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# Influence of sex, migration distance, and latitude on life history expression in steelhead and rainbow trout (*Oncorhynchus mykiss*)

Haley A. Ohms, Matthew R. Sloat, Gordon H. Reeves, Chris E. Jordan, and Jason B. Dunham

**Abstract:** In partially migratory species, such as *Oncorhynchus mykiss*, the emergence of life history phenotypes is often attributed to fitness trade-offs associated with growth and survival. Fitness trade-offs can be linked to reproductive tactics that vary between the sexes, as well as the influence of environmental conditions. We found that *O. mykiss* outmigrants are more likely to be female in nine populations throughout western North America (grand mean 65% female), in support of the hypothesis that anadromy is more likely to benefit females. This bias was not related to migration distance or freshwater productivity, as indicated by latitude. Within one *O. mykiss* population we also measured the resident sex ratio and did not observe a male bias, despite a high female bias among outmigrants in that system. We provide a simulation to demonstrate the relationship between sex ratios and the proportion of anadromy and show how sex ratios could be a valuable tool for predicting the prevalence of life history types in a population.

**Résumé :** Chez les espèces partiellement migratrices comme la truite arc-en-ciel anadrome (*Oncorhynchus mykiss*), l'apparition de phénotypes associés au cycle biologique est souvent attribuée à des compromis adaptatifs reliés à la croissance et à la survie. Ces compromis peuvent être liés à des tactiques de reproduction qui varient selon le sexe, ainsi qu'à l'influence de conditions du milieu. Nous avons constaté que, dans neuf populations de l'Ouest de l'Amérique du Nord, les *O. mykiss* migrant vers la mer sont plus susceptibles d'être des femelles (grande moyenne de 65 % de femelles), ce qui appuie l'hypothèse selon laquelle l'anadromie est probablement plus avantageuse pour les femelles que pour les mâles. Ce biais n'est pas relié à la distance de migration ni à la productivité du milieu d'eau douce, reflétée par la latitude. Dans une population d'*O. mykiss*, nous avons également mesuré le rapport des sexes des individus résidents et n'avons observé aucun biais en faveur des mâles, malgré un fort biais en faveur des femelles parmi les individus migrant vers la mer dans ce système. Nous présentons une simulation pour illustrer la relation entre les rapports des sexes et la proportion d'anadromie et démontrons que ces rapports peuvent constituer un outil intéressant pour la prédiction de la prévalence des types de cycle biologique dans une population donnée. [Traduit par la Rédaction]

## Introduction

Partially migratory salmonid populations consist of migratory individuals that undergo either marine or freshwater migrations before reaching maturity as well as freshwater residents that complete their entire life cycle in fresh water (Jonsson and Jonsson 1993). Understanding the evolutionary and ecological factors influencing the prevalence of anadromy within partially migratory salmonid populations is a fundamental challenge to their effective management. Anadromous and resident life histories are characterized by major trade-offs between survival to first reproduction and the size and age at reproduction. For anadromous fish, migration to the food-rich marine environment delays maturity, lowers the probability of surviving to reproduce, but results in a larger size at reproduction (Fleming and Reynolds 2004). Freshwater residents typically mature at a much smaller size, but have an earlier age at maturation, higher survival to reproduction, and a greater probability of iteroparity than their anadromous counterparts (Fleming and Reynolds 2004).

The balance of these trade-offs may vary across environmental gradients (Hendry et al. 2004). For example, the food availability

hypothesis of Gross et al. (1988) suggests that decreasing freshwater growth opportunity at higher latitudes, in combination with increasing ocean productivity, increases the relative benefits of anadromy. Consequently, latitude can be a strong predictor of life history expression in partially migratory salmonids (e.g., Valiente et al. 2005). Migration distance should also influence life history expression, since more difficult migrations increase the cost of anadromy through increased mortality, stress, or energy expenditure (Hendry et al. 2004). The prevalence of anadromy in partially migratory populations, therefore, should decrease with increasing freshwater productivity or increasing migration distance.

In addition to these environmental influences, the costs and benefits of anadromy are likely to differ between the sexes. For female salmonids, potential reproductive success is primarily limited by egg production (i.e., fecundity  $\times$  egg size; Jonsson and Jonsson 1993), which increases exponentially with body size (Quinn 2005; Quinn et al. 2011). In contrast with females, male reproductive success is typically limited by access to mates rather than gamete production (Fleming 1998). Obtaining a large body

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H.A. Ohms\* and M.R. Sloat. Oregon State University, Department of Fisheries and Wildlife, 104 Nash Hall, Corvallis, OR 97331, USA.

G.H. Reeves. US Department of Agriculture Forest Service, Pacific Northwest Research Station, 3200 Southwest Jefferson Way, Corvallis, OR 97331, USA.

C.E. Jordan. NOAA-Fisheries, Northwest Fisheries Science Center, 2725 Montlake Blvd. E., Seattle, WA 98112, USA.

J.B. Dunham. US Geological Survey, Forest and Rangeland Ecosystem Science Center, 3200 Southwest Jefferson Way, Corvallis, OR 97331, USA.

Corresponding author: Haley A. Ohms (e-mail: haley.ohms@oregonstate.edu).

\*Present address: Oregon State University, Department of Zoology, 3029 Cordley Hall, Corvallis, OR 97331, USA.

size is less critical for male reproduction because they can secure matings either through aggressive defense of females, a tactic typically displayed by larger anadromous males (Esteve 2005), or through the “sneaking” tactic adopted by smaller resident males (Hutchings and Myers 1988). In partially migratory species, where the main advantage of migration is increased body size, females are often hypothesized to receive a much stronger benefit from anadromy than males (Jonsson and Jonsson 1993; Thériault et al. 2007). What remains unclear is how the sexes differ in the strength of their response to environmental factors influencing the costs and benefits of anadromy.

The objective of this study was to determine how freshwater productivity and migration difficulty influence differences between male and female *Oncorhynchus mykiss* in the expression of anadromy. Steelhead and rainbow trout are common names for alternative life-history forms within this species, with “steelhead” referring to anadromous individuals, and “rainbow trout” referring to freshwater residents. *Oncorhynchus mykiss* is a useful model species because it inhabits a large geographic range and has considerable life history plasticity present in both males and females. Steelhead and rainbow trout are sympatric, interbreed, and may produce offspring with a life history different from their own (i.e., steelhead parents can produce rainbow trout offspring and vice versa; Christie et al. 2011; Courter et al. 2013).

To test the prediction that steelhead are more likely to be female, we measured outmigrant sex ratios in nine North American populations of partially migratory *O. mykiss*. If females receive a greater relative benefit from anadromy than males, we expected to find a consistently female-biased sex ratio within the outmigrants of partially migratory populations. We also tested whether freshwater productivity and migration difficulty influence the strength of female-biased anadromy by sampling streams across a wide range of latitude and migration distance (Fig. 1). We expected that males would more readily shift to resident life histories as the relative benefits of anadromy decreased, resulting in increased female-biased anadromy in streams at either lower latitudes or with longer migration distances. Lastly, we compared the sex ratios of age-0 juveniles, mature freshwater residents, and anadromous outmigrants in one study stream to determine how sex ratios differ across life-stage categories. We extend inferences from this single study stream using a simple mathematical model to explain demographic conditions under which female-biased outmigrant sex ratios may or may not result in correspondingly male-biased sex ratios in freshwater residents.

