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RESEARCH ARTICLE

The impact of small irrigation diversion dams on the recent migration rates of steelhead and redband trout (*Oncorhynchus mykiss*)

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Abstract Barriers to migration are numerous in stream environments and can occur from anthropogenic activities (such as dams and culverts) or natural processes (such as log jams or dams constructed by beaver (*Castor canadensis*)). Identification of barriers can be difficult when obstructions are temporary or incomplete providing passage periodically. We examine the effect of several small irrigation diversion dams on the recent migration rates of steelhead (*Oncorhynchus mykiss*) in three tributaries to the Methow River, Washington. The three basins had different recent migration patterns: Beaver Creek did not have any recent migration between sites, Libby Creek had two-way migration between sites and Gold Creek had downstream migration between sites. Sites with migration were significantly different from sites without migration in distance, number of obstructions, obstruction height to depth ratio and maximum stream gradient. When comparing the sites without migration in Beaver Creek to the sites with migration in Libby and Gold creeks, the number of obstructions was the only significant variable. Multinomial logistic regression identified obstruction height to depth ratio and maximum stream gradient as the best fitting model to predict the level of migration among sites. Small irrigation diversion dams were limiting population interactions in Beaver Creek and collectively blocking steelhead migration into the stream. Variables related to stream resistance (gradient, obstruction number and obstruction height to depth ratio) were better predictors of recent migration rates than distance, and can provide important insight into migration and population demographic processes in lotic species.

Keywords Migration · Isolation by resistance · Isolation by distance · Landscape genetics · Steelhead

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Introduction

Populations across a landscape interact to exchange individuals providing demographic support and genetic variation. The meta-population theory is often used to describe this inter-dependence between populations where local populations support each other in a source–sink dynamic important to the long term persistence of species in stochastic environments (Hanski and Gilpin 1996; McCullough 1996). The emergence of this theory in conservation biology resulted in resource management strategies that focus on maintaining and improving connectivity between populations (Crooks and Sanjayan 2006; Kettunen et al. 2007). Barriers to migration and gene flow alter these ecological and evolutionary processes which may reduce fitness (Reed and Frankham 2003) and/or increase the risk of extinction through loss of adaptive potential (Swindell and Bouzat 2005). Yet, barriers can also have the beneficial effect of preventing the invasion of non-native species or strains that may inter-breed with native species or stocks (Novinger and Rahel 2003; Fausch et al. 2009).

Hybridization with introduced species threatens many species of invertebrates, fish, birds and mammals (Rhymer and Simberloff 1996). Hybridization can spread widely and become an uncontrollable problem for scientists trying to protect native species (Rhymer and Simberloff 1996; Allendorf et al. 2001). In aquatic environments, hatchery fish are widely stocked for mitigation and conservation purposes to support recreational and commercial fisheries (e.g. Thurow et al. 1997). These introduced fish oftentimes reproduce in the natural environment which, in some cases, can directly reduce fitness of the native stock (e.g. Epifanio et al. 1999; Miller et al. 2004). Although barriers can preserve the native genotypes from these threats, this situation is not ideal because these populations are still subject to the effects of fragmentation and isolation.

Loss of habitat threatens 50 % of species in the United States (Richter et al. 1997). Small barriers, such as diversion dams and culverts, adversely impact aquatic fauna and are more numerous and widely distributed across the landscape than the larger mainstem dams (Moyle and Williams 1990; Sheer and Steel 2006). As numerous species of fish have declined in abundance over the last several decades, extensive efforts have been made to remove or modify these barriers to allow passage of target fish species (Bernhardt et al. 2005). Steelhead, the anadromous life history of *Oncorhynchus mykiss*, are threatened and declining in many areas of the native range in western North America due to numerous impacts during freshwater and ocean rearing and associated migratory habitats (McClure et al. 2003). Studies indicate a genetic component is important to the successful completion of the anadromous life cycle in this species (Thrower et al. 2004; Hendry and Stearns 2004); therefore, maintaining connectivity for the migratory life history to access breeding habitat is crucial to the conservation and recovery of this life history.

Genotypic data can be used to identify migrants and estimate migration rates between populations (Rannala and Mountain 1997; Pritchard et al. 2000). Recent migration rates within the last one to two generations can be estimated using disequilibrium methods described in Wilson and Rannala (2003) allowing the assessment of the current conditions on a landscape. Steelhead are a spring spawning species migrating during peak flows can alter temporary barriers such as beaver (*Castor canadensis*)dams, log jams and small irrigation diversions creating passage opportunities over or around these obstacles. Therefore, determining the level of connectivity or pass-ability of an obstacle may be difficult. Direct observations of tagged individuals may be impractical if passage is periodic (such as every few years) and/or very small. In addition, movement (or dispersal) of individuals based on tag information does not provide an estimate of successful migration (or genotypic exchange) between sites.

In this study, we use population genetic parameters to compare *O. mykiss* populations in a tributary stream basin with numerous irrigation diversion dams to two nearby tributary basins to the Methow River, Washington. The objectives of our study are to: (1) estimate the level of migration; (2) identify the relative proportion of hatchery admixture; and (3) identify the relative effect of stream obstructions and distance on migration rates and hatchery admixture in *O. mykiss* from Beaver, Libby and Gold creeks, tributaries to the Methow River, WA.

Study area

The Methow Basin is located on the east side of the Cascade Mountain Range in north-central Washington. The Methow River is a tributary of the Columbia River located about 843 km upstream from the estuary. Beaver Creek is a third order tributary that flows west into the Methow River 91.1 km upstream from the mouth (Fig. 1). Libby and Gold creeks are third and fourth order tributaries, respectively, that flow east into the Methow River. Libby Creek is 42.5 km and Gold Creek is 35.1 km from the mouth of the Methow River. Basin areas for Beaver, Libby and Gold basins are 290.1, 104.4 and 230.5 km^2, respectively. The upper portions of these basins are managed forest land administered by state or federal agencies. The lower portion of these basins are irrigated, privately-owned residences and farms.

Access for fish into Beaver Creek was disconnected due to water withdrawal and diversion dams for more than 100 years (Martens and Connolly 2010). Seven small irrigation diversion dams (1.0–2.0 m high) were located along Beaver Creek. Six of these structures were “push up” dams made of various materials such as wood, rock and plastic sheets or tarps. The most downstream irrigation diversion was a 2.0 m high concrete diversion dam. These irrigation diversion structures were modified to allow fish passage from 2000 to 2004. Although Libby and Gold creek basins support irrigation withdrawals, residences and road systems, these streams maintained connectivity for spring migrating steelhead. Steelhead/rainbow trout were the most abundant species of salmonid throughout the Beaver, Libby and Gold creek basins.

Hatchery releases

The Grand Coulee Fish Maintenance Project mitigated for the loss of fish habitat and production from the construction of Grand Coulee Dam during the 1930s. Hatchery production was intended to replace lost natural production of anadromous salmon and steelhead from tributaries upstream blocked by the dam. The State of Washington also manages a hatchery program to mitigate for other hydropower facilities on the Columbia River.

