AN ABSTRACT OF THE THESIS OF

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Abstract approved:

Jason B. Dunham

Partial migration is a common migratory behavior where some individuals in a population migrate and others do not. Patterns of partial migration can vary dramatically, especially for species that inhabit a wide range of environments. I described and predicted spatial variation in marine migration (anadromy) of female *Oncorhynchus mykiss* (steelhead and rainbow trout) in the John Day River catchment basin, Oregon. This large catchment (20,500 km^2), where *O. mykiss* is known to exhibit partial migration, encompasses a broad range of environmental conditions. I collected 149 juvenile *O. mykiss* across 72 sites and identified locations used by anadromous females by assigning maternal origin (anadromous versus non-anadromous) to each juvenile. These assignments used comparisons of strontium to calcium ratios in otolith primordia and freshwater growth regions to indicate maternal origin. Individuals within sites were more likely to have the same maternal origin than expected at random (χ^2 test, $P < 0.001$). I used logistic regression to predict probability of anadromy among sites in relation to stream size (as indicated by mean annual runoff). Stream size and maternal origin for single fish collected from 69 sites were used to construct a predictive model. I examined the ability of this model to predict new individuals at 47 of these sites (where a second fish was collected) using a variety of diagnostics, including kappa statistics and receiver operating characteristic curves. The model predicted anadromy in this second set of individuals with a moderate level of accuracy (e.g. 68% correctly predicted with a 0.5 classification threshold). Residuals from the models were not spatially autocorrelated, as indicated by Mantel tests. This result also suggested that remaining variability in the expression of anadromy was due to localized influences, as opposed to broad-scale gradients unrelated to stream size. The importance of stream size implies that occurrence of migratory females was related to environmental variability, but stream size is an indicator of many potential processes, and I was unable to identify a specific likely mechanism. However, I was able to demonstrate 1) that it is possible to predict the probability of anadromy across broad environmental gradients, and 2) the validity of a sampling approach that minimizes the need for sacrificial sampling of individuals. These results are important for the management of *O. mykiss* because anadromous individuals (steelhead) within the John Day River watershed are listed as a threatened species, and it is difficult to discern steelhead from non-anadromous individuals (rainbow trout). My results provide managers with the first broad-scale description and prediction of locations supporting anadromy, and provide a broad template that can guide future habitat restoration, monitoring, and research to better manage and understand the expression of anadromy in *O. mykiss*.

Description and Prediction of Broad-scale Spatial Variability in Expression of Anadromy in Female *Oncorhynchus mykiss* in the John Day River, Oregon, USA

by

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Justin S. Mills, Author

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CONTRIBUTION OF AUTHORS

Jason B. Dunham was involved in the study design, data analysis, and editing of all sections of this manuscript. Gordie Reeves and Chris Jordan were involved in the study design and planning.

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CHAPTER 1 – GENERAL INTRODUCTION

Migration is common among animals, often encompassing diverse migratory behaviors among and within species (Dingle 1996; Dingle and Drake 2007). Within migratory species, some individuals may migrate while others remain to complete their life cycle in their respective natal habitats; a condition often termed “partial migration.” Partial migration has been described in diverse animal taxa including insects, birds, mammals, and fish, and encompasses a range of variable individual- and population-level behaviors (reviewed in Swingland 1983; Kaitala et al. 1993). Factors influencing partial migration vary widely and derive from the costs and benefits of migration versus residency. Among individuals, alternative migratory behaviors affect survival and reproduction, and ultimately individual fitness (Cox 1968; Lundberg 1988; Kaitala et al. 1993). Environments providing a wide range of conditions can favor alternative migratory behaviors through time or among localities (Kaitala et al. 1993; Hendry et al. 2003). Accordingly, broad-scale spatial variability in these factors can manifest as spatial patterns of differential migratory tendencies (Olsson and Greenberg 2004). Furthermore, the fitness consequences of migratory behaviors can differ dramatically between the sexes, since males and females often face contrasting selection pressures (Jonsson and Jonsson 1993; Quinn and Kinnison 1999; Hendry et al. 2004; Neville et al. 2006b).

In this study, we examined the expression of marine-migratory or anadromous migrations in *Oncorhynchus mykiss* within the John Day River, Oregon. Individuals of this species exhibiting anadromy are referred to as steelhead trout whereas those residing within freshwaters throughout their life cycle are considered rainbow trout. The former is listed as a threatened species (Busby et al. 1996; Cooney 2005) and is the focus of this study.

CHAPTER 2 – DESCRIPTION AND PREDICTION OF BROAD-SCALE SPATIAL VARIABILITY IN EXPRESSION OF ANADROMY IN FEMALE *ONCORHYNCHUS MYKISS* IN THE JOHN DAY RIVER, OREGON, USA

INTRODUCTION

Partial migration is common in salmonid fishes (Hendry et al. 2003), and includes relatively short migrations between freshwater habitats and long-distance migrations to the ocean. Spatial variability in migratory behavior of individuals occurs in many salmonids. For example, brown trout (*Salmo trutta*) (Olsson and Greenberg 2004), Dolly Varden char (*Salvelinus malma*) (Koizumi et al. 2006), and rainbow trout/steelhead (*Oncorhynchus mykiss*) (McMillan et al. 2007; Narum et al. 2008a) exhibit a basic pattern of increasing tendency for residency with increasing upstream distance. Migratory behavior is variably heritable (e.g., brook trout, *S. fontinalis*) (Thériault et al. 2007), but in all species it appears to be a flexible response to variability in environmental conditions (Jonsson and Jonsson 1993; Aubin-Horth et al. 2006). The implication is that environmental variability could provide a useful means for predicting the distribution of migratory behaviors across a landscape.

The tendency for migration in salmonids is sex-dependent, as males and females have substantially different costs and benefits of anadromy (Jonsson and Jonsson 1993; Northcote 1997; Hendry et al. 2004). Males benefit less from greater size resulting from anadromy than females (Northcote 1997), and male *O. mykiss* and other salmonids commonly adopt non-migratory tactics such as early maturation and sneaking (Fleming and Reynolds 2003; Esteve 2005; McMillan et al. 2007). Among partially migratory salmonids, females tend to predominate among migrants (Jonsson and Jonsson 1993; Thériault and Dodson 2003; Koizumi et al. 2006). On their return from the ocean, females may home to specific spawning habitats, whereas males may exhibit little spatial patterning (Neville et al. 2006a). Given these differences between sexes, it seems appropriate to consider expression of migratory behavior in salmonids separately for males and females, at least when considering specific populations or localities.

Current analytical techniques favor examination of female anadromy. Otolith microchemistry provides a means for determining the maternal origin of individuals through comparing the ratio of strontium (Sr) to calcium (Ca) within different regions of their otoliths (Kalish 1990; Volk 1999). Otoliths are primarily composed of calcium carbonate ($CaCO_3$), and Sr is substituted for Ca relative to the concentration in the environment (Kalish 1990). Freshwater Sr concentration tends to be much lower than seawater. By comparing Sr to Ca ratios in otolith primordia and subsequent freshwater growth regions it is possible to assign individuals to mothers that resided in marine or freshwater environments. This is because otolith primordia begin forming during the egg stage and strongly reflect the Sr:Ca ratio of the maternal environment during formation of yolk precursors (Kalish 1990). Zimmerman and Reeves (2002) successfully used this method to determine maternal life-history of juvenile *O. mykiss* progeny of both anadromous and non-anadromous females in the Deschutes River, Oregon.

Here, we examine whether there is predictable broad-scale variation in female anadromy of *O. mykiss* within the John Day River, a large river basin located in northeast Oregon. We sampled juvenile *O. mykiss* from streams throughout the John Day basin and used otolith microchemical analysis to determine the migratory life histories of their mothers. By assuming juveniles were captured close to their natal site and that their mothers spawned near their respective natal sites, we were able to use otolith analysis to test whether female anadromy varied across the landscape and if it could be predicted from patterns of environmental variability. Specific objectives of this study were to: 1) establish accurate measures of female anadromy across a broad spatial area with a protocol that minimized sacrificial sampling; 2) predict patterns of female anadromy in relation to broad-scale environmental gradients; and 3) assess the potential importance of local variability in determining the expression of anadromy.

METHODS

Study area

The John Day River (45°44'N, 120°39'W) is a free-flowing tributary to the Columbia River draining about 20,500 km^2 of north-central Oregon (Figure 2-1). Elevation in the catchment basin ranges from 80 m near the mouth to 2,700 m in the headwaters, and annual precipitation varies from about 25 cm to 145 cm (Anonymous 2006a). Most precipitation occurs during the winter and spring. Peak stream flows tend to be in the spring, linked to high rainfall and snowmelt. Climate, vegetation, geology, and hydrology vary widely across the basin, including heavily wooded ponderosa pine (*Pinus ponderosa*) forests in the uplands of the northeastern part of the basin, high desert in the central basin, and the Ochoco and Strawberry Mountain ranges along the southern edge of the basin.

Both anadromous and non-anadromous *O. mykiss* occur throughout the basin, though spawning and rearing of both is generally restricted to areas with relatively cool water, away from the lower river mainstem. Other salmonine species in the basin include Chinook salmon (*O. tshawytscha*), westslope cutthroat trout (*O. clarkii lewisi*), bull trout

(*Salvelinus confluentus*), and introduced brook trout (*S. fontinalis*). To reduce confusion, hereafter "*O. mykiss*" is used to refer to the species as a whole and the common names are used for the migratory life histories: steelhead for anadromous individuals and rainbow trout for non-anadromous individuals (Nelson et al. 2004).

Study design and data collection

In this study, we characterized occurrence of anadromy by determining the maternal origins of juvenile *O. mykiss* as an indicator of the presence of spawning steelhead (i.e., identifying individuals with anadromous mothers). We focused our sampling at sites throughout the study area used for monitoring of steelhead by the State of Oregon (J. Ruzycki, Oregon Department of Fish and Wildlife, personal communication). These sites (Figure 2-1) were selected using generalized random tessellation stratified sampling (Stevens and Olsen 2004). This sampling process uses hierarchical randomization to produce a spatially balanced equal probability sample, optimized for efficient environmental sampling. Our sampling frame included only streams appearing on a 1:100,000-scale digital streams layer that were accessible to anadromous fish and presumed to be suitable for use by *O. mykiss* by local fisheries biologists (Lloyd and Bowers 2002, 2004). We did not sample stream reaches known to have populations of cutthroat trout due to the difficulty of differentiating their juveniles from *O. mykiss* juveniles (Pollard et al. 1997).

Whenever possible we collected two fish by electrofishing at each site between June–September 2007, one between 50 and 75 mm fork length (FL) and the other between 75 and 100 mm FL. The separate size ranges were collected to reduce the chance of sampling siblings and to avoid bias due to variable spawn timing (Zimmerman and Reeves 2000) or growth rate (Chernoff and Curry 2007) related to maternal origin (anadromous vs. non-anadromous mothers). If either size was unavailable after 30-45 minutes of sampling, we substituted one from the other size range, or a fish over 100 mm FL if no others were captured. We killed each fish with an overdose of tricaine methanesulfonate (MS-222) and removed both sagittal otoliths, storing them dry in polyethylene vials until returning to the lab, where the vials were filled with ethanol (95% EtOH, ACS).

We prepared otoliths following methods in Zimmerman and Reeves (2000) and Donahoe et al. (2008). We cleaned and mounted at least one otolith from each fish sulcus side up on glass microscope slides, or a cover slip attached to a slide, with Crystal Bond 509 thermoplastic resin (Structure Probe, Inc, West Chester, Pennsylvania[1]). We ground them on 1200 and 2000 grit aluminum-oxide sandpaper to the level of the primordia, and then polished them with a slurry of 0.05 µm alumina paste in deionized water. After polishing, we aged each fish by examination of otolith banding. We mounted groups of polished otoliths on petrographic slides for microprobe analysis and washed each slide with deionized water and mild detergent before air drying and coating them with a 40 nm carbon layer.

Elemental analysis was conducted with a Cameca SX-100 wavelength dispersive electron microprobe (Cameca SAS, Gennevilliers, France). For all analyses, the incident

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[1] Use of trade or firm names is for reader information only and does not constitute endorsement of any product or service by the U.S. Government

electron beam had an accelerating voltage of 15 kV, a 50 nA current, and a 10 µm beam diameter. We measured Sr and Ca simultaneously for all otoliths, using strontianite ($SrCO_3$ – USNM R10065) and calcite ($CaCO_3$ – USNM 136321) as standards, respectively. Sr was measured using a large TAP and regular TAP crystal simultaneously; Ca was measured with a large PET crystal. Counting time for the first 42 otoliths was 60 s on peak, 60 s on background, and 40 s on peak, 40 s on background for the remainder. The average lower detection limit for the 60 s counting time for Sr was 140 ppm, and 171 ppm for 40 s. On these otoliths, we probed three (on the 60 s otoliths) or four points (on the 40 s otoliths) in the maternal growth region near the primordia, and an equal number of points in the freshwater growth region along a roughly proximal transect. We discarded probed points with total weight percent below 90% or above 110%.

