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Corresponding author mail id :- chris.p.tatara@noaa.gov

Age-at-release, size, and maturation status influence residualism in hatchery steelhead trout, *Oncorhynchus mykiss*

Christopher P. Tatara
Environmental and Fisheries Sciences Division
Northwest Fisheries Science Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
Manchester Research Station, Post Office Box 130, Manchester, Washington 98353, USA

Donald A. Larsen
Environmental and Fisheries Sciences
Northwest Fisheries Science Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
2725 Montlake Boulevard East, Seattle, Washington 98112, USA

Matt R. Cooper
U.S. Fish and Wildlife Service, Mid-Columbia Fish and Wildlife Conservation Office, 7501 Icicle Road, Leavenworth, Washington 98826, USA

Penny Swanson

Environmental and Fisheries Sciences
Northwest Fisheries Science Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
2725 Montlake Boulevard East, Seattle, Washington 98112, USA

Mollie A. Middleton
School of Aquatic and Fisheries Science, University of Washington
Under contract to Northwest Fisheries Science Center
National Marine Fisheries Service, National Oceanic and Atmospheric Administration
2725 Montlake Boulevard East, Seattle, Washington 98112, USA

Jon T. Dickey
School of Aquatic and Fisheries Science, University of Washington
Under contract to Northwest Fisheries Science Center
National Marine Fisheries Service, National Oceanic and Atmospheric Administration
2725 Montlake Boulevard East, Seattle, Washington 98112, USA

Deborah Harstad
Environmental and Fisheries Sciences
Northwest Fisheries Science Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
2725 Montlake Boulevard East, Seattle, Washington 98112, USA

Michael Humling
U.S. Fish and Wildlife Service, Mid-Columbia Fish and Wildlife Conservation Office, Winthrop
Field Office, 453A Twin Lakes Road, Winthrop, Washington 98862

Chris R. Pasley
U.S. Fish and Wildlife Service, Winthrop National Fish Hatchery, 453A Twin Lakes Road,
Winthrop, Washington 98862

Barry Berejikian

Environmental and Fisheries Sciences Division
Northwest Fisheries Science Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
Manchester Research Station, Post Office Box 130, Manchester, Washington 98353, USA

Running Title: Steelhead smolt-age and residualism

<A>Abstract

Steelhead trout (*Oncorhynchus mykiss*) that fail to emigrate seaward after release from hatcheries, commonly referred to as “residuals”, can have negative impacts on natural populations ranging from competition and predation to interbreeding with returning anadromous adults. We investigated how age-at-release, size, and maturation status influence the rate of residual production in hatchery summer-run steelhead released from the Winthrop National Fish Hatchery (Methow River, Washington) between 2010 and 2015. Migration data from 21,598 individuals implanted with passive integrated transponder (PIT) tags identified 1,783 residual steelhead expressing two distinct phenotypes, immature male and female parr and precociously mature males. We found that age-at-release significantly affected the predominant residual phenotype. Age-1 (S1) steelhead residuals were dominated by smaller parr of both sexes (fish under < 146 mm FL), while age-2 (S2) residuals were dominated by mature males, though both phenotypes were present in both S1 and S2 residual groups. Collections of residual steelhead in the Methow River indicated that parr phenotype residuals grew as well as juvenile *O. mykiss*, suggesting potential competition for food resources and habitat. PIT tag detections within the Methow River Basin indicated that precocious male residuals may overlap both spatially and temporally with previously documented spawning anadromous adults, posing a potential genetic management risk. Both residual phenotypes had poor overwinter survival and only 1 out of 1,783 of these fish eventually returned to the Methow River as an anadromous adult. We conclude that the ecological and genetic consequences of residual steelhead far outweigh their potential contribution to anadromous production, and measures should be taken to reduce their production by changing hatchery rearing practices.

