hypothesized that density would influence outmigration tendencies as a result of higher competition resulting in increased outmigration probability. Additionally, I predicted there would be inter-annual variation in drivers and magnitude of outmigration as a result of differences in intraspecific densities and temperatures. Lastly, I predicted that because our study sites demonstrate bioenergetic challenges for fish in warm years, warmer years will favor higher rates of outmigration.

Methods

Study area

The Lapwai Creek watershed, draining an area of approximately 694 km^2, is located in Nez Perce and Lewis counties in North-Central Idaho (Fig. 1). The Lapwai Creek watershed terminates as a fourth-order stream where it drains into the Clearwater River. The headwaters of the Lapwai watershed are located at Craig Mountain at an elevation of 1463 meters above sea level (MASL) and it is joined by second to third order tributaries of Upper Lapwai, Mission, Sweetwater, and Webb Creeks before meeting the Clearwater River at 236 MASL. In addition to supporting a naturally-reproducing, ESA threatened population of *O. mykiss*, which is identified as an "A-run", or early-returning with relatively small adult body size, part of the Snake River Distinct Populations Segment (DPS) (NFMS 2006), the watershed supports native populations of dace (*Rhinichthys* spp.), sculpin, (*Cottus* spp.), northern pikeminnow (*Ptychocheilus oregonensis*), bridgelip sucker (*Catostomus columbianus*), chislemouth (*Acrocheilus alutaceus*), and redside shiner (*Richardsonius balteatus*). Since 2005, the Nez Perce Tribe has released approximately 275,000 coho salmon (*Oncorhynchus kisutch*) smolts into the Lapwai watershed annually in the spring. Dams on Sweetwater and Webb Creeks divert water to a reservoir where it is stored for irrigation use. Both diversions withdraw water from February-October, although a provision exists to bypass all inflow to the diversions in February and March if minimum flows are not met.

Sampling sites

Six sites of approximately 100 m in length were selected for inclusion in the subsequent analysis (Fig. 1). These six sites represent a subset of sites from an ongoing research and monitoring effort in the basin (see Hartson and Kennedy 2014, Myrvold and Kennedy 2014). Sites chosen were the only sites that were continuously sampled every year from 2011-2013 that had sufficient numbers of recaptured yearling *O. mykiss* to allow for survival and outmigration analysis. Sampling began at or near the onset of base flows each summer and I visited each site five times, with sampling intervals at each site spaced approximately 30 days apart. In 2012 and 2013, sampling began mid-June and concluded in mid-October. High flows in 2011 precluded effective sampling early in the season, thus forcing us to begin sampling in late-June and concluding in mid-November that year.

O.mykiss sampling

I placed block nets at each end of each sampling reach to prevent immigration and emigration of *O. mykiss* during sampling. Block nets were removed at the conclusion of each sampling occasion. I used a Smith-Root LR-24 electrofisher (Smith-Root Inc., Vancouver, WA, USA) to capture steelhead, conducting three passes at each site during sampling occasions. After each pass, individuals were placed into aerated buckets and fish were not returned to the stream until all three passes had been completed.

Captured individuals were anesthetized using a solution of tricaine methanesulfonate (MS-222). Once fish were anesthetized, I measured fork length (FL) to the nearest mm and mass to the nearest 0.1 g for each individual. I inserted a 12 mm 134.2 kHz ISO PIT tag (Biomark Inc., Boise, ID, USA) into the ventral cavity of each steelhead ≥65 mm FL. Steelhead were then moved to an in-stream livewell where they were given a minimum of 30 minutes to recover before being released back into the stream. All fish sampling, and handling procedures were permitted as part of the Section 7 consultation for the Lewiston Orchards Biological Opinion (NMFS 2006) Idaho Department of Fish and Game (permit F-07-05-10), and the University of Idaho Institutional Animal Care and Use Committee.

O. mykiss densities and growth rates

To calculate juvenile *O. mykiss* densities ($\#/m^{-2}$), I used 3-pass depletion estimates for each site based on Carle and Strub (1978). I calculated both age 1+ density and total density (all age classes combined) for each sampling occasion at all sites. I categorized individuals as age 0+ or 1+ based on site- and time-specific length distributions. Length distributions were generally bimodal, allowing us to easily determine age class for each individual.

I calculated mean individual growth rate (%body weight/day) between sampling intervals at each site for all recaptured individuals. This resulted in 4 growth intervals in 2012 and 2013, and 3 in 2011. Mean growth intervals were used for each site to summarize summer growth rates for individual sites during each sampling year.

Temperature

At each site I deployed a HOBO TidbiT v2 water temperature data logger (Onset Computer Corporation, Bourne, MA, USA). The loggers collected temperatures (°C) at 15 minute intervals for the duration of the study. On rare occasions, temperature data at a given site was unavailable due to the logger malfunctioning or not being completely submerged. In these instances, I created linear regressions to recreate temperatures during the missing intervals. Using known temperatures from the site with the missing data and its nearest site from the same tributary, I was able to create a regression to estimate temperatures during the missing time period, (all R^2 values > 0.972) leaving me confident that estimated temperature values were representative of actual conditions.

Apparent survival analysis

To estimate apparent survival, I used a Huggins version (Huggins 1989) of Pollock's Robust Design (Pollock 1982, Kendal et al. 1995, 1997) in Program MARK (White and Burnham 1999). Pollock's Robust Design uses primary (monthly visits to each site) and secondary (discrete electrofishing passes during each visit) sampling occasions to estimate apparent monthly survival (ϕ) and capture probability (p). A major advantage of Pollock's Robust Design over traditional Cormack-Jolly-Seber (CJS) models (Cormack 1964, Jolly 1965, Seber 1965), is that the robust design allows for temporary immigration (γ') and emigration (γ'') of individuals between primary sampling periods. Accounting for temporary movement of individuals reduces bias in apparent survival estimates, as compared to CJS models (Fujiwara and Cassell 2002). The robust design also contains a parameter for recapture probability (*c*), the probability that an individual will be recaptured within a primary sampling period. Since individuals were not returned to the stream until completion of the third electrofishing pass, *c* was fixed to 0.

To estimate apparent survival (ϕ) I first needed to determine the most parsimonious models for *p*, *γ'*, and *γ''*. For each parameter of interest, I built a model set to test various hypotheses (i.e. effects of density, length, time, site), while placing no constraints on the remaining parameters. I then chose the top model based on AIC_c (Burnham & Anderson 2002) and used the resulting structure of each parameter for all apparent survival models (Horton et al. 2009). I assumed capture probability to be equal during all three secondary sampling periods. For the temporary movement parameters, I assumed a random emigration model and set temporary emigration and immigration equal to one another (henceforth referred to as *γ*). Additionally, I set *γ* constant over time, allowing the survival parameter for the last interval to be estimable. The top models for *p* were time in 2011 and 2012, and site in 2013. The top models for *γ* were length, site, and total density in 2011, 2012, and 2013 respectively.

To estimate monthly apparent survival, I developed a set of candidate models which reflected the suite of factors indicated by the literature to be drivers of survival for juvenile salmonids (Table 1). These included effects of time, site, total density, and yearling density. I also created models that included multiple predictions with additive and interaction effects. Additionally, I included site-specific relative length (RL) as a covariate in the candidate models. RL is a site- and time-specific ratio of an individual's FL to the average FL of all yearlings present at the specific time and site (Hartson and Kennedy 2014). I used model averaging based on Akaike weights (w_i) to estimate apparent monthly survival.

Oumigration analysis

To determine the potential migrants (the individuals that were estimated to be alive at the beginning of the outmigration period) I used our estimates of apparent survival (see *Apparent survival analysis*) for each year. I applied the product of monthly apparent survival estimates from the last capture occasion for each tagged individual and then grouped individuals by survival probability to the outmigration period, binned to 5% probabilities. Individuals were then randomly removed within each binned survival probability group, so that the number of surviving individuals was closest to the product of the number of individuals in the group and the group's apparent survival probability. For example, if a group of 10 tagged individuals had an average apparent survival probability of 0.78, I would randomly select 8 of those individuals as having survived to the beginning of the outmigration period. I applied this analysis for all age 1+ individuals encountered over all sampling occasions to create a pool of individuals modeled to be alive at the beginning of the outmigration period.

In order to identify outmigrating individuals, a PIT-antenna array at the mouth of Lapwai Creek (Fig. 1) as well as the antennas associated with hydropower projects throughout the Snake and Columbia River basins were used to distinguish individual outmigrants. Migrants were defined as any individual recorded passing one of these antennas at any time between the last sampling interval and mid-June of the subsequent year. I determined detection efficiency at the Lapwai array (E_L) using the following equation,

$$E_L = N_D/N_{LD} \text{(eq. 1)}$$

where N_D represents the number of individuals that were recorded at an array downstream of the Lapwai antenna and N_{LD} represents the number of individuals detected downstream of the Lapwai array that were also recorded at the Lapwai array.

I calculated detection efficiency at the Lapwai antenna to be 0.79 in 2012 and 0.93 in 2013. Since 83.7% and 96.9% of all fish detected as outmigrants were detected at the Lapwai antenna in 2012 and 2013, respectively, I felt the detection efficiencies at the Lapwai antenna were a good proxy for overall detection efficiency, as the majority of all migrants were detected at this array. We had no way of estimating detection efficiency in 2011, as the Lapwai antenna was non-operational during the outmigration period. We selected 0.70 as our detection efficiency for 2011 models, as we would expect lower detection efficiencies than 2012 and 2013, due to the Lapwai antenna being non-functional.

I developed multistate live-recapture models (Hestbeck et al. 1991, Brownie et al. 1993) in Program Mark to analyze outmigration patterns of *O. mykiss*. Multistate models are used to estimate the probability of transitioning between multiple states (ψ), which in the case of this study, was the probability that a stream-dwelling juvenile will become a migrant. In addition to generating estimates of ψ, these models develop estimates of survival (*S*) during migration to and recapture probability (*p*). I fixed survival probability during migration to 1. Since the majority of migrants were detected at the mouth of Lapwai Creek, I assumed no mortality during migration.

I fixed the recapture probability in the headwaters to 0, as we did not conduct multiple capture periods in the headwaters during the outmigration period. I fixed recapture probability from the headwaters to migration using calculated estimates of detection efficiency for each year. Additionally, I set ψ from migration to the headwaters as 0, because we observed no fish moving back into Lapwai Creek after they had been detected moving out. I built models that considered individual- and site-specific effects on outmigration probability. I also considered models that included temperature effects on outmigration probability, as well as models that included interactions between temperature and some of our individual and site-specific variables (Table 2). I considered all models within 2 AIC_c of the top model to be supported by the data (Burnham and Anderson 2002).

Results

O. mykiss densities and growth rates

In all years, three sites (UMU, USU and UWM) had consistently higher yearling *O. mykiss* densities than the remaining three sites (ULU, UMM and USM) (Table 3). The highest yearling densities were recorded in 2013, with average monthly densities over two times larger than densities in 2011, the year with the lowest yearling densities. In 2012, yearling densities generally fell between 2011 and 2013, however, average yearling densities in 2012 were much closer to those in 2013 than they were to 2011. Total *O. mykiss* densities were highly variable between sites and years. For example, UMM had the highest density (fish/100 m^{-2}) among sites in 2012 (42.4), the lowest in 2013 (6.8), and an intermediate value in 2011 (19.6). At some sites, total densities varied by almost an order of magnitude between years. 2012 had significantly higher total densities than 2011 or 2013, and 2013 had slightly lower total *O. mykiss* densities than 2011. Average monthly growth rates were highest in 2011 and lowest in 2013 (Table 3). Site-specific growth rates were highly variable among years with no clear trends.

Temperature

Temperature differences among sites were consistent for the entire duration of the study. In all three years, temperatures were the highest at the lowest elevation sites, UWM and UMM (Table 3). Peak temperatures for 2011, 2012, and 2013, generally occurred in late-August, mid-July, and early-July, respectively. The coolest year was 2011, with only two sites reaching temperatures of >20.5°C and maximum temperatures at each site never exceeding maximum temperatures in 2012 or 2013. 2013 was the warmest year, with each site reaching a higher maximum temperature greater than in 2012.