Some freshwater areas have high Sr:Ca ratios that may obscure maternal origin (Rieman et al. 1994; Donohoe et al. 2008). To avoid misidentification of maternal origin resulting from unknown freshwater microchemistry, we tested Sr:Ca ratios in water samples from juvenile sampling sites. We collected water samples at all sample sites except those with restricted access and those directly upstream of another site where water was collected, with no major tributaries in between. Similar to the methods of Wells et al. (2003), we collected two water samples and vacuum-filtered them with 0.45-µm polyethersulfone membranes pre-washed with deionized water, then stored 125 ml of each sample in acid-rinsed HDPE bottles pre-preserved with 1 ml ultrapure nitric acid. After transporting samples from the field, we stored samples in a 40^{o} cold room until analysis with a Varian AA240FS flame atomic absorption spectroscope (Varian, Inc, Palo Alto, California). We calculated mean ionic concentration and molar ratios of Sr:Ca for each site, and compared the results for each site to an anadromy detection threshold of 4.75 mmol/mol: roughly half the Sr:Ca ratio in the Pacific Ocean (de Villiers 1999; Zimmerman 2005; Donohoe et al. 2008). We did not use fish samples from sites with water Sr:Ca ratios over this threshold.

Determination of maternal origin

We assigned maternal origin to each fish by comparing Sr:Ca ratios in the maternal and freshwater growth regions of each otolith. A fish was determined to be of anadromous maternal origin if the Sr:Ca ratio in the maternal growth region was significantly higher than in the freshwater growth region, based on a one-tailed *t*-test with $\alpha = 0.05$. We generally included in our analysis only those juveniles in their first or second summer (age 0+ or 1+, respectively) after emergence to avoid potential bias from outmigrating smolts and the effects of within-basin movement of juveniles (Tattam 2006).

Data analysis

We first tested for non-random distribution of individuals with different maternal origins within sites, to evaluate the degree to which juveniles with similar life histories were clustered within samples. Then, we divided our sample data into two sets by randomly drawing individuals from all sites where more than one individual was collected. With these data we developed a predictive model of the relationship between stream size and the probability of anadromy at each site. Finally, we tested for spatial autocorrelation to determine if the variability remaining in the model residuals was related to broad-scale gradients unrelated to stream size or more likely a result of local conditions.

Tests for non-random distribution of life histories

With only two individuals sampled at each site (to minimize the number of sacrificial samples), we could not estimate proportions of juveniles of anadromous versus freshwater maternal origin. Given that the fecundity of an anadromous female exceeds that of a freshwater resident female by an order of magnitude (Jonsson and Jonsson 1993), we assumed that sites where steelhead females had spawned would harbor a relatively large number of their offspring relative to those from rainbow trout females. This also assumes that numbers of steelhead and rainbow trout females are not drastically different (e.g., a large number of rainbow trout females could equal the production of offspring by only a few anadromous females). Under this assumption, we expected that samples of two juveniles would be more likely to contain two steelhead progeny where steelhead females were present. Accordingly, we expected that relatively few sites would harbor a mix of rainbow trout and steelhead offspring (one of each in our sample of two). Alternatively, if rainbow trout and steelhead females were spatially segregated, we expected a similar pattern: clustering of steelhead and rainbow trout offspring sampled at sites. If neither of these processes was important, we expected to find random associations or lack of clustering between juveniles with different maternal origins.

We tested for non-random distribution of juveniles with contrasting maternal origins within sites by using a χ^2 test. This test compared the observed and expected frequencies of sites where juveniles shared maternal origin and those where there was one of each. We estimated expected frequencies based on the null hypothesis of random distribution of juveniles across all sites. Table 2-1 shows the calculations used to derive observed and expected frequencies. We calculated χ^2 as follows:

$$\chi^2 = \sum_{i=1}^{n} \frac{(O_i - E_i)^2}{E_i}$$

where O represents the observed frequency, E represents the expected frequency, and n represents the number of possible outcomes: two, in this case.

Prediction of anadromy

To relate occurrence of steelhead to broad-scale environmental gradients, we developed a model to predict the probability of individuals with anadromous maternal origin in relation to stream size. We tested model accuracy with several cross-validation techniques. Stream size, indicated for this study by mean annual runoff (m^3/s), is an indicator representing a variety of associated environmental gradients, described below. We estimated mean annual stream runoff (m^3/s) for the 1:100,000-scale NHDPlus (Anonymous 2005) reach containing each sampling site. Because measured stream runoff information was not available for most sites, we used a regression model for variable flow regime streams developed by Sanborn and Bledsoe (2006). This model estimates runoff based on basin area contributing to the sampling site stream reach (km^2) and area-weighted mean annual precipitation (mm) across the basin (Anonymous 2006b).

For the purposes of model development and evaluation we divided the fish data into a fitting data set—containing one fish drawn randomly from each site—and a validation set containing the remaining fish from each site. At sites with only one fish available, that fish was only included in the fitting data set. To predict probability of anadromy among sites in relation to stream size (as indicated by mean annual runoff), we developed a binary logistic regression model and fit it with the fitting data set. Natural $\log_e$ transformation of mean annual runoff resulted in the best fitting models (using the score statistic) (Hosmer and Lemeshow 2000). Unless further specified, all further reference to this variable refers to the transformed value. We tested variable significance with Wald's X^2, and model significance with the likelihood ratio chi-square, using $\alpha = 0.05$ for both tests.

The models were evaluated for sensitivity and specificity relative to their ability to make predictions about presence or absence of anadromy. It is important at this point to clarify that we could not interpret absence of anadromy as presence of residents, due to asymmetries in probability of sampling residents described above (see Tests for non-random distribution of life histories above). We used with receiver-operating characteristic (ROC) plots and area-under-the-curve (AUC) analysis with a 10,000-iteration bootstrapping algorithm to estimate 95% confidence intervals for the AUC (Gönen 2007). To aid in predicting the occurrence of anadromy, we also determined the classification threshold for each model that maximized kappa (Manel et al. 2001; Freeman and Moisen 2008).

Spatial variability of predictions

Unexplained or residual variability in the distribution of anadromy remained after our model analysis, so we tested for spatial autocorrelation of model residuals as an indicator of spatial dependence remaining after the influence of stream size was accounted for (Legendre 1993). If we omitted influential broad-scale landscape variables that were unrelated to stream size from the model, spatial autocorrelation could result from the effects of gradients of conditions among sites. This result would also indicate non-independence among observations, which would violate a key assumption of logistic regression and result in inflated model degrees of freedom. Lack of spatial autocorrelation would support the assumption of independence and suggest that variability in local conditions is responsible for model residuals.

We conducted Mantel tests to determine if model residuals were spatially autocorrelated. First, we calculated pairwise Euclidean geographic distances between sampling sites using the ArcGIS Spatial Analyst extension, and pairwise stream network distances using the 1:100,000-scale medium-resolution National Hydrography Dataset (NHD). We used the PASSaGE software package (Rosenberg 2005) to generate distance matrices for model residuals and perform Mantel tests. We used both Euclidean distances and pairwise stream network distances because both could indicate underlying gradients that directly or indirectly influence the expression of anadromy. For example, geology, terrestrial vegetation, topography, or climate could be associated more closely with Euclidean than stream network distances. Alternatively, stream network distances should be more strongly associated with connectivity of locations within streams due to transport of materials within streams or fish movement.

Significance for Mantel tests was determined using a permutation test that held one matrix constant while randomly reordering the other, then calculating the correlation coefficient. This was repeated 9,999 times for each model being tested and the correlation coefficient for the measured data was compared to the null distribution to determine significance ($\alpha = 0.05$, one-tailed). A significant result would indicate the model residuals were spatially autocorrelated in relation to Euclidian or stream network distance.

RESULTS

Determination of maternal origin

We determined maternal origin for 149 juveniles at 72 sites (Figure 2-2). The sites we sampled were almost entirely on federal lands, due to limited access to private land. Because of this constraint, we collected few samples from the interior and lower mainstem portions of the river basin near the mouth.

Ninety-one (60.3%) were steelhead progeny and 58 (39.7%) were rainbow trout progeny. Steelhead progeny occurred at 52 of 72 sites. Overall, most juveniles were < 2 years old (Table 2-2), but at three sites we collected only fish > 2 years old, so we excluded those sites from further analysis. There was clear separation in the distribution of fork length between ages (Figure 2-3). The proportion of steelhead progeny was not different between ages (for fish under 3 years old Pearson $\chi^2 = 0.86$, $df = 2$, $P = 0.65$).

The mean water Sr:Ca ratio across all sampling sites (*n* = 64) was 2.58 mmol/mol (95% CI 2.36, 2.81; Figure 2-4). Increasing water Sr:Ca ratio was correlated with increasing longitude (Spearman's $\rho = 0.47$, $N = 116$, $P = 0.34$) One site (#115, on Hideaway Creek) had a mean Sr:Ca ratio of 5.61, high enough to warrant exclusion of otolith microchemistry results from this site (even though Sr concentration was below reliable detection limits).

Tests for non-random distribution of life histories

When considering only sites with two juveniles < 2 years old (*n* = 47 sites), the maternal life histories of both juveniles tended to be same more often than expected from the overall proportion of maternal origins (Table 2-3; $\chi^2 = 11.15$, $df = 1$, $P < 0.001$,). Both juveniles had the same maternal life histories at 36 of these sites.

Prediction of anadromy

Increasing stream size was associated with increasing probability of anadromy (Figure 2-5). The logistic regression model using stream size correctly classified 78% of the observations of anadromy and non-anadromy in the fitting data set (*n* = 69; Table 2-4) and 68% of the validation data set observations (*n* = 47; Table 2-5) with a probability cutoff of 0.50. At this probability threshold, the model correctly classified 32 of 40 observations of anadromy (80%) and 21 of 29 observations of non-anadromy (72%) for the fitting data. The optimal threshold for the fitting data (0.51, $K = 0.56$) was substantially lower than that of the validation data (0.62, $K = 0. 32$). There was no correlation between absolute value of model residuals and fish length (Spearman's $\rho =$ 0.09, $N = 116$, $P = 0.34$; Figure 2-6) or fish age (Spearman's $\rho = 0.058$, $N = 116$, $P =$

0.54). The ROC area-under-the-curve (AUC) score was high for the fitting data set (0.82; 95% confidence interval 0.71, 0.91), but moderate for the validation data set (0.69; 95% CI 0.53, 0.84; Figure 2-7).

Spatial variability of predictions

Mantel tests with Euclidian and stream network measures of pairwise geographic distances indicated that model residuals were not spatially autocorrelated among sites (Table 2-6). Plots of pairwise model residual distances in relation to geographic distances showed no obvious spatial patterns (Figure 2-8), nor did Mantel correlograms (Figure 2-9). Thus, the stream size gradient included in the predictive model accounted for the broad-scale variation in the expression of anadromy. However, there was remaining unexplained variability, pointing to the potential importance of local factors influencing expression of anadromy.

DISCUSSION

We found that female anadromy occurred widely across the John Day River basin, and that variation in stream flow predicted much of the spatial pattern of female anadromy. Our analysis of otolith and water microchemistry successfully identified maternal life histories at almost all sites. Within sites, both juveniles had the same maternal origin more frequently than expected, though we were not able to estimate the proportion of steelhead or rainbow trout progeny overall. A logistic regression model predicting probability of anadromy based on stream size showed moderate accuracy as indicated by cross-validation. Lack of spatial autocorrelation among model residuals indicated the simple stream size model explained most variability in anadromy at the broad spatial scale we sampled, implying remaining variation is due to local conditions and associated influences.

Our sampling approach was intended to characterize female anadromy across a broad spatial range while minimizing sacrificial sampling of a threatened species. By foregoing more intensive sampling at each site, we were able use a relatively small total sample size to develop a robust predictive model across a broad spatial extent encompassing large environmental gradients. Our intent was to describe and predict the occurrence of anadromy, rather than to predict the prevalence of steelhead and rainbow trout at each site. Estimated proportions of steelhead offspring are unlikely to correspond to the proportion of steelhead females supported by the site; fecundity of large steelhead may be an order of magnitude greater than small rainbow trout (Jonsson and Jonsson 1993).

Maternal life history

Microchemical analysis of freshwater Sr:Ca ratios supported broad-scale use of otolith Sr:Ca ratios to identify maternal origin in similar landscapes. The strong spatial gradient of increasing Sr:Ca concentration with increasing latitude and longitude likely reflects underlying geologic gradients, a key concern when we began our sampling effort. However, only one site in our study was rejected for having a Sr:Ca ratio likely to mask maternal origin, and we did not have difficulty identifying the offspring of stream-maturing fish. Other studies observed similar spatial variability in freshwater Sr:Ca ratios (Rieman et al. 1994; Wells et al. 2003; Donohoe et al. 2008). This variability implies the need for sample validation, but the paucity of sites with unacceptable Sr:Ca ratios suggests that a subsample of sites may be adequate to validate an extensive sampling effort.

Relatively few sites yielded a mix of steelhead and rainbow trout offspring, suggesting steelhead offspring numerically dominated the sites where they were present or that there was spatial separation between steelhead and rainbow trout spawning. It is difficult to identify which scenario is more plausible without further sampling. In either case, our small sample may not have detected anadromy at all sites where steelhead progeny were present. However, we were still able to estimate the relative (not absolute) probability of occurrence of anadromy within our sample (Johnson et al. 2006).

The relationship between maternal origin of juveniles and their subsequent migratory behavior (Tattam 2006) is unclear, but by sampling fish below 100 mm and only using 0+ and 1+ age fish, we minimized the bias associated with potential emigration of 2+ fish as steelhead smolts from our sampled locations. Similarly, we found no bias toward or against anadromous origin associated with fish size, though other work suggests that offspring of anadromous fish would have higher growth rates and therefore greater size-at-age (Chernoff and Curry 2007).