<A>Introduction

Oncorhynchus mykiss display extensive life-history variation including both anadromous (steelhead) and resident (rainbow trout) forms (Kendall et al. 2015) that interbreed with one another (Docker and Heath 2003; McPhee et al. 2007). In the natural environment, both forms can either follow the parental phenotype or produce the alternate life-history (Quinn and Myers 2004; Courter et al. 2013). The complexity in life-history variation may constitute a portfolio effect that functions to maintain population viability (Waples et al. 2008; Shindler et al. 2010; Moore et al. 2014). Life history variation is influenced by maternal and genetic effects, environmental conditions (water temperature, nutrition, and competition) and their interactions (Kendall et al. 2015). However, hatcheries intentionally produce either rainbow trout or steelhead and typically constrain natural life history variability to achieve program or management objectives.

Steelhead hatchery programs throughout the Pacific Northwestern United States and British Columbia, Canada were implemented to mitigate for stock declines resulting from loss of habitat, overharvest, and hydropower development, among other factors (Lichatowich 1999). The primary goal of steelhead hatchery programs is to increase the number of returning anadromous adults for broodstock, and sport, tribal and commercial fisheries. However, hatchery fish differ from wild fish behaviorally and physiologically (Weber and Fausch 2003; Kostow 2004; Naish et al. 2007; Fraser et al. 2008) and exhibit reduced reproductive fitness relative to wild fish (Araki et al. 2008; Christie et al. 2016; Ford et al. 2016). Growth patterns of hatchery and naturally reared steelhead in freshwater profoundly differ (Berejikian et al. 2012). Wild steelhead typically spend two or more years in freshwater before undergoing the physiological changes to allow for life in seawater (smolting) and migrating to the ocean (Randall et al. 1987; Peven 1994). By contrast, for economy of time, space, and expense, most hatchery steelhead are reared on an accelerated growth regime and released to produce seaward migrants ('smolts') after a single year (hereafter 'S1'). Doing so may require intentional artificial selection for advanced spawn timing in hatchery broodstocks (Mackey et al. 2001; McClean et al. 2005). Programs that aim to supplement natural populations for recovery purposes, are mandated by hatchery reform guidelines to use natural origin broodstock that exhibit natural spawn timing (USFWS, 2009), and such programs have recently been developing methods to produce age-2 smolts (hereafter ‘S2’).

Regardless of age-at-release, steelhead hatcheries are deemed successful if they achieve high percentages of juveniles completing smoltification by the release date. Anadromous salmonids that do not undergo smoltification and migrate during the primary migration period are referred to as “residuals” and can occur in both S1 and S2 steelhead programs (Berejikian et al. 2012). Reduced age at smoltification in S1 programs has been associated with selection for higher growth rates in culture (Berejikian et al. 2017). Male and female steelhead with lower growth rates do not reach threshold sizes for smolting during their year of hatchery rearing and residualize as immature male or female parr. These fish will remain in the freshwater environment and either delay migration to the ocean by one or more years, or do not migrate at all (see review by Hausch and Melnychuk 2012). Although both S1 and S2 programs produce residuals with the parr and precocious mature male phenotypes, the parr phenotype tends to predominate in S1 programs, while the mature male phenotype is more common in S2 programs (Berejikian et al. 2012). While residual steelhead may represent an important component of the natural life-history portfolio for steelhead (Moore et al. 2014), excessively high rates of residualism can increase rates of interbreeding and competition with wild stocks and reduce anadromy (McMichael et al. 1997, 1999; McMichael and Pearsons 2001; Huntingford 2004; Tatara and Berejikian 2012; Snow et al. 2013).