## Materials and methods

### Study species

North American populations of partially migratory *O. mykiss* are distributed along the eastern Pacific Rim from southern California to southcentral Alaska. Steelhead inhabit coastal stream systems, as well as interior streams requiring migrations as far as 1500 km to reach the ocean (Busby et al. 1996). Anadromous individuals generally spend between 1 and 5 years rearing in fresh water prior to emigrating to the ocean and from 1 to 3 years at sea (Busby et al. 1996). Resident rainbow trout reach maturity after 1 to 8 years, often breeding several times (Schill et al. 2010). The timing of spawning migrations for steelhead varies with both latitude and migration distance (Busby et al. 1996). Generally, interior populations migrate upstream during the summer and complete maturation prior to their winter–spring spawning period, whereas most coastal populations enter fresh water as mature adults just before spawning. Relative to steelhead, little is known about the spawning behavior of rainbow trout within partially migratory populations (Busby et al. 1996).

Given the potential confusion associated with common names, the fact that individuals may express life histories that differ from their parents and are indistinguishable as juveniles, we use the

term “juvenile” to identify an individual with an undetermined life history, “anadromous” or “outmigrant” to indicate an individual that has adopted an anadromous life history and has either smolted or migrated downstream from its natal habitat, and “freshwater resident” or “resident” to indicate an individual that has adopted a freshwater resident life history and shows signs of maturation in fresh water. In all cases, these names apply to individuals regardless of their parent’s life history.

### Study areas and capture methods

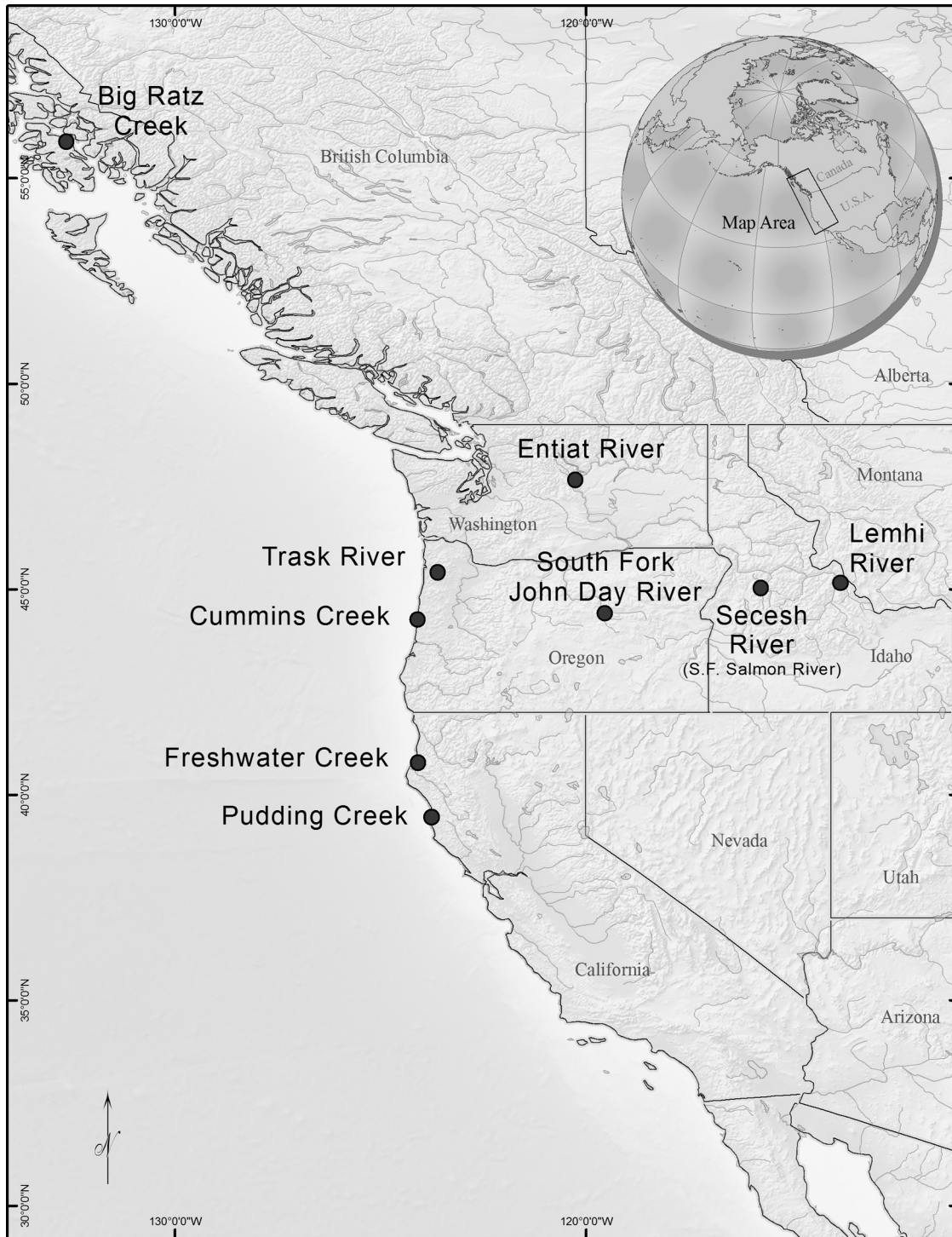
To test the prediction that the anadromous component of partially migratory *O. mykiss* populations is female-biased and that migration distance and latitude influence the strength of that bias, we sampled outmigrants in nine streams located from 39.5° to 55.9° latitude on the west coast of North America in the spring of 2011 and 2012 (Table 1; Fig. 1). All study systems support self-sustaining, wild *O. mykiss* populations without hatchery supplementation. We determined the sex ratios of outmigrants because this life stage provides the earliest time at which to identify the anadromous component of a population and because sex ratios at this stage are not confounded by sex-specific mortality rates that can occur within the marine environment (Spidle et al. 1998; Tamate and Maekawa 2004) or after first reproduction (Keefer et al. 2008).

Outmigrants were captured using rotary screw traps operated by local state agencies during the emigration season at each location (roughly April to May) in 2011 and 2012. Dates of operation at each trap varied slightly according to local emigration timing and stream conditions (Table 2). Seven of the nine rotary screw traps operated in 2011 and the two remaining were operated in 2012. We developed a systematic sampling scheme based on site-specific capture data from previous years to estimate the proportion of the total expected catch at each site that would be required to yield approximately 200 outmigrant samples (Table 2). Outmigrants were then sampled proportionally to the daily, site-specific catch to ensure that samples were dispersed throughout the emigration period.