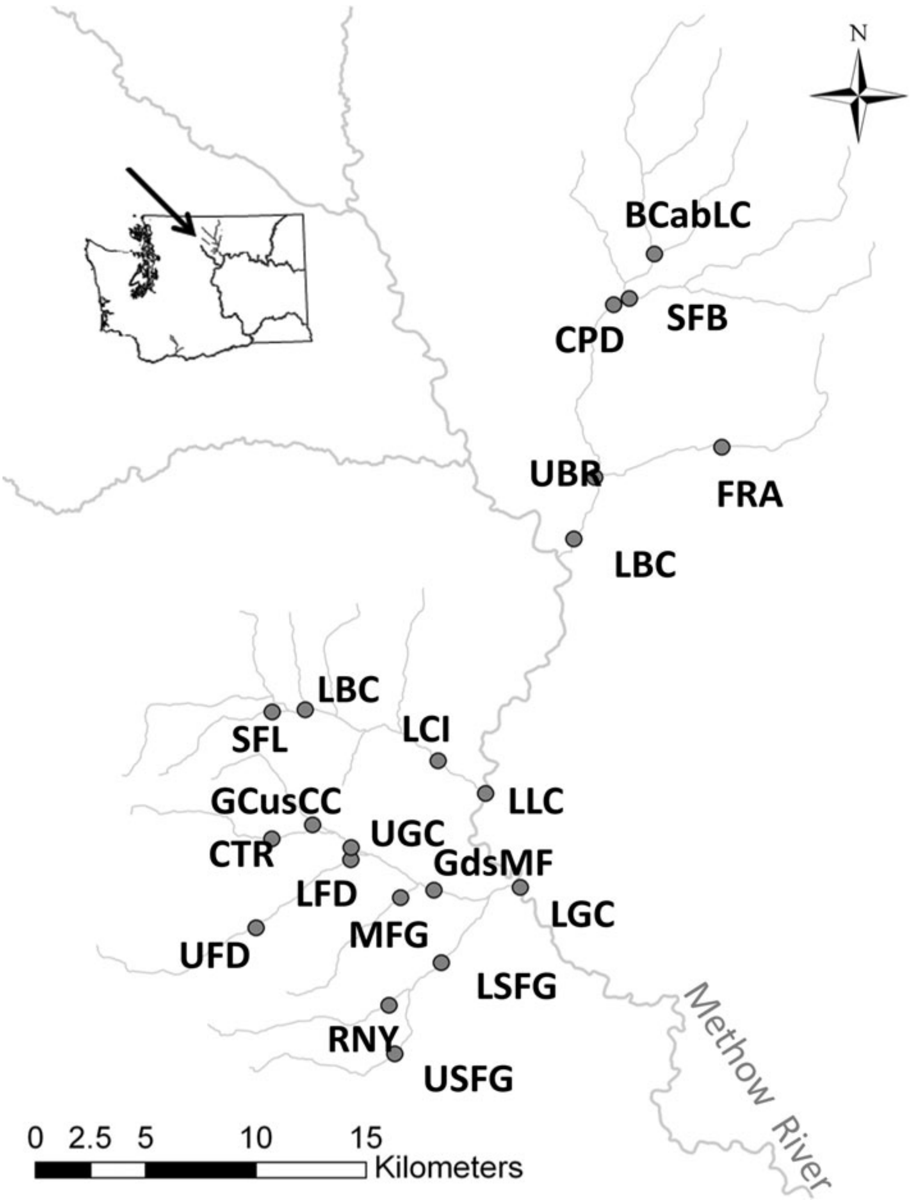

Fig. 1 Study area and sites in Beaver, Libby and Gold creeks, tributaries to the Methow River, Washington

Currently state and federal hatchery programs in the Methow Basin release 450,000–550,000 steelhead smolts per year. Returning adult steelhead are spawned and the eggs are reared at Wells Hatchery on the Columbia River downstream from the mouth of the Methow River. Current practices include intentional breeding between hatchery and naturally produced adults, and progeny from these crosses are primarily released in the Methow River basin (C. Snow, Washington Department of Fish and Wildlife, personal communication). Hatchery steelhead are released as age 1 smolts in the Methow and Chewuch rivers upstream from the town of Winthrop, WA. All hatchery-origin steelhead were marked with an internal tag (such as PIT tag), external tag (such as elastomer tag) and/or fin clip.

Methods

Fish collections and movements

Juvenile *O. mykiss* were sampled at 6 sites in the Beaver Creek Basin, 4 sites in the Libby Creek Basin and 11 sites in the Gold Creek Basin (Fig. 1). This study is intended to assess the connectivity of populations of *O. mykiss* in Beaver Creek prior to the completion of diversion dam modifications that would improve fish passage in the stream particularly for the anadromous life history. In Beaver Creek, one site was downstream of the lowest diversion dam (LBC), 1 site was located between the various diversion dam modifications (UBR), 3 sites were located upstream from the diversion dams (CMP, SFB, BCusLC) and one site was located on a tributary that flows into Beaver Creek between the diversion dams (FRA) (Fig. 1). Sites were selected in a stratified random design to spatially represent populations located in these basins. Collections were made during the fall of 2004 or the summer of 2005 sampling age 1+ juvenile *O. mykiss* in the stream.

Juvenile *O. mykiss* were collected using a backpack electrofisher (Smith Root Inc. LR-24). Trout were measured to the nearest mm fork length and weighed to the nearest 0.01 g using a digital scale (Ohaus, Scout Pro SP 400). Juvenile and adult trout were scanned for PIT tags and coded wire tags and inspected for any other external tags (such as fin clips, elastomer tags, etc.). If the trout did not have a PIT tag, a tag was inserted in the body cavity for trout >65 mm (12.5 mm tag, full duplex 134.2 kHz). A tissue sample was removed from the caudal fin of juvenile and adult trout and stored in 95 % non-denatured ethanol. Anadromous outmigration rates were estimated for each site based on the proportion of PIT tags read at passage facilities on the mainstem Columbia River out of the total number released at a site.

Stream segments between the mouth of each creek and each site were walked to measure obstructions and gradients. Obstructions were beaver dams, log jams, culverts and diversion dams that could prevent adult *O. mykiss* passage in the stream. The obstruction type, height and jump pool depth were measured. Maximum stream gradient was measured between each site using a clinometer. Stream temperature was measured at each site using Hobo tidbit loggers reading every 30 min during the summer 2009. Elevation at each site and stream distances were measured using GIS.

Laboratory methods

Tissue samples from the Wells Hatchery brood years 2005 and 2006 (hatchery × hatchery crosses) were provided by the Washington Department of Fisheries and Wildlife (WDFW). Sixteen microsatellite markers were used to identify individuals. Thirteen of these markers are standardized across the Columbia River Basin and are cited in Stephenson et al. (2009). Additional primer sets analyzed were: *One102* (Olsen et al. 2000), *Omm1036* and *Omm1046* (Rexroad et al. 2002).

DNA was isolated from fin clips preserved in ethanol using Qiagen DNEasy tissue extraction kits following standard manufacturer's protocols. Sixteen microsatellite loci were amplified using the polymerase chain reaction (PCR) in three multiplex reactions using Qiagen Multiplex PCR Master Mix on Applied Biosystems GeneAmp PCR System 9700 thermal cyclers in 96 well plates. PCR products were run on an Applied Biosystems 3730 genetic analyzer. Peaks were scored using GeneMapper version 3.7 software (Applied Biosystems, Foster City, California), and labeled following the Stevan Phelps Allele Nomenclature (SPAN) convention (Stephenson et al. 2009). Forward primers were fluorescently labeled (Applied Biosystems).

Amplification (PCR) reactions consisted of 5 ul reactions containing 2.5 ul Qiagen Multiplex PCR Master Mix, five or six primer sets and water, added to 2 μl of extract dried down in a 96 well plate. Cycling conditions included initial denaturation for 15 min at 95 °C, followed by 28 cycles for 30 s at 94 °C, 90 s at 51 °C (Multiplex A) or 57 °C (Multiplex B and Multiplex C), and 60 s at 72 °C, followed by a final cycle for 30 min at 60 °C. Multiplex A contained *Oki23*, *Oke4*, *Oneu14*, *Ssa289*, and *Ssa408*; Multiplex B contained *Ots4*, *Omy7*, *Ogo4*, *One102*, *Omm1046*, and *Ssa407*; Multiplex C contained *Ots100*, *Omy1011*, *Omy1001*, *Ots3m*, and *Omm1036*.