Historically, the Winthrop National Fish Hatchery (WNFH) on the Methow River in northcentral Washington State, USA released only S1 steelhead smolts, but beginning with release year (RY) 2010 the WNFH implemented hatchery reform measures to transition to using natural-origin broodstock and began releasing S2 steelhead smolts (USFWS 2009; Tatara et al. 2017). As a hedge against the uncertainty associated with full transition from an S1 to an S2 rearing regime, both S1 and S2 steelhead were released from WNFH for six consecutive years. Evaluations of outmigration behavior and survival of 142,990 S1 and S2 steelhead implanted with passive integrated transponder (PIT) tags were conducted during the six paired release years. Migration rates of S2 steelhead from the WNFH to the Columbia River were equivalent or better than that of S1 steelhead, and fish size at release largely explained significant migration and survival differences between S1 and S2 fish in some RYs (Tatara et al. 2017). In this study we evaluated how age-at-release affects residualism in hatchery steelhead. This investigation had three central objectives. Objective 1) Conduct pre-release smoltification and maturation surveys to identify characteristics and phenotypes predictive of S1 and S2 residual steelhead, and to estimate percentages of residual phenotypes. Objective 2) Use detection data for PIT tagged steelhead to determine propensity to residualize and to infer the fate of residual S1 and S2 steelhead in the Methow and Columbia Rivers. Objective 3) Collect residual steelhead near WNFH (Spring Creek) after the primary migration period had ended to determine characteristics and post-release growth rates of S1 and S2 residuals.

<A>Materials and Methods

<B>Study area

The study investigated direct evidence of residualism in the vicinity of the hatchery and indirect evidence of residualism by evaluating PIT tag detection patterns in the Methow and Columbia Rivers (Figure 1). Steelhead were released from the WNFH, near the town of Winthrop, Washington, USA, on the Methow River approximately 81.1 river kilometers (rkm) from the confluence with the Columbia River (Lat: 48.4736822°N, -Long:120.1909727°W). Once entering the Columbia River, migrating juvenile salmonids from the WNFH pass nine hydroelectric dams along the additional 843 km migration corridor leading to the Pacific Ocean. Juvenile-specific PIT tag interrogation sites occur downstream at Rocky Reach, McNary, John Day, and Bonneville dams and in close proximity to the WNFH (Figure 1).

Residual steelhead collections and PIT tag detections occurred in a hydrologically complex focal area near the WNFH (Figure 1). The WNFH receives surface water diverted from the Methow River through the 5.4-km long Foghorn Canal. A small, natural, groundwater-fed stream (approximatley 1 – 7 meters in width and 0.1 – 1.5 meters in depth), "Spring Creek", is entirely captured by the Foghorn Canal approximately 450 meters upstream of the hatchery's point of diversion. A portion of the Foghorn Canal's flow is diverted (unscreened to downstream fish passage) behind the hatchery, maintaining the name Spring Creek, while additional flows are diverted into the hatchery or further downstream to irrigators (both screened to fish passage). Most of the water used at the hatchery is returned via the adult fish ladder into Spring Creek, which flows an additional 825 meters to the Methow River. The focal zone for residual collection was restricted to Spring Creek below the screened diversion, adjacent to and downstream of the WNFH, as depicted in Figure 1. Due to the locations of fish screens and impassable culvert structures, juvenile salmonids are not able to ascend upstream of sampled locations in Spring Creek.

<B>Fish culture and tagging

The S1 and S2 steelhead in this study were reared at the WNFH (operated by the United States Fish and Wildlife Service, USFWS) and released into the Methow River between 2010 and 2015. The S1 and S2 broodstock collection, spawning and hatchery rearing protocols are as described in Tatara et al. (2017). Rearing parameters were different for the S1 and S2 steelhead, but the goal of the two regimes was to produce similar sized smolts with an average fork length of 198 mm and an average mass of 75.6 g at the time of release (USFWS 2009). Lower daily rations and rearing temperatures were implemented for the S2 group than for the S1 group (Tatara et al. 2017, supplement). Both S1 and S2 juveniles were reared on Methow River water in the month(s) prior to their release in mid-April in order to facilitate homing to the Methow River. All steelhead were differentially implanted in the snout with a coded-wire tag (CWT) uniquely batch coded according to brood year and rearing treatment. Each year, a subset of approximately 15,000 fish per rearing treatment were also implanted with 12 mm PIT tags following the guidelines established by the Columbia Basin Fish and Wildlife Authority, PIT Tag Steering Committee (1999). Both CWT and PIT tag implantation occurred annually in October, when the S1 steelhead were approximately 7 months old and the S2 steelhead were approximately 16 months old. PIT tag implanted fish were distributed evenly among replicate raceways in each rearing treatment.