Outmigrants were characterized differently at each site based on the expertise of local agency personnel operating each trap and their regional metrics for differentiating between anadromous outmigrants and freshwater residents. At Cummins Creek, fish greater than a 120 mm length threshold were sampled; at Trask River, fish greater than a 100 mm length threshold were sampled; and at Big Ratz Creek, fish greater than a 150 mm length threshold were sampled. No length threshold was applied at the remaining sites (Pudding Creek, Freshwater Creek, Entiat River, Lemhi River, and Secesh River). We acknowledge that some smaller fish sampled at these latter sites may have been migrating to estuarine or mainstem habitats for additional rearing prior to smolting and entering the ocean (Shapovalov and Taft 1954; Hayes et al. 2011). However, we included these fish in our analyses because they are part of the anadromous component of their respective populations even though they may not have fully completed the physiological transformations necessary for ocean entry. Outmigrants selected for sampling were anesthetized, measured for fork length to the nearest mm, and a small fin clip and scales were collected for sex determination and age analysis, respectively. Scales were removed from an area a few rows above the lateral line, between the anterior insertion of the anal fin and the posterior insertion of the dorsal fin (Devries and Frie 1996). Scales and fin tissue were stored on Whatman chromatography paper (Whatman, Maidstone, UK), except at Big Ratz Creek (Fig. 1), where tissue samples were initially placed in vials containing 90% ethanol and later transferred to Whatman chromatography paper in the lab.

In addition to sampling outmigrants, we selected one population in which we determined the sex ratios of age-0 juveniles and freshwater residents. Although previous laboratory (Magerhans and Hörstgen-Schwark 2010; Sloat 2013) and field studies (Rundio

**Fig. 1.** Locations of study streams where outmigrants were collected in 2011 and 2012. Age-0 juveniles, freshwater residents, and anadromous outmigrants were collected during 2011 in the South Fork John Day (Oregon) *Oncorhynchus mykiss* population.



et al. 2012) have demonstrated that juvenile sex ratios of *O. mykiss* are typically 1:1 prior to the expression of anadromous or resident life histories, we wished to verify whether outmigrant sex ratios reflected differences in life history expression between the sexes or whether they were simply proportional to the relative abundance of males and females at age-0. We sampled juvenile and resident *O. mykiss* in the South Fork (SF) John Day River, Oregon (Fig. 1). We selected 16 sampling locations using a generalized random tessellation stratified survey design (Stevens and Olsen

2004). The SF John Day River has a waterfall at river kilometre 45 that acts as a barrier to upstream migration of anadromous adults, and therefore, all individuals above the barrier are offspring from resident fish. Eight sampling locations were located above the waterfall, eight were located below, and we stratified sampling locations above and below the waterfall by stream order (Strahler 1957). Sites above the waterfall were chosen to contrast the sex ratio of a freshwater resident population with that within the partially migratory population below the waterfall.

**Table 1.** Geographic locations, environmental conditions, and biological characteristics of study streams where outmigrants were collected in 2011 and 2012 (Fig. 1).

River	Trap location (state)	Latitude (°N)	Longitude (°W)	Migration distance (km)	Drainage area (km <sup>2</sup> )	Elevation (m)	Climate type (precipitation as rain)	Stream conditions
Big Ratz	Alaska	55.8900	132.6334	1	41	296	Pacific maritime (152–559 cm·year <sup>-1</sup> )	Lake- and rainwater-fed.
Entiat River	Washington	47.6636	120.2505	770	816	1298	Semi-arid high desert (25–254 cm·year <sup>-1</sup> )	Originates from 11 glaciers and snowfields in the Cascade Range. Limit to anadromy is Entiat Falls at rkm 54.4.
Trask River	Oregon	45.4156	123.6023	45	75	499	Pacific maritime (318–508 cm·year <sup>-1</sup> )	Flashy stream, high flows November to March.
Lemhi River	Idaho	45.1526	113.8135	1090	3160	2182	Semi-arid high desert (mean 51 cm·year <sup>-1</sup> )	Fed by snowmelt runoff and groundwater springs. Major irrigation diversion.
Secesh River	Idaho	45.0382	115.7421	1240	626	2055	Semi-arid high desert (51–152 cm·year <sup>-1</sup> )	Peak discharge results from snowmelt runoff in late May and June.
South Fork John Day River	Oregon	44.4189	119.5394	690	1441	1466	Semi-arid high desert (25–51 cm·year <sup>-1</sup> )	Fed by snowmelt runoff and groundwater springs. Waterfall at rkm 45 restricts upstream movement of steelhead. Some irrigation diversion.
Cummins Creek	Oregon	44.2670	124.0890	1	21	332	Pacific maritime (180–230 cm·year <sup>-1</sup> )	High-gradient stream, peak flows November to March, no estuary.
Freshwater Creek	California	40.7837	124.0831	21	77	281	Pacific maritime (100–150 cm·year <sup>-1</sup> )	Lower 6 km has cattle grazing, is low-gradient, and confined by levees.
Pudding Creek	California	39.4541	123.7576	7	39	156	Mediterranean (mean 98 cm·year <sup>-1</sup> )	Impoundment 1 km upstream of ocean mouth; resulting reservoir inundates 4.3 km of stream.

**Table 2.** Dates of rotary screw trap operation, sampling protocol, and outmigrant sample size at each study stream.

River	Sampling protocol	Sample size	Dates of operation
Big Ratz	1 in 7 outmigrants captured	198	17 April to 14 June 2011
Entiat River	1 in 10 outmigrants captured	147	17 March to 14 May 2011
Trask River	All outmigrants captured	366	7 March to 18 June 2012
Lemhi River	All outmigrants captured	218	19 April to 24 May 2011
Secesh River	All outmigrants captured	99	1 May to 5 July 2011
SF John Day River	1 in 7 outmigrants captured	119	12 April to 17 June 2011
Cummins Creek	1 in 3 outmigrants captured	154	3 March to 4 June 2012
Freshwater Creek	All outmigrants captured	122	12 April to 1 June 2011
Pudding Creek	1 in 3 outmigrants captured	193	10 April to 13 June 2011

At each site, we attempted to collect at least three fish in each of five size categories (<65, 65–100, 100–150, 150–200, and >200 mm) using a combination of electrofishing, seining, and hook-and-line sampling. Fish were euthanized with an overdose of MS-222, measured to fork length (mm), and fin tissue and scales were collected as described for the sampling of outmigrants. In addition, we removed gonads and extracted otoliths from euthanized fish to determine maturity status and age. Gonads were fixed in 10% buffered formalin then transferred to vials with ethyl alcohol for preservation and storage.