When analyzing the relationship between anadromy and environmental variability, we assumed the juveniles were captured within the stream reach where their mothers spawned. Whereas some *O. mykiss* may migrate long distances in freshwater (Tattam 2006), there is little evidence that the < 2 year old juveniles used in this study would do so (Kahler et al. 2001). Juvenile density is correlated to redd density in both *S.*

salar (Beland 1996) and *S. trutta* (Beard and Carline 1991), indicating limited movement from natal areas is a reasonable assumption. During the summer juvenile trout may move frequently within a stream reach, but they are unlikely to move more than a few hundred meters (Kahler et al. 2001). *O. mykiss* juveniles may move downstream from spawning areas in substantial numbers in the fall or spring after their first summer (Van Dyke et al. 2001), but many juveniles return upstream seasonally (Tattam 2006). Therefore, we conclude that movement of juvenile *O. mykiss* is unlikely to affect our analysis of the distribution of anadromy, and that sampling bias by size or age is probably negligible.

Predicting probability of anadromy

Female anadromy was predictable across the study area, and we found no evidence of serious bias from assignment of maternal origin, juvenile movement, or sampling that could be attributed to our approach. However, it is important to clarify that model predictions should be interpreted as indicating the relative probability of anadromy. Due to the chance that we failed to detect anadromous individuals when indeed they were present at some sites, the absolute probability of anadromy overall is likely underestimated and thus we can only make inferences about relative probabilities (Johnson et al. 2006). For example, at sites where the two sampled juveniles were of different maternal origin, only one data set indicated anadromy at a site, thus the other set is known to under-represent anadromy. Furthermore, we cannot infer anything about the relative or absolute probability of occurrence of freshwater resident individuals. These issues likely contributed to the variable model performance between the fitting and validation data, as these mixed sites were randomly distributed among the data sets.

Regardless, the model explained much of the spatial variability in expression of anadromy and provides a useful picture of the occurrence of this life history across a large stream network.

Processes affecting anadromy

Based on work with other salmonines (e.g., Jonsson and Jonsson 1993), it is likely that expression of anadromy in *O. mykiss* in our system is driven by environmental variation that is manifested across a range of spatial and temporal scales. Our model based on stream size used data from a short temporal scale: sampling within one year and confined largely to two juvenile cohorts. Furthermore, whereas stream size was a useful predictor of anadromy, the exact processes associated with stream size, and ultimately anadromy, remain unclear. Stream size is an indicator of a range of ecological and physical processes (Vannote et al. 1980). It is often associated with gradients of hydrologic and biological organization, but is only loosely linked to the physiological processes governing migration. For example, large fish are less vulnerable to predation in large streams and deep pools (Power 1984; Quinn and Kinnison 1999), so large anadromous fish may avoid spawning in small or shallow streams. Furthermore, stream discharge can be used to directly estimate sediment transport (Barry et al. 2004), which is a key component of stream habitat disturbance regimes and development of in-stream habitat (Reice et al. 1990; Reeves et al. 1995). Patterns of disturbance by sediment transport may govern broad-scale distribution of steelhead spawning (Montgomery et al. 1999), providing a simple process-based explanation to the relative effectiveness of our model. In addition, gradients of stream size may also match gradients in water temperature regime (Torgersen et al. 1999). This has direct bioenergetic consequences for growth, survival, and smolting (Thorpe and Metcalfe 1998; Tattam 2006; Madrinan 2008), as well as affecting how fish communities respond to local geomorphology (Torgersen et al. 2006).

Broad-scale environmental gradients were predictably associated with the expression of anadromy, but we also found evidence to suggest the importance of local influences. Our analysis of spatial autocorrelation of the residual variability in anadromy after removing the influence of stream size provided no additional evidence of the influence of spatial gradients, leaving the possibility that localized conditions may play an important role. Within localities, it is likely that variability in thermal conditions, food availability, and population density could be important. For example, brown trout given restricted food rations develop migratory morphology more frequently than those on a more liberal diet (Olsson et al. 2006; Wysujack et al. in press). Brown trout in high density stream segments migrated at a much higher rate than those in segments with low population density (Olsson and Greenberg 2004). Ecological processes and organisms' responses to them are scale-dependent (Wiens 2002), and it is impossible to fully understand and describe these relationships without multi-scale sampling and modeling beyond the scope of this study (Wiens 2002; Boyce 2006).

Research implications

Our predictive model performed well with the timeframe of this study, but interannual variability in spawner distribution and reproductive success may have important effects on model predictions and the effectiveness of a simple model. A limited window of interannual variability was captured in our consideration of 0+ and 1+ age fish at each site, but our study lacked the temporal depth needed to capture multi-year variability. The occurrence of anadromy could vary from year to year with spawner abundance and habitat availability. In years of low abundance, spawning may be restricted to a short time period at high-quality spawning sites, becoming more dispersed in time and space as abundance increases, as is the case with other salmonines (Isaak et al. 2003; Isaak and Thurow 2006). Furthermore, when the steelhead run size is small the reproductive contribution from rainbow trout may increase to keep the overall steelhead effective population size (N_e) stable (Araki et al. 2007). Estimated steelhead spawner abundance in the upper John Day River has fluctuated from almost 10,000 to below 1000 since the mid-1980s (Good et al. 2005). About 8,700 steelhead spawned in the John Day River in 2007, up from about 5,300 in 2006 and about 3,700 in 2005 (James et al. 2007), so our results reflect relatively high spawner abundance. Accordingly, continued sampling at these and other sites, with better understanding of the probability of detection of anadromy under varying conditions, could lead to a more robust model that would transfer well across years and to other river basins.

Our model provides a basic tool for predicting anadromy, but conservation efforts will benefit from a more comprehensive strategy that integrates other lines of evidence into the overall understanding of the occurrence of steelhead (Peterson and Dunham 2003). These could include additional indirect techniques for assessing anadromy, such as microchemical sampling or genetic studies. However, lethal sampling techniques severely restrict the number of individuals on which we can conduct otolith analysis and preclude studying individuals over their entire lifespan. Non-lethal microchemical analysis of scales is useful for assessing lifetime patterns of adult migration (Courtemanche et al. 2005; Courtemanche et al. 2006), but juvenile salmonids do not begin to grow scales until after they emerge from the gravel to begin feeding (Quinn 2005) and any maternal strontium signature is likely to be insubstantial. Genetic techniques may be useful where there is evidence for reproductive isolation (e.g., Narum et al. 2008b) or where entire populations can be sampled (Araki et al. 2007). However, there is little evidence for such isolation or genetic distinctiveness of life histories in similar populations elsewhere (McCusker et al. 2000; Olsen et al. 2006; McPhee et al. 2007). In addition to inferences based on juveniles, direct observations of redds or spawning adults may provide additional opportunities to quantify the occurrence of anadromy (e.g., Zimmerman and Reeves 2000; Gallagher et al. 2005; Crawford et al. 2006).

CHAPTER 3 – GENERAL CONCLUSIONS

Results of this study have important implications for the management and conservation of *O. mykiss*. Within the John Day River basin, steelhead are federally protected as threatened, but rainbow trout are not (Busby et al. 1996; Cooney 2005). The *O. mykiss* population of the John Day River basin produces one of the last remaining intact wild populations of steelhead in the Columbia River basin, with little historical hatchery influence (Howell et al. 1985; Busby et al. 1996). Planning for conservation and recovery depends on effectively planning and prioritizing activities and resources (Roni et al. 2002; Beechie et al. 2003). For example, managers could use results of this work to target their activities more effectively in areas supporting anadromy within the John Day basin. Alternatively, if the uncertainty in predictions from the model presented herein is a concern, additional work could focus on refining model predictions (e.g., using Bayesian posterior probabilities to incorporate additional lines of evidence) (Peterson and Dunham 2003) or on understanding processes that directly influence expression of anadromy (Jonsson and Jonsson 1993; Hendry et al. 2004). This uncertainty about patterns and processes also relates to the design of monitoring programs focused on quantifying numbers of juvenile steelhead in freshwater, as well as estimating juvenile to adult survival or rates of return. We were not able to address the absolute proportion or occurrence of freshwater resident *O. mykiss* in this study, and thus inferences about anadromy based on numbers of *O. mykiss* alone remain uncertain. Finally, it is worth noting that this study focused on factors influencing anadromy in one sex: females. We suspect that expression of anadromy in males is driven by a different suite of evolutionary pressures (e.g., Fleming 1998; McMillan et al. 2007; Wysujack et al. in press).

In conclusion, we find that variable expression of anadromy in *O. mykiss* is associated with broad-scale environmental factors. Variability remaining after accounting for these factors that suggests the importance of localized environmental factors, but much remains to be learned. We can look to other salmonines for evidence of general processes likely to influence the expression of anadromy (e.g., Jonsson and Jonsson 1993; Hendry et al. 2003), but the influence of specific environmental factors on the expression of anadromy in *O. mykiss* is likely to be a fruitful area for future investigation.

TABLES

Table 2-1 Calculations used to conduct χ2 test for clustering of juvenile *O. mykiss* maternal life histories within sites in the John Day River in 2007. Only sites with two juveniles > 2 years old were included. The observed number of sites where both individuals were rainbow trout or steelhead progeny is represented by RbtRbt or StSt, respectively, and the number of sites where one individual was each type is represented by RbtSt. The expected proportions of each combination under the null hypothesis of no association were calculated from the observed proportions of rainbow trout and steelhead progeny across these sites (Rbt and St, respectively), where n is the number of sites.

Combination	Observed	Expected
Same maternal type	RbtRbt + StSt	$(\mathrm{Rbt}^2 + \mathrm{St}^2) \times n$
Different maternal type	RbtSt	$2 \times \mathrm{Rbt} \times \mathrm{St} \times n$

Table 2-2 Count, mean lengths (mm; with 95% confidence intervals), and proportion of steelhead progeny (P_a) among all juveniles analyzed (n = 149) from the John Day River in 2007.

			95% CI			95% CI	
Age	n	Mean length (mm)	Lower	Upper	P_a	Lower	Upper
0	48	56.1	53.6	58.5	0.69	0.55	0.80
1	74	79.4	76.4	82.3	0.55	0.44	0.66
2	24	94.0	88.6	99.4	0.63	0.43	0.79
3	3	85.7	45.7	125.6	0.67	0.20	0.94

Table 2-3 Count (proportions) of combinations of juvenile *O. mykiss* maternal life histories at sites (n = 47 sites) in the John Day River with two juveniles < 2 years old collected in 2007.

Combination	Observed	Expected
Same maternal type	36 (0.77)	24.6 (0.52)
Both steelhead	23 (0.49)	17.3 (0.37)
Both rainbow trout	13 (0.28)	7.3 (0.15)
Different maternal type	11 (0.23)	22.4 (0.48)

Table 2-4 Results from logistic regression analysis of the effects of mean annual runoff on the probability of maternal anadromy for fish in the fitting data set.

			95% CI (Wald's)						95% CI (Wald's)	
Predictor	β	SE	Lower	Upper	Wald's χ^2	df	*P*	Odds ratio	Lower	Upper
Intercept	2.90	0.79	1.34	4.46	13.34	1	0.0003			
Mean annual runoff	1.24	0.33	0.58	1.90	13.71	1	0.0002	3.45	1.79	6.66

Table 2-5 Results from logistic regression analysis of the effects of mean annual runoff on the probability of maternal anadromy for juvenile *O. mykiss* in the validation data set.

			95% CI (Wald's)						95% CI (Wald's)	
Predictor	β	SE	Lower	Upper	Wald's χ^2	df	*P*	Odds ratio	Lower	Upper
Intercept	1.57	0.63	0.33	2.82	6.17	1	0.013			
Mean annual runoff	0.56	0.26	0.04	1.08	4.45	1	0.035	1.75	1.04	2.94

Table 2-6 Mantel test matrix correlations of pairwise differences in model residuals in relation to two measures of between-site distance. Probabilities are for a one-tailed test (to test alternative hypothesis that geographically proximate sites are more similar).