<B> Phenoytpe and sex of S1 and S2 reared steelhead

In RYs 2011 through 2015, fork lengths (mm) and weights (g) were collected on a subsample of up to 3,000 PIT-tagged steelhead per rearing treatment per year as described in Tatara et al. (2017). In all years, pre-release data was collected in late March, approximately three weeks prior to release from the hatchery. A qualitative categorization based on visible physical characteristics (phenotype) was assigned to each steelhead sampled (adapted from Gorbman et al. 1982). Fish categorized as parr displayed distinct parr marks. Fish categorized as transitional displayed fading parr marks. Fish characterized as smolts displayed loss of parr marks and silver coloration. Finally, fish categorized as sexually mature males displayed secondary sex characteristics and/or expression of milt (Figure 2). Pre-release data were collected on a total of 21,258 steelhead between RYs 2011 and 2015, and this data was distributed approximately evenly between the S1 and S2 rearing treatments (Table 1). A chi-square test of independence was performed to examine the relationship between rearing strategy (S1 or S2) and pre-release phenotype.

Genetic sex was determined for a subsample of approximately 1,000 PIT-tagged fish per rearing treatment in RYs 2011 and 2012, and approximately 2,000 PIT-tagged fish per rearing treatment in RY 2013 (Table 1). Fin clips were mounted and dried on Whatman chromotography paper (GE Healthcare, Chicago, IL) imprinted with a numbered grid to track which fish the fin tissue belonged. A smaller piece of each mounted fin was subsequently removed using a 2mm Harris micropunch (GE Healthcare, Chicago, IL) and transferred to a 96-well plate. For genomic DNA extraction, 80ul of a 10% Chelex 100 (BioRad, Hercules, CA) solution in nuclease-free water was added to each well, the plate was sealed with heat sealing foil and heated in a thermal cycler for 20 minutes at 100°C. The genomic DNA extraction solution was then centrifuged at 900 × g for 5 minutes. A 5-fold dilution of the supernatant, excluding any Chelex resin, was made in nuclease-free water. Duplex PCR for sdY (primers sdY E2S1 (forward) and sdY E2AS4 (reverse) as described by Yano et al. 2013) and 18S (primers 18S S (forward) and 18S AS (reverse) as described by Yano et al. 2013) was performed. PCR conditions were as follows: 10ul GoTaq Green Master Mix (Promega, Madison, WI), 5.68ul nuclease-free water, 0.33ul of each primer (10uM stock for sdY and 2.5uM stock for 18S), and 3ul of diluted template DNA. Cycling parameters were: 95°C for 2 minutes; 33 cycles of 94°C for 50 seconds, 60°C for 50 seconds, 72°C for 1 minute; and 72°C for 2 minutes. Gel electrophoresis was performed on a 2% agarose gel run for 1 hour at 90 volts. Gels were stained in a solution of 300ml 1xTAE and 30ul GelRed (Phenix Research, Candler, NC). Presence of a single band indicated a female, duplicate banding indicated a male. Genetic sex was recorded and linked to the PIT tag code and other prerelease sampling data via the tracking number.

We conducted two analyses to determine sex bias in migratory behavior for RYs 2011-2013. First, a two-sample t-test looked for differences in the percentage of S1 and S2 males detected migrating, followed by a binary logistic regression model with detection during migration as the response and pre-release fork length as a continuous predictor variable, and rearing strategy (S1 or S2), phenotype, and genetic sex as categorical predictors.