### Sex determination

To determine the genotypic sex of all fish sampled (age-0 juveniles, residents, and outmigrants) we used polymerase chain reaction (PCR) in 2011 and single nucleotide polymorphisms (SNP) in 2012 to determine the presence of a Y-linked sex marker (OmyY1)

described by Brunelli et al. (2008) DNA was extracted from fin tissue using DNeasy 96 Tissue kits with a BioRobot 8000 (QIAGEN Inc., Valencia, Calif.) for all samples in both years. For the 2011 samples, the PCR was performed on approximately 25 ng of DNA to amplify OmyY1. We used ND3 as the internal control (5 pmol each; Domanico and Phillips 1995) and OmyY primer (12 pmol each), which differed slightly from the methods described by Brunelli et al. (2008). PCR products were electrophoresed through 2% agarose gels in Tris-acetate-EDTA (TAE) buffer and stained with GelRed nucleic acid stain (PHENIX, Candler, N.C.). The male band (792 bp) was clearly distinguishable from the ND3 control band (368 bp). For the 2012 samples, approximately 10–20 ng of DNA was used as a template in the TaqMan 5' nuclease assay (Applied Biosystems, Carlsbad, Calif.). All PCRs were done in a 5 µL volume containing TaqMan GTXpress Master Mix, SNP genotyp-

ing primers and minor groove binding probes for OmyY1-2SEXY based on the OmyY1 locus (Brunelli et al. 2008). The amplification consisted of 95 °C for 10 min and 40 cycles of 95 °C for 15 s and 60 °C for 1 min. The 7900 Real-Time PCR System (Applied Biosystems) was used for SNP genotyping and the data were analyzed using the Sequence Detection System 2.4 (Applied Biosystems). Positive and negative controls were used on each plate and the assay was tested on 150 samples from 2011 to ensure the quality of allele discrimination. These samples had 100% concordance of sex determination across methods.

We compared the genotypic sex results with the phenotypic sex determined by histology to assess the error rate associated with the genotypic sex determination for freshwater residents collected in the SF John Day River. These samples had 100% concordance between genotypic and phenotypic sex ( $n = 115$ ).

### Age determination

Fish age was determined using scales (all populations) and otoliths (SF John Day River only). Scales from Big Ratz Creek, and Cummins Creek and Trask River, were aged by trained personnel at the respective state agencies collecting the outmigrant samples (Alaska Department of Fish and Game and Oregon Department of Fish and Wildlife, respectively). Because of the large number of outmigrants captured at Trask River, a stratified random subsample of outmigrants were selected for age analysis ( $n = 262$ ). Scales from the remainder of the study streams were aged by trained personnel at Oregon State University, Corvallis, following the methods of Devries and Frie (1996). Otoliths of fish collected from the SF John Day River were aged following the methods of Devries and Frie (1996).

### Maturity status of SF John Day River *O. mykiss*

We assessed the maturity status of SF John Day River *O. mykiss* by histological examination of gonads from fish captured during stream sampling. Ovaries and testes were fixed in formalin, dehydrated through a graded series of ethanol baths and embedded in paraffin wax, thin-sectioned (thickness, 5  $\mu\text{m}$ ), and stained with hematoxylin–eosin. Stages of development (oogenesis and spermatogenesis) were determined by light microscopy, using the protocol of Nagahama (1983) as a guide. We classified males as freshwater residents if spermatozoa were present within the testis and females as freshwater residents if oocytes in the ovary had advanced to oil drop stage (Nagahama 1983). We considered individuals that did not have gonads with these characteristics to be juveniles, with an undetermined life history.

### Data analysis

We measured the number of stream kilometres from each rotary screw trap to the ocean to calculate migration distance and the latitude at each trapping location using a geographic information system (ArcGIS 9.3.1, ESRI, Redlands, Calif.). Rotary screw traps were located near the downstream distribution boundary for anadromous *O. mykiss* within each study stream, and therefore, this approach likely underestimated the total migration distance for each study population. However, this discrepancy is very small compared with the variation in migration distances among the study populations (Table 1) and is unlikely to introduce any systematic bias into our analysis.

We performed exact binomial tests to determine whether outmigrant sex ratios from each of the nine study streams deviated significantly from 1:1. We constructed two separate generalized linear mixed-effects logistic regression models to test the effect of migration distance and latitude, with outmigrant sex as the binomial response variable (i.e., female = 1, male = 0) and site as the random effect. Because of potential differences between the sexes in age, length, and emigration date, these variables were also included as predictors in each model. Age was normalized by assigning a relative age of zero to the modal value within each

study stream to control for a potential increase in outmigrant age with latitude (Metcalf and Thorpe 1990). We also standardized outmigrant length by subtracting the stream-specific mean value from the length of each individual outmigrant to avoid interpreting the model intercept for a fish of length zero (Zuur et al. 2009). For migration date, we normalized the date of capture relative to the start of trap operation within each study stream. These data transformations eliminated collinearity among predictor variables. In addition, we used a natural log transformation of migration distance because of the extreme range of migration distances among study streams and because untransformed values caused poorly conditioned model matrices.

To verify whether latitude was a suitable proxy for variation in freshwater growth opportunity among study streams, we modeled mean outmigrant age as a function of latitude, sex, outmigrant length, and latitude  $\times$  outmigrant length interaction, using a generalized linear mixed-effects model, with latitude included as a random effect. As with the logistic regression, we centered outmigrant length. We used drop-in-deviance tests to determine the significance of each parameter and then reduced the model to contain only statistically significant predictors. Sex and latitude  $\times$  outmigrant length interaction were not significant, so we reduced the model to include only latitude and outmigrant length as predictor variables. If latitude was a suitable proxy for freshwater growth opportunity, we expected to observe a significant effect of latitude on outmigrant age for a given length (i.e., when holding length constant).

We assessed potential variation among males and females in the size at emigration by modeling fork length as a function of sex, age, and emigration date for each study stream using a generalized linear mixed-effects model with site as a random effect. We used a similar approach to assess variation in emigration timing as a function of sex, age, and length (with site as a random effect), as well as variation in age as a function of sex, emigration date, and length (with site as a random effect). These combinations of predictor variables were not collinear, so we did not apply any data transformations in this analysis.

To determine whether sex ratios of SF John Day River age-0 juveniles and freshwater residents differed from 1:1, we used exact binomial tests. We performed an odds ratio test to compare the sex ratios of freshwater residents above and below the barrier waterfall in the SF John Day River. All analyses were performed in R version 2.14.1 (R Development Core Team 2012).