Apparent survival analysis

A total of 289, 629, and 675 yearlings were captured in 2011, 2012 and 2013, respectively. In 2011, the best supported apparent survival models included effects of site and yearling density (Table 4). Within sites, survival was negatively associated with yearling density. Additionally, models including the site-specific length covariate received moderate support, with small fish experiencing higher apparent survival than larger fish. However, after model averaging, the effect of size on survival was marginal, as the difference between average monthly survival probabilities between the largest and smallest fish at any given site was never greater than 5%.

Survival models in 2012 showed similar trends to 2011, with models including site and yearling density receiving strong support from AIC_c selection (Table 4). Similarly, there was a negative relationship between survival and yearling density, as well as between survival and length. Within sites, there was relatively little variation between months, with the exception of the June survival period for ULU, during which we estimated apparent survival at 0.015 (Fig. 2). This apparent survival rate is approximately 30 times lower than any other apparent survival estimate for 2012. Although yearling density (0.332) during this apparent survival interval would explain the low survival rates, this apparent survival estimate likely has a higher proportion of permanent emigrants to mortalities, relative to other apparent survival estimates in 2012. A large spike in the flows (U.S. Geological Service, http://waterdata.usgs.gov/id/nwis) indicated a flash flood is likely responsible for the relatively low rates of apparent survival.

In 2013, the temporal and spatial effects model was the most supported (w_i =0.59; Table 4). Although length appears in the second most supported model with site and time, a ΔAICc of 1.94 with the addition of 1 parameter to the top model suggests length carries very little weight. Generally, survival was high during September, with mean survival rates of 0.930-0.981.

Outmigration analysis

Based upon apparent survival models, we estimated 175, 315, and 386 surviving fish to the beginning of the outmigration period in 2011, 2012, and 2013 respectively (Table 5). Of the individuals projected to be alive at the beginning of the outmigration period, we observed 50 migrants in 2011, 86 in 2012, and 66 in 2013 (Table 5). Overall, modeling results showed individual length was a strong predictor of outmigration tendencies for all years. Site and density effects are also present in top outmigration models, although their relative importance is variable between years.

In 2011, we found strong support for the site+length and the survival+site-specific length models (Table 6). For the top model (site+length), proportional representation of migrants ranged from 0.85 to 0.15 across the six sites, with average outmigration probability being 0.53 (Table 7). The top model also showed that migration probability decreased with increasing body length (Fig 3). Additionally, supported models indicated increasing outmigration probability with decreasing modeled survival probability (Fig 4).

All 2012 models with ΔAICc <2.0 included one of the two length covariates (Table 6). This indicates that length was the strongest driver influencing migratory decisions. Mean estimated outmigration probability was 0.34 with SE of 0.03. Results from 2011 shows that the length and site-specific length covariates were similar, as replacing one length covariate for the other generally resulted in ΔAICc <1.2 between the two models. Similarly to 2011, supported models in 2012 showed increasing outmigration probability with decreasing modeled survival probability (Fig 4). Conversely, 2012 showed opposite trends regarding body length and outmigration probability to 2011, with supported models in 2012 exhibiting increasing outmigration probability with increasing body length (Fig. 3).

In 2013, both supported models included yearling density and one of the length covariates (Table 7). ΔAICc of 0.247 between the two models indicates that the two length covariates are very similar for 2013. Additionally, the next most supported model is the yearling density only model (ΔAICc=3.184), showing that yearling density has the strongest influence on outmigration probability. Similarly to 2012, outmigration probability was positively correlated to body size (Fig 3). Further, outmigration rate was negatively correlated with yearling density (Fig 5).

The top model for each year showed the highest overall outmigration probability in 2011 (0.41) and the lowest in 2013 (0.18), with 2012 being a relatively intermediate year, in terms of outmigration (0.35). The proportion of migrants in 2011 is likely higher than the top model indicates, as setting detection efficiency at 0.70 is likely an overestimate of actual detection. Overestimating detection efficiency in 2011 would result in an underestimate in outmigration rates, thus we are reasonably confident that 2011 represents the highest rates of outmigration.

Discussion

A fundamental property of interest among salmonids is the diversity of migratory strategies they employ (Gross 1985, 1991, Bourret et al. 2014). Life-history variability of *O. mykiss* has garnered particular interest among researchers due to the species' relatively diverse life-history portfolios and high rates of residency compared to other salmonids (Withler 1966, Waples et al. 2001, Schindler et al. 2010, Moore et al. 2014, Kendall et al. 2015). Understanding underlying processes that influence migratory decisions in *O. mykiss* has become increasingly important to conservation and management decisions as anthropogenic change has resulted in a decrease in life history variation of *O. mykiss* (Pearse et al. 2009, Satterthwaite et al. 2010), an attribute that is important for long-term population stability and persistence (Greene et al. 2010, Schindler et al. 2010, Moore et al. 2014). While much is known about general factors influencing *O. mykiss* migratory strategies (reviewed by Kendall et al. 2015), less research has focused on mechanisms driving and maintaining life-history strategies within populations and the variability of these mechanisms between years.

In this study, my overall objective was to determine the relative strength of biotic and abiotic drivers of migratory decisions in a population of *O. mykiss* with facultative migration. Additionally across three years of study that varied considerably in terms of climate, I sought to quantify the relative differences in migratory strategies among years and how causative factors differed amongst these years. My results show that between years, cool temperatures, relatively low densities, and associated high growth rates, were correlated with an increase in the proportion of outmigrating individuals. In relatively warm years with high densities (2012 and 2013), the best supported models indicated that large individuals had the highest probability of becoming migrants, with the opposite being true in 2011, a relatively cold and low-density year. Additionally, models indicated a strong negative correlation between individual survival probability and outmigration probability in 2011 and 2012, and a negative correlation between densities and outmigration probability in 2013.

Through an intensive 3-year field effort that studied the fate of over 1500 individuals, I was able estimate apparent survival probabilities of yearling *O. mykiss* and relate modeled probabilities to hypothesized mechanisms influencing survival, as well as likelihood of outmigration. My apparent survival estimates are likely underestimations of true survival, as they confound true survival with permanent emigration. Dispersal of stream-dwelling *O. mykiss* is generally limited (Edmundson et al. 1968, Rodriguez 2002). Thus, it can be assumed that the majority of the fish remained within the study sites for the duration of the study. This suggests that my models of apparent survival largely reflect mortality, rather than permanent emigration. Although I found similar factors influenced survival and outmigration, my research was able to determine how size, density, and year effects influenced migratory decisions, independent of survival.

For *O. mykiss*, decisions regarding residency vs. anadromy hinge on fitness tradeoffs between survival to reproduction, fecundity, and probability of iteroparity. Anadromous migrants generally achieve larger sizes, and thus greater fecundity (Gross 1987) than their resident counterparts, at the cost of reduced survival to first spawning and lower rates of iteroparity (Fleming and Reynolds 2004). Thus, it has been suggested that optimally behaving individuals must weigh their experienced growth condition against potential opportunities for growth in alternative environments when making migratory decisions. Our results were consistent with previous studies that have indicated that individuals with lower freshwater survival probabilities tend to have higher rates of outmigration (Satterthwaite et al. 2010, Hartson and Kennedy 2014). While survival probability is an ultimate cause of migration, our results also uncovered proximate causes for selection of migratory tactics.

For stream-dwelling salmonids large body-size confers a fitness advantage, as large fish are more competitive in defending territories relative to smaller, subordinate individuals, resulting in greater resource acquisition and growth rates for large individuals (Abbott and Dunback 1985). However, increased metabolic costs associated with large size may counteract this competitive advantage (Myrvold and Kennedy 2014). In all three years of analysis, body length appeared in one of the supported models though the direction of its effect was not consistent. In relatively warm years, 2012 and 2013, I found a positive correlation between body-size and outmigration probability. Our results provide evidence to support the thermal tolerance hypothesis (Chapman et al. 2011) in which individuals under the most energetic stress are most likely to migrate. At warm temperatures, large fish have low growth efficiencies relative to small fish (Morinville and Rasmusen 2003), thus faced with limited opportunity for growth, large individuals should become migrants. Conversely, in 2011, temperatures were ideal for growth of *O. mykiss*, rarely exceeding 20.5°C (Moyle 1976), and the models indicated a negative relationship between body-size and outmigration probability. Free from energetic stress imposed in 2012 and 2013, the competitive advantage for large fish in 2011 would have countered metabolic costs associated with large body size. Consequently, increased activity of large bodied individuals would impose both exploitative and interference competition on smaller individuals and pressure them to outmigrate in search of better habitat. McMillan et al. (2012) observed a similar trend in male *O. mykiss*, concluding that freshwater maturation was positively correlated with body-size in the summer prior to spawning.

Temperature serves as an important factor in controlling *O. mykiss* growth rates (Myrick and Cech 2004). Our study has shown how variability in growth rates, shaped by temperature, influence migratory tendencies in a partially anadromous salmonid population. However, impacts of temperature on life-history decisions are mediated by intraspecific densities, individual body size, and site effects. Thus, developing climate models to account for these interactive effects is important for understanding future shifts in relative abundance of life-history strategies in partially migratory populations (Nilsson et al. 2006, Finstad and Hein 2012).

In addition to body-size, I found strong effects of yearling density on outmigration probabilities in 2013, the year with the highest yearling densities, with low-density sites having the highest proportions of migrants. This was a surprising result as most studies of density-dependent effects on migratory strategies of other salmonids has indicated either a positive correlation between densities and proportion of migrants (Krogius 1981, Moriata et al. 2000, Olsson et al. 2006) or no effect (Aubin-Horth et al. 2006). Stream-dwelling salmonids exhibit density-dependent growth (Keeley 2001), thus low densities may serve as a mechanism for relatively high growth rates in our study. Although I incorporated growth into outmigration models, I was unable to describe individual variation in yearling growth due to infrequent recapture events between sampling periods. While none of the top models predicting outmigration in 2013 included growth measures, we did observe the highest and lowest rates of outmigration at sites with the lowest and highest yearling densities, respectively. Thus, it appears that relatively high growth rates in 2013 are correlated with high outmigration probabilities, a trend consistent with and Beakes et al. (2010) and Soggard et al. (2012), but contradictory to Olsson et al. (2006) and Sloat and Reeves (2014) which indicate a negative correlation between growth and outmigration.

Size-dependent predation in ocean environments, may result in relatively high survival for large smolts at sea (Holtby et al. 1990). This is likely a response to increased smolt-to-adult survival for large individuals (Ward and Slaney 1988, Ward et al. 1999). Increased growth opportunities often lead to larger size at outmigration for salmonid smolts. Interannual trends in outmigration patterns showed a strong relationship between growth rates and outmigration probability. Overall, increased rates of outmigration were associated with low densities, low temperatures, and high growth rates. In 2011, the coolest year with the lowest yearling densities, models estimated migration rates more than twice that of 2013, the year with the highest temperatures and yearling densities. These results provide evidence that selection for migrants favors large, fast-growing individuals.

Results from this study have implications for conservation of anadromous salmonids, as well as understanding processes that drive migratory decisions, at both local and regional scales. This study highlights the importance of understanding fine-scale variation in outmigration tendencies between populations, an aspect that is often overlooked in studies of partial migration (Chapman et al. 2011). Due to conflicting trends regarding causes of outmigration in salmonids (Kendall et al. 2015), studies that only consider one or two populations, or span only one migration season, may be oversimplifications of the processes responsible for shaping the entire suite of decisions involved in migration. Due to the high degree of plasticity associated with salmonid phenotype selection and the general decline in populations of migratory species (Wilcove and Wileski 2008), understanding how global change may affect life-history selection in partially migratory species has become increasingly important. In addition to decreasing available habitat (Wenger et al. 2011), studies have shown the potential for climate change to cause dramatic shifts in life-histories of salmonids (Satterthwaite et al. 2010). My results show the likelihood of a decreasing proportion of migrants in response to increasing temperatures. Although salmonids are capable of evolving in the face of rapidly changing environmental conditions (Hendry et al. 2000, Theirault et al. 2008), a loss of life history-diversity associated with climate change (Benjamin et al. 2013), may reduce long-term viability of anadromous salmonids (Schindler et al. 2010). Thus, understanding processes and patterns shaping variation in life-history expression is necessary for making informed management and conservation decisions.