<B> Collection and characterization of residuals near the hatchery

Residual collections were conducted annually over several days from mid-July to mid-September 2010-2015 within the 0.7 river kilometer section of Spring Creek (Figure 1). Fish were captured using a variety of methods including angling, backpack electrofishing and dipnetting (Table 2). Backpack electrofishing with one operator and two netters was the primary means of capture in water depths of less than one meter. In areas over one meter deep, generally in the vicinity of the hatchery ladder, angling and dipnetting were utilized. Captured fish were held up to 48 hours in indoor hatchery holding tanks until they were sampled to determine origin, sex and maturation status. We calculated a residualism index by RY and by smolt age using the catch data with the following formula.

$$\text{Residualism index} = \text{captured residuals} / \text{steelhead released} \times 100$$

The residualism index was then standardized using the CPUE data, so that comparisons could be made among RYs with differing amounts of effort. For RYs 2010 through 2015, we tested for differences in the standardized residual index between the S1 and S2 rearing treatments, using two-sample t-tests. For RYs 2011 through 2015, we used Pearson’s correlation coefficients to examine the relationship between the standardized residual index for S1 and S2 steelhead and mean fork length at release and estimated annual percentage of fish categorized as residual phenotypes (parr and mature males). Each captured residual steelhead was inspected for presence or absence of the adipose fin and scanned for CWT and PIT-tags to determine hatchery or natural origin, brood year and treatment. Natural-origin fish were released. Hatchery origin fish were humanely euthanized, assigned an identification number, measured for fork length (mm) and weight (g), and dissected to determine sex and state of maturational development. For male fish, the testes were removed and weighed on a microbalance for calculation of the gonadosomatic index (GSI) according to the following formula: gonad weight (g) / body weight (g) × 100. The heads of fish with CWTs present were placed in a plastic bag with their corresponding identification number and frozen for future CWT recovery and reading.

The GSI values for male steelhead were $\log_{10}$ transformed to meet the assumption of normality and plotted as a histogram to determine the distribution of male maturation phenotypes and to determine criteria for characterization of male fish as either immature or maturing (ranging from initiation of testes development to fully mature). We used finite mixture models to compare the fit of the $\log_{10}$ transformed GSI data as one mode (AIC = 1204.6), two mode (AIC = 992.2), three mode (AIC = 919.1), and four mode (AIC = 922.2) distributions. The $\log_{10}$ transformed GSI data was best fit (lowest AIC) to a distribution comprised of three modes (immature, maturing, and mature). This model was used to predict the probability of falling into each of the three modes for each $\log_{10}$ GSI value. We set the boundary between modes to be where the probability = 0.5 (equal chance of falling within each of two modes). This analysis showed the boundary between the lower mode and the middle mode to be -0.86 $\log_{10}$ GSI (corresponding to an untransformed GSI value of 0.138, Figure 3). Males with GSI values at or below 0.138 were classified as “immature” and those above as “mature” in subsequent analyses requiring categorical variables. The two upper modes corresponded to male fish that were initiating maturation for the following year and those that had already matured the previous spring.

Differences in the number of each sex among captured S1 and S2 residuals and differences in maturation status among S1 and S2 male residuals were analyzed using the Chi-square test. Within each rearing strategy, we compared the estimated percentage of phenotypes from the prerelease samples to the percentages of phenotypes captured during the Spring Creek sampling, respectively using two sample t-tests.