	Stream network distance		Euclidean distance	
Data set	*r*	*P*	*r*	*P*
Fitting data	0.02	0.31	-0.03	0.71
Validation data	0.01	0.38	-0.01	0.58

FIGURES

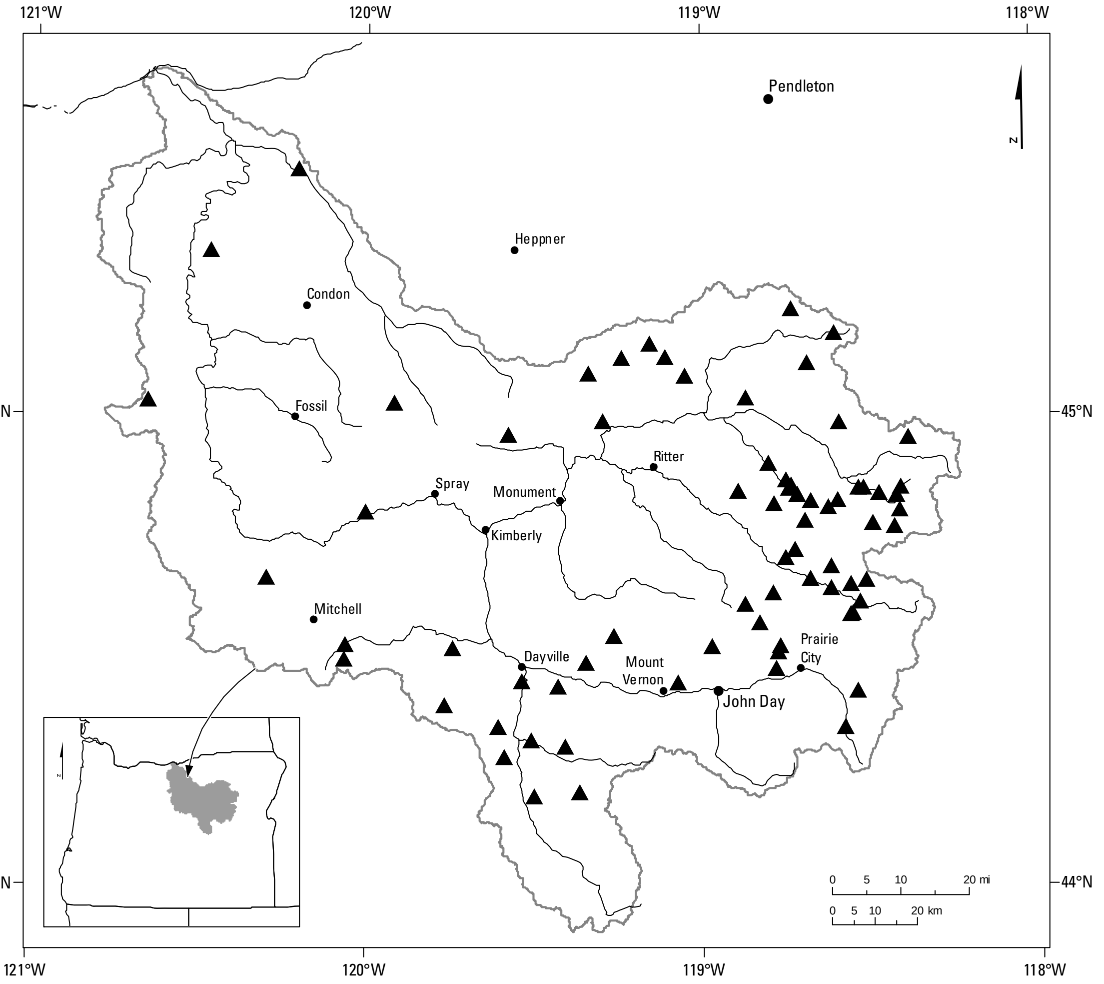

Figure 2-1 Map of 2007 juvenile *O. mykiss* sampling sites (▲) in relation to the John Day River basin, with selected cities and localities (●).

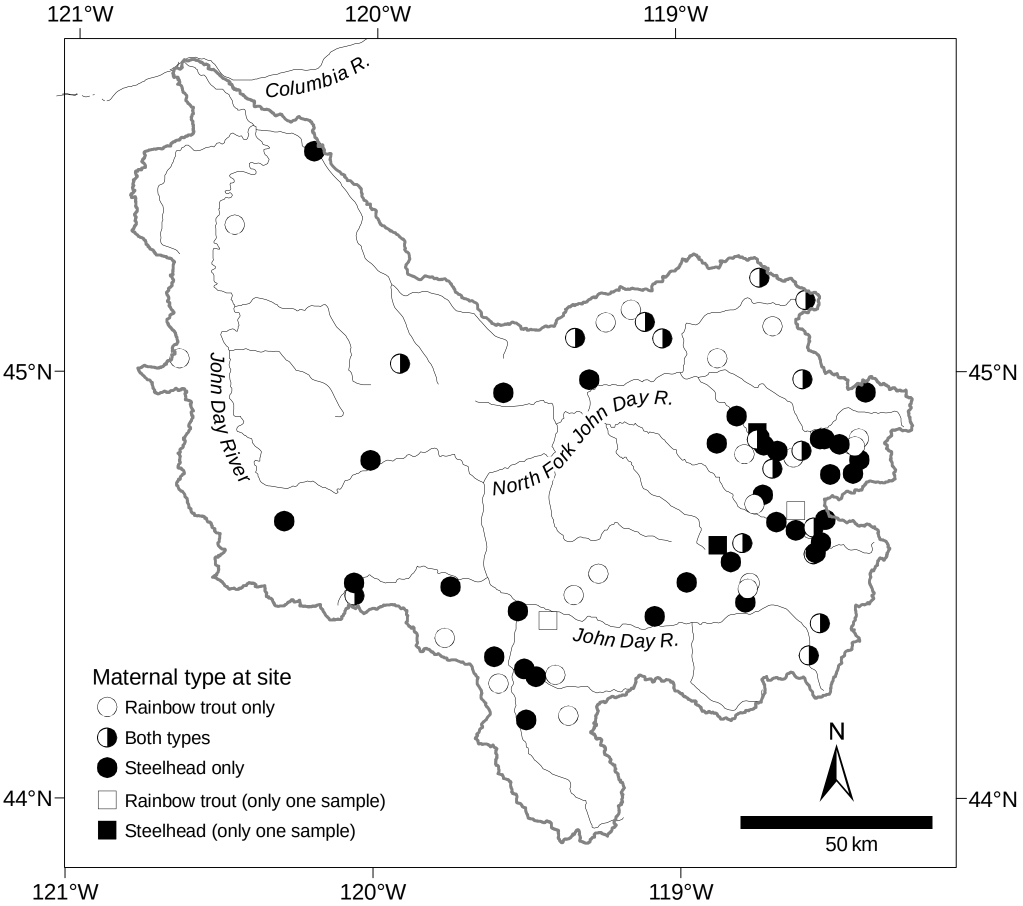

Figure 2-2 Maternal types identified for juveniles at study sites in the John Day River in 2007. Sites where two or more juveniles were sampled are indicated with circles (○/●); those where only one juvenile was sampled are indicated with squares (□/■). Hollow markers (○/□) indicate sites where all juveniles were the offspring of rainbow trout, solid markers (●/■) indicate those with all steelhead offspring, and mixed markers indicate at least one offspring of each type (◑).

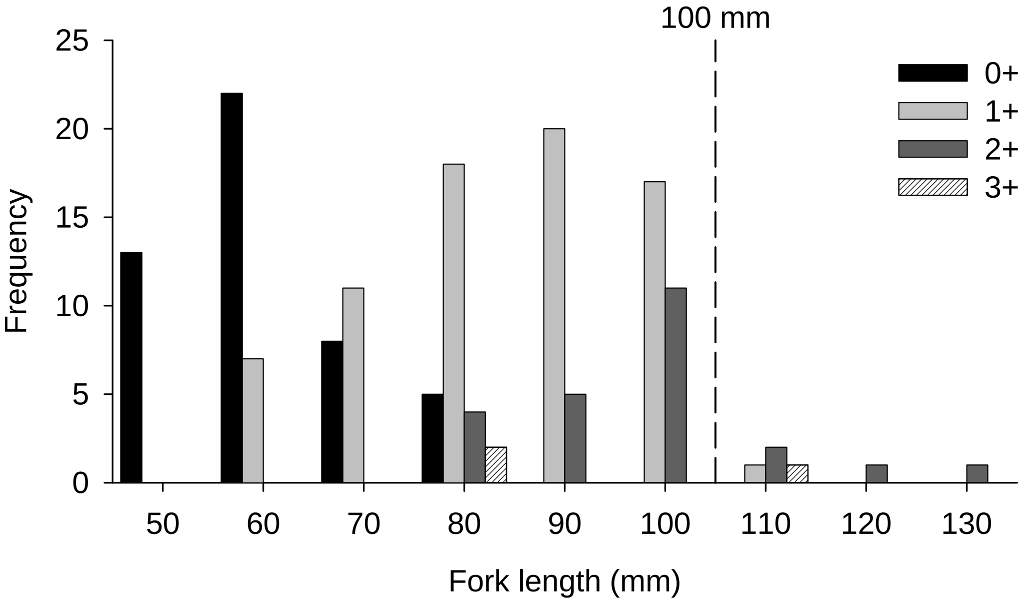

Figure 2-3 Length-frequency histogram for juveniles of each age class of *O. mykiss* juveniles collected from sites in the John Day River (Figure 2-1) in 2007. Our sampling targeted 50-100 mm fish, collecting larger or smaller fish when the target size was unavailable.

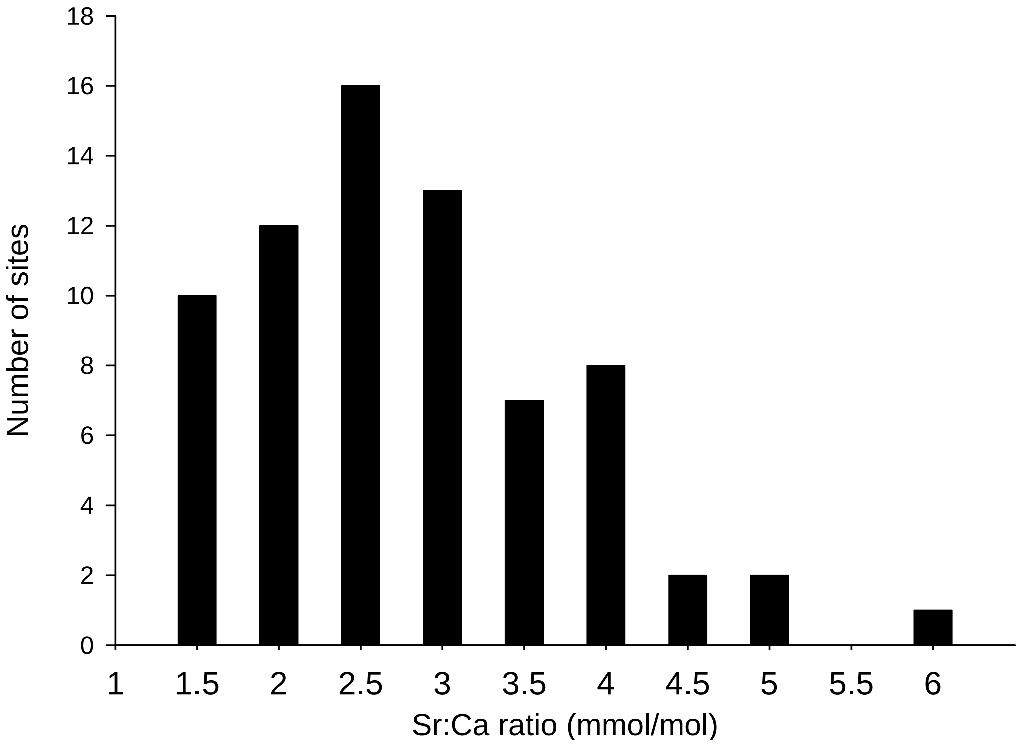

Figure 2-4 Histogram of mean freshwater Sr:Ca ratios (mmol/mol) from our 2007 sample sites (*n* = 64) in the John Day River. We did not include sites greater than 4.75 mmol/mol in our analysis, as we could not discern marine or freshwater maternal origin at sites past that threshold. We removed one site from analysis with Sr:Ca ratio of 5.61 mmol/mol. Two sites had Sr:Ca ratios between 4.5 and 4.75 mmol/mol.

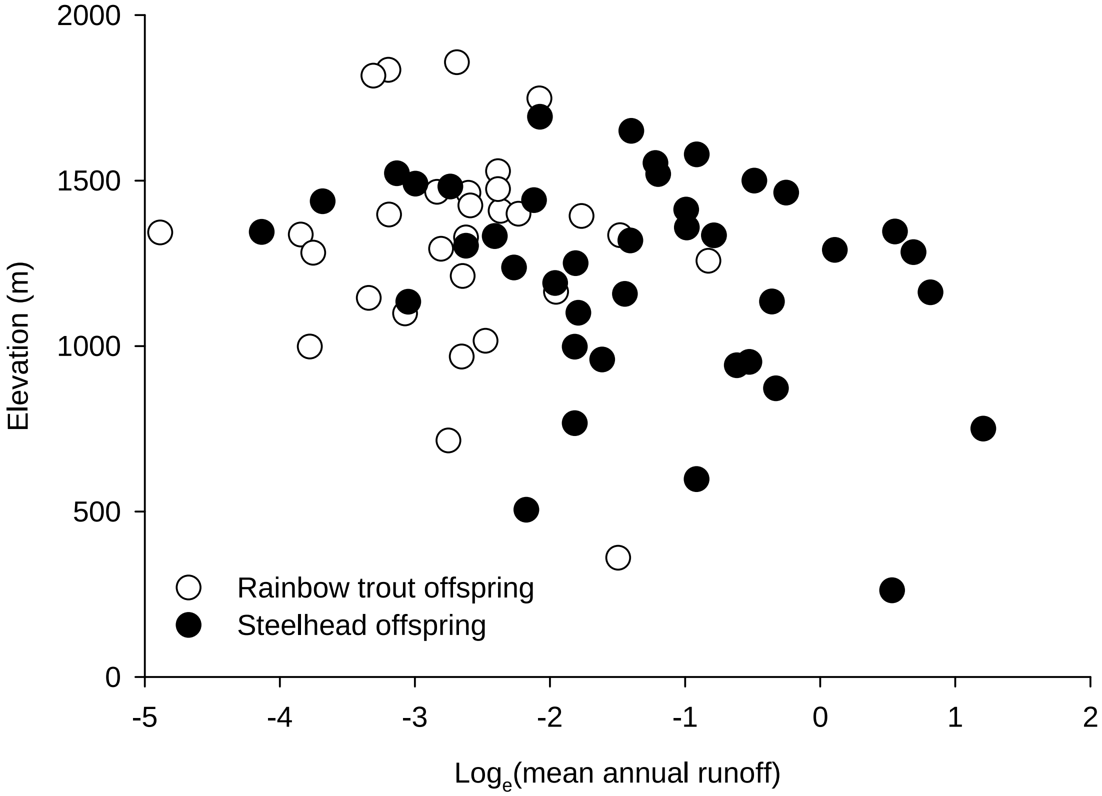

Figure 2-5 Increasing stream size (represented by $\log_e$-transformed mean annual runoff (m^3/s)) was associated with increasing occurrence of anadromy at sites sampled in 2007 in the John Day River basin. Steelhead offspring (●) occurred at sites across the range of stream sizes, but rainbow trout offspring (○) occurred only at the smaller streams.