Figures

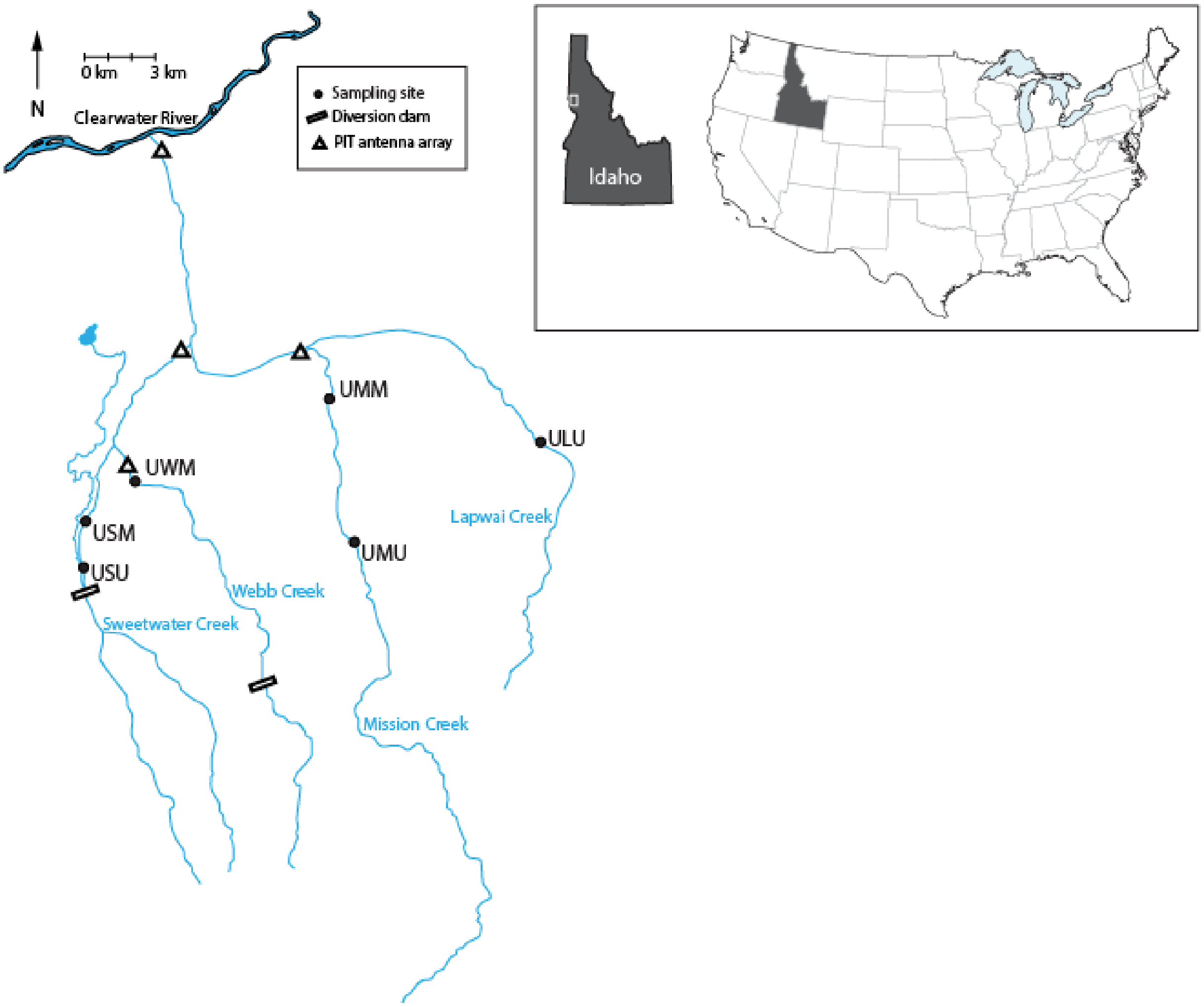

Fig 1. Map of Lapwai Creek basin and sampling sites in Idaho, USA.

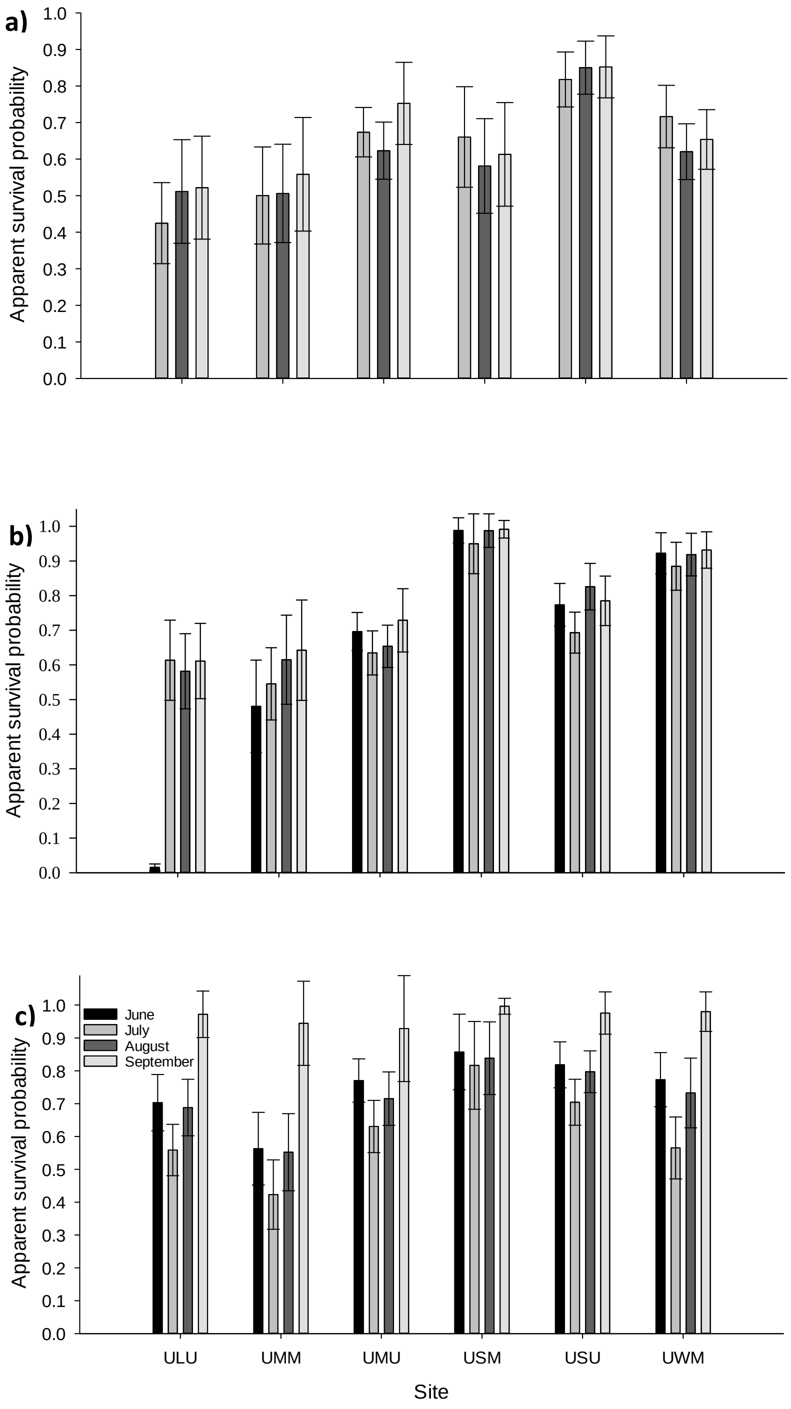

Fig. 2 Model averaged monthly apparent survival rates from mark-recapture analysis for yearling *O. mykiss* at study sites in summer 2011 (a), 2012 (b) and 2013 (c). Sites were not sampled in June 2011 due to high flows. Error bars represent 1 SE.

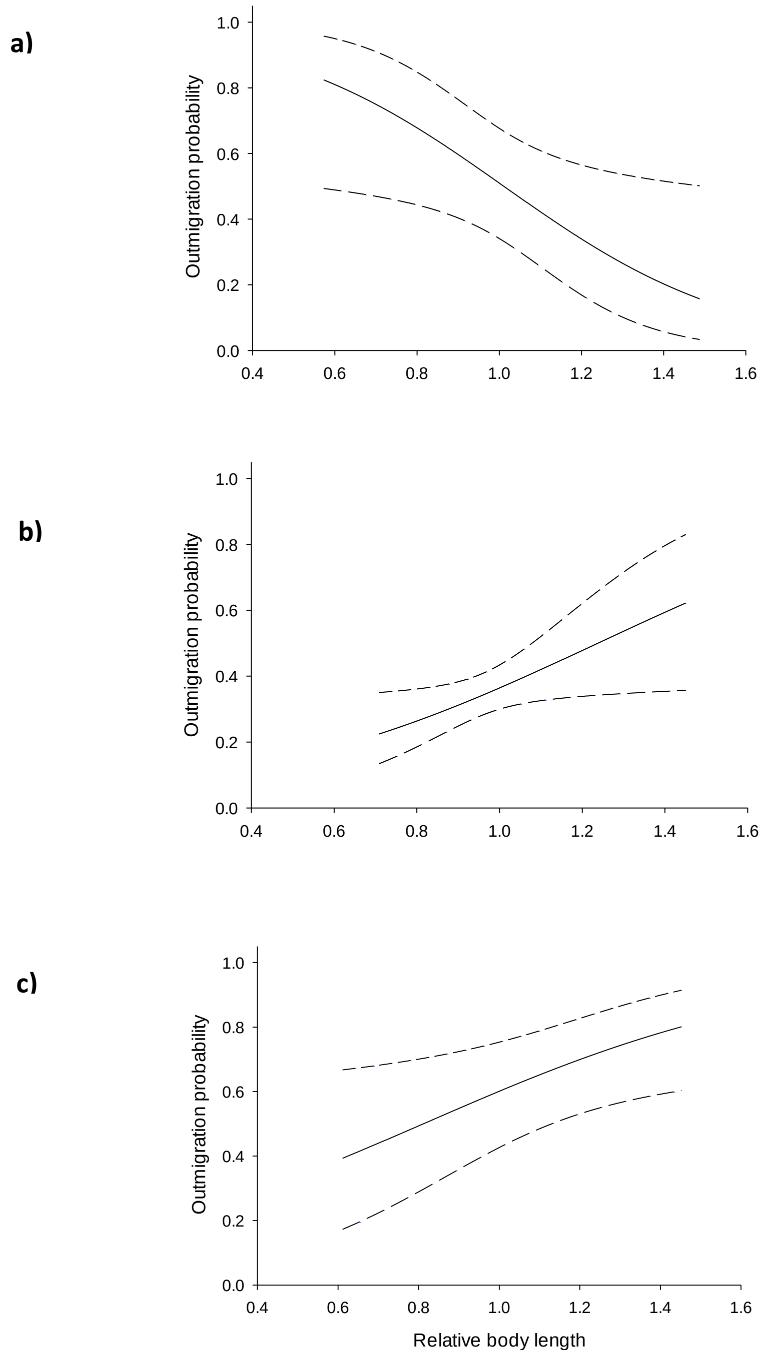

Fig. 3 Outmigration probabilities and relative body length for yearling O. mykiss in the Lapwai Creek basin using multi-state live recaptures models for individuals tagged in a) 2011 at site UWM b) 2012 (all sites) and c) 2013 (all sites) using the most supported model for each year. Solid lines represent mean probabilities, and dashed lines represent 95% confidence intervals.