<B>Indirect assessment of residualism in the Methow and Columbia Rivers

We used the Columbia Basin PIT Tag Information System (PTAGIS) to obtain and manage PIT tag detection data for steelhead released from WNFH. PTAGIS is an online (http://www.ptagis.org/) centralized database for PIT-tagged fish in the Columbia River Basin that houses and provides the software necessary for the tagging and interrogation data submitted by contributors. All tag codes from fish that died or were lethally sampled prior to release, were removed from the initial tag file before uploading to PTAGIS. Hatchery steelhead smolts from the WNFH migrate to the ocean between mid-April and June 30th of their RY. A minimal number of PIT-tagged fish released from WNFH are detected as migrants at PIT tag interrogation sites in the Columbia River after 30 June of their release year (Tatara et al. 2017). We defined migratory steelhead as fish that left the Methow River and were detected at least once at any of the four main stem Columbia River hydroelectric dams (Rocky Reach, McNary, John Day, or Bonneville, Figure 1) equipped with PIT tag interrogation systems by 30 June of each release year. However, it is not possible to identify all migratory and residual hatchery steelhead solely from PIT tag detections because PIT tag interrogation arrays located within juvenile bypass facilities at main stem hydroelectric dams in the Columbia River are not 100% efficient and some routes across the hydroelectric dams are not equipped with PIT tag interrogators. Therefore, we had to develop criteria to distinguish residuals from steelhead that migrated without detection.

We used PIT tag detections of all steelhead sampled prior to release between 2011 and 2015 to determine phenotypes and size characteristics of steelhead with a high likelihood of residualization after release, and to track the long-term fate of identified residual steelhead in the Methow and Columbia Rivers. We combined Columbia River detection data for steelhead from all five RYs and rearing treatments and ran separate logistic regression models for fish categorized according to phenotype (parr, transitional, smolt, mature male) to predict the probability of not being detected as a migrant. Each model included prerelease fork length (mm) and a quadratic term for fork length as continuous covariates, because previous results (Tatara et al. 2017) found that models including the quadratic term best estimated survival during outmigration. The goodnessof-fit tests indicated that the data fit the logistic regression models (Pearson and Hosmer-Lemeshow tests, all $P \geq 0.05$). The predicted probability of not being detected migrating was calculated for each phenotype across the entire range of fork lengths. We estimated the number of undetected fish of each phenotype by multiplying the size-dependent probability of not being detected migrating by the size distribution of fork lengths within each phenotype. These undetected fish were then compared to the size distribution of fish detected migrating (i.e., known migrants) to discern which undetected individuals were most likely to die during migration or residualize. The logistic regression equation for parr was used to determine a size criteria for likely residuals by selecting fish with a fork length corresponding to a ≥ 95% probability of not being detected migrating. All precociously mature males were classified as putative residuals. After identifying the putative residuals using the phenotype and size criteria, we then used our knowledge of migration timing for steelhead released from WNFH to set date ranges in PTAGIS queries designed to determine if the putative residuals migrated to the ocean in a subsequent year by setting the query start date as 1 July of each release year.

<B>Growth rates of residuals and natural-origin *O. mykiss*

The post-release instantaneous growth rates of PIT-tagged residual S1 and S2 steelhead captured in the Methow River were calculated using the masses of the fish collected during the pre-release sampling and from the sampling of residuals captured in Spring Creek with the following formula (Ricker 1979):

$$G = (\log_e Y2 - \log_e Y1)/(t_2 - t_1)$$

Where t_1 and t_2 are the dates of prerelease and residual sampling, respectively, and Y_1 and Y_2 are the masses of the fish at those times. Growth of residual steelhead was compared to growth of PIT-tagged natural-origin *O. mykiss* in the Methow River using data obtained from Martens et al. (2014). Instantaneous growth rates of natural-origin *O. mykiss* were calculated using the same formula as for residual steelhead. We tested for differences in instantaneous growth rate among S1 and S2 residuals and natural-origin *O. mykiss* using one-way ANOVA and Tukey pair-wise comparisons. All statistical analyses were performed with Mintab 17 software (State College, PA), with the exception of the finite mixture model analysis, which was performed with STATA software (College Station, TX). Statistical significance was set at an alpha level of 0.05.

<A>Results

<B>Rearing effects on phenotype

The Chi-squared test revealed a significant association between rearing type (S1 and S2) and the proportion of each phenotype (parr, transitional, smolt, mature male) in the release populations in all RYs ($P < 0.001$ in all release years). With the exception of RY 2013, steelhead classified as parr were overrepresented in the S1 rearing strategy. In each RY, mature male steelhead were overrepresented in the S2 rearing strategy (Table 1). There were fewer differences in the proportion of steelhead classified as transitional or smolts between the S1 and S2 rearing groups in all RYs (Table 1).