Lastly, we conducted a mathematical simulation to determine the conditions under which a female-biased sex ratio in the anadromous component of a given population would correspond with a male-biased sex ratio in the resident component of that population. The sex ratio of one component of a partially migratory population is determined by both the relative proportion of males and females, as well as the overall ratio of anadromous and resident individuals in the population. Assuming a juvenile sex ratio of 1:1, the relationship between these proportions can be expressed as

$$r = (s - 0.5)/(s - m)$$

where  $r$  is the proportion of residents within a population,  $s$  is the proportion of outmigrants that are male, and  $m$  is the proportion of residents that are male. This equation best represents the dynamics of an individual cohort from juvenile rearing until the expression of anadromous or resident phenotypes, but does not explicitly account for variation in the age at emigration and at maturity, and it assumes no differences in mortality rates between sexes prior to life history expression. Based on these simplifying assumptions, this equation can provide an approximate estimate of the relative proportion of resident and anadromous

**Table 3.** Outmigrant sex ratios from all study streams sampled in 2011 and 2012.

River	Percentage of females (%)	95% confidence interval (%)	p value	Sample size
Big Ratz	71	64–77	<0.01	198
Entiat River	62	54–70	<0.01	147
Trask River	56	51–61	0.02	366
Lemhi River	60	53–67	<0.01	218
Secesh River	65	54–74	<0.01	99
SF John Day River	76	67–83	<0.01	119
Cummins Creek	58	50–66	0.04	154
Freshwater Creek	71	62–79	<0.01	122
Putding Creek	63	56–70	<0.01	193

**Note:** Binomial test results and p values indicate all populations differ from a 1:1 sex ratio and are female-biased.

fish within a partially migratory population given information on the sex ratios of outmigrants and residents.

**Results**

The number of outmigrants sampled per study stream ranged from 99 to 366 (Table 3). Outmigrant sex ratios from all study streams were female-biased, with the proportion of females in each population ranging from 56% to 76% (Table 3). Contrary to our initial hypotheses, latitude was not a significant predictor of outmigrant sex ratios (drop in deviance test,  $\chi^2 = 0.02$ ,  $p = 0.89$ ; Fig. 2), nor was migration distance ( $\chi^2 = 0.01$ ,  $p = 0.74$ ; Fig. 3).

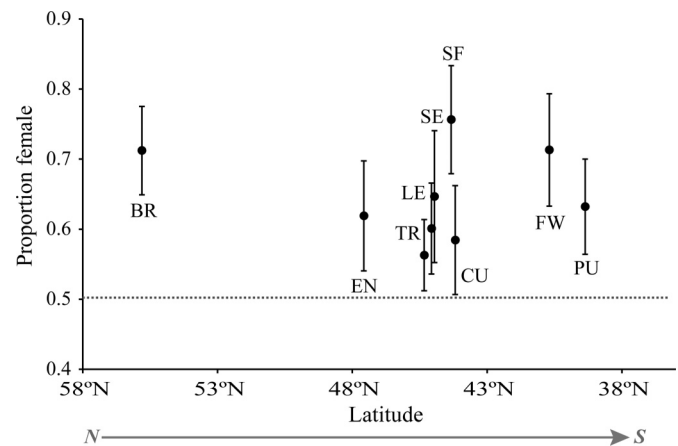
Mean outmigrant age increased with latitude after accounting for outmigrant length (95% confidence interval (CI): 0.05–0.14 years,  $p < 0.01$ ; Fig. 4), such that for every 10.45° increase in latitude there was an estimated 1 year increase in mean outmigrant age. This result indicates that fish of a given age were smaller at northern latitudes than at southern latitudes.

Within the study populations, we did not observe phenotypic differences between male and female outmigrants. After controlling for age and emigration date, mean outmigrant length was similar between males and females (mixed-effects linear regression, 95% CI: -2.7–2.2 mm,  $p = 0.85$ ; Fig. 5). Similarly, neither mean outmigrant age nor mean emigration date differed between males and females (mean outmigrant age 95% CI: -0.10–0.01 years,  $p = 0.10$ ; mean emigration date 95% CI: -0.393–0.044 days,  $p = 0.12$ ).

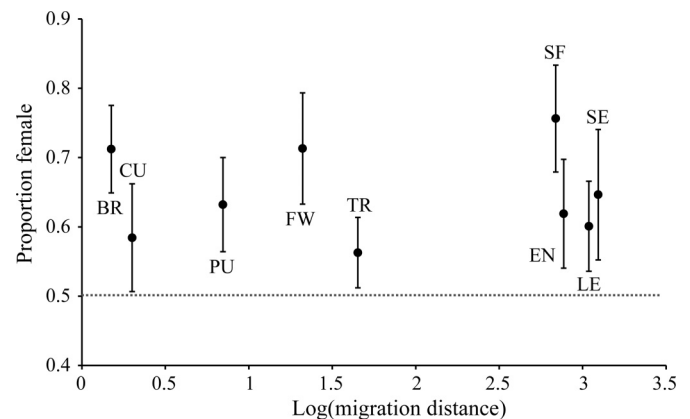
The sex ratio of age-0 juveniles was slightly male-biased and included 56% males in age-0 juveniles above the barrier falls ( $n = 36$ ) and 57% males below the barrier falls ( $n = 44$ ). However, neither of these estimates differed significantly from 1:1 (exact binomial tests, above falls 95% CI: 38%–72% male,  $p = 0.62$ ; below falls 95% CI: 41%–72% male,  $p = 0.45$ ; Fig. 6). Of the 68 age-1 or older fish captured above the SF John Day River barrier waterfall, 49 (72%) were maturing, and within this sample, the estimated sex ratio was 51% male, which was not significantly different from 1:1 (95% CI: 36%–66% males,  $p = 0.99$ ). Of the 71 age-1 or older fish captured below the barrier waterfall, 31 (44%) were maturing, and within this sample, the estimated sex ratio was 58% male, which was not significantly different from 1:1 (95% CI: 39%–75% female,  $p = 0.47$ ). Furthermore, the sex ratios of mature fish above and below the barrier waterfall were not significantly different from each other (odds ratio test,  $p = 0.54$ ).

Our mathematical simulation indicated that a highly skewed sex ratio within outmigrants may not result in an equally skewed sex ratio within freshwater residents because of a large effect of the relative abundance of anadromous and freshwater residents on complementary sex ratios (Fig. 7). For example, when the proportion of residents in the population is large and outmigrants are highly female-biased, residents will have only a very slight male bias as a result of the high overall proportion of residents. In cases where the proportion of residents in the population is small, the resident sex ratio can be highly male-biased even when the

**Fig. 2.** Estimated proportion of female steelhead (*Oncorhynchus mykiss*) outmigrants and 95% confidence intervals from all populations arranged by latitude. PU, Putding Creek, California; FW, Freshwater Creek, California; SE, Secesh River, Idaho; CU, Cummins Creek, Oregon; EN, Entiat River, Washington; SF, South Fork John Day River, Oregon; TR, Trask River, Oregon; LE, Lemhi River, Idaho; and BR, Big Ratz Creek, Alaska.