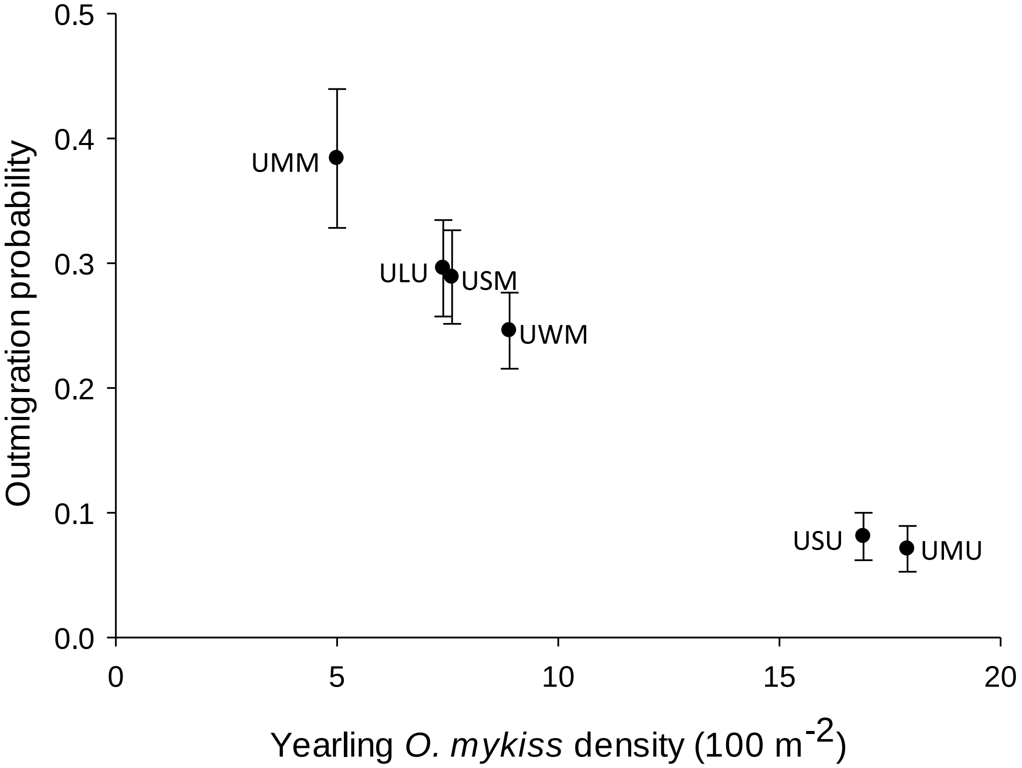

Fig. 4 Modeled outmigration probabilities generated using multi-state live mark-recapture models and mean monthly yearling *O. mykiss* densities (m^{-2}) for individuals tagged during 2013 at each of the 6 study sites. Estimates were generated using the yearling density+site-specific length candidate model.

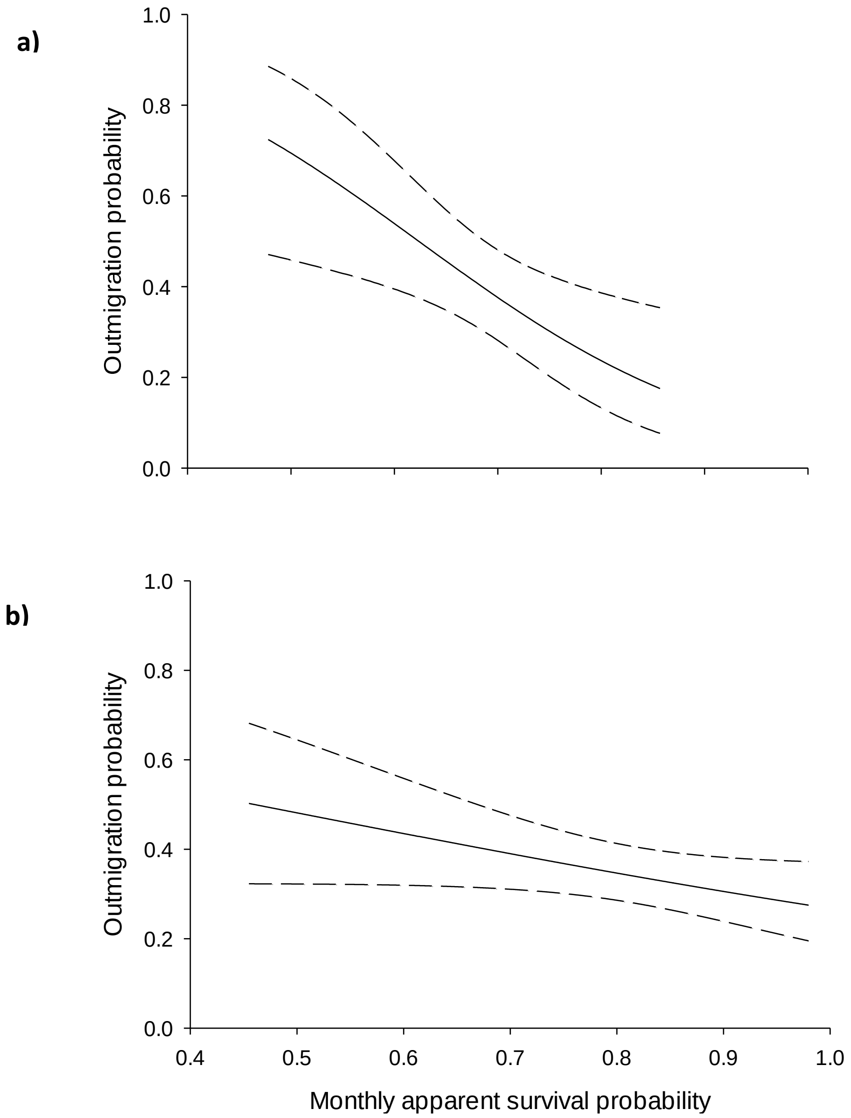

Fig. 5 Yearling *O. mykiss* Outmigration probability generated using multistate live mark-recapture models and modeled apparent survival probability, generated with Pollock's robust design mark-recapture model for individuals tagged in a) 2011 and b) 2012. Apparent survival estimates are model averaged values and outmigration probabilities are from the survival+site-specific models for both years. Solids lines are mean values and dashed lines are 95% confidence intervals.

Tables

Table 1 Model description and number of parameters for each model used in yearling *O. mykiss* apparent survival mark-recapture analysis using Pollock's Robust Design for summer 2011-2013. An additional 10 models were created by the adding site-specific length covariate to each model, resulting in a 1 extra parameter for each model.

	No. parameters		
Model	2011	2012	2013
Site	12	17	14
Time	9	15	12
Site + time (additive)	14	20	17
Site * time (interaction)	24	35	32
Yearling density	8	13	10
Total density	8	13	10
Site + yearling density (additive)	13	18	15
Site * yearling density (interaction)	18	23	20
Site + total density (additive)	13	18	15
Site * total density (interaction)	18	23	20
Site-specific length	8	13	10
Null	7	12	9

Table 2 Model description and number of parameters for each model used in yearling *O. mykiss* outmigration analysis using multi-state live recaptures models for fish tagged in summer 2011-2013. Each model including density is two separate models, one including yearling density and one including total density. Each model including length is two separate models, one including site-specific relative length (RL) and one including overall relative length (WRL).

Model	No. parameters
Site	8
Density	4
Growth	4
Max temp.	4
Temp. ≥20.5	4
Survival	4
Length	4
Site, length	9
Site, survival	9
Density, length	5
Density, survival	5
Growth, length	5
Growth, survival	5
Max temp., length	5
Max temp. survival	5
Temp. ≥20.5, length	5
Temp. ≥20.5, survival	5
Length, survival	5
Null	3

Table 3. Mean monthly yearling and total densities (100 m^{-2}), average individual monthly growth rate (%body weight/day), maximum temperature (°C) and days in which maximum temperature exceeded 20.5 °C for study sites during sampling period (approx. Jun.-Oct.) in 2011-2013. Mean values are in bold.

Year	Site	Yr. *O. mkyiss* density (100 m^{-2})	Total *O. mkyiss* density (100 m^{-2})	Max. (°C)	Days Max. >20.5 (°C)	Mean monthly growth rate (%BW/d)
2011	ULU	2.1	27.0	18.7	0	0.17
	UMM	1.7	19.6	23.1	10	0.48
	UMU	8.6	15.4	19.8	0	0.05
	USM	2.8	6.2	19.9	0	0.57
	USU	6.7	16.9	19.0	0	0.74
	UWM	9.2	23.7	21.2	10	0.64
		5.2	**18.1**	**20.3**	**3.3**	**0.44**
2012	ULU	8.1	11.5	21.2	3	0.26
	UMM	2.1	42.4	25.1	49	-0.01
	UMU	12.2	31.5	21.8	11	0.02
	USM	8.7	18.7	21.7	12	0.07
	USU	12.4	21.3	20.9	1	0.10
	UWM	11.1	17.0	22.4	16	0.21
		9.1	**23.8**	**22.2**	**15.3**	**0.11**
2013	ULU	7.4	26.1	21.4	11	0.19
	UMM	5.0	6.8	25.3	80	-0.08
	UMU	17.9	18.3	22.8	8	-0.11
	USM	7.6	8.2	22.9	7	0.32
	USU	17.0	17.6	21.5	1	0.07
	UWM	8.9	11.4	26.2	51	0.07
		10.6	**14.8**	**23.4**	**26.3**	**0.07**

Table 4. Model results for yearling *O. mykiss* apparent survival analysis for summer 2011-2013 using Pollock's Robust design. For each year, the table includes ΔAICc, ΔAICc weight (w_i), and the number of parameters from each model with ΔAICc ≤ 2.0.

Year	Model	ΔAIC_c	w_i	No. Parameters
2011	Site + yr. density	0	0.34	13
	Site	1.47	0.16	12
	Site + yr. density +site-specific length	1.82	0.14	14
2012	Site + yr. density	0	0.38	18
	Site * total density	0.93	0.24	23
	Site + year density + site-specific length	1.98	0.14	19
2013	Site + time	0	0.59	17
	Site + time + site-specific length	1.94	0.22	18

Table 5. Modeled surviving yearling *O. mykiss* to the beginning of the outmigration period (approx. early-mid Oct.) using Pollock's Robust Design and the number of migrants, defined as modeled survivors recorded at the PIT antenna at the mouth of Lapwai Creek or any other downstream PIT array (proportion of migrating survivors in parentheses), with totals in bold.

	2011		2012		2013	
Site	Survivors	Migrants	Survivors	Migrants	Survivors	Migrants
ULU	10	6 (0.60)	13	6 (0.46)	42	17(0.41)
UMM	8	5 (0.63)	13	3 (0.23)	35	12 (0.34)
UMU	48	8 (0.17)	64	24 (0.38)	126	8 (0.06)
USM	13	3 (0.23)	62	16 (0.26)	48	10 (0.21)
USU	35	6 (0.17)	75	15 (0.20)	93	6 (0.07)
UWM	61	22 (0.36)	88	22 (0.25)	42	13 (0.40)
Total	**175**	**50 (0.29)**	**315**	**86 (0.27)**	**386**	**66 (0.17)**

Table 6. Model results for yearling *O. mykiss* outmigration analysis for individuals tagged in summer 2011-2013 using multi-state live recaptures models. For each year, the table includes ΔAICc, and the number of parameters from each model ≤ 2.0 ΔAICc.

Year	Model	ΔAIC_c	No. Parameters
2011	Site, length	0	9
	Survival, site-specific length	1.49	5
2012	Survival, length	0	5
	Site-specific length	0.33	4
	Survival, site-specific length	0.42	5
	Length	1.44	4
	Site, length	1.76	9
	Total density, site-specific length	1.79	5
2013	Yr. density, length	0	5
	Yr. density, site-specific length	0.27	5

Table 7. Mean individual outmigration probabilities for sites in 2011, using the site+yearling density model. Standard deviation in parentheses.