There were no significant differences in the percentage of estimated parr between S1 and S2 steelhead over five RYs (two-sample T-test, T = 1.67, $P = 0.17$, df = 4). There was a significantly higher percentage of mature male residuals in the S2 rearing treatment (two-sample T-test, T = -5.36, $P = 0.01$, df = 4, Figure 4). Despite the higher percentage of mature male residuals in the S2s, there were no significant differences in the total percentage of residuals (parr + precocious males) between rearing treatments (two-sample T-test, T = 0.74, $P = 0.50$, df = 4, Figure 4).

<B>Direct evidence of residualism near the hatchery

We collected 966 residual steelhead from Spring Creek between 2010 and 2015 (Table 2). Of these, 467 (48.3%) were from the S1 rearing treatment, 443 (45.9%) from the S2 treatment, and the remaining 56 (5.8%) were of unknown origin. Among release years, the percentages of S1 and S2 residuals was highly variable, but over the six release years there was no difference in the percentage of each rearing group recaptured (two sample t-test, T = 0.1, df = 9, $P = 0.92$). The recaptured residual population was male-biased for both the S1 and S2 rearing treatments (Chi-square = 30.99, df = 1, $P < 0.001$; Table 3) with sex ratios (male:female) of 1.78:1 and 5.71:1, respectively. There were also differences in maturation status between rearing treatments for recaptured residual males (Chi-square = 116.77, df = 2, $P < 0.001$,). Immature S1 male residuals (76.1%) and maturing S2 male residuals (72.0%) were both overrepresented in the recaptured residual population. S1 maturing males made up a greater proportion (26.1%) of the recaptured residual population than estimated in the release population (1.5%; T = -2.83, df. = 4, *P* = 0.047). The proportion of recaptured S2 maturing male residuals (57.1%) was similar to the proportion estimated in the release population (56.7% T = -0.03, df. = 7, *P* = 0.974).

The catch per unit effort (CPUE) during Spring Creek sampling averaged 4.7 fish/hour over all years (Table 2). The standardized residual indices for RYs 2010-2015 were not different between the S1 (mean = 0.203; SE = 0.047) and S2 (mean = 0.197; SE = 0.056) rearing groups (T-value = 0.09, *P* = 0.929, df = 9). There were no significant correlations between mean fork length at release and the standardized residual index for S1 steelhead (r = 0.042, *P* = 0.937) or S2 steelhead (r = -0.493, *P* = 0.320). There were no significant correlations between the annual estimated percentage of parr in the prerelease sample and the standardized residual index for S1 steelhead (r = 0.642, *P* = 0.243) or S2 steelhead (r = 0.284, *P* = 0.643). Similarly, there were no significant correlations between the annual estimated percentage of mature males in the prerelease sample and the standardized residual index for S1 steelhead (r = -0.021, *P* = 0.973) or S2 steelhead (r = 0.287, *P* = 0.639).

<B>Indirect evidence from PIT detections in the Methow and Columbia Rivers

For parr, transitional, and smolt phenotypes, fork length, fork length^2, and smolt age all had significant effects on the probability of a fish not being detected migrating (all *P* < 0.002). The logistic regression model for mature males was not significant (*P* = 0.937) indicating that fork length was not useful for predicting the probability of not being detected migrating.