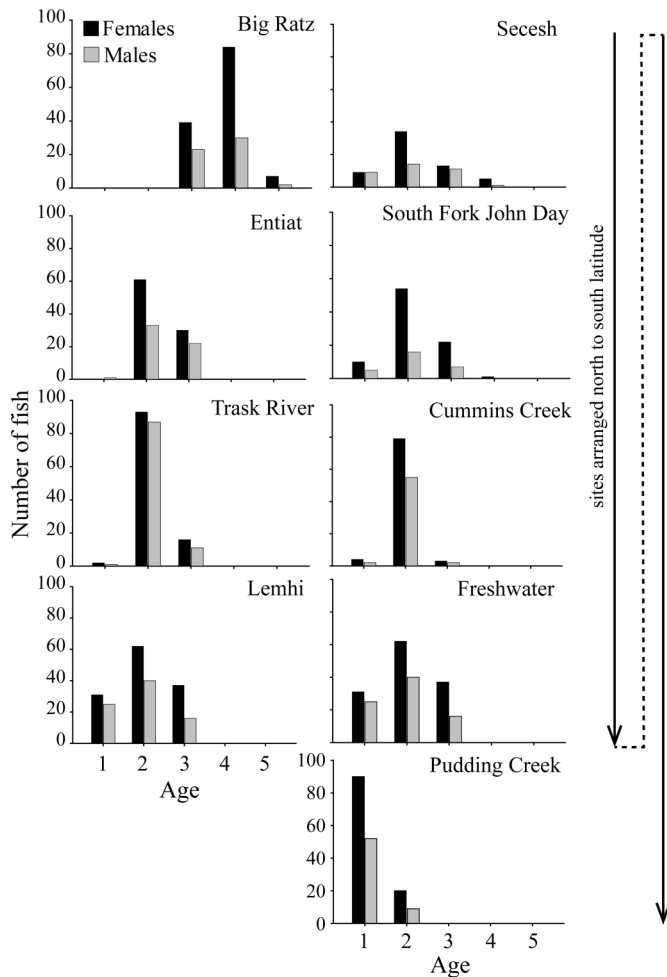


**Fig. 3.** Proportion and 95% confidence intervals of female steelhead (*Oncorhynchus mykiss*) outmigrants along gradient of migration distance (natural log, km). BR, Big Ratz Creek, Alaska; CU, Cummins Creek, Oregon; PU, Putding Creek, California; FW, Freshwater Creek, California; TR, Trask River, Oregon; SF, South Fork John Day River, Oregon; EN, Entiat River, Washington; LE, Lemhi River, Idaho; and SE, Secesh River, Idaho.



outmigrant sex ratio is only slightly female-biased. Only when there is an equal proportion of residents and anadromous individuals in the population are outmigrant and resident sex ratios complementary.

**Fig. 4.** Age at emigration of *Oncorhynchus mykiss* outmigrants sampled in 2011 and 2012. The mean outmigrant age measured in each stream increases with increasing latitude ( $p < 0.01$ ).



## Discussion

We found a consistent female bias in *O. mykiss* outmigrants across a broad geographic range, supporting the hypothesis that females and males of this species differ in migratory tendency (e.g., Jonsson and Jonsson 1993; Hendry et al. 2004). Data on sex ratios in *O. mykiss* are limited, especially for outmigrants, but our results are consistent with the relatively strong (63%) female bias in steelhead outmigrants in the mid-Columbia River (Peven et al. 1994). Ward and Slaney (1988) also observed a slight (54%), but consistent, female bias in *O. mykiss* outmigrants over three years of sampling in the Keogh River, British Columbia. However, because of small sample sizes, they could not rule out the possibility that this deviation from a 1:1 sex ratio had occurred by chance. The higher prevalence of females within *O. mykiss* outmigrants supports the notion that anadromy confers greater benefits to females than males. Females are more likely to dominate the anadromous component in populations of other partially migratory salmonids (*Salvelinus fontinalis* (Thériault et al. 2007), *Salmo salar* (Jonsson et al. 1998), *Oncorhynchus masou* (Tamate and Maekawa 2004), and *Salvelinus malma* (Koizumi et al. 2006)), and in several extreme examples, salmonid mating systems consist primarily of anadromous females and almost exclusively resident males (Hutchings and Jones 1998; Valiente et al. 2005).

Contrary to our expectations, we did not find more highly female-skewed smolt sex ratios in streams at either lower latitudes or with longer migration distances. Both of these factors

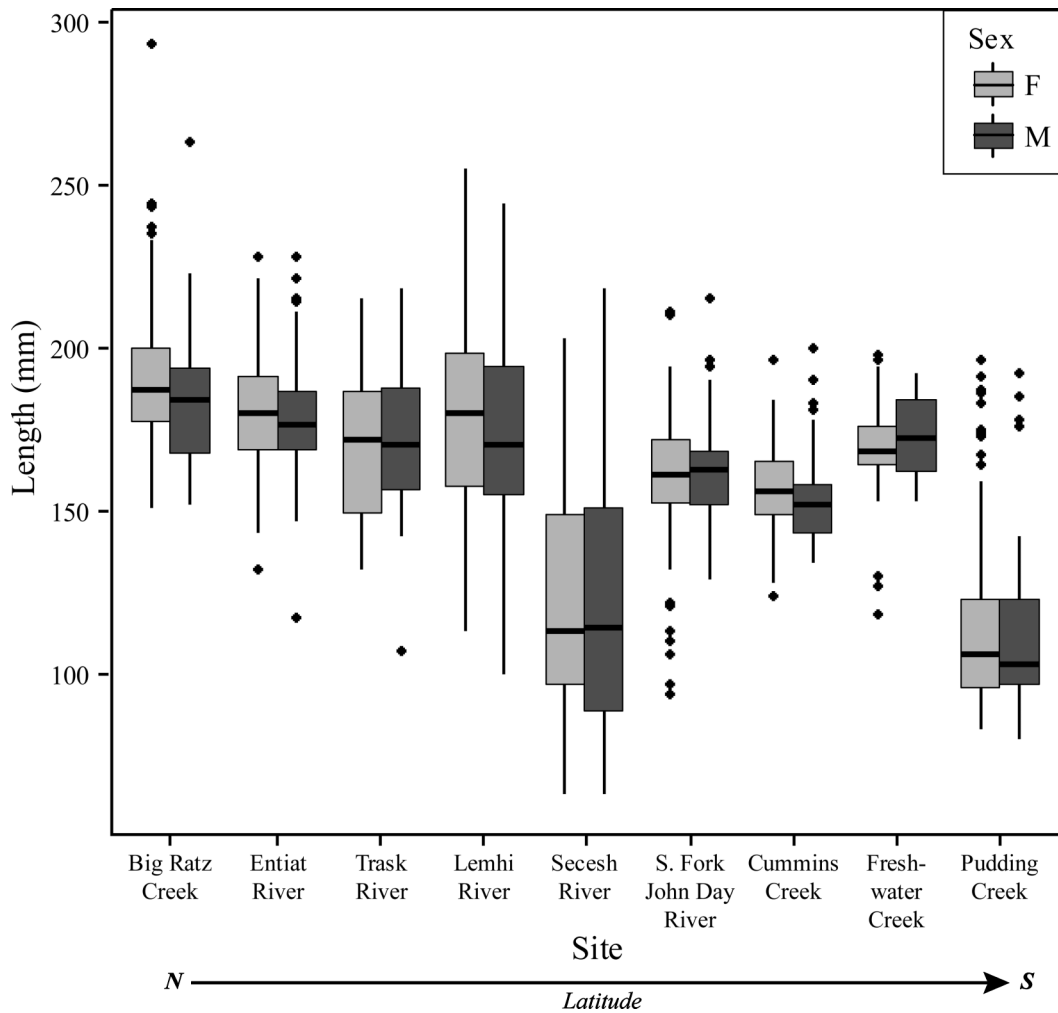
should alter the relative costs and benefits of anadromy and, therefore, influence the prevalence of anadromy within the sexes (Hendry et al. 2004). Latitude appears to be a reasonable proxy for freshwater growth opportunity within our study populations, given that the mean size for a given outmigrant age decreased with increasing latitude. Increased parr growth at lower latitudes (e.g., L'Abée-Lund et al. 1989; Morita and Nagasawa 2010) should decrease the relative benefits of anadromy by increasing developmental opportunities within fresh water. For example, latitude is a strong predictor of the rate of male residency in Atlantic salmon (Valiente et al. 2005) and masu salmon (Morita and Nagasawa 2010) populations spanning a latitudinal range similar to our study. Latitudinal clines in the degree of anadromy (sensu Rounsefell 1958) are well established in other salmonid species (e.g., Elliott 1994; Yamamoto et al. 1999; Maekawa and Nakano 2002). Increasing migration distance should also decrease the relative benefits of anadromy by increasing the survival and energy costs of more difficult migrations (Hendry et al. 2004). Although this has not been shown directly in *O. mykiss*, migration distance has been shown to affect the frequency of anadromy in sockeye salmon (*Oncorhynchus nerka*; Wood 1995), brown trout (*Salmo trutta*; Bohlin et al. 2001; but see Jonsson and Jonsson 2006), and Arctic char (*Salvelinus alpinus*; Kristoffersen et al. 1994; Finstad and Hein 2012).