Amplification products were diluted with 10 μl DNA grade water and 1 μl of each dilution added to 10 μl of LIZ/formamide solution (30 μl LIZ600 to 1 ml formamide). Completed runs were analyzed automatically using Genemapper, followed by manual analysis of all peaks for verification. All homozygous results were checked for small allele dropout and large allele dropout. Peaks were also visually checked for conformity to expected profiles. Laboratory error rates for the 13 standardized loci are <2 % (Stephenson et al. 2009). Duplicate samples indicate laboratory error rates <1 % for our study.

Statistical analysis

Passage over obstacles for adult *O. mykiss* require 1–1.25 height to pool depth based on jumping ability and associated hydraulics (Bjornn and Reiser 1991). Therefore, we considered stream obstacles exceeding this 0.8 ratio obstructions. The number of obstructions was standardized to stream distance. For migration rate analyses, all environmental variables were summarized pair-wise between sites within each tributary basin. For hatchery admixture analyses, all environmental variables were summarized from the mouth of the tributary to the site. Stream temperature data were averaged between July 1 and September 10, 2009 for relative maximum summertime temperature across sites.

Prior to statistical tests, full siblings were identified and removed from the data set using ML-RELATE (Kalinowski et al. 2006). Exact tests of Hardy–Weinberg Equilibrium and linkage disequilibrium were performed using GENEPOP version 4.0.10. Expected heterozygosity and exact tests for allele frequencies were calculated using GENEPOP version 4.0.10 (Raymond and Rousset 1995). Unbiased estimates of allelic richness and private alleles were calculated using HP-RARE (Kalinowski 2005). All comparisons were adjusted for multiple comparisons using a Bonferroni correction (Rice 1989).

Migration rates were estimated between each site within each of the tributary basins using Bayesian inference of migration rates (BIMR) (Faubet and Gaggiotti 2008). Sites without significant allele frequency differences were not included in this analysis and one site was used to represent all the similar comparisons. In Libby Creek, site LLC was not included in the migration rate analysis. In Gold Creek, sites LGC, LSF, LFD, UGC were not included in this analysis. BIMR was run using 2 million iterations for burn in and 20 million iterations for sampling with a thinning interval of 2,000 using a Markov Chain Monte Carlo resampling algorithm as described in Wilson and Rannala (2003). The default values were used for all other parameter settings. The best run was selected with the lowest log likelihood. We also calculated the deviance as described in Faubet et al. (2007) to identify runs that did not converge. Sites with migration were compared to sites without migration using a Wilcoxon test. To avoid excessive numbers of sites with 0 migration estimates, we analyzed the Beaver Creek sites separately. Therefore, sites with and without migration were compared in Gold and Libby basins, and then sites with migration from Gold and Libby basins were compared to Beaver Creek.

Multinomial logistic regression was used to predict migration rates between each site within a tributary basin from measured environmental variables. Migration estimates were grouped into one of three categories for the response variable: no migration, low migration (0.001–0.07) and high migration (0.10–0.32). The purpose of these models was to evaluate the relative model fit for isolation by distance to isolation by resistance (obstruction number, obstruction height to depth, maximum gradient). Average maximum summertime stream temperature was used as an alternative variable to distance that would have an expected longitudinal gradient in the stream. A global model included the candidate predictor variables for distance and resistance and interaction variables. From this global model, subsets of predictor variables were chosen for comparison to the global model. The relative plausibility of the models were compared using Akaike's Information Criteria using the small sample adjustment (AICc, Akaike 1973; Burnham and Anderson 1998) with the best fitting model having the lowest AICc value. Model weights and evidence ratios were calculated as described in Burnham and Anderson (1998). A goodness-of-fit test was used on the best fitting model to test whether the data could plausibly arise from the model. All regressions and goodness-of-fit tests were performed using R (R Development Core Team 2010).

The proportion of hatchery admixture was estimated using STRUCTURE version 2.3.3 (Pritchard et al. 2000) for each site in the sample using known hatchery steelhead from Wells Hatchery ($n = 99$) as a reference. The two hatchery brood years were not statistically different and were combined for our analysis. STRUCTURE is a Bayesian based model that clusters individuals according to allelic frequencies minimizing Hardy–Weinberg and linkage disequilibrium. The admixture model was run in STRUCTURE using 10,000 iterations for burn in and 100,000 iterations using a Markov Chain Monte Carlo resampling algorithm as described in Pritchard et al. (2000). The number of populations (K) was set to 2 and all other settings were run using default values. Ten runs were performed for each site and the run with the lowest log likelihood was selected as the best run. The percent hatchery admixture for each individual was averaged for each sample collection at each site. A logistic regression was used to predict percent hatchery admixture from measured environmental variables, and models were compared using AICc values (Akaike 1973; Burnham and Anderson 1998).

Results

The total number of alleles detected at each locus ranged from 7 to 24 with the average allelic richness ranging from 4.5 to 6.8 (Table 1). Tests of Hardy–Weinberg Equilibrium detected significant departures in two comparisons (One 102 at SFL and Omy1011 at CTR). Linkage disequilibrium detected significant departures at 6 pairs of loci from the samples from Beaver, Libby and Gold creek sites. Tests on the Wells Hatchery samples did not detect any significant departures from Hardy–Weinberg Equilibrium but did detect linkage disequilibrium at 6 pairs of loci. There was no discernable pattern to the pairs of loci in the linkage disequilibrium tests.

Percent tag outmigration was used as an indication of the dominant life history at a site. Percent tag outmigration and percent Wells Hatchery admixture both followed a declining trend from the largest values at the most downstream sites in each tributary basin and smallest values in the upstream sites and were highly correlated ($r > 0.80$) (Table 1; Fig. 2). Genetic differentiation (F_{ST}) ranged from 0.02 to 0.15 in Beaver Creek. Libby and Gold creeks had slightly lower F_{ST} values ranging from 0 to 0.09 (Table 2). Allele frequency exact tests were significantly different for all pairs of sites in Beaver Creek. In Libby Creek, the two most downstream sites were not significantly different (LLC and LCI). In Gold Creek, the mainstem sites (LGC, GCdsMF, UGC), LSF and LFD were not significantly different. All other comparisons were significant (Table 2).

Pair-wise migration estimates generated by BIMR indicated that there was no migration between sites for the

Table 1 Sample sizes (*n*), expected heterozygosity (He), average allelic richness (AR), average private allelic richness (PA), percent PIT tags that out migrated, percent hatchery admixture and elevation (m) for sample sites in Beaver, Libby and Gold creeks

	n	He	AR	PA	% tag out	% hatchery	Elev (m)
Beaver Creek							
LBC	28	0.81	6.6	0.2	7.0	40	474.5
UBR	19	0.79	6.0	0.2	6.0	27.4	547.5
CMP	36	0.76	5.9	0.1	0.4	6	803.1
SFB	28	0.73	5.2	0.1	1.0	1.8	888.3
BCabLC	22	0.70	4.8	0.1	0.0	0.9	1028.2
FRA	25	0.67	4.5	0.1	0.0	1.8	851.7
Libby Creek							
LLC	36	0.82	6.8	0.1	8.0	31.5	425.9
LCI	23	0.81	6.8	0.2	3.0	25.6	486.7
LCBen	32	0.78	6.1	0.1	0.4	14.1	778.7
SFL	15	0.72	4.7	0.1	0.0	0.6	1052.5
Gold Creek							
LGC	46	0.82	6.8	0.2	6.0	42.6	401.5
GCdsMF	30	0.82	6.8	0.1	6.0	37.1	486.7
UGC	16	0.83	6.8	0.2	5.0	28	669.2
GCusCC	25	0.79	6.1	0.2	2.0	9.5	790.9
LSFG	28	0.81	6.5	0.1	6.0	56.9	644.9
USFG	39	0.77	5.8	0.1	2.0	13.7	876.1
RNY	19	0.74	5.1	0.1	1.0	3.8	754.4
MFG	15	0.76	5.5	0.1	0.0	9.6	681.4
LFD	35	0.83	6.9	0.3	3.0	29.3	730.1
UFD	25	0.79	5.9	0.2	0.0	3.3	882.2
CTR	7	0.82	6.7	0.6	2.0	3.8	924.7