Site	Modeled outmigration probability
ULU	0.85 (0.17)
UMM	0.93 (0.45)
UMU	0.15 (0.07)
USM	0.51 (0.22)
USU	0.21 (0.11)
UWM	0.52 (0.09)

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Chapter 2: Effects of Barriers on Movement, Gene Flow, and Life-History Expression of *Oncorhynchus mykiss* in Lapwai Creek, Idaho

Abstract

Large-scale habitat modification and population isolation are processes that define the evolutionary history of salmon and their relatives. In the Anthropocene, salmonid populations in the Columbia River basin have experienced unnatural levels of habitat fragmentation due to impassable dams and barriers throughout much of their range, with many of these populations maintaining isolated populations above these barriers to upstream movement. Even though the area above barriers may only represent a small fraction of a system's total available fish habitat in some cases, previous research has shown that occasional gene flow from these above-barrier populations to the central population is critical in maintaining genetic diversity, and even contributing to long-term population persistence. The objectives of this study were to understand how putative barriers to movement have influenced life-history expression, movement patterns, and potential for gene flow between fragmented populations of *Oncorhynchus mykiss* across the entire Lapwai Creek watershed, Idaho. Additionally, I sought to determine how historic impacts of habitat fragmentation have affected gene flow potential between populations in the Lapwai Creek basin and nearby Snake River populations. I hypothesized that barriers in the Lapwai watershed would serve as barriers to upstream adult migration, but that some individual juvenile *O. mykiss* upstream of these barriers would either disperse downstream or exhibit recognizable smolting behavior due to the maintenance of migratory tendencies in the population as a whole. From 2012-2013, I took fin clips from over 200 individuals in both above- and below-barrier populations for genetic analysis. In addition, at above-barrier sites, I collected otoliths from 43 individuals for maternal life history analysis and PIT-tagged 83 juvenile *O. mykiss* to monitor potential downstream passage across barriers Results from tagging and otolith analysis above one stream diversion, Webb Creek, showed no movement of *O. mykiss* in either direction (spawning adults passing upstream or smolts migrating downstream) across the Webb Creek diversion. However, analyses of Sweetwater Creek populations indicated limited movement in both directions across the diversion in that stream. Genetics results support these findings, in addition to providing evidence for introgression between a population of O. *mykiss* isolated upstream of the Webb Creek diversion, and non-native, coastal-origin, hatchery rainbow trout. Results also indicated that below-barrier populations in Webb and Sweetwater Creeks are relatively genetically unique, in relation to the rest of the Clearwater River metapopulation. Results from this study highlight the importance of the Webb Creek and Sweetwater Creek populations as potentially important sources of genetic diversity to other Clearwater River *O. mykiss* populations through occasional gene flow. Although we did not directly examine exchange of genetic material between populations, our results indicate this occurrence likely happens at low to moderate levels. Throughout the Pacific Northwest where small dams fragment habitat, these isolated populations likely serve as sources of genetic and life-history diversity for salmonids and are important for the long-term viability of these threatened and populations.

Introduction

Habitat fragmentation, the process of dividing continuous habitat into smaller, isolated patches, is a common occurrence in both terrestrial and freshwater habitats. While advances in landscape ecology have aided our understanding and approaches for understanding habitat connectivity, our increased appreciation for fish dispersal and movement over many spatial scales has necessitated the integration of riverscape tools with population biology in river systems (Fausch et al. 2002). In stream corridors, natural habitat fragmentation occurs in the form of waterfalls (Pearse et al. 2009) and drought events (Chapman and Warburton 2006). In addition to natural sources of fragmentation, hydroelectric dams and irrigation diversions serve to further disrupt habitat connectivity in riverine systems. The effects of dams on fish populations have been well-documented and may ultimately lead to increased likelihood of extirpation (Morita and Yamomoto 2002).

Dams and other barriers fragment spawning and rearing habitat of Pacific salmon (*Oncorhynchus spp.*) and char (*Salvelinus spp.*) (henceforth referred to as salmonids) in much of their native range. These anthropogenic barriers block anadromous salmonids from reaching upstream spawning habitat (Nehlsen et al. 1991), a circumstance that is in part responsible for declines of salmonid populations in recent decades (McClure et al. 2003). Dauble et al. (2003) showed that 87% and 80% of historic spawning habitat of ocean-type Chinook salmon (*Oncorhynchus tshawytscha*) in the Columbia and Snake River basins, respectively, is currently inaccessible due to impassable dams. Neraas and Spruell (2001) argue that restricted movement between populations, as a result of hydropower and diversion dams, may inhibit life-history diversity, a consequence that may lead to local extirpation of salmonid populations.

Salmonids exhibit a diversity of life-histories, with migratory strategies within populations ranging from completely anadromous (Berejikian et al. 2013), to entirely resident in landlocked populations (Nielsen and Sage 2001). Additionally, some species of Pacific salmonids are facultative migrants (i.e. *O. mykiss*, *O. nerka*), meaning migratory tendencies are not fixed, but can be flexible in response to changing environmental conditions. In these facultative migrating species, we often see a mix of resident and anadromous individuals within a single population (i.e. Nordeng 1983-*S. alplinus*, Docker and Heath 2003-*O. mykiss*) a phenomenon known as partial migration (Lundberg 1988, Jonsson and Jonsson 1993). While some studies have shown reproductive isolation between sympatric resident and anadromous individuals within partially migratory populations (Zimmerman and Reeves 2000, Narum et al. 2004), many have demonstrated the ability for each parental phenotype to produce offspring that exhibit the alternate strategy (Hayes et al. 2012, Courter et al. 2013), or have found evidence of spawning between the two-life histories (McPhee et al. 2007).

While dams and natural barriers may preclude passage of adult salmonids to upstream spawning habitat, partially migratory species may persist above barriers as isolated populations (Northcote 2010). In these populations, there would appear to be selective pressure against downstream movement over dams or waterfalls, as any individual that crosses over one of these barriers is permanently lost from the above-barrier gene pool. However, due to retention of adaptive plasticity in these isolated salmonid populations, researchers have observed evidence of downstream movement and smolting behavior over barriers among *O. mykiss* above both waterfalls (Wilzbach et al. 2012, Boersox et al. in press) and dams (Holecek et al. 2012). While rates of downstream movement over natural barriers may be low in some instances (e.g. Pearse et al. 2009, Bowersox et al. *In press*), migration rates of isolated salmonids over barriers may be higher among more recently isolated populations. Thrower and Joyce (2004) observed that experimental breedings between *O. mykiss* isolated above an impassable migration barrier for 70 years and anadromous below-barrier individuals produced offspring that showed smolting rates of 32-56%, indicating the potential for significant interaction between above- and below-barrier populations.

Studies have shown significant genetic differentiation between salmonid populations isolated above barriers, and their downstream counterparts (Thrower et al. 2004, Van Doornik et al. 2013). Occasional dispersal from these divergent, isolated populations into the central below-barrier population may serve as an important source of genetic variability (Northcote and Hartman 1988), a trait which is vital to long-term population persistence (Allendorf et al. 1987). Conversely, introgression of primarily resident populations of *O. mykiss* into below-barrier populations may reduce fitness of anadromous individuals through outbreeding depression (Waples 1994). Understanding metapopulation dynamics and rates of dispersal and gene flow among these populations is important for informing conservation and management measures involving anadromous salmonids.

In this study I sought to quantify connectivity and gene flow for an *Oncorhynchus mykiss* population living in a typically fragmented watershed in the Pacific Northwest. The overall objective of this study was to describe dispersal and gene flow between populations of *O. mykiss* isolated from one another by both natural and anthropogenic barriers in the Lapwai Creek basin, Idaho, a tributary of the Clearwater River. I used a spatially-scaled and multidisciplinary approach, implementing PIT-tagging, otolith microchemistry, and genetic analysis to quantify connectivity between above-and below barrier populations in the system. Additionally, I examine the Lapwai Creek watershed's significance and potential importance in relation to the larger Clearwater River metapopulation. Finally, I discuss implications that interactions between these populations have for future conservation and management efforts.

Methods

Study area

The Lapwai Creek watershed, draining an area of approximately 694 km^2, is located in Nez Perce and Lewis counties in North-Central Idaho (Fig. 1). The Lapwai Creek watershed terminates as a fourth-order stream where it drains into the Clearwater River. The headwaters of the Lapwai watershed are located at Craig Mountain at an elevation of 1463 meters above sea level (MASL) and it is joined by second to third order tributaries of Upper Lapwai, Mission, Sweetwater, and Webb Creeks before meeting the Clearwater River at 236 MASL. The watershed supports a naturally-reproducing, ESA-threatened population of *O. mykiss*, which is identified as an “A-run”, or early-returning with relatively small adult body size, part of the Snake River Distinct Populations Segment (DPS) (NFMS 2006).

Dams on Sweetwater and Webb Creeks have been continuously diverting water for irrigation since 1917. Originally privately owned, the Bureau of Reclamation (BOR) has been operating and maintaining the diversions since 1947. Water for irrigation is collected at the headwaters at Craig Mountain and is then stored at Lake Waha and Soldiers Meadow Reservoir before a series of diversions on Sweetwater and Webb Creeks ultimately transport it to Mann Lake Reservoir for storage (Fig. 1). Water diversion occurs from February through October, annually. Before 2006 and 2009 for Sweetwater and Webb Creeks, respectively, no minimum flow requirements were mandated. Thus, large sections (up to 6.4 km) of stream below the diversions in Sweetwater and Webb Creeks were historically left dewatered during the summer months (Chandler 2004).

Located at stream km 14.3, the Sweetwater Creek diversion is approximately 3.7 m in height and NMFS (2006) classified it as a “complete or nearly complete barrier to upstream migration of adult steelhead and a downstream barrier during much of the irrigation season”. Nez Perce Tribe (NPT) Department of Fishery Resources reports have concluded that the Sweetwater diversion blocks upstream passage to 17.7 km of habitat currently inhabited by *O. mykiss* (Chandler and Parot 2003, Chandler and Richardson 2006). The Webb Creek diversion, located at stream km 15.4, is approximately 6.1 m in height. Additionally, a natural 7.6 m high waterfall is located 0.6 km downstream of the Webb diversion, creating an impassable barrier for upstream migration (NMFS 2006). Researchers have identified the presence of juvenile (of unknown life-history) and mature resident *O. mykiss* 1 km upstream of the Webb Creek diversion (Chandler and Richardson 2005). As this site represents the furthest upstream extent of sampling on Webb Creek, the *O. mykiss* distribution beyond 1 km upstream of the Webb Creek diversion is unknown.

Sampling sites

Six sites downstream of the diversions approximately 100 m in length were selected for inclusion in this study (Fig. 1). These six sites represent a subset of sites from an ongoing research and monitoring effort in the basin (see Hartson and Kennedy 2014, Myrvold and Kennedy 2014). Below-barrier sites were chosen for inclusion in this study based on having ample number of individuals needed for the genetic analysis. These sites were visited once in June 2013. Due to limited access, sites upstream of the diversions were chosen based on landowner permission. Thus, this study included one site each above the Webb and

Sweetwater diversions. Above-barrier sampling occurred opportunistically, in October 2013 at Webb Creek, and November and December 2012 and June and August 2013 at Sweetwater Creek.

O. mykiss sampling

I used a Smith-Root LR-24 electrofisher (Smith-Root Inc., Vancouver, WA, USA) to capture juvenile *O. mykiss* at all study sites. Captured individuals were anesthetized using a solution of tricaine methanesulfonate (MS-222). Once fish were anesthetized, I measured fork length (FL) to the nearest mm and mass to the nearest 0.1 g for each individual. For 237 individuals in both above- and below-barrier populations, I collected caudal fin clips for genetic analysis (Table 1). I inserted a 12 mm 134.2 kHz ISO PIT tag (Biomark Inc., Boise, ID, USA) into the ventral cavity of 83 individuals ≥65 mm FL at above-barrier sites (Table 2). Since there were no PIT antenna arrays upstream of the diversions, I did not tag individuals below diversions, as there was no way of detecting juvenile *O. mykiss* potentially moving upstream past the barriers. Additionally, I sampled 43 individuals at above-diversion sites in order to collect otoliths for maternal life-history analysis (Table 3). All fish sampling and handling procedures were permitted as part of the Section 7 consultation for the Lewiston Orchards Biological Opinion (NMFS 2006), Idaho Department of Fish and Game (permit F-07-05-10), and the University of Idaho Institutional Animal Care and Use Committee.

Movement monitoring

In order to identify the potential presence of downstream movement of juveniles over the diversions, four PIT-antenna arrays in the Lapwai watershed (Fig. 1), as well as the antennas associated with hydropower projects throughout the Snake and Columbia River basins were used to distinguish migratory individuals. I categorized any individual detected at the PIT array at the mouth of Lapwai Creek or further downstream as an “anadromous migrant”. Individuals detected at the Mission, Webb, or Sweetwater antennas, but not recorded at the Lapwai antenna or further downstream were labeled as “local migrants”. Since the PIT arrays on Sweetwater and Webb were not directly downstream of the diversions, it is possible that individuals from above-barrier populations moved downstream over the diversions without being recorded.