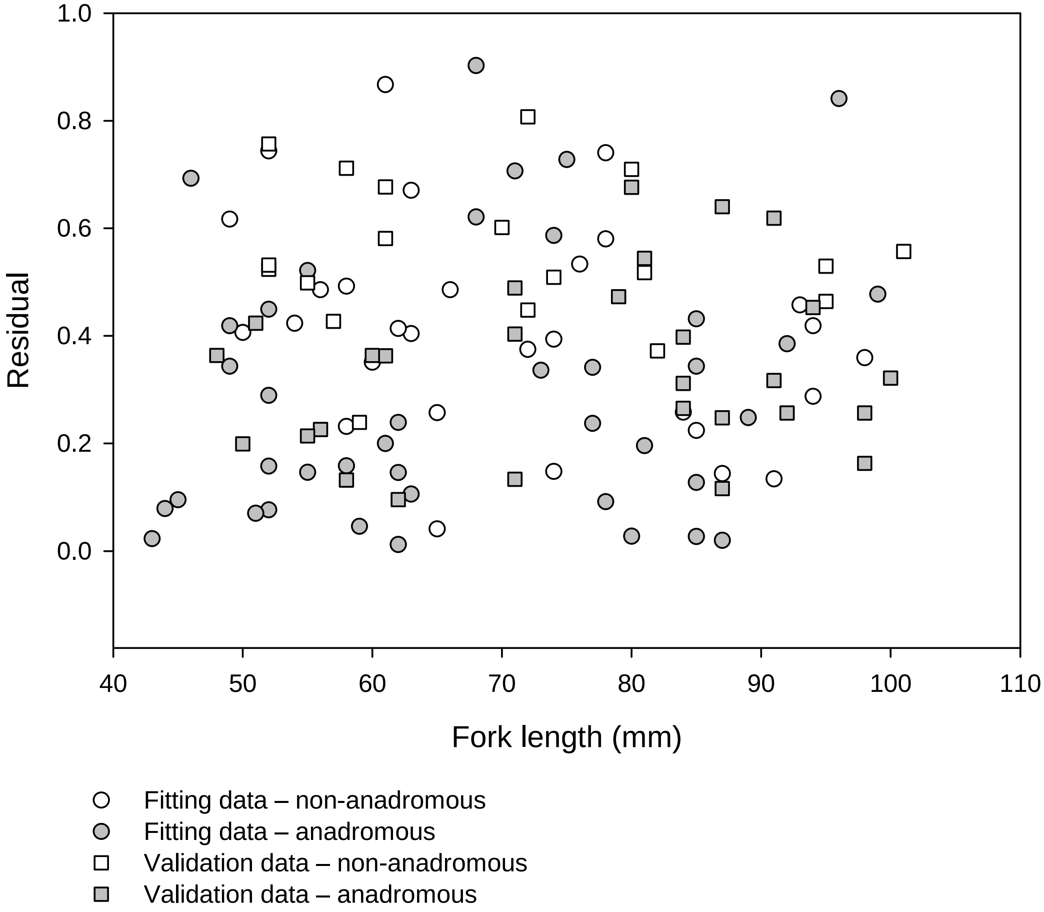

Figure 2-6 We found no relationship between fish fork length (mm) and model residual for the stream size predictive model of expression of anadromy in the John Day River. Grey markers indicate steelhead progeny, white indicate rainbow trout progeny. Circles (○) represent fitting data, squares (□) represent validation data.

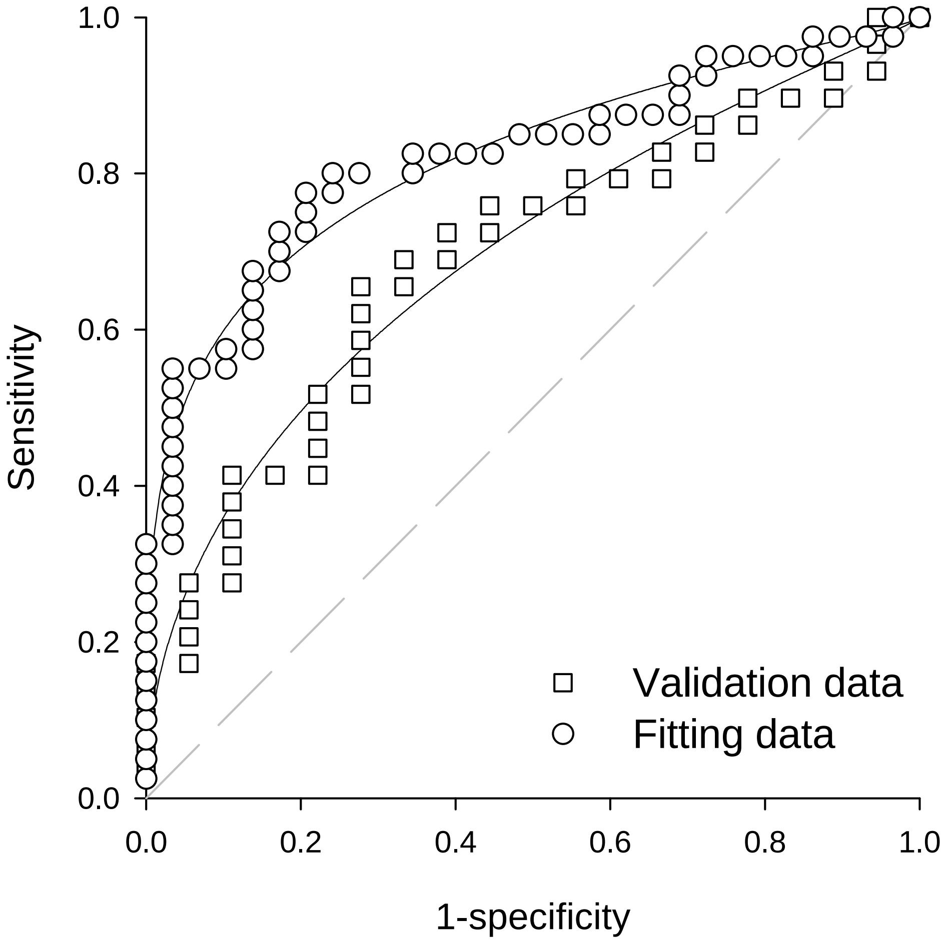

Figure 2-7 Receiver operating characteristic (ROC) curves for mean annual runoff model using fitting (circles; AUC = 0.82; 95% CI 0.71, 0.91) and validation data (squares; AUC = 0.69; 95% CI 0.53, 0.84). The optimal threshold (based on maximum kappa) for the fitting data curve is $p = 0.51$ ($k = 0.56$). For the validation data curve the optimal threshold is $p = 0.62$ ($k = 0.32$).

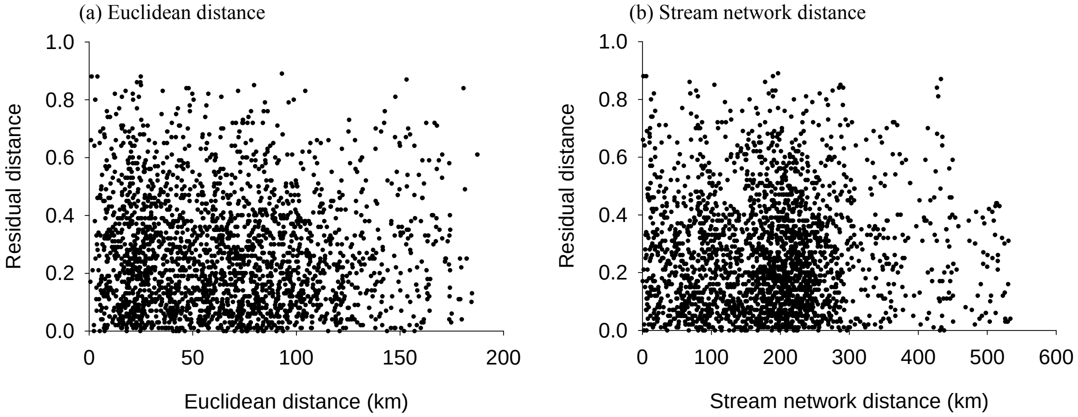

Figure 2-8 Plots of pairwise model residual distances (absolute values) and geographic distances (km) used in Mantel tests for (a) Euclidean distances and (b) stream network distances between sampling sites.

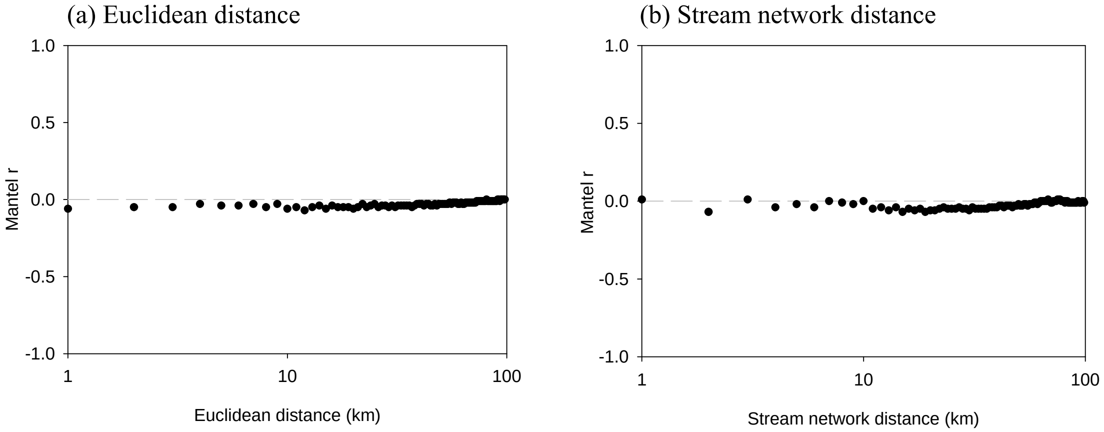

Figure 2-9 Mantel correlograms for both Euclidean (a) and stream network (b) distances (km; $\log_{10}$ scale) showing little or no effect of scale on spatial autocorrelation of model residuals for the fitting data within our broad-scale sampling effort in the John Day River in 2007. These plots present 1-km distance classes for pairwise between-site distances of 100km or smaller.

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APPENDICES

APPENDIX A – WATER CHEMISTRY ANALYSIS

Table A-1 Mean freshwater microchemistry for otolith sampling sites in the John Day River in 2007. The flame atomic absorption method used was not sensitive enough to consistently detect the levels of Ba and Mn in our water samples. In similar analysis, an inductively coupled plasma (ICP) optical emission spectrophotometer provided adequate sensitivity to measure all these parameters in similar sampling conditions and parent material (Wells et al. 2003).

ODFW Site ID	Concentration (ppm)					Molar ratio (mmol/mol)			
	Ca	Sr	Mg	Mn	Ba	Sr:Ca	Mn:Ca	MgCa	BaCa
OJD03458-007	38.93	0.1	16.665	0.025	0.2	1.17	0.47	706	1.50
OJD03458-011	45.895	0.13	11.1	0.005	0.2	1.30	0.08	399	1.27
OJD03458-017	27.775	0.21	10.17	0	0.2	3.46	0.00	604	2.10
OJD03458-019	6.16	0.05	2.365	0.02	0.1	3.71	2.37	633	4.74
OJD03458-020	23.71	0.06	10.56	0	0.1	1.16	0.00	734	1.23
OJD03458-027	10.86	0.07	5.785	0	0.1	2.95	0.00	878	2.69
OJD03458-031	26.545	0.14	9.815	0	0.2	2.41	0.00	610	2.20
OJD03458-033	58.515	0.2	20.725	0	0.3	1.56	0.00	584	1.50
OJD03458-034	32.475	0.075	24.96	0.025	0.25	1.06	0.56	1267	2.25
OJD03458-042	17.7625	0.075	7.8325	0.01	0.225	1.93	0.41	727	3.70
OJD03458-044	17.965	0.07	8.425	0	0.25	1.78	0.00	773	4.06
OJD03458-050	11.47	0.08	5.525	0.02	0.1	3.19	1.27	794	2.54
OJD03458-052	15.09	0.08	8.565	0	0.1	2.42	0.00	936	1.93
OJD03458-062	10.265	0.07	3.795	0.01	0.1	3.12	0.71	610	2.84
OJD03458-066	56.17	0.21	5.665	0	0.3	1.71	0.00	166	1.56
OJD03458-074	9.755	0.04	6.71	0	0.1	1.88	0.00	1134	2.99
OJD03458-086	3.39	0.02	1.07	0	0.1	2.70	0.00	520	8.61
OJD03458-087	10.585	0.04	4.115	0	0.1	1.73	0.00	641	2.76
OJD03458-090	3.815	0.02	12.93	0	0.1	2.40	0.00	5589	7.65
OJD03458-094	12.645	0.04	4.94	0	0.1	1.45	0.00	644	2.31
OJD03458-095	18.225	0.11	4.925	0	0.2	2.76	0.00	446	3.20
OJD03458-097	19.435	0.05	7.91	0	0.2	1.18	0.00	671	3.00
OJD03458-106	39.935	0.31	23.2	0.005	0.3	3.55	0.09	958	2.19
OJD03458-107	15.11	0.1	3.765	0	0.2	3.03	0.00	411	3.86
OJD03458-108	8.18	0.05	3.905	0	0.2	2.80	0.00	787	7.14
OJD03458-111	16.94	0.11	7.27	0	0.1	2.97	0.00	708	1.72
OJD03458-115	1.63	0.02	0.44	0	0	5.61	0.00	445	0.00
OJD03458-116	23.485	0.06	10.98	0	0.1	1.17	0.00	771	1.24
OJD03458-122	24.39	0.11	8.295	0	0.2	2.06	0.00	561	2.39
OJD03458-129	30.97	0.16	10.7925	0	0.2	2.36	0.00	575	1.88
OJD03458-132	20.815	0.07	8.805	0.005	0.2	1.54	0.18	698	2.80
OJD03458-133	8.575	0.07	3.295	0	0.15	3.73	0.00	634	5.11
OJD03458-134	45.86	0.31	22.13	0.195	0.3	3.09	3.10	796	1.91
OJD03458-140	17.94	0.045	6.66	0	0.2	1.15	0.00	612	3.25
OJD03458-146	32.16	0.1	13.6	0	0.25	1.42	0.00	697	2.27
OJD03458-148	20.88	0.18	11.675	0	0.2	3.94	0.00	922	2.80