The apparent lack of influence of latitude and migration distance on outmigrant sex ratios does not necessarily indicate that these factors have no effect on the overall prevalence of anadromy within the study populations, but it does raise the possibility that the proportional response of male and female life histories to these environmental factors was similar. Females are often hypothesized to have less plasticity than males in life history expression because of their higher energy requirements for gamete production and the premium on body size for female reproductive potential (e.g., Fleming 1996; Fraser, In press). This perspective may be appropriate for Atlantic salmon, a species with a suite of life histories similar to *O. mykiss*, but for which freshwater maturation in females is extremely rare in fluvial populations (Fleming 1998). However, female *O. mykiss* demonstrate considerable capacity to adjust their maturation schedules in response to local opportunities for freshwater growth and development (e.g., Sogard et al. 2012; Pavlov et al. 2008). A recent laboratory study of *O. mykiss* reared under contrasting temperature regimes determined that males and females demonstrated a similar proportional decrease in the rate of freshwater residency in response to changing temperature (Sloat 2013). Males had an overall rate of maturation that was 30% higher than females across temperature treatments, but both males and females exhibited an approximately 20% (range: 18%–26%) reduction in freshwater maturation in response to increasing water temperature (Sloat 2013). A similar proportional response to environmental factors associated with latitude and migration distance would tend to reduce variation in outmigrant sex ratios among populations even if these factors influence the overall prevalence of anadromy within the study populations. Overall this could indicate that traits other than size at reproduction, such as age at maturity, survival to maturity, and level of iteroparity, as well as potential intrasexual competition for oviposition sites (Dodson et al. 2013), may play larger roles for female *O. mykiss* fitness than has previously been appreciated.

An alternative explanation for a lack of an environmental effect on outmigrant sex ratios is the potential for interacting effects of latitude and migration distance on the prevalence of anadromy in partially migratory populations. Finstad and Hein (2012) found this to be true in populations of Arctic char in Norway. Neither migration difficulty nor freshwater productivity alone successfully predicted the Arctic char life history expression, but the interaction between the two significantly predicted the prevalence of anadromy among populations. Given that we only had nine observations of migration distance and latitude, we could not investigate this statistical interaction (Zuur et al. 2009). This



**Fig. 5.** Comparison of *Oncorhynchus mykiss* outmigrants' fork lengths between males and females and among sampled streams. Mean lengths did not differ between males and females in any population ( $p = 0.85$ ); however, mean fork length increased with increasing latitude ( $p < 0.01$ ). The solid line represents the median length, while the lower and upper limits of the box represent the 25th and 75th percentiles. The lower and upper ends of the whiskers represent the 10th and 90th percentiles, respectively, and the dots represent length values outside the 10th and 90th percentiles.

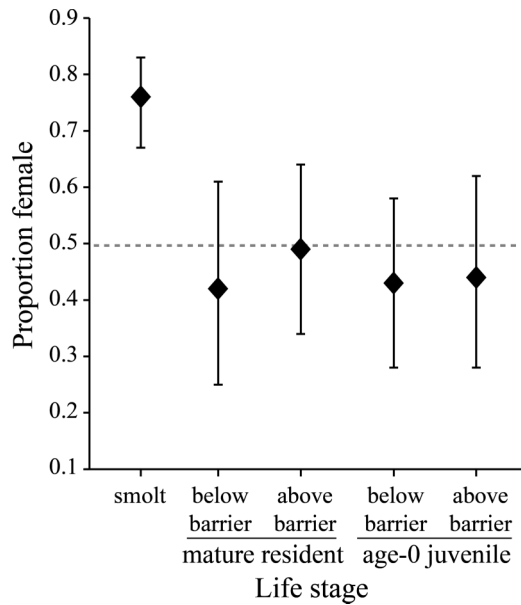


interaction may be important for our study streams because migration distance and elevation are typically correlated, and reduced growth at higher elevations may counter the higher relative cost of anadromy associated with increased migration distance. However, the relatively low variation in smolt sex ratios in the populations we measured suggests that interactions would still not explain variation among populations. Interactions of other environmental factors operating at local scales may also influence life history patterns more acutely than the large-scale environmental gradients we measured. For example, both Sogard et al. (2012) and Pavlov et al. (2008) found that freshwater growth varied considerably in neighboring streams, and resulted in very different life history patterns in the *O. mykiss* populations, despite their geographic proximity.