Maternal life-history

Otoliths collected from juvenile *O. mykiss* at above-barrier sites were analyzed for strontium isotope ratios (^{87}Sr/^{86}Sr) at the otolith’s primordia (core) and freshwater growth regions (edge), in order to determine individual maternal life history. The ratio of ^{87}Sr/^{86}Sr in marine environments (~0.709) is constant (Kennedy et al. 1997, 2000) and elevated relative to that of freshwater habitats (Lapwai basin ~0.706). Since the ^{87}Sr/^{86}Sr ratio of an otolith’s edge is similar to the environment it inhabits (Kennedy et al. 2000, 2002) and chemical composition of the core is representative of the origin of an individual’s mother (Bacon et al. 2004, Miller and Kent 2009), higher ^{87}Sr/^{86}Sr ratios in the core versus the edge of the otolith would indicate that an individual has an anadromous mother. Observation of juveniles in above-barrier populations with anadromous maternal parentage would refute assumptions that barriers on Webb and Sweetwater Creeks are complete barriers to upstream movement of adults.

I sampled 43 juvenile *O. mykiss* at above-barrier sites in 2012 and 2013 (Table 3) to collect otoliths for analysis. Otoliths were prepared for analysis using the methods outlined by Hegg et al. (2013) and analyzed at the Washington State University Geoanalytical Laboratory in Pullman, WA. I measured 20 points at both the core and the edge of each otolith. To identify potential anadromous parentage, I ran a one-sided, 2-sample t-tests to test for differences between 87Sr/^{86}Sr ratios in the core and edge of each otolith, with an alternative hypothesis of core ^{87}Sr/^{86}Sr < edge ^{87}Sr/^{86}Sr. For each individual with a significant difference ($p<.05$) between core and edge region ^{87}Sr/^{86}Sr, I ran a two-sided, 1-sample t-test, comparing mean ^{87}Sr/^{86}Sr ratio across the core transect, to the expected marine ^{87}Sr/^{86}Sr value (0.70918), using the null hypothesis of equal means. Non-significant differences between core and marine standard ^{87}Sr/^{86}Sr ratios would confirm the presence of an anadromous mother. Since there is no way to determine paternal origin through otolith chemical analysis, some individuals with confirmed resident maternal origin may have anadromous fathers, as the two life-histories may occasionally spawn with one another (McMillan et al. 2007, Christie et al. 2011).

Genetic analysis

Genomic DNA extraction and single nucleotide polymorphism (SNP) amplification for all genetic samples (n=237) were performed at Idaho Department of Fish and Game's Eagle Fish Genetics Laboratory in Eagle, ID, USA according to methods described in Bowersox et al. (*In press*). All samples were screened at 190 SNPs (Bowersox et al. (*In press*), unless otherwise noted. Three of those SNPs were used to identify potential *O. mykiss* x cutthroat trout (*Oncohrynchus clarkii)* hybrids. None of the individuals from this study were identified as hybrids, so these SNPs were excluded from further analysis leaving 187 for genetic analyses. Genomic DNA extraction and amplification and SNP genotyping using multiplex 5'-nuclease reactions are described in detail in Seeb et al. (2009). Due to the close proximity, and thus assumed genetic similarity (Allendorf and Waples 1996) between sites UMM and UMU, as well as USU and USM, I combined individuals from the two sites, in both instances for the genetic analysis. For a more detailed description of the subsequent genetic analysis, see Bowersox et al. (*In press*).

Genetic diversity, Hardy-Weinberg expectation, and intra-basin population differentiation

For samples from the Lapwai watershed, I evaluated genetic diversity within populations as well as differentiation among populations to describe the degree of isolation between above-and below barrier populations. Across all SNPs, I used GenAlEx 6.5 (Peakall and Smouse 2012) to calculate expected heterozygosity (H_E) and percent polymorphic SNPs. Another measure of genetic diversity, allelic richness (AR), was calculated using FSTAT v2.9.3.2 (Goudet 1995). I tested for differences among mean H_E and AR among all study populations using a Kruskal-Wallis test (Kruskal and Wallis 1952) and followed up with Dunn's tests (Dunn 1964) to compare between pairs of populations. I also calculated deviation from Hardy-Weinberg expectation (HWE) for each population, using GENEPOP v4.1.2 (Rousset 2008).

Potential coastal O. mykiss introgression

Historic stocking records, dating back to 1967, show that approximately 1,000 juvenile *O. mykiss* were stocked annually above the Webb Creek diversion from 1979-1981 (fishandgame.idaho.gov/public/fish/stocking/). A sub-species of *O. mykiss*, *O. m. irideus*, is generally used for stocking of recreational fisheries, and is easily genetically distinguishable from the native sub-species, *O. m. gairdneri* (e.g. Malta et al. 2014, Bowersox et al. *In press*). To identify potential genetic introgression between *O. m. irideus*, and our Lapwai basin *O. m. gairdneri* populations, I used STRUCTURE 2.3.4 (Pritchard et al. 2000) to estimate relative contribution of each group to the ancestry of sampled individuals in the watershed. In STRUCTURE, I set K=2 populations (*O. m. irideus* and native *O. m. gairdneri*). For reference *O. m. irideus* populations, I used four populations of hatchery-origin coastal *O. mykiss* (Eagle Lake (n=47), Fish Lake (47), Troutlodge (47), and Kamloops (23)) that had previously been screened using the same SNPs used in this study. These were then compared to the combined above-and below-barrier study sites in the Lapwai basin. I used a burn-in length of 100,000 with 250,000 repeats of the Monte Carlo Markov Chain to estimate group membership for each collection. Populations with greater than 10% assignment to the coastal group, were considered to be hybridized (Vaha and Primer 2006).

Population structure

Pairwise F_{ST} values were calculated in GenAlEx to assess the degree of population differentiation between Lapwai basin populations. Specifically, I was interested in determining the degree of interaction between above-barrier populations, and their below-barrier counterparts in Webb and Sweetwater Creeks. Additionally, I compared genetic structure between Lapwai basin collections and nearby *O. mykiss* populations in the Snake and Clearwater River basins. I compared Lapwai populations to 4 Clearwater River populations that had been previously genotyped over the same 187 SNPs (Table 4, Fig. 2) (Ackerman et al. 2012). I then generated a multivariate principal coordinate analysis (PCoA) based on pairwise F_{ST} values to visualize genetic differentiation among Lapwai and Clearwater populations.

Results

Movement monitoring

A total of 8 of 63 tagged individuals tagged above the Sweetwater diversion were observed having passed downstream over the Sweetwater diversion dam, as recorded by PIT antenna arrays in the basin (Table 2). 6 out of 8 individuals were recorded at the Lapwai antenna or further downstream, while the other 2 recorded individuals were only observed at the array on Sweetwater Creek. None of the 31 individuals tagged upstream of the Webb diversion were recorded at any of downstream PIT arrays. Tagging results indicate the Sweetwater diversion is not a complete barrier to downstream passage of juveniles and movement of juveniles over the Webb diversion is likely limited or nonexistent.

Maternal life-history

6 out of 35 otoliths collected from populations upstream of the Sweetwater diversion had significantly elevated ^{87}Sr/^{86}Sr ratios in the core relative to that of the freshwater growth region ($p<.0001$). Five of these individuals had core regions with ^{87}Sr/^{86}Sr ratios that were not significantly different from the global marine standard ($p=0.64$-0.94), suggesting anadromous maternal parentage (Table 3), while one individual had core ^{87}Sr/^{86}Sr that significantly deviated from 0.70918 ($p=.0025$). This individual had core ^{87}Sr/^{86}Sr of 0.7217, a value similar to the Clearwater River ^{87}Sr/^{86}Sr signature of 0.7134. None of the 10 individuals collected above the Webb diversion showed evidence of anadromous maternal parentage (Table 3), with ^{87}Sr/^{86}Sr mean values (±SE) of 0.70591 ± 0.00004 and 0.705990 ±0.00005 in the core and edge regions, respectively.

Genetic diversity and Hardy-Weinberg expectation

While allelic richness was lower at above barrier-sites EFS (1.82) and WAD (1.84) relative to the four below-barrier collections (1.89-1.96) (Table 1), Kruskal-Wallis tests found differences between populations to be non-significant (p=0.76). Significance testing of differences in H_E between populations yielded similar results, revealing no differences between populations (p=0.79). EFS had the lowest H_E (27.8%) and while WAD had a lower H_E (28.5%) than all other below-barrier sites, with the exception of Sweetwater (28.1%). In terms of polymorphic loci, above-barrier collections exhibited lower genetic diversity than below-barrier sites. WAD (84.9% polymorphic loci) and EFS (88.2%) had 10.8% and 7.5% fewer polymorphic loci than below-barrier sites with the fewest poloymorhpic loci (Sweetwater and Lapwai), respectively. The highest proportion of SNPs out of HWE occurred in the Sweetwater (11.8%) and EFS (11.3%) collections. Of those deviations, 12 in the Sweetwater, and 15 in the FES collections were due to an excess of heterozygotes, suggesting a relatively large number of full-siblings were present in each respective sample. Additionally, 10 deviations in the Sweetwater population sample were due to a deficit in heterozygotes, indicating potential sub-population structure in the Sweetwater collection.

Potential coastal O. mykiss introgression

Five of the six study collections showed minimal or no introgression with coastal *O. m. irideus*, suggesting these populations are composed of wild native individuals (Fig 3). Mean membership to the native *O. mykiss* group, averaged across individuals, ranged from 96.4-99.5% for these collections. One of the study collections, WAD, displayed likely introgression between wild and non-native *O. mykiss*, with average membership of 44.0% and 56.0% to the wild and non-native groups, respectively. Non-native collections had 98.1% or greater membership to the coastal group, with the exception of the Fish Lake collection (93.8%).

Population structure

The WAD collection showed a high degree of genetic differentiation from the below-barrier population in Webb Creek (F_{ST}=0.89, Table 4). This supports my results from the movement and maternal life-history analysis, suggesting no movement between above- and below-barrier populations in Webb Creek. Conversely, F_{ST} values between EFS and Sweetwater collections (0.29) indicate some limited movement between populations, a result that is also supported by the movement and maternal life-history analysis. For reference, the Sweetwater and EFS collections showed a level of genetic differentiation that is similar to that between Sweetwater and Webb collections (0.31). The PCoA analysis shows that the above-barrier collections, EFS and WAD, are highly differentiated from the reference Snake/Clearwater basin populations (Fig. 3b). This is not surprising given the degree of isolation observed between these above-barrier populations and the rest of the Lapwai basin. Interestingly, the PCoA analysis shown in Fig. 3a indicates relatively high levels of genetic differentiation between below-barrier Sweetwater and Webb collections relative to Snake/Clearwater populations, even though below-barrier Mission and Lapwai populations show little differentiation to the reference populations.

Discussion

The results of this study characterize the relationships between above- and below-barrier *O. mykiss* populations in the Lapwai Creek drainage, as well as the potential significance of the basin as a contributor of genetic diversity to the larger Clearwater metapopulation. Movement and otolith microchemistry analysis show that while the population of *O. mykiss* above the Webb Creek diversion exists in complete or near-complete isolation from the stream's below-barrier population, restricted movement of both adults and juveniles occurs between above- and below-barrier populations in Sweetwater Creek. Genetics results confirm the likelihood of the Webb diversion as a complete barrier and the Sweetwater diversion as a partial barrier to migration. Additionally, I identified collections from below-barrier populations in Sweetwater and Webb Creeks with increased differentiation relative to nearby Clearwater and Snake River *O. mykiss* populations.

There has been a tremendous amount of interest and research on the life-history diversity and movement patterns of Pacific salmonids at the watershed scale (reviewed by Kendall et al. 2015 for *O. mykiss*). As such, most studies of genetic structure at large scales focus on genetic differentiation rather than connectivity (Allendorf and Waples 1996, Waples 1998). However, much less is known about how populations interact with one another at large spatial scales and how these interactions potentially provide genetic and population resilience. There is an abundance of evidence to suggest that many salmon populations function as a metapopulation with local extinctions or population declines being countered by dispersal among sub-populations. However, very few studies have been able to address the metapopulation structure of salmon populations, perhaps because of their generally depressed population sizes and impacted connectivity (Hanski and Simberloff 1996). However, understanding metapopulation dynamics of Pacific salmonids has been identified as a critical component in aiding future conservation work for these threatened and endangered species (Rieman and Dunham 2000). The results of this study give insight in understanding these processes, as well as their potential implications for management and conservation efforts.