ODFW Site ID	Concentration (ppm)					Molar ratio (mmol/mol)			
	Ca	Sr	Mg	Mn	Ba	Sr:Ca	Mn:Ca	MgCa	BaCa
OJD03458-369	25.31	0.11	8.1	0	0.1	1.99	0.00	528	1.15
OJD03458-496	19.165	0.14	7.635	0.01	0.15	3.34	0.38	657	2.28
OJD03458-497	14.85	0.07	4.36	0	0.1	2.16	0.00	484	1.97
OJD03458-505	25.245	0.135	10.12	0	0.1	2.45	0.00	661	1.16
OJD03458-514	25.225	0.13	11.495	0	0.2	2.36	0.00	751	2.31
OJD03458-516	4.95	0.025	1.695	0	0.1	2.31	0.00	565	5.90
OJD03458-517	3.485	0.02	1.61	0	0.1	2.63	0.00	762	8.37
OJD03458-519	42.49	0.28	20.135	0	0.3	3.01	0.00	781	2.06
OJD03458-522	20.76	0.16	4.19	0	0.15	3.53	0.00	333	2.11
OJD03458-524	64.385	0.27	10.93	0	0.35	1.92	0.00	280	1.59
OJD03458-531	4.88	0.05	1.295	0	0.1	4.69	0.00	438	5.98
OJD03458-532	73.65	0.34	11.04	0.005	0.4	2.11	0.05	247	1.59
OJD03458-533	18.94	0.12	5.68	0	0.25	2.90	0.00	495	3.85
OJD03458-535	7.645	0.06	5.105	0	0.2	3.59	0.00	1101	7.63
OJD03458-536	10.43	0.06	9.655	0	0.2	2.63	0.00	1526	5.60
OJD03458-548	36.665	0.17	11.56	0	0.2	2.12	0.00	520	1.59
OJD03458-549	5.69	0.05	2.415	0	0.1	4.02	0.00	700	5.13
OJD03458-558	8.945	0.04	3.695	0	0.1	2.05	0.00	681	3.26
OJD03458-561	9.145	0.07	3.44	0	0.1	3.50	0.00	620	3.19
OJD03458-564	10.105	0.06	3.985	0.07	0.1	2.72	5.05	650	2.89
OJD03458-565	15.41	0.09	8.98	0.01	0.1	2.67	0.47	961	1.89
OJD03458-567	8.63	0.04	6.33	0	0.1	2.12	0.00	1209	3.38
OJD03458-569	13.13	0.07	5.085	0.01	0.15	2.44	0.56	639	3.33
OJD03458-570	7.425	0.07	2.495	0	0.15	4.31	0.00	554	5.90
OJD03458-571	30.06	0.13	7.83	0	0.15	1.98	0.00	430	1.46
OJD03458-573	5.8	0.06	2.1	0	0.1	4.73	0.00	597	5.03
OJD03458-584	6.15	0.04	8.15	0	0.1	2.98	0.00	2185	4.75
OJD03458-585	12.255	0.08	6.91	0	0.2	2.99	0.00	930	4.76
OJD03458-586	6.11	0.04	10.655	0	0.2	2.99	0.00	2876	9.55
OJD03458-587	18.05	0.05	9.405	0.01	0.1	1.27	0.40	859	1.62
OJD03458-595	9.735	0.05	4.29	0	0.15	2.35	0.00	727	4.50
OJD03458-596	19.58	0.08	7.395	0	0.2	1.87	0.00	623	2.98
OJD03458-600	10.74	0.045	12.445	0	0.1	1.92	0.00	1911	2.72
OJD03458-604	5.82	0.045	1.89	0	0.1	3.54	0.00	535	5.01
OJD03458-608	5.99	0.03	7.17	0	0.1	2.29	0.00	1974	4.87

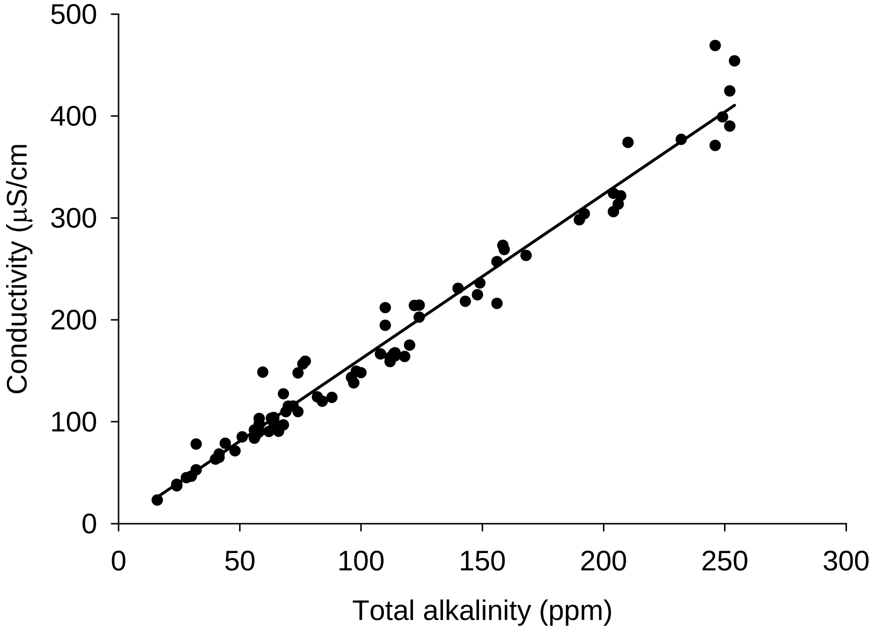

Figure A-1 Water total alkalinity (ppm) and conductivity (µS/cm), with linear regression, as tested at otolith sampling sites in the John Day River in 2007. Stream water conductivity and alkalinity were highly correlated, as in previous studies (e.g. Silsbee and Larson 1982; Koetsier et al. 1996; Kney and Brandes 2007). A simple linear regression model on conductivity with no intercept parameter explained almost all of the variation in alkalinity (r2 = 0.99, $P < 0.0001$; df = 1; n = 81).

APPENDIX B – FISH AND SITE DATA

Table B-1 Data from juvenile fish collected in the John Day River basin in 2007 and used for logistic regression modeling on expression of anadromy.

ODFW Site ID	Stream name	Sample date	FishID	Fork length (mm)	Age	Steelhead progeny?	Data set
OJD03458-011	Service Creek	7/17/2007	011A	52	0	1	Fitting
OJD03458-017	West Fork Lick Creek	8/6/2007	017B	98	1	0	Fitting
OJD03458-019	Tribble Creek	7/9/2007	019A	94	1	0	Fitting
OJD03458-020	Belshaw Creek	6/29/2007	020B	84	1	0	Fitting
OJD03458-027	Middle Fork John Day River	7/18/2007	027A	87	1	1	Fitting
OJD03458-033	Deer Creek	6/28/2007	033A	89	1	1	Fitting
OJD03458-034	Caribou Creek	7/18/2007	034B	91	1	0	Fitting
OJD03458-042	Rock Creek	8/3/2007	042A	52	0	1	Fitting
OJD03458-044	Flat Creek	6/29/2007	044A	87	1	0	Fitting
OJD03458-048	Bear Wallow Creek	8/4/2007	048A	58	1	0	Fitting
OJD03458-050	Bull Run Creek	8/5/2007	050A	58	0	1	Fitting
OJD03458-052	Granite Creek	7/19/2007	052A	43	0	1	Fitting
OJD03458-062	Fivemile Creek	7/9/2007	062A	52	0	1	Fitting
OJD03458-068	Ferry Canyon	7/15/2007	068B	78	0	0	Fitting
OJD03458-074	Clear Creek	9/4/2007	074A	62	0	1	Fitting
OJD03458-078	Beech Creek	7/5/2007	078A	45	0	1	Fitting
OJD03458-087	Baldy Creek	6/30/2007	087A	65	1	0	Fitting
OJD03458-090	North Fork Desolation Creek	8/4/2007	090B	78	1	0	Fitting
OJD03458-094	Indian Creek	7/1/2007	094A	60	1	0	Fitting
OJD03458-095	Granite Creek	7/20/2007	095A	56	1	0	Fitting
OJD03458-097	North Fork Wind Creek	6/27/2007	097A	94	1	0	Fitting
OJD03458-106	Bear Creek	8/1/2007	106A	50	0	0	Fitting
OJD03458-107	Myrtle Creek	7/10/2007	107B	96	1	1	Fitting
OJD03458-108	Granite Boulder Creek	7/17/2007	108A	63	1	0	Fitting
OJD03458-111	East Fork Beech Creek	8/2/2007	111A	92	1	1	Fitting
OJD03458-116	Cummings Creek	8/3/2007	116A	63	0	0	Fitting
OJD03458-122	Davis Creek	7/18/2007	122A	62	1	0	Fitting
OJD03458-129	South Fork John Day River	6/27/2007	129B	62	0	1	Fitting
OJD03458-132	Wilson Creek	7/8/2007	132A	52	0	1	Fitting
OJD03458-133	Fivemile Creek	7/20/2007	133A	44	0	1	Fitting
OJD03458-134	Bear Creek	7/2/2007	134A	73	1	1	Fitting
OJD03458-140	Black Canyon Creek	8/2/2007	140G	49	0	1	Fitting
OJD03458-145	Buckhorn Creek	7/12/2007	145B	93	1	0	Fitting
OJD03458-148	Coyote Creek	8/5/2007	148B	65	0	0	Fitting
OJD03458-369	Murderers Creek	9/9/2007	369B	63	1	1	Fitting
OJD03458-496	Beaver Creek	7/20/2007	496A	68	1	1	Fitting
OJD03458-505	Camp Creek	7/11/2007	505A	46	0	1	Fitting
OJD03458-514	Pine Hollow	8/25/2007	514A	72	1	0	Fitting
OJD03458-516	Indian Creek	7/17/2007	516A	58	1	0	Fitting

ODFW Site ID	Stream name	Sample date	FishID	Fork length (mm)	Age	Steelhead progeny?	Data set
OJD03458-517	Big Creek	7/10/2007	517A	74	1	0	Fitting
OJD03458-519	Bear Creek	8/1/2007	519A	49	0	0	Fitting
OJD03458-522	Beaver Creek	7/17/2007	522A	71	0	1	Fitting
OJD03458-524	Deer Creek	6/28/2007	524B	76	1	0	Fitting
OJD03458-531	Meadow Creek	8/26/2007	531B	81	1	1	Fitting
OJD03458-533	Granite Creek	7/20/2007	533A	66	1	0	Fitting
OJD03458-536	Vinegar Creek	7/18/2007	536B	77	1	1	Fitting
OJD03458-548	Lick Creek	7/19/2007	548A	68	1	1	Fitting
OJD03458-549	Reynolds Creek	7/20/2007	549A	61	1	0	Fitting
OJD03458-552	Badger Creek	9/10/2007	552B	62	1	1	Fitting
OJD03458-557	Rock Creek	6/28/2007	557B	80	0	1	Fitting
OJD03458-558	Indian Creek	7/23/2007	558B	99	1	1	Fitting
OJD03458-561	Ditch Creek	8/20/2007	561A	52	0	0	Fitting
OJD03458-564	Bridge Creek	8/25/2007	564A	74	1	0	Fitting
OJD03458-565	Granite Creek	8/21/2007	565B	85	1	1	Fitting
OJD03458-567	Desolation Creek	8/20/2007	567A	59	0	1	Fitting
OJD03458-569	Camas Creek	8/26/2007	569A	55	0	1	Fitting
OJD03458-570	North Trail Creek	8/27/2007	570C	49	0	1	Fitting
OJD03458-571	Bear Creek	9/6/2007	571C	55	0	1	Fitting
OJD03458-573	John Day River	8/22/2007	573B	85	1	1	Fitting
OJD03458-575	Davis Creek	8/22/2007	575A	74	1	1	Fitting
OJD03458-584	Desolation Creek	8/21/2007	584B	78	1	1	Fitting
OJD03458-585	Sponge Creek	8/21/2007	585A	75	1	1	Fitting
OJD03458-586	North Fork Desolation Creek	8/21/2007	586A	77	1	1	Fitting
OJD03458-587	Mallory Creek	8/20/2007	587B	85	1	1	Fitting
OJD03458-595	Lake Creek	8/28/2007	595A	61	0	1	Fitting
OJD03458-596	Duncan Creek	8/18/2007	596B	85	1	0	Fitting
OJD03458-600	Vinegar Creek	8/21/2007	600B	85	1	1	Fitting
OJD03458-604	Pole Creek	8/19/2007	604B	54	0	0	Fitting
OJD03458-605	Desolation Creek	8/21/2007	605A	51	0	1	Fitting
OJD03458-017	West Fork Lick Creek	8/6/2007	017A	55	1	1	Validation
OJD03458-019	Tribble Creek	7/9/2007	019B	95	1	0	Validation
OJD03458-020	Belshaw Creek	6/29/2007	020A	72	1	0	Validation
OJD03458-027	Middle Fork John Day River	7/18/2007	027B	87	1	1	Validation
OJD03458-033	Deer Creek	6/28/2007	033B	91	1	1	Validation
OJD03458-034	Caribou Creek	7/18/2007	034A	87	1	1	Validation
OJD03458-042	Rock Creek	8/3/2007	042B	50	0	1	Validation
OJD03458-050	Bull Run Creek	8/5/2007	050B	84	1	1	Validation
OJD03458-068	Ferry Canyon	7/15/2007	068A	61	0	0	Validation
OJD03458-074	Clear Creek	9/4/2007	074B	98	1	1	Validation
OJD03458-090	North Fork Desolation Creek	8/4/2007	090A	70	1	0	Validation
OJD03458-097	North Fork Wind Creek	6/27/2007	097B	95	1	0	Validation
OJD03458-106	Bear Creek	8/1/2007	106C	52	0	0	Validation
OJD03458-107	Myrtle Creek	7/10/2007	107A	91	1	1	Validation
OJD03458-122	Davis Creek	7/18/2007	122B	79	1	1	Validation
OJD03458-129	South Fork John Day River	6/27/2007	129A	62	0	1	Validation