Both temporal replication of our outmigrant data and a better understanding of ocean growth conditions could have improved the assessment of our results. There are no longterm outmigrant sex ratio data sets for *O. mykiss*. However, two longterm studies of Atlantic salmon outmigrant sex ratios do show temporal variation. Jonsson et al. (1998) measured outmigrant sex ratios for 11 years and observed a range of 50% to 76% females (grand mean 64% females) over that time, whereas Páez et al. (2011) measured outmigrant sex ratios for 7 years and observed a range of 50% to

64% females (grand mean 59% females). If the temporal patterns in *O. mykiss* outmigrant sex ratios are similar to that of Atlantic salmon outmigrants, then any possible patterns could have been obscured, but may also not be very biologically relevant. In addition to temporal variation, it is not clear how latitudinal variation in growth opportunity at sea may also influence the relative benefit of anadromy in these different populations. Ocean growth is an important component of the life history trade-offs experienced by partially migratory species and could also influence the prevalence of anadromy in *O. mykiss*. There is some evidence that ocean productivity increases with latitude (Gross et al. 1988), but whether this influences ocean growth and the benefits of anadromy at higher latitudes is unknown. North American steelhead appear to be widely dispersed and highly mixed in the Pacific Ocean east of 167° longitude and 41° latitude (Light et al. 1988), which may render any latitudinal clines in ocean growth unimportant. Adult steelhead are generally older and larger in northern latitude populations (Withler 1966), which may indicate slower ocean growth for these fish, but could also represent an adaptive advantage to being bigger upon returning to spawn. In any case, existing data suggest that ocean productivity either increases with latitude or ocean growth is similar for steelhead at the latitudes we sampled, and therefore, the trade-offs moving north should lean towards anadromy.

**Fig. 6.** Proportion of female *Oncorhynchus mykiss* in different life histories collected from the South Fork John Day River in the summer of 2011. The sex ratio of outmigrants was the only sex ratio significantly different from 1:1 ( $p < 0.001$ ,  $n = 119$ ). Maturing residents below the waterfall, maturing residents above the waterfall, age-0 below the waterfall, and age-0 above the waterfall did not differ from 1:1 (all  $p$  values  $> 0.45$ ,  $n = 31, 49, 44$ , and  $36$ , respectively).

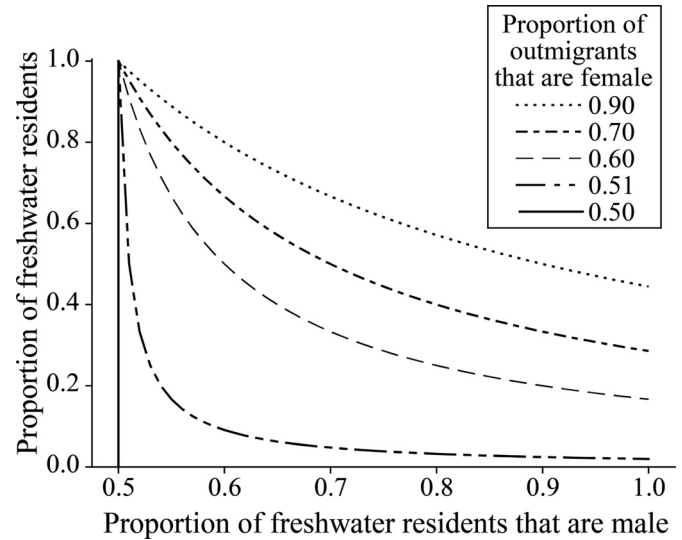


Aside from the higher proportion of females among outmigrants, we found no phenotypic differences between males and females. We investigated differences between males and females in outmigrant length, age, and emigration date and found both sexes to be similar. There is some indication from other studies that freshwater growth differs for males and females (Morita and Nagasawa 2010); however, we did not find evidence of this difference, possibly because those differences take place in an earlier life stage than when we measured. There may also be other factors, such as lipids (Thorpe et al. 1998; McMillan et al. 2012), not considered here that may influence life history expression and may differ between the sexes. However, despite the lack of differences in these characteristics, the strong female bias observed in all study streams underscores the importance of investigating proximate cues and mechanisms of life history choice separately in males and females.

We found no evidence of sex bias in age-0 juveniles in the SF John Day River, which supports our assumption that *O. mykiss* sex ratios are not skewed from the start. Our results are consistent with results from other studies that have measured juvenile (age-0 and age-1 combined) sex ratios of *O. mykiss* in nature (Rundio et al. 2012) and age-0 under artificial propagation (Magerhans and Hörstgen-Schwark 2010; Sloat 2013). Because the age-0 sex ratio was not different from 1:1, we assumed that any change in sex ratio at later life stages indicated a sex-dependent difference in the adoption rate of life history phenotypes.

Contrary to our predictions, we did not observe a strong male bias among residents, despite a high female bias among steelhead outmigrants in the SF John Day River. Our lack of a statistically significant result is likely due to low sample size; however, our estimate was still much less male-biased than expected. We hypothesize that this was due to a high abundance of resident *O. mykiss* that overwhelmed any male bias associated with the female-biased outmigrants. As demonstrated with our sex ratio simulation, when the proportion of residents in a population is high, the

resident sex ratio can be close to 1:1, even when the outmigrant sex ratio is highly female-biased (Fig. 7). Also, if the resident sex ratio is highly male-biased (e.g., 80%), the outmigrant sex ratio is equivalently female-biased only when the proportion of residents in the population is approximately 50%. This highlights how the sex ratio from one life history phenotype provides very little information about the sex ratio of the other, unless the relative proportions of life history phenotypes in the population are known. This is also a plausible explanation for why our results differed from the highly male-biased resident sex ratio reported by Rundio et al. (2012). Their study reported only the sex ratio of residents, not outmigrants, and therefore, the high male bias observed among residents may be the result of a low proportion of residents in the population, a high female bias in outmigrants, or some combination of both. This simulation also demonstrates how estimates of the sex ratios of both residents and outmigrants within a population can be used to approximate the relative proportion of life history phenotypes for that population. For example, using our estimates from the SF John Day River of the outmigrant sex ratio (76% female, 95% CI 67%–83%) and resident sex ratio (42% female, 95% CI 25%–61%), we estimate that approximately 85% of the population is resident. The high proportion of residents may be the result of habitat conditions that allow for freshwater maturation in females, inputs from residents above the barrier falls (Berejikian et al. 2013), or both. This estimate has considerable implications for management and conservation of this population and could certainly be useful in other systems. We acknowledge that this model may oversimplify sex- and age-specific mortality and life history expression timing; however, it does provide an estimate for how the sex ratios and proportion of life history variants are related and could be a relatively simple, nonlethal way to infer a population-level dynamic that can otherwise be difficult to measure.



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In summary, we demonstrated that sex is an important predictor of an individual's life history, likely as the result of differences

in fitness determinants between males and females. However, sex biases may not always be equivalent between life history types (i.e., residents and steelhead), and this may be controlled by population-level trade-offs that differ from male–female trade-offs. For example, we found that sex ratios did not vary along environmental gradients of latitude and migration distance, possibly because males and females respond similarly to these conditions. Whether the sexes respond similarly to environmental conditions is an important question for understanding the overall resilience of the species, as well as predicting future effects of climate change. We emphasize the importance of considering sex when investigating proximate and ultimate controls on life history and propose that sex ratios could be a powerful tool for investigating frequencies of life histories within populations.

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