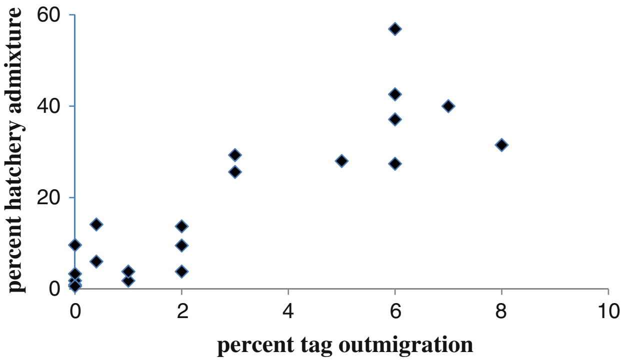

Fig. 2 Percent hatchery admixture and percent *O. mykiss* with PIT tags that out migrated. Outmigration was determined as anadromous outmigration when tags were detected on the Columbia River downstream from the Snake River confluence

generation prior to 2004 in Beaver Creek (Table 3). Libby Creek maintained migration in both directions between the three tested sites in this basin (Table 4). In Gold Creek, there was migration from sites in the upper tributaries into the mainstem Gold Creek sites and lower South Fork Gold and lower Foggy Dew (Table 5). However, there was no detectable migration upstream to these upper sites from the mainstem in Gold Creek. When the level of migration among sites in Libby and Gold creeks were categorized, 75 % of the sample had no migration, 17 % of the sample low migration and 8 % of the sample high migration.

Wilcoxon rank sum tests comparing sites in Libby and Gold creeks with migration to sites without migration found significant differences in distance, number of obstructions, obstruction height to depth, and gradient ($p < 0.02$) (Figs. 3, 4). When comparing the Beaver Creek sites to the sites in Libby and Gold that had migration, the number of obstructions was the only significantly different comparison ($p < 0.03$). Model selection found that the model with obstruction height to depth and maximum gradient was the best fit predicting the level of migration with an AICc of 23.66 (Table 6). Evidence ratios indicated that this model was 294 times more likely than the next best fitting model (Table 6). Obstruction height to depth ratio and maximum gradient were inversely related to increased migration, and the interaction term was positively related to migration (Table 7). The goodness of fit test for this model was not significant ($p > 0.98$).

The models predicting percent hatchery admixture did not clearly indicate relationships in the data. The top two models (distance alone and gradient alone) were less than 0.01 AICc value and the top four models were within 0.6 AICc value of each other. Each of the top models used only one of the predictors. None of these predictors were significant. The goodness of fit tests for the top two models were not significant ($p = 1.0$).

Discussion

Disconnected or fragmented habitats can impact the demographic exchange and genetic diversity among populations by restricting gene flow and increasing the effects of genetic drift (Allendorf and Luikart 2007). Loss of genetic diversity is associated with losses in fitness (Reed and Frankham 2003) and reduced adaptive potential (Swindell and Bouzat 2005). Overall, the *O. mykiss* in our study had similar genetic measurements as those in other studies of this species (Heath et al. 2002; Narum et al. 2004, 2008; Nielsen et al. 2009). Our study did not include populations upstream of waterfalls, therefore we document slightly lower maximum F_{ST} values and slightly higher minimum heterozygosity than Narum et al. (2008). The pre-treatment barrier effects indicate the highest F_{ST} and lowest heterozygosity in the upper Beaver Creek sites (FRA and BCusLC), little to no recent migration and reduced Wells Hatchery admixture among sites in the

Table 2 Pairwise F_{ST} values among sample sites in Beaver, Libby and Gold creeks

	LBC	FRA	UBR	CMP	SFB	BCusLC	LLC	LCI	LCB	SFL
FRA	0.091									
UBR	0.018	0.1089								
CMP	0.0269	0.0743	0.0455							
SFB	0.0464	0.1125	0.0625	0.0289						
BCusLC	0.0868	0.1466	0.0965	0.0567	0.0989					
LLC	0.0039*	0.0866	0.0211	0.028	0.0447	0.0741				
LCI	0.0122	0.0763	0.0247	0.0196	0.0344	0.0708	0.0046*			
LCB	0.0432	0.1091	0.0393	0.0408	0.051	0.0842	0.0282	0.0178		
SFL	0.1	0.1818	0.1075	0.1067	0.1165	0.1515	0.0916	0.0931	0.08	
LGC	0.0063*	0.0825	0.025	0.0164	0.0416	0.0565	0.0000*	0.0048*	0.0263	0.0935
LSF	0.0138	0.0953	0.0267	0.0191	0.0411	0.061	0.0043*	0.01	0.0191	0.0896
USF	0.0268	0.0979	0.0387	0.027	0.0537	0.0674	0.0235	0.0263	0.0476	0.1108
RNY	0.0407	0.1188	0.0491	0.0486	0.0631	0.099	0.0317	0.0407	0.0467	0.1078
UGC	0.006	0.0713	0.0255	0.0247	0.0488	0.0831	0.0067*	0.0047*	0.0301	0.0946
LFD	0.019	0.0884	0.0337	0.0274	0.0453	0.073	0.0077	0.0085	0.0265	0.087
UFD	0.0237	0.094	0.0418	0.0308	0.0497	0.089	0.0208	0.0191	0.0397	0.0991
GCusCC	0.065	0.1229	0.0776	0.0633	0.0887	0.0904	0.045	0.0488	0.0516	0.1048
CTR	0.0605	0.1497	0.0823	0.0821	0.0966	0.1254	0.0525	0.0665	0.085	0.0917
MFG	0.0504	0.0974	0.0564	0.0485	0.0639	0.1036	0.0373	0.0393	0.0516	0.1389
GCdsMF	0.0016*	0.08	0.0235	0.0142	0.0363	0.0615	0.0007*	0.0054*	0.0255	0.0905
LSF	0.0000*									
USF	0.0137	0.011								
RNY	0.0327	0.0253	0.0437							
UGC	0.007*	0.0077	0.0224	0.0406						
LFD	0.0074	0.0055	0.0277	0.0351	0.009*					
UFD	0.0182	0.0166	0.0356	0.0447	0.0253	0.0177				
GCusCC	0.0408	0.0445	0.0672	0.0722	0.0477	0.0397	0.0541			
CTR	0.0582	0.0642	0.0747	0.0859	0.0424	0.0541	0.0769	0.0637		
MFG	0.0324	0.0361	0.0544	0.0488	0.0318	0.0335	0.0509	0.0705	0.0941	
GCdsMF	0.000*	0.003*	0.0198	0.0324	0.0054*	0.0056*	0.0114	0.0397	0.0586	0.0367

* Denotes not significant allele frequency exact test after Bonferroni correction

basin. The reference streams in our study found connectivity among sites throughout the basins, and migration was generally biased in the downstream direction. There was high migration of individuals between the lower two sites in Libby Creek (LLC, LLI) and the five lower-most sites in Gold Creek (LGC, GCdsMF, UGC, LSF, LFD).