Despite the categorization of the Sweetwater diversion as a complete or near-complete barrier to in-stream movement (NMFS 2006), my results indicate that dispersal and gene flow between above-and below barrier populations in Sweetwater Creek occurs at low to moderate rates. Genetic divergence between above- and below-barrier populations in Sweetwater Creek (F_{ST}=0.029) was similar to that between our below-barrier Sweetwater population and *O. mykiss* in the South Fork of the Clearwater River (F_{ST}=0.031) (Vu et al. 2015), populations separated by more than 200 river kilometers (RKM). This is inconsistent with research showing a strong positive correlation between genetic and geographical distance in Pacific salmonids (Allendorf and Waples 1996), suggesting the diversion is an additional factor in creating genetic isolation between the two populations. However, genetic differentiation between barrier-separated Sweetwater sites was considerably less than what was observed by Clemento et al. (2008) between populations of *O. mykiss* separated by a dam for approximately 60 years (F_{ST}=0.097). This indicates that the Sweetwater diversion likely serves as a partial, rather than complete, barrier to migration.

Surprisingly however, maternal origin analysis revealed the presence of anadromous *O. mykiss* spawning above the Sweetwater diversion. Anadromous mothers produced 14.3% of juveniles sampled upstream of the diversion, while previous research in the basin using similar methods of otolith analysis identified 91.7% of individuals in below-barrier populations throughout the basin as being progeny of anadromous females (Kennedy, unpublished). This disparity in proportion of anadromously produced *O. mykiss* in above- and below-barrier populations indicates the Sweetwater diversion may only block upstream migration of returning adults during certain years or months. Powers and Orsborn (1985) calculated the maximum jumping height of adult steelhead to be 3.3 m. Although the Sweetwater diversion has a vertical drop of 3.7 m during summer base flows, this height is likely less during the spawning season, as the water level rises from spring rains and snowmelt. Thus, the diversion likely creates a barrier in Sweetwater Creek that pushes the upper extent of steelhead leaping capabilities, resulting in only some individuals achieving successful passage during optimal windows of flow (Reiser et al. 2006).

In systems in which introduced species are present, above-to-below barriers to gene flow may result in deleterious effects for the central population. Hybridization between native and non-native taxa is an increasingly important threat to persistence of rare species (Rhymer and Simberloff 1996, Allendorf et al. 2001). In particular, genetic introgression between native and non-native *O. mykiss* is prevalent throughout the Columbia and Snake River basins and is likely partly responsible for the decline of these stocks (Williams et al. 1996, Kozfkay et al. 2009). *O. mykiss* are the most extensively introduced salmonid in North America (Lever 1996), so it unsurprising that I detected genetic admixture of native and non-native *O. mykiss* above the Webb Creek diversion, a result of the stocking of approximately 3,200 coastal *O. m. irideus* from 1979-1981. While I did not observe downstream movement over the Webb diversion, individuals likely occasionally pass over the dam, however, those individuals may remain reproductively isolated from their below-barrier counterparts (Pearse et al. 2009).

Barrier removal is a frequently recommended action to aid in conservation efforts of ESA-listed salmonid populations in the Pacific Northwest (Roni et al. 2002, Bernhardt et al. 2005). While such practices may restore habitat connectivity for these populations, an unintended consequence of barrier removal may be outbreeding depression between the previously isolated populations. Individuals isolated above-barriers may not be locally adapted to downstream environments, thus, successful interbreeding with downstream populations may result in a decrease in fitness in these instances (Krueger and May 1991). In a population of naturalized adfluvial steelhead in Lake Superior, Miller et al. (2009) found that crosses between naturalized and hatchery-produced steelhead produced young that were nearly three times less likely to survive to age 1 than individuals from naturalized x naturalized crosses. Although removal of the Webb diversion would not establish connectivity between above-and below dam populations due to an impassable waterfall shortly downstream of the diversion, our results offer managers a cautionary tale in regards to potential risks of barrier removal when non-native *O. mykiss* may be present.

Conversely to the Webb population, observed occasional gene flow between isolated Sweetwater populations may represent an important source of life-history diversity for *O. mykiss* in the watershed. Maintenance of life-history diversity is important for long-term population persistence, as populations with more diverse life-history portfolios may be better able to withstand extreme environmental events than populations that only express a single life-history (Greene et al. 2010). Above-barrier populations, such as the one in Sweetwater Creek, are generally comprised of primarily resident individuals, due to intense selection against downstream movement (Northcote and Hartman 1988). However, many of these may still undertake downstream movements over barriers (Wilzbach et al. 2012), and thus may end up living sympatrically with below-barrier anadromous life-histories. Van Doornik et al. (2013) showed evidence of breeding between the two life-histories, thus indicating the potential for gene flow between above- and below barrier populations. Therefore, above-barrier populations of *O. mykiss* may act as sources of life-history diversity, through downstream dispersal of resident *O. mykiss* into below-barrier anadromous populations.

Above-barrier populations, such as the one observed in Sweetwater Creek, may also contribute to long-term persistence of below-barrier populations through recolonization after extirpation or low abundances. Weigel et al. (2014) showed that resident *O. mykiss* had a significant role in recolonizing a tributary of the Methow River in the two subsequent years after barrier removal, with 81% of parr in the study coming from fluvial parentage in one year. Another study in the same basin showed that not only do resident *O. mykiss* contribute a significant proportion of offspring to the population post-barrier removal, but that their progeny can adopt an anadromous life-history, as evidenced by observed smolting behavior (Weigel et al. 2013). This ability of resident individuals to produce anadromous offspring is a commonly overserved phenomenon (Zimmerman and Reeves 2000, Pascual et al. 2001). Thus, resident populations isolated above barriers, such as the one in Sweetwater Creek, have the ability to reestablish below-barrier anadromous populations after extirpation.

Similarly to how above-barrier populations in Sweetwater Creek may act as sources of life-history diversity for the Lapwai Creek basin, my results show that below-barrier populations in Webb and Sweetwater Creeks may act as sources of genetic diversity for the Clearwater and Snake River metapopulation. Although anadromous salmonids generally return to their natal streams as adults to breed, a small percentage may venture elsewhere to spawn, a phenomenon known as straying (reviewed by Quinn 1993). In anadromous salmonids, straying may serve to maintain genetic diversity and improve resiliency in peripheral populations (Consuegera et al. 2005, Walter et al. 2009). As populations in Sweetwater and Webb Creeks are relatively genetically distinct to nearby Clearwater River *O. mykiss* populations, they may be particularly important as sources of novel genetic material to these populations. Although we did not attempt to observe or quantify straying in the course of this study, Keefer et al. (2005) observed straying rates of up to 6.7% for O. mykiss in nearby Snake River populations. Thus, it is probable that individuals from the Lapwai basin contribute to genetic diversity of populations in the Clearwater River through straying.

Figures

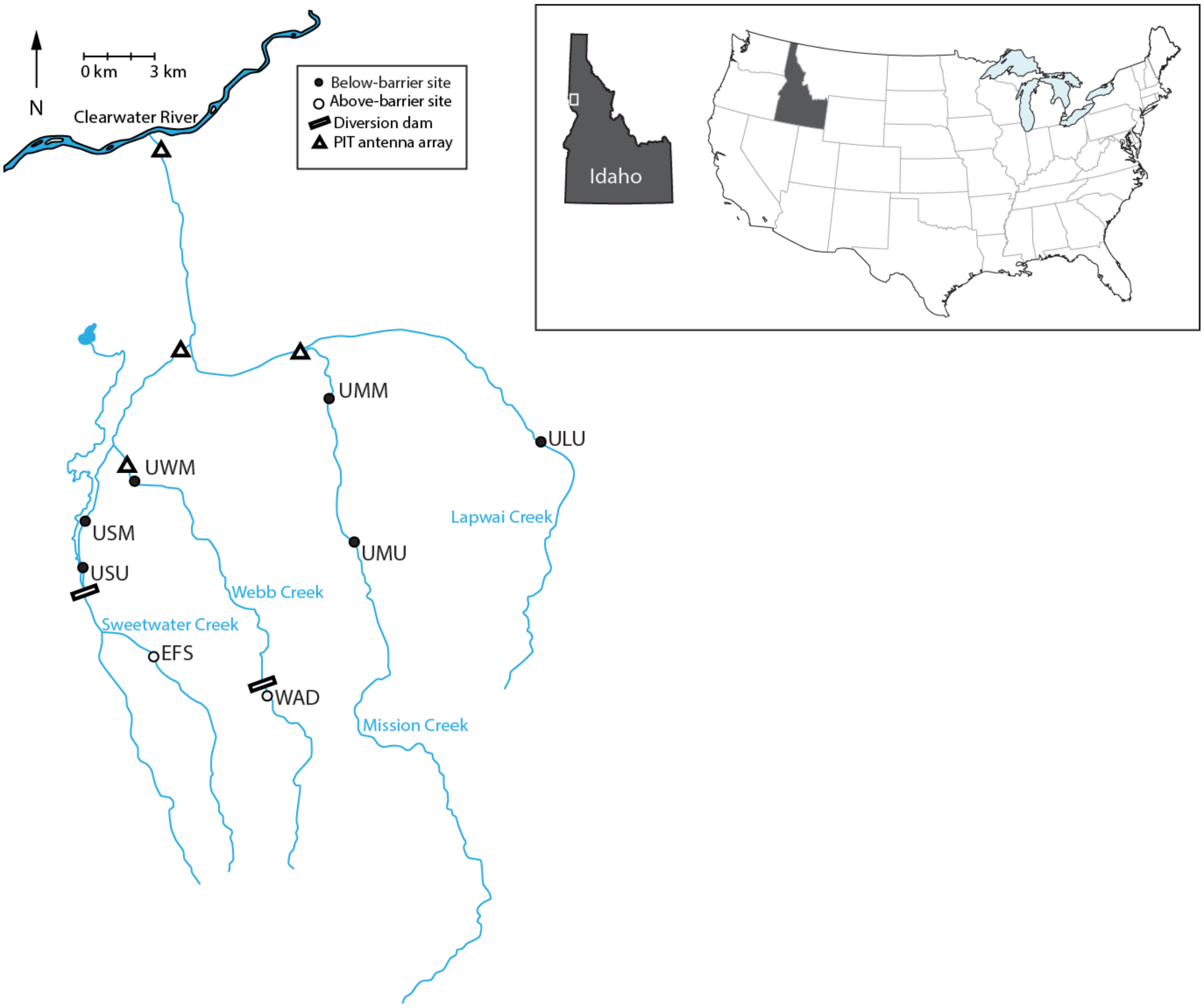

Fig. 1 Map of Lapwai Creek basin and sampling sites in Idaho, USA.