ODFW Site ID	Stream name	Sample date	FishID	Fork length (mm)	Age	Steelhead progeny?	Data set
OJD03458-140	Black Canyon Creek	8/2/2007	140D	48	0	1	Validation
OJD03458-145	Buckhorn Creek	7/12/2007	145A	94	1	1	Validation
OJD03458-148	Coyote Creek	8/5/2007	148A	59	0	0	Validation
OJD03458-369	Murderers Creek	9/9/2007	369A	56	1	1	Validation
OJD03458-496	Beaver Creek	7/20/2007	496B	71	1	1	Validation
OJD03458-514	Pine Hollow	8/25/2007	514B	74	0	0	Validation
OJD03458-517	Big Creek	7/10/2007	517C	81	1	0	Validation
OJD03458-524	Deer Creek	6/28/2007	524A	61	0	0	Validation
OJD03458-531	Meadow Creek	8/26/2007	531A	58	1	0	Validation
OJD03458-536	Vinegar Creek	7/18/2007	536A	61	1	1	Validation
OJD03458-548	Lick Creek	7/19/2007	548B	80	1	1	Validation
OJD03458-549	Reynolds Creek	7/20/2007	549B	87	1	1	Validation
OJD03458-557	Rock Creek	6/28/2007	557A	71	0	1	Validation
OJD03458-558	Indian Creek	7/23/2007	558A	51	0	1	Validation
OJD03458-561	Ditch Creek	8/20/2007	561B	100	1	1	Validation
OJD03458-564	Bridge Creek	8/25/2007	564B	82	1	0	Validation
OJD03458-565	Granite Creek	8/21/2007	565A	58	0	1	Validation
OJD03458-567	Desolation Creek	8/20/2007	567B	98	1	1	Validation
OJD03458-569	Camas Creek	8/26/2007	569B	101	1	0	Validation
OJD03458-570	North Trail Creek	8/27/2007	570B	84	1	1	Validation
OJD03458-571	Bear Creek	9/6/2007	571B	92	1	1	Validation
OJD03458-573	John Day River	8/22/2007	573A	52	0	0	Validation
OJD03458-584	Desolation Creek	8/21/2007	584A	55	0	1	Validation
OJD03458-585	Sponge Creek	8/21/2007	585B	81	1	1	Validation
OJD03458-586	North Fork Desolation Creek	8/21/2007	586B	84	1	1	Validation
OJD03458-587	Mallory Creek	8/20/2007	587A	60	0	1	Validation
OJD03458-595	Lake Creek	8/28/2007	595B	80	1	0	Validation
OJD03458-596	Duncan Creek	8/18/2007	596A	57	0	0	Validation
OJD03458-600	Vinegar Creek	8/21/2007	600A	71	1	1	Validation
OJD03458-604	Pole Creek	8/19/2007	604A	52	0	0	Validation
OJD03458-605	Desolation Creek	8/21/2007	605B	72	1	0	Validation
OJD03458-106	Bear Creek	8/1/2007	106B	90	1	0	N/A
OJD03458-140	Black Canyon Creek	8/2/2007	140C	55	0	1	N/A
OJD03458-140	Black Canyon Creek	8/2/2007	140F	50	0	1	N/A
OJD03458-140	Black Canyon Creek	8/2/2007	140E	48	0	1	N/A
OJD03458-570	North Trail Creek	8/27/2007	570A	50	0	1	N/A
OJD03458-571	Bear Creek	9/6/2007	571A	56	0	1	N/A
OJD03458-011	Service Creek	7/17/2007	011B	135	2	1	N/A
OJD03458-031	Camp Creek	7/11/2007	031B	89	2	1	N/A
OJD03458-048	Bear Wallow Creek	8/4/2007	048B	80	2	1	N/A
OJD03458-052	Granite Creek	7/19/2007	052C	90	2	1	N/A
OJD03458-052	Granite Creek	7/19/2007	052B	95	2	1	N/A
OJD03458-078	Beech Creek	7/5/2007	078B	104	2	1	N/A
OJD03458-086	Hideaway Creek	8/4/2007	086A	72	2	0	N/A
OJD03458-086	Hideaway Creek	8/4/2007	086B	79	2	0	N/A
OJD03458-087	Baldy Creek	6/30/2007	087B	87	2	0	N/A

ODFW Site ID	Stream name	Sample date	FishID	Fork length (mm)	Age	Steelhead progeny?	Data set
OJD03458-094	Indian Creek	7/1/2007	094B	99	2	1	N/A
OJD03458-095	Granite Creek	7/20/2007	095B	76	2	0	N/A
OJD03458-111	East Fork Beech Creek	8/2/2007	111B	95	2	1	N/A
OJD03458-116	Cummings Creek	8/3/2007	116B	93	2	0	N/A
OJD03458-132	Wilson Creek	7/8/2007	132B	102	2	1	N/A
OJD03458-133	Fivemile Creek	7/20/2007	133B	99	2	0	N/A
OJD03458-134	Bear Creek	7/2/2007	134B	85	2	1	N/A
OJD03458-505	Camp Creek	7/11/2007	505B	93	2	1	N/A
OJD03458-516	Indian Creek	7/17/2007	516B	98	2	0	N/A
OJD03458-517	Big Creek	7/10/2007	517B	95	2	1	N/A
OJD03458-519	Bear Creek	8/1/2007	519B	98	2	0	N/A
OJD03458-522	Beaver Creek	7/17/2007	522B	84	2	1	N/A
OJD03458-533	Granite Creek	7/20/2007	533B	99	2	0	N/A
OJD03458-552	Badger Creek	9/10/2007	552A	112	2	1	N/A
OJD03458-575	Davis Creek	8/22/2007	575B	97	2	1	N/A
OJD03458-062	Fivemile Creek	7/9/2007	062B	104	3	0	N/A
OJD03458-505	Camp Creek	7/11/2007	505C	74	3	1	N/A
OJD03458-535	Battle Creek	7/21/2007	535A	79	3	1	N/A

Table B-2 Location and estimated mean annual runoff (MAR), both untransformed (m^3/s) and log$_e$-transformed, for our 2007 John Day River juvenile *O. mykiss* sampling sites. Mean annual runoff was estimated from area (km^2) and area-weighted mean precipitation (mm) for each sampling site's catchment basin.

ODFW Site ID	Stream name	Latitude	Longitude	Mean annual runoff (MAR)	log(MAR)	Mean precipitation	Catchment area
OJD03458-011	Service Creek	44.79682	-120.00257	0.113	-2.18	40298	79.8
OJD03458-017	West Fork Lick Creek	44.62336	-118.78790	0.060	-2.81	57483	18.8
OJD03458-019	Tribble Creek	45.15449	-119.15273	0.074	-2.60	78889	10.8
OJD03458-020	Belshaw Creek	44.53354	-119.26309	0.041	-3.19	50971	17.4
OJD03458-027	Middle Fork John Day River	44.63412	-118.61401	2.261	0.82	67656	405.5
OJD03458-031	Camp Creek	44.60097	-118.87055	0.163	-1.82	57613	48.3
OJD03458-033	Deer Creek	44.19360	-119.50019	0.236	-1.45	43352	134.7
OJD03458-034	Caribou Creek	44.64153	-118.55532	0.021	-3.85	59649	6.4
OJD03458-042	Rock Creek	44.50770	-119.74091	0.721	-0.33	58827	189.8
OJD03458-044	Flat Creek	44.42628	-119.42728	0.023	-3.78	42006	15.7
OJD03458-048	Bear Wallow Creek	45.22742	-118.72467	0.094	-2.37	71292	17.2
OJD03458-050	Bull Run Creek	44.79897	-118.40674	0.370	-0.99	67422	72.8
OJD03458-052	Granite Creek	44.84769	-118.52988	1.993	0.69	70596	325.2
OJD03458-062	Fivemile Creek	45.12524	-119.10756	0.373	-0.99	76931	53.6
OJD03458-068	Ferry Canyon	45.34986	-120.47140	0.224	-1.50	33789	232.0
OJD03458-074	Clear Creek	44.77083	-118.48808	0.401	-0.91	84378	46.1
OJD03458-078	Beech Creek	44.43464	-119.07295	0.591	-0.53	47877	256.1
OJD03458-086	Hidaway Creek	45.11297	-118.68184	0.253	-1.38	72232	43.0
OJD03458-087	Baldy Creek	44.38572	-119.76490	0.041	-3.20	77706	6.4
OJD03458-090	North Fork Desolation Creek	44.80559	-118.61960	0.125	-2.08	83300	15.7
OJD03458-094	Indian Creek	44.48385	-120.06390	0.059	-2.84	66866	12.8
OJD03458-095	Granite Creek	44.84840	-118.40235	0.092	-2.39	73715	15.6
OJD03458-097	North Fork Wind Creek	44.27581	-119.58758	0.046	-3.07	47907	22.5
OJD03458-106	Bear Creek	44.51233	-118.76595	0.071	-2.65	62503	18.0
OJD03458-107	Myrtle Creek	44.71561	-118.72069	0.025	-3.68	61678	6.9
OJD03458-108	Granite Boulder Creek	44.67955	-118.61349	0.171	-1.77	87374	18.8
OJD03458-111	East Fork Beech Creek	44.51110	-118.96850	0.141	-1.96	52976	51.2
OJD03458-115	Hidaway Creek	45.08664	-118.62640	0.101	-2.29	76051	15.8
OJD03458-116	Cummings Creek	44.47586	-119.34471	0.070	-2.65	46561	35.9
OJD03458-122	Davis Creek	44.57730	-118.55510	0.073	-2.62	63275	17.9
OJD03458-129	South Fork John Day River	44.43691	-119.53686	3.343	1.21	44954	1552.2
OJD03458-132	Wilson Creek	44.96017	-119.57648	0.199	-1.61	46307	98.1
OJD03458-133	Fivemile Creek	45.08600	-119.04873	0.700	-0.36	73469	109.0
OJD03458-134	Bear Creek	44.46270	-118.77982	0.167	-1.79	57621	49.4
OJD03458-140	Black Canyon Creek	44.34071	-119.60557	0.163	-1.82	57292	48.8
OJD03458-145	Buckhorn Creek	45.02804	-119.91830	0.084	-2.48	46765	42.0
OJD03458-148	Coyote Creek	44.69783	-118.74801	0.008	-4.89	51494	3.4
OJD03458-369	Murderers Creek	44.31244	-119.50710	0.540	-0.62	41714	325.4
OJD03458-496	Beaver Creek	44.76508	-118.42291	0.065	-2.74	65026	15.0
OJD03458-505	Camp Creek	44.56040	-118.82856	0.050	-3.00	63017	12.6