Longitudinal trends in streams are directly correlated with environmental variables such as distance from the mouth, elevation, temperature, width, depth, and channel gradient. These longitudinal gradients of environmental variables are typically correlated with species distributions (Weigel and Sorensen 2001 and citations therein). Similarly, life history of *O. mykiss* has a longitudinal gradient in the stream with anadromous sites located lower in the tributary basins and resident sites higher in the basins (Narum et al. 2004, 2008). Sites intermediate between these have a moderate level of anadromy. Gradients in the landscape and the associated environment may result in spatial autocorrelation in the data (Legendre 1993; Smouse and Peakall 1999; Neville et al. 2006a). We address non-independence among variables in our data by standardizing variables to distance prior to statistical analysis, using variables with little direct correlation with elevation or distance from the mouth of the stream and using only select variables with longitudinal gradients in a hypothesis testing framework. Maximum gradient was used instead of average channel gradient to represent the most difficult obstacle a fish had to pass when traveling upstream between sites, and this variable is related to underlying geology more so than the longitudinal trend in the channel.

In our study, we use the percent of tags that out migrated as an index of anadromy at a site. This variable has a longitudinal gradient and also is highly correlated with the percent of Well Hatchery admixture ($r = 0.80$). Percent

Table 3 Mean pairwise migration estimates and 95 % posterior probability in parentheses among sites in Beaver Creek

From/into	LBC	UBR	SFB	BCusLC	CMP	FRA
LBC	1	0	0	0	0	0
	(1.0, 1.0)	(5.8×10^{-12}, 5.7×10^{-10})	(5.6×10^{-12}, 1.1×10^{-9})	(4.1×10^{-12}, 7.4×10^{-10})	(1.1×10^{-12}, 6.7×10^{-10})	(6.7×10^{-12}, 5.7×10^{-10})
UBR	0	1	0	0	0	0
	(1.9×10^{-12}, 1.5×10^{-9})	(1.0, 1.0)	(7.4×10^{-12}, 1.1×10^{-9})	(3.3×10^{-12}, 7.0×10^{-10})	(1.1×10^{-12}, 6.3×10^{-10})	(8.3×10^{-12}, 5.7×10^{-10})
SFB	0	0	1	0	0	0
	(1.8×10^{-12}, 1.5×10^{-9})	(6.1×10^{-12}, 5.8×10^{-10})	(1.0, 1.0)	(3.3×10^{-12}, 7.3×10^{-10})	(9.3×10^{-13}, 6.7×10^{-10})	(5.5×10^{-12}, 5.9×10^{-10})
BCusLC	0	0	0	1	0	0
	(2.2×10^{-12}, 1.5×10^{-9})	(4.8×10^{-12}, 5.6×10^{-10})	(6.5×10^{-12}, 1.2×10^{-9})	(1.0, 1.0)	(1.1×10^{-12}, 6.6×10^{-10})	(5.7×10^{-12}, 5.9×10^{-10})
CMP	0	0	0	0	1	0
	(2.0×10^{-12}, 1.4×10^{-9})	(4.2×10^{-12}, 5.8×10^{-10})	(7.0×10^{-12}, 1.1×10^{-9})	(4.0×10^{-12}, 8.1×10^{-10})	(1.0, 1.0)	(6.0×10^{-12}, 5.9×10^{-10})
FRA	0	0	0	0	0	1
	(2.4×10^{-12}, 1.4×10^{-9})	(5.0×10^{-12}, 5.7×10^{-10})	(6.3×10^{-12}, 1.2×10^{-9})	(4.0×10^{-12}, 7.5×10^{-10})	(8.3×10^{-13}, 6.4×10^{-10})	(1.0,1.0)

Table 4 Mean pairwise migration estimates and 95 % posterior probability in parentheses among sites in Libby Creek

From/into	LCI	LCB	SFL
LCI	0.63	0.18	0
	(0.43, 0.82)	(0.04, 0.32)	(3.6×10^{-9}, 0.01)
LCB	0.32	0.75	0
	(0.13, 0.50)	(0.58, 0.91)	(3.7×10^{-9}, 0.01)
SFL	0.06	0.07	1
	(0.01, 0.13)	(0.02, 0.15)	(0.98, 1.0)

hatchery admixture is linked to anadromy via the local hatchery brood practices. Although matings between hatchery and wild anadromous steelhead are possible in the natural habitat, they were rare in Beaver Creek and did not result in offspring that survive to return as an adult (Weigel et al. 2013). Other studies indicate drastic reductions in relative reproductive success when hatchery steelhead spawn in the natural stream habitat (Araki et al. 2007a). In addition, parentage data indicates incomplete isolation between the fluvial and anadromous life history (Araki et al. 2007b; Christie et al. 2011; Weigel 2013). In Beaver Creek, the wild steelhead is the link between the hatchery population (with intentional cross breeding in the hatchery) and the fluvial rainbow trout (Weigel 2013). Interestingly, the percent tag outmigration data indicates an anadromous life history present at UBR even though there was very little to no recent migration into the site. The anadromous life history can arise from a resident rainbow trout (Thrower et al. 2004), and juvenile outmigration (anadromy) occurred at this site prior to barrier treatment (Weigel et al. 2013).

Asymmetrical migration is documented for numerous species including humans (*Homo sapiens*) (Faubet and Gaggiotti 2008), plants (*Centaurea corymbosa*), wolves (*Canis lupis)* (Wilson and Rannala 2003) and cutthroat trout (*O. clarki hewshawi*) (Neville et al. 2006b). Stream habitats lend to asymmetrical movement due to the longitudinal gradient with larger habitats in downstream areas, as well as the resistance that the stream flow presents for upstream movement. This resistance results in greater energy expenditure to travel against the current and climb in elevation. Previous applications of stream barriers examine waterfalls that exceed the jumping ability of the study species. These studies treat the barriers as complete or non-existent with a binomial response variable (Costello et al. 2003; Meeuig et al. 2010). Yet, barriers (or obstructions) can also be incomplete or temporary. Incomplete barriers are passable under specific stream flow conditions whereas temporary barriers would eventually move or deteriorate.

Obstructions can occur naturally (such as log jams or beaver dams) or arise from anthropogenic activities (such

Table 5 Mean pairwise migration estimates and 95 % posterior probability in parentheses among sites in Gold Creek