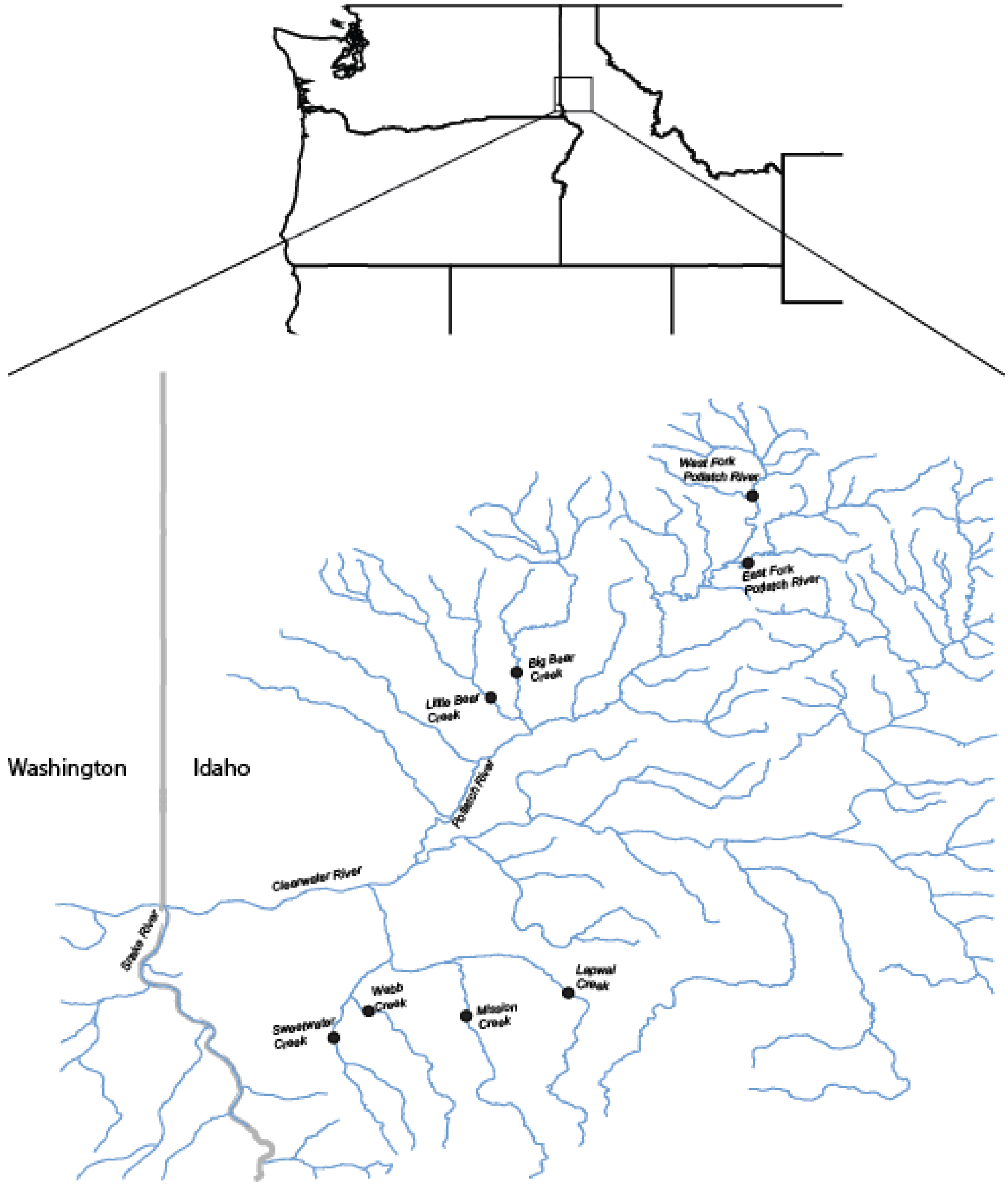

Fig. 2 Map of below-barrier Lapwai Creek basin populations and reference Clearwater populations used in the principal coordinate analysis (PCoA).

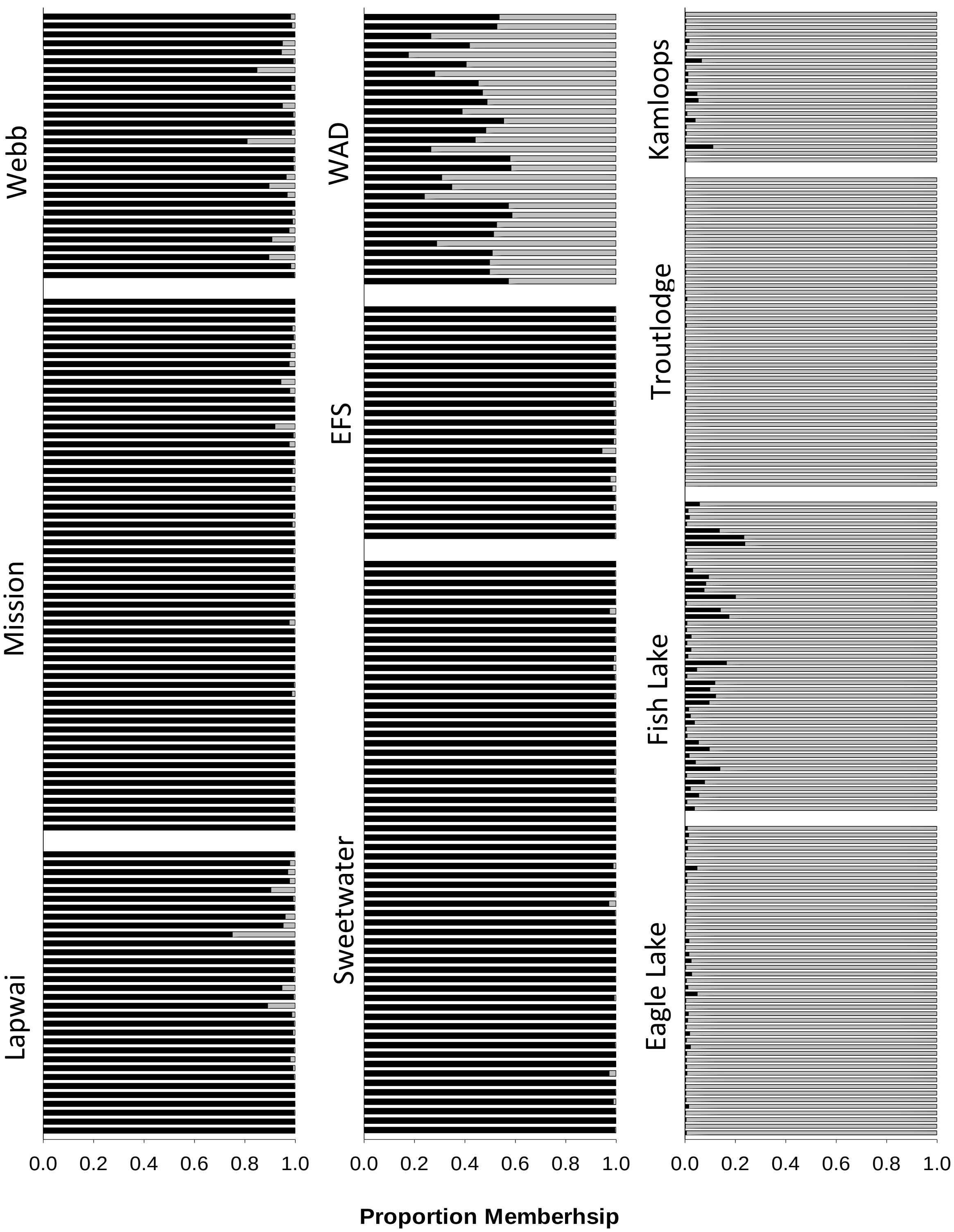

Fig. 3 Proportion membership of each individual to $k = 2$ inferred groups representing native *O. m. gairdneri* (black) and non-native coastal *O. m. irideus* (gray), analyzed in STRUCTURE v2.3.4.

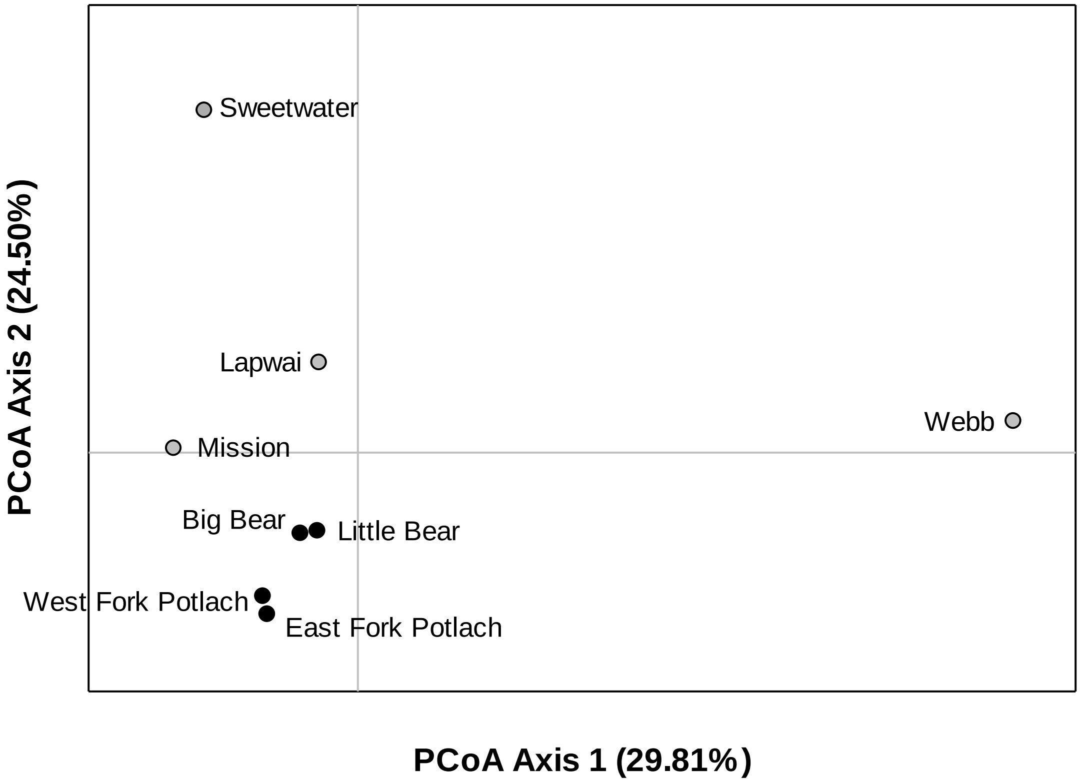

Fig 4. Principal coordinate analysis (PCoA) based on pairwise F_{ST} values between below-barrier Lapwai Creek basin collections (○) and Clearwater basin collections (●). Percent variation in data explained by each axis in is parentheses.

Tables

Table 1. Collection year, sample size (n), location relative to diversion dams, deviations from Hardy-Weinberg expectation (HWE) expressed in number of SNPs with significant excess of deficit of heterozygotes and percentage of total SNPS out of HWE, allelic richness (AR), expected heterozygosity, and percent polymorphic SNPs for above- and below-barrier Lapwai basin collections.

Collection	Collection year	n	Above/below barrier?	Het. exc.	Het. def.	% SNPs	AR	H_E	Polymorphic SNPs
Lapwai	13	32	Below	4	5	4.8%	1.96	29.7%	95.7%
Mission	13	60	Below	4	6	5.4%	1.92	30.0%	96.7%
Webb	13	30	Below	6	3	4.8%	1.89	28.9%	95.7%
Sweet	13	61	Below	12	10	11.8%	1.89	28.1%	96.2%
EFS	12	25	Above	15	6	11.3%	1.82	27.8%	88.2%
WAD	12	29	Above	6	1	3.8%	1.84	28.5%	84.9%

Table 2. Results of movement analysis, indicating tagging year, sample size (n), number of individuals recorded at PIT arrays at the mouth of Lapwai Creek or further downstream (anadromous migrants), and number of individuals only detected at PIT arrays upstream of the mouth of Lapwai Creek (local migrants).

Site	Tagging year	n	Anadromous migrants	Local migrants
EFS	12, 13	63	6	2
WAD	13	31	0	0

Table 3. Results of maternal life-history analysis, indicating collection year, sample size (n), and number of individuals determined to have anadromous mothers based on analysis of otolith ^{87}Sr/^{86}Sr ratios.

Site	Collection year	n	Anadromous mothers
EFS	12, 13	35	5
WAD	13	10	0

Table 4. Pairwise F_{ST} values of Lapwai basin collections.

Collection	Lapwai	Mission	Webb	Sweetwater	EFS	WAD
Lapwai	0.000	-	-	-	-	-
Mission	0.018	0.000	-	-	-	-
Webb	0.024	0.030	0.000	-	-	-
Sweetwater	0.017	0.024	0.031	0.000	-	-
EFS	0.024	0.031	0.035	0.029	0.000	-
WAD	0.082	0.094	0.089	0.085	0.093	0.000

Table 5. Reference Snake and Clearwater basin populations used in principal coordinate analysis (PCoA).

Site	n	Collection year
West Fork Potlatch River	84	09, 10
East Fork Potlatch River	158	08, 09, 10
Big Bear Creek	151	07, 08, 09, 10
Little Bear Creek	99	07, 08, 09, 10

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