ODFW Site ID	Stream name	Latitude	Longitude	Mean annual runoff (MAR)	log(MAR)	Mean precipitation	Catchment area
OJD03458-514	Pine Hollow	45.03202	-120.65720	0.064	-2.75	35583	61.8
OJD03458-516	Indian Creek	44.81330	-118.77988	0.037	-3.31	73904	6.4
OJD03458-517	Big Creek	44.77869	-118.68729	0.068	-2.69	82116	9.1
OJD03458-519	Bear Creek	44.49842	-118.77325	0.141	-1.96	60293	37.9
OJD03458-522	Beaver Creek	44.65334	-118.67642	0.047	-3.05	59765	13.6
OJD03458-524	Deer Creek	44.20258	-119.36282	0.107	-2.23	44572	59.6
OJD03458-531	Meadow Creek	44.98503	-118.58683	0.301	-1.20	73528	48.7
OJD03458-533	Granite Creek	44.83014	-118.41477	0.092	-2.39	73715	15.6
OJD03458-535	Battle Creek	44.86302	-118.74783	0.067	-2.71	67932	14.0
OJD03458-536	Vinegar Creek	44.60401	-118.52987	0.164	-1.81	69749	30.8
OJD03458-548	Lick Creek	44.84689	-118.51470	0.016	-4.13	63507	4.2
OJD03458-549	Reynolds Creek	44.41558	-118.53768	0.437	-0.83	75261	65.7
OJD03458-552	Badger Creek	44.51409	-120.06242	0.245	-1.41	65912	51.9
OJD03458-557	Rock Creek	45.52502	-120.20999	1.702	0.53	38349	1188.2
OJD03458-558	Indian Creek	44.84148	-118.88882	0.104	-2.27	65419	23.2
OJD03458-561	Ditch Creek	45.08971	-119.33817	0.227	-1.48	67688	45.3
OJD03458-564	Bridge Creek	45.03931	-118.86542	0.023	-3.75	59360	7.1
OJD03458-565	Granite Creek	44.83441	-118.46748	1.738	0.55	70924	282.2
OJD03458-567	Desolation Creek	44.89838	-118.79784	1.114	0.11	74419	164.8
OJD03458-569	Camas Creek	45.17624	-118.60058	0.090	-2.41	61222	23.7
OJD03458-570	North Trail Creek	44.95257	-118.37917	0.126	-2.07	81344	16.6
OJD03458-571	Bear Creek	44.65589	-120.29679	0.400	-0.92	45817	195.9
OJD03458-573	John Day River	44.33977	-118.57430	0.455	-0.79	85052	51.1
OJD03458-575	Davis Creek	44.58075	-118.54922	0.073	-2.62	63275	17.9
OJD03458-584	Desolation Creek	44.83331	-118.71411	0.614	-0.49	83300	71.5
OJD03458-585	Sponge Creek	44.85342	-118.73034	0.044	-3.13	68297	9.2
OJD03458-586	North Fork Desolation Creek	44.81998	-118.67335	0.247	-1.40	81198	31.8
OJD03458-587	Mallory Creek	44.99014	-119.29386	0.163	-1.82	56812	49.8
OJD03458-595	Lake Creek	44.82154	-118.59303	0.295	-1.22	84336	34.5
OJD03458-596	Duncan Creek	44.29899	-119.40613	0.035	-3.34	42810	22.7
OJD03458-600	Vinegar Creek	44.65052	-118.51015	0.120	-2.12	73715	20.2
OJD03458-604	Pole Creek	45.12322	-119.23701	0.075	-2.59	82895	9.7
OJD03458-605	Desolation Creek	44.84586	-118.73676	0.777	-0.25	79017	101.4

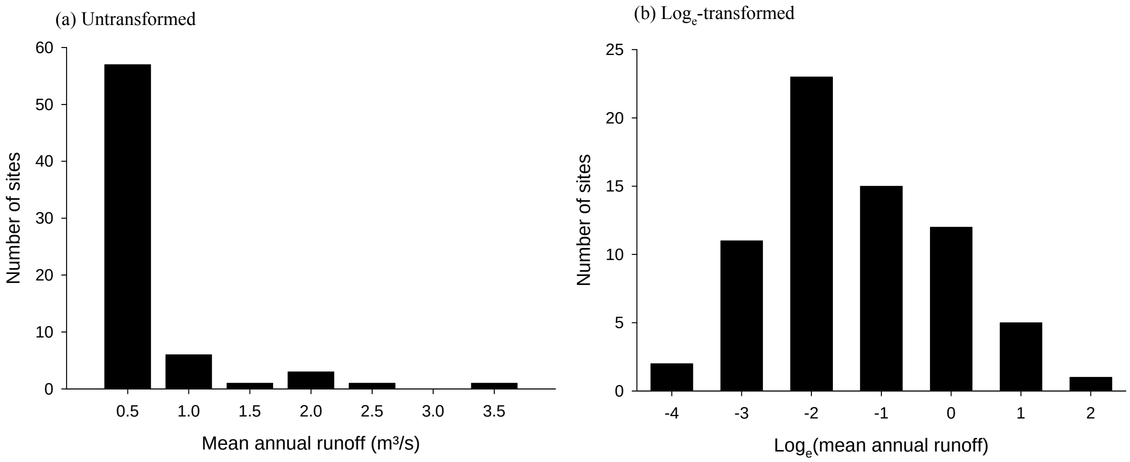

Figure B-1 Histograms of mean annual runoff for the John Day River sample sites, (a) untransformed and (b) $\log_e$-transformed. Data are modeled using 1971-2000 mean annual precipitation data (Anonymous 2006a) for stream sampling sites (n = 69) using parameters from Sanborn and Bledsoe (2006).

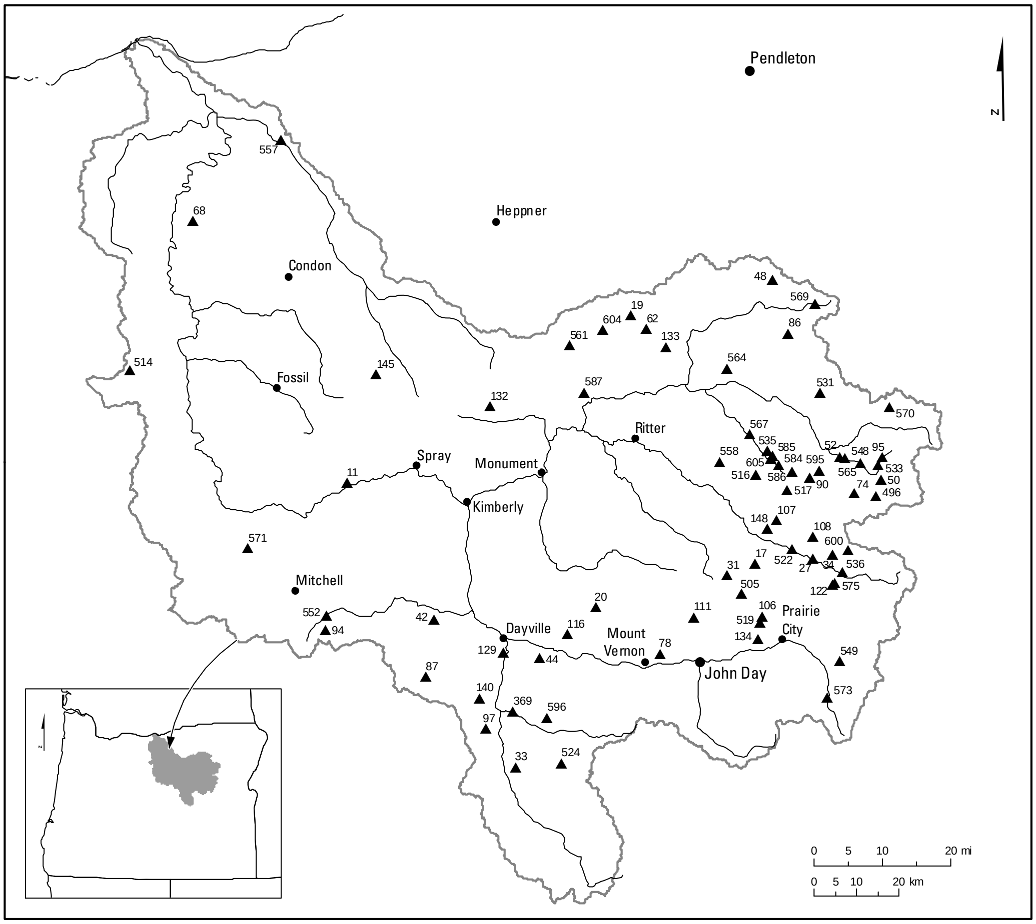

Figure B-2 Sites where juvenile *O. mykiss* were collected during summer 2007 in the John Day River basin, with site numbers as in Tables B-1 and B-2.

APPENDIX C – OTHER VARIABLES CONSIDERED

Table C-1 We considered these other variables during our model design process: elevation (m); slope (m/m); conductivity (µS/cm); downstream distance from site to the Pacific Ocean (km); and area-weighted mean winter (December, January, and February) air temperature.

ODFW Site ID	Elevation	Slope	Conductivity	Distance to ocean	Mean winter temperature
OJD03458-011	505	0.03	377.0	597	0.15
OJD03458-017	1294	0.05	230.7	775	-2.11
OJD03458-019	1463	0.01	63.0	758	-1.93
OJD03458-020	1397	0.05	211.7	719	-1.83
OJD03458-027	1162	0.01	120.0	786	-3.57
OJD03458-031	1326	0.03	224.3	778	-2.07
OJD03458-033	1157	0.04	424.3	726	-1.81
OJD03458-034	1336	0.06	321.5	790	-3.15
OJD03458-042	872	0.02	257.0	682	-1.48
OJD03458-044	998	0.10	158.8	696	-0.78
OJD03458-048	1407	0.03	83.7	768	-2.24
OJD03458-050	1412	0.01	115.2	794	-3.94
OJD03458-052	1283	0.02	147.6	782	-3.94
OJD03458-062	1357	0.02	100.8	754	-1.89
OJD03458-068	360	0.02	314.0	434	0.52
OJD03458-074	1578	0.03	103.0	802	-4.20
OJD03458-078	952	0.01	--	730	-1.33
OJD03458-086	1363	0.02	38.3	773	-3.04
OJD03458-087	1834	0.06	91.6	708	-3.12
OJD03458-090	1748	0.05	109.7	774	-4.00
OJD03458-094	1465	0.06	115.1	714	-1.85
OJD03458-095	1528	0.03	148.5	796	-4.16
OJD03458-097	1098	0.05	163.8	717	-1.08
OJD03458-106	1211	0.04	399.0	764	-2.33
OJD03458-107	1437	0.11	96.6	780	-2.35
OJD03458-108	1393	0.09	78.0	787	-4.02
OJD03458-111	1190	0.02	166.3	749	-1.53
OJD03458-115	1605	0.03	22.9	782	-3.42
OJD03458-116	968	0.03	218.0	706	-1.00
OJD03458-122	1327	0.03	166.7	793	-3.15
OJD03458-129	750	0.01	268.7	686	-1.79
OJD03458-132	959	0.02	202.5	702	-0.68
OJD03458-133	1134	0.03	90.3	744	-1.76
OJD03458-134	1100	0.02	390.0	756	-1.91
OJD03458-140	997	0.05	149.4	709	-1.83
OJD03458-145	1015	0.03	238.6	485	-0.88
OJD03458-148	1342	0.09	214.0	773	-1.66
OJD03458-369	941	0.01	216.0	713	-1.47
OJD03458-496	1481	0.02	164.6	801	-3.85
OJD03458-505	1490	0.03	214.3	787	-2.25
OJD03458-514	714	0.02	263.0	508	0.27
OJD03458-516	1816	0.05	45.0	763	-4.00

ODFW Site ID	Elevation	Slope	Conductivity	Distance to ocean	Mean winter temperature
OJD03458-517	1857	0.06	37.0	767	-3.90
OJD03458-519	1163	0.03	371.0	762	-2.10
OJD03458-522	1133	0.05	148.0	780	-2.59
OJD03458-524	1399	0.03	373.9	740	-2.29
OJD03458-531	1519	0.01	52.7	771	-3.24
OJD03458-533	1473	0.03	159.2	796	-4.16
OJD03458-535	1498	0.05	89.9	762	-3.22
OJD03458-536	1250	0.03	127.3	794	-3.65
OJD03458-548	1345	0.12	273.0	784	-3.38
OJD03458-549	1257	0.02	68.3	778	-3.50
OJD03458-552	1319	0.01	--	714	-1.78
OJD03458-557	262	0.00	--	401	0.09
OJD03458-558	1237	0.05	84.9	754	-3.10
OJD03458-561	1335	0.03	96.9	710	-1.57
OJD03458-564	1282	0.03	98.4	743	-1.86
OJD03458-565	1345	0.01	156.6	788	-3.99
OJD03458-567	1290	0.01	97.7	755	-3.42
OJD03458-569	1332	0.01	143.3	781	-2.63
OJD03458-570	1692	0.03	71.2	805	-4.27
OJD03458-571	597	0.02	304.0	573	0.06
OJD03458-573	1334	0.03	64.8	782	-4.09
OJD03458-575	1303	0.03	174.9	793	-3.15
OJD03458-584	1499	0.02	92.2	767	-3.90
OJD03458-585	1521	0.05	124.3	765	-3.08
OJD03458-586	1649	0.04	109.7	770	-3.90
OJD03458-587	767	0.03	163.0	700	-0.99
OJD03458-595	1552	0.04	90.2	786	-4.01
OJD03458-596	1145	0.04	167.5	722	-1.69
OJD03458-600	1440	0.04	138.0	800	-3.69
OJD03458-604	1425	0.03	78.6	722	-2.26
OJD03458-605	1463	0.02	87.9	763	-3.68

Table C-2 Spearman's ρ correlation matrix for environmental variables for sample sites in the John Day River catchment basin possibly implicated in anadromy. Only significant correlations are shown. Bold indicates significance at $\alpha = 0.01$; others are significant at $\alpha = 0.05$.

	Mean annual runoff	Site elevation	Slope	Catchment area	Mean annual precipitation	Conductivity	River km to ocean
Site elevation							
Slope[a]	**-0.69**	0.26					
Catchment area	**0.86**	**-0.57**	**-0.70**				
Mean annual precipitation[b]		**0.78**		-0.27			
Conductivity[c]		**-0.59**			**-0.80**		
River km to ocean		**0.62**		**-0.36**	**0.61**	-0.30	
Winter temperature[d]		**-0.77**		0.29	**-0.82**	**0.54**	**-0.85**

[a] Slope for 1:100,000-scale NHD+ reach

[b] Area-weighted mean PRISM annual precipitation for site catchment

[c] Water conductivity measured at site

[d] Area-weighted mean PRISM December, January, February mean temperature for site catchment