From/into	CTR	UFD	GCusCC	GCdsMF	MFG	RNY	USF
CTR	1	0	0	0.02	0	0	0
	(1.0, 1.0)	$(1.0 \times 10^{-14}, 3.8 \times 10^{-10})$	$(9.1 \times 10^{-12}, 1.3 \times 10^{-9})$	$(6.5 \times 10^{-4}, 0.08)$	$(4.9 \times 10^{-13}, 4.8 \times 10^{-11})$	$(5.0 \times 10^{-12}, 9.0 \times 10^{-10})$	$(2.0 \times 10^{-12}, 1.5 \times 10^{-10})$
UFD	0	1	0	0.19	0	0	0
	$(5.3 \times 10^{-12}, 1.0 \times 10^{-9})$	(1.0, 1.0)	$(7.0 \times 10^{-12}, 1.3 \times 10^{-9})$	(0.06, 0.35)	$(4.6 \times 10^{-13}, 4.6 \times 10^{-11})$	$(6.0 \times 10^{-12}, 1.0 \times 10^{-9})$	$(1.4 \times 10^{-12}, 1.7 \times 10^{-10})$
GCusCC	0	0	1	0.08	0	0	0
	$(5.2 \times 10^{-12}, 1.1 \times 10^{-9})$	$(8.3 \times 10^{-15}, 4.2 \times 10^{-10})$	(1.0, 1.0)	(0.01, 0.17)	$(4.6 \times 10^{-13}, 4.3 \times 10^{-11})$	$(6.4 \times 10^{-12}, 9.7 \times 10^{-10})$	$(1.3 \times 10^{-12}, 1.7 \times 10^{-10})$
GCdsMF	0	0	0	0.46	0	0	0
	$(4.2 \times 10^{-12}, 1.2 \times 10^{-9})$	$(6.4 \times 10^{-15}, 3.8 \times 10^{-10})$	$(9.2 \times 10^{-12}, 1.4 \times 10^{-9})$	(0.27, 0.69)	$(4.1 \times 1^{0-13}, 4.6 \times 10^{-11})$	$(5.3 \times 10^{-12}, 1.0 \times 10^{-9})$	$(9.3 \times 10^{-12}, 1.9 \times 10^{-10})$
MFG	0	0	0	0.07	1	0	0
	$(5.3 \times 10^{-12}, 1.1 \times 10^{-9})$	$(8.6 \times 10^{-15}, 4.0 \times 10^{-10})$	$(8.2 \times 10^{-12}, 1.3 \times 10^{-9})$	(0.005, 0.17)	(1.0, 1.0)	$(6.7 \times 10^{-12}, 1.0 \times 10^{-9})$	$(1.6 \times 10^{-12}, 1.7 \times 10^{-10})$
RNY	0	0	0	0.03	0	1	0
	$(5.3 \times 10^{-12}, 1.0 \times 10^{-9})$	$(8.7 \times 10^{-15}, 3.7 \times 10^{-10})$	$(7.6 \times 10^{-12}, 1.4 \times 10^{-9})$	$(8.0 \times 10^{-4}, 0.09)$	$(3.9 \times 10^{-13}, 4.6 \times 10^{-11})$	(1.0, 1.0)	$(1.6 \times 10^{-12}, 1.6 \times 10^{-10})$
USF	0	0	0	0.15	0	0	1
	$(4.8 \times 10^{-12}, 1.1 \times 10^{-9})$	$(5.6 \times 10^{-15}, 3.8 \times 10^{-10})$	$(7.0 \times 10^{-12}, 1.3 \times 10^{-9})$	(0.04, 0.29)	$(3.7 \times 10^{-13}, 4.4 \times 10^{-11})$	$(7.0 \times 10^{-12}, 9.7 \times 10^{-10})$	(1.0, 1.0)

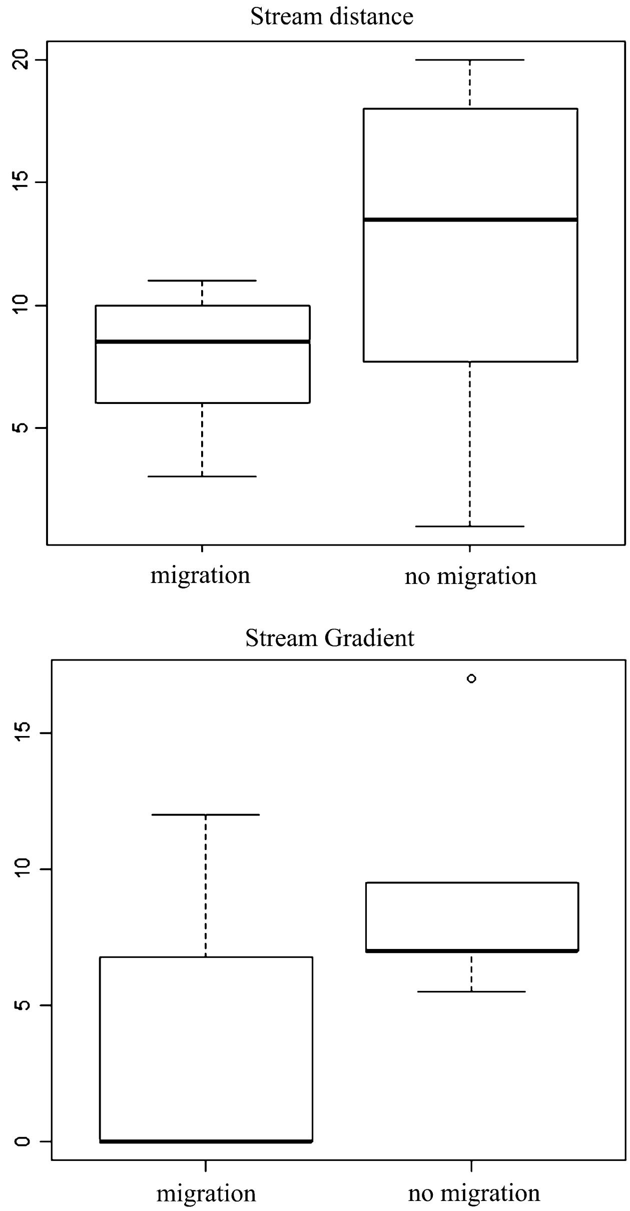

Fig. 3 Stream distance (km) and stream gradient (%) at sites with migration and sites without migration

as culverts or irrigation diversion dams). These types of smaller obstructions are often more numerous on the landscape than waterfalls and can have cumulative effects on the migration and dispersal of aquatic species. In our study, migration was biased in the downstream direction among the sites in the reference streams, Libby and Gold creeks. Libby Creek had higher levels of two directional migration among sites whereas Gold Creek had migration solely from the upper sites into the mainstem and lower sites. However, it is important to note that the lower-most sites were lumped for this analysis due to indistinguishable population genetic differences indicating high migration rates among these sites.

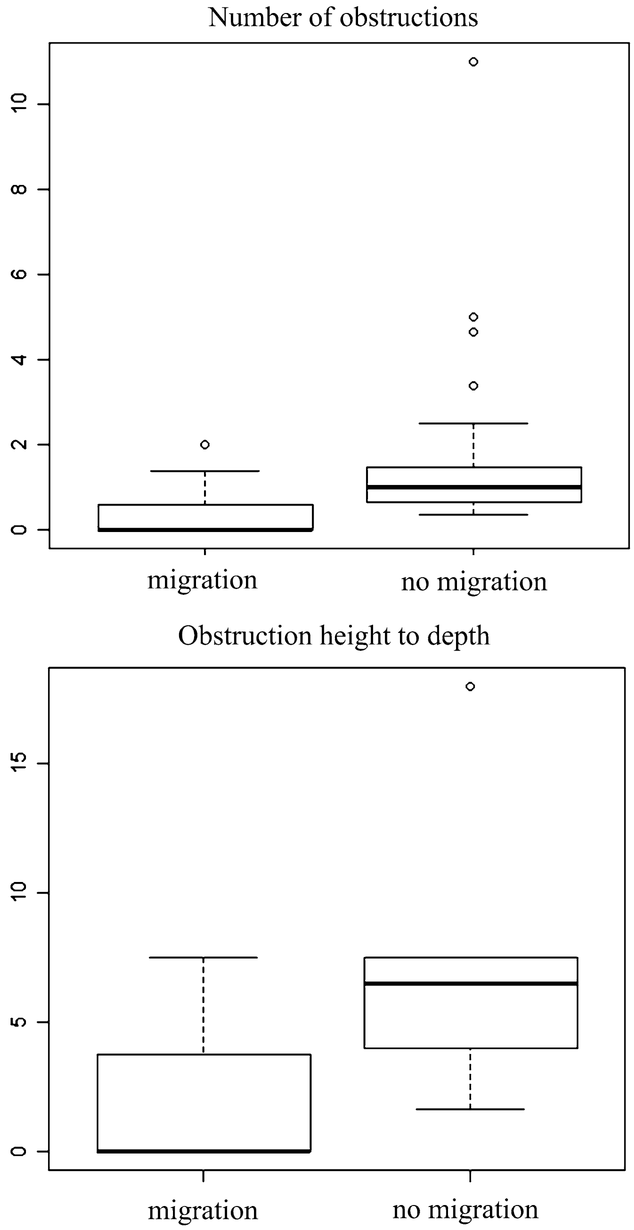

Fig. 4 Number of obstructions per km and obstruction height to depth ratio for sites with migration and sites without migration

Table 7 Model coefficients and standard errors for the multinomial models predicting the level of migration in Libby and Gold creeks

Model	Variable	Coeff	Std error
Low migration	Intercept	220.25	36.49
	ob_htd	−99.39	49.15
	max_grad	−45.37	19.35
	interaction	13.82	8.34
High migration	Intercept	219.33	36.5
	ob_htd	−92.57	56.53
	max_grad	−45.17	19.34
	interaction	13.15	9.13

Faubet and Gaggiotti (2008) similarly combine populations with no detectable genetic differences. Simulation studies indicate that migration estimation can be inaccurate particularly when genetic differentiation is low ($F_{ST} = 0.01$); however, the estimation can be fairly accurate when differentiation is higher (Faubet et al. 2007; Faubet and Gaggiotti 2008). Higher migration rates (>0.3 Wilson and Rannala 2003; >0.7 Faubet and Gaggiotti 2008) are also difficult to detect. These inaccuracies influence the parameter estimates, increase unexplained variation and result in greater posterior probability intervals (Faubet et al. 2007; Faubet and Gaggiotti 2008). In this study, potential inaccuracies in the exact estimated rates are addressed by using categorical classifications of the relative rates of estimated migration. We also only analyze sites with detectable genetic differences, thereby avoiding the source of some of these inaccuracies.

Geographic distance is commonly correlated with genetic distance (Wright 1943). Distance is related to the dispersal ability of the organism. Isolation by distance is commonly detected in steelhead populations (Heath et al. 2002; Narum et al. 2008; Nielsen et al. 2009). Basin is also often associated with genetic distances in salmonids with sites from different basins having greater genetic distances (Costello et al. 2003; Narum et al. 2004, 2008; Nielsen et al. 2009). Strong relationships between genetic distance

Table 6 Multinomial logistic regression results and model comparison values

Variables	AIC	K	AICc	Δ_i	£($g_i|x$)	w_i/w_t	Evid ratio
ob_htd, max grad	27.16	3	23.66	0	1	0.995	
grad, temp	39.20	4	35.033	11.37	0.003	0.003	294.9
ob_htd, ob_km, max grad	43.15	8	37.15	13.49	0.001	0.001	849.8
ob_htd, temp	50.16	4	45.99	22.33	1.4E–05	1.4E–05	70732.9
ob_km, grad	61.02	4	56.85	33.19	6.2E–08	6.2E–08	16137667
temp	65.82	2	63.07	39.41	2.8E–09		
dist	70.13	2	67.38	43.72	3.2E–10		
ob_km, ob_htd, grad, temp	70.56	16	64.89	41.23	1.1E–09		
dist, ob_km, ob_htd, grad	71.75	16	66.08	42.42	6.1E–10		

and geographic distance could be an artifact of the assumption of symmetrical migration rates inherent in genetic distance values. When considering asymmetrical migration rates, the strength of the relationship with geographic distance will decline as the pair-wise migration rate can have two different values for the same geographic distance. Additionally, the sites in our data that did not have significant allele frequencies in Libby and Gold Creeks would be considered one population and any distance between the nearest or furthest collection site could be used in the pairwise comparisons. Lastly, the migration relationships in Beaver Creek also indicate that landscape variables other than distance are influencing migration and population genetic measures.

Although distance often provides good predictive models, ecologists are often striving for more mechanistic relationships that could drive an organism's preference for habitats or ability to survive and reproduce. Resistance has been used to explain the path and associated likelihood of movement by organisms (Cushman et al. 2006; Spear et al. 2010). In this hypothesis, certain pathways may be less preferred but still available and characteristics of the site are associated with a resistance or permeability value (Spear et al. 2010). In anadromous fish, resistance is potentially important due to the long migration distances traveled by adults returning to natal areas that deplete limited energy reserves. This could influence the distance or the ability to navigate obstructions in the stream environment. In our analysis, we compared the level of migration between sites using three resistance variables (number of obstructions, obstruction height to depth ratio and maximum upstream gradient) to the null hypothesis of isolation by distance. In the reference streams, we found that isolation by resistance was a better predictor of the level of migration than distance. The resistance variables that provided the best fit for the data included obstruction height to depth ratio, maximum gradient and their interaction. Interestingly, the percent Wells Hatchery admixture did not provide as clear model results when comparing resistance variables to distance. We suspect that this is a result of the hatchery brood practices that link the wild anadromous alleles to the hatchery alleles resulting in an association between these alleles and the anadromous gradient longitudinally in the stream. Alternatively, it is possible that the migration of hatchery steelhead into these sites is unrelated to the variables tested resulting in a spurious correlation, where hatchery steelhead that successfully spawn at sites in the study area use other cues such as presence of a mate or presence of spawning gravel.

In summary, small irrigation diversion dams were limiting population interactions in Beaver Creek and collectively blocking steelhead migration into the stream. However, these barriers also limited the percent Wells Hatchery admixture in this stream providing some protection to native genotypes in the basin. The patterns of migration and associated environmental variables were different when comparing Beaver Creek to the reference streams indicating that the higher level of anthropogenic impacts in the creek resulted in fragmentation of the *O. mykiss* population. Variables related to stream resistance, such as obstruction height to depth ratio and maximum gradient, were better predictors of the level of migration than stream distance. Re-connecting Beaver Creek re-established a local population of steelhead that returned to the creek as adults to spawn (Weigel et al. 2013). Connectivity projects that restore access to historically occupied habitats will contribute to the restoration and recovery of this declining life history. However, in situations with depressed populations or stocks, numbers of colonizing individuals is a concern and should be monitored and evaluated to maintain sufficient genetic diversity in the newly established habitat.

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References

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. In: Prtrov BN, Csaki F (eds) Second international symposium on information theory. Akademiai Kiado, Budapest, pp 267–281

Allendorf FW, Luikart G (2007) Conservation and the genetics of populations. Blackwell Publishing, Malden

Allendorf FW, Leary RF, Spruell P, Wenburg JK (2001) The problems with hybrids: setting conservation guidelines. Trends Ecol Evol 16:613–622

Araki H, Ardren WR, Olsen E, Cooper B, Blouin MS (2007a) Reproductive success of captive-bred steelhead trout in the wild: evaluation of three hatchery programs in the Hood River. Conserv Biol 21:181–190

Araki H, Waples RS, Ardren WR, Cooper B, Blouin MS (2007b) Effective population size of steelhead trout: influence of variance in reproductive success, hatchery programs, and genetic compensation between life history forms. Mol Ecol 16:953–966

Bernhardt ES et al (2005) Synthesizing U.S. river restoration efforts. Science 308:636–637

Bjornn TC, Reiser DW (1991) Habitat requirements of salmonids in streams. Am Fish Soc Special Publ 19:83–138

Burnham KP, Anderson DR (1998) Model selection and inference: an information-theoretic approach. Springer, New York

Christie MR, Marine ML, Blouin MS (2011) Who are the missing parents? Grandparentage analysis identifies multiple sources of gene flow into a wild population. Mol Ecol 20:1263–1276

Costello AB, Down TE, Pollard SM, Pacas CJ, Taylor EB (2003) The influence of history and contemporary stream hydrology on the evolution of genetic diversity within species: an examination of microsatellite DNA variation in bull trout, *Salvelinus confluentus* (Pisces: Salmonidae). Evolution 57:328–344

Crooks KR, Sanjayan MA (eds) (2006) Connectivity and conservation. Cambridge University Press, Cambridge

Cushman SA, McKelvey KS, Hayden J, Schwartz MK (2006) Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. Am Nat 168:486–499

Epifanio JM, Hooe M, Buck DH, Philipp DP (1999) Reproductive success and assortative mating among *Pomoxis* species and their hybrids. Trans Am Fish Soc 128:104–120

Faubet P, Gaggiotti OE (2008) A new Bayesian method to identify the environmental factors that influence recent migration. Genetics 178:1491–1504

Faubet P, Waples R, Gaggiotti OE (2007) Evaluating the performance of a multilocus Bayesian method for the estimation of migration rates. Mol Ecol 16:1149–1166

Fausch KD, Rieman BE, Dunham JB, Young MK, Peterson DP (2009) Invasion versus isolation: trade-offs in managing native salmonids with barriers to upstream movement. Conserv Biol 23:859–870

Hanski IA, Gilpin ME (eds) (1996) Metapopulation biology: ecology, genetics, and evolution. Academic Press, New York

Heath DD, Busch C, Kelly J, Atagi DY (2002) Temporal change in genetic structure and effective population size in steelhead trout (*Oncorhynchus mykiss*). Mol Ecol 11:197–214

Hendry AP, Stearns SC (eds) (2004) Evolution illuminated Salmon and their relatives. Oxford University Press, New York

Kalinowski ST (2005) HP-RARE: a computer program for performing rarefaction on measures of allelic diversity. Mol Ecol Notes 5:187–189

Kalinowski ST, Wagner AP, Taper ML (2006) ML-RELATE: a computer program for maximum likelihood estimation of relatedness and relationship. Mol Ecol Notes 6:576–579

Kettunen M, Terry A, Tucker G, Jones A (2007) Guidance on the maintenance of landscape connectivity features of major importance for wild flora and fauna. Institute for European Environmental Policy (IEEP), Brussels

Legendre P (1993) Spatial autocorrelation: trouble or new paradigm? Ecology 74:1659–1673

Martens KD, Connolly PJ (2010) Effectiveness of a redesigned water diversion using rock vortex weirs to enhance longitudinal connectivity for small salmonids. North Am J Fish Manag 30:1544–1552

McClure MM, Holmes EE, Sanderson BL, Jordan CE (2003) A large-scale multispecies status assessment: anadromous salmonids in the Columbia River Basin. Ecol Appl 13:964–989

McCullough DR (ed) (1996) Metapopulations and wildlife conservation. Island Press, Washington, p 429

Meeuig MH, Guy CS, Kalinowski ST, Fredenberg WA (2010) Landscape influences on genetic differentiation among bull trout populations in a stream-lake network. Mol Ecol 19:3620–3633

Miller LM, Close T, Kapuscinski AR (2004) Lower fitness of hatchery and hybrid rainbow trout compared to naturalized populations in Lake Superior tributaries. Mol Ecol 13:3379–3388

Moyle PB, Williams JE (1990) Biodiversity loss in the temperate zone: decline of the native fish fauna of California. Conserv Biol 4:275–284

Narum SR, Contor C, Talbot A, Powell MS (2004) Genetic divergence of sympatric resident and anadromous forms of *Oncorhynchus mykiss* in the Walla Walla River, USA. J Fish Biol 65:471–488

Narum SR, Zendt JS, Graves DG, Sharp WR (2008) Influence of landscape on resident and anadromous life history types of *Oncorhynchus mykiss*. Can J Fish Aquat Sci 65:1013–1023

Neville HM, Dunham JB, Peacock MM (2006a) Landscape attributes and life history variability shape genetic structure of trout populations in a stream network. Landsc Ecol 21:901–916

Neville HM, Isaak DJ, Dunham JB, Thurow RF, Rieman BE (2006b) Fine-scale natal homing and localized movement as shaped by sex and spawning habitat in Chinook salmon: insights from spatial autocorrelation analysis of individual genotypes. Mol Ecol 15:4589–4602

Nielsen JL, Byrne A, Graziano SL, Kozfkay CC (2009) Steelhead genetic diversity at multiple spatial scales in a managed basin: Snake River, Idaho. North Am J Fish Manag 29:680–701

Novinger DC, Rahel FJ (2003) Isolation management with artificial barriers as a conservation strategy for cutthroat trout in headwater streams. Conserv Biol 17:772–781

Olsen JB, Wilson SL, Kretschmer EJ, Jones KC, Seeb JE (2000) Characterization of 14 tetranucleotide microsatellite loci derived from sockeye salmon. Mol Ecol 9:2185–2187

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155:945–959

R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. http://www.R-project.org

Rannala B, Mountain JL (1997) Detecting immigration by using multilocus genotypes. Proc Natl Acad Sci USA 94:9197–9201

Raymond M, Rousset F (1995) GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. J Hered 86:248–249

Reed DH, Frankham R (2003) Correlation between fitness and genetic diversity. Conserv Biol 17:230–237

Rexroad CE, Coleman RL, Gustafson AL, Hershberger WK, Killefer J (2002) Development of rainbow trout microsatellite markers from repeat enriched libraries. Mar Biotechnol 4:12–16

Rhymer JM, Simberloff D (1996) Extinction by hybridization and introgression. Annu Rev Ecol Syst 27:83–189

Rice WR (1989) Analyzing tables of statistical tests. Evolution 43:223–225

Richter BD, Braun DP, Mendelson MA, Master LL (1997) Threats to imperiled freshwater fauna. Conserv Biol 11:1081–1093

Sheer MB, Steel EA (2006) Lost watersheds: barriers, aquatic habitat connectivity, and salmon persistence in the Willamette and Lower Columbia River Basins. Trans Am Fish Soc 135:1654–1669

Smouse PE, Peakall R (1999) Spatial autocorrelation analysis of individual multiallele and multilocus genetic structure. Heredity 82:561–573

Spear S, Balkenhol N, Fortin M, McRae BH, Scribner K (2010) Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. Mol Ecol 19:3576–3591

Stephenson JJ et al (2009) A centralized model for creating shared, standardized, microsatellite data that simplifies inter-laboratory collaboration. Conserv Genet 10:1145–1149

Swindell WR, Bouzat JL (2005) Modeling the adaptive potential of isolated populations: experimental simulations using Drosophila. Evolution 59:2159–2169

Thrower FP, Hard JJ, Joyce JE (2004) Genetic architecture of growth and early life-history transitions in anadromous and derived freshwater populations of steelhead. J Fish Biol 65(Suppl A): 286–307

Thurow RF, Lee DC, Rieman BE (1997) Distribution and status of seven native salmonids in the interior Columbia River Basin and portions of the Klamath River and Great Basins. North Am J Fish Manag 17:1094–1110

Weigel DE (2013) Colonization of steelhead (*Oncorhynchus mykiss*) after barrier removal in a tributary to the Methow River, WA. Ph.D. Thesis. University of Idaho, Moscow

Weigel DE, Sorensen PW (2001) The influence of habitat characteristics on the longitudinal distribution of brook, brown and rainbow trout in a small Midwestern stream. J Freshw Ecol 16:599–613

Weigel DE, Connolly PJ, Martens KD, Powell MS (2013) Colonization of steelhead in a natal stream after barrier removal. Trans Am Fish Soc 142:920–930

Wilson GA, Rannala B (2003) Bayesian inference of recent migration rates using multilocus genotypes. Genetics 163:1177–1191

Wright S (1943) Isolation by distance. Heredity 28:114–138