Comparing the size distributions by phenotype of known migrants to non-detected fish revealed insight into which non-detected were more likely to residualize in the Methow River, and which were likely to die while migrating (Figure 5). A large percentage of transitional S1 (34.2%) and S2 (37.4%) and smolt S1 (38.8%) and S2 (39.8%) phenotypes were detected migrating. The size distributions of known migrant and non-detected S1 and S2 transitional and smolt phenotypes were similarly shaped with a peak in the distributions near a fork length of 200 mm. That is, detected and non-detected transitional or smolt phenotypes were similar in size. Very few S1 (3.8%) and

S2 (5.4%) steelhead classified as parr were detected migrating. The size distributions of non-detected and known migrant parr (Figure 5, top row) were strikingly different from that of transitional and smolt phenotypes. The non-detected S1 parr were smaller and more numerous than the S2 parr with the majority of the non-detected fish having fork lengths under 150 mm. Because the non-detected parr were smaller than the phenotypes with known migratory behavior, it is more likely that fish classified as parr residualized in the Methow River than attempted migration and died without detection.

We estimated the number of residual steelhead based on phenotype and size prior to release using the previously developed binary logistic regression models. Parr < 146 mm were post-hoc categorized as putative residuals because their probability of not being detected in the Columbia River was greater than 95% (Figure 6). All mature males were determined to be residuals because only four of 555 mature male steelhead were detected as known migrants in the year of their release. Based on these criteria, 1,783 estimated PIT tagged residual steelhead were released out of the 21,598 PIT tagged steelhead measured in the prerelease samples between 2011 and 2015 (Table 4). The PIT tag codes for the 1,783 putative (or inferred) residuals were queried in PTAGIS to gain further insight into the fate of parr and mature male residual steelhead after the primary migration period had ended.

According to the genetic sex data, in RYs 2011- 2013 there were 5.3% fewer S1 males and 8.1% fewer S2 males fewer males detected in the migrating population than were present in the release population, but there were no differences in the percentage of migrating males between the S1 and S2 rearing groups (T = 0.49, $P = 0.673$, df = 2). The binary logistic regression model of migratory behavior was significant ($X^2 = 544.3$, df = 6, 7,137, $P < 0.001$). Neither the rearing strategy ($X^2 = 0.32$, df = 1, 7,137, $P = 0.57$), nor the genetic sex ($X^2 = 0.06$, df = 1, 7,137, $P = 0.81$) influenced whether a steelhead was detected in the Columbia River after release. The probability of being detected as a migrant in the Columbia River was significantly affected by pre-release fork length ($X^2 = 53.44$, df = 1, 7,137, $P < 0.001$) and prerelease phenotype ($X^2 = 232.06$, df = 3, 7,137, $P < 0.001$). The odds-ratio indicated that the probability of being detected as a migrant increased 10% with each additional centimeter of fork length. Mature male steelhead were 24.4, 21.9, and 3.1 times less likely to migrate than steelhead classified as smolts, transitional, and parr, respectively. Steelhead classified as parr were 7.9 and 7.1 times less likely to migrate than steelhead classified as smolts or transitional fish, respectively.

<B>Fate and growth of residuals

Parr < 146 mm were post-hoc categorized as putative residuals. The post-release fates of these 1,228 PIT-tagged S1 and S2 parr were inferred from their detection locations in the Methow and Columbia Rivers. 583 (47.5%) of the 1,228 PIT-tagged residual steelhead classified as parr were never detected after release. Eighteen (1.5%) parr were detected in the Columbia River during the year of release, and another 7 (0.6%) in the year after release. Only 1 (0.08%) residual parr returned as an anadromous adult. The greatest number (594, 48.4%) of parr phenotype residuals were detected only in Spring Creek, while 6 (0.5%) were detected upstream of WNFH, and 10 (0.8%) downstream of WNFH. The tags of 8 (0.7%) parr were detected at fish-eating bird colonies in the Columbia River and were assumed to be mortalities.

The fate and behavior of 555 PIT-tagged mature male residuals was different from the parr phenotype. A greater percentage of released mature male residuals (82.8%) were detected than released parr (52.5%). Only 4 (0.7%) mature males were detected in the Columbia River during the year of their release, and none were detected in the Columbia River in a subsequent release year, nor returned as anadromous adults. The majority (434, 78.1%) of released mature males were detected in Spring Creek, while 11 (2.0%) were detected in the Methow River upstream of WNFH and 8 (1.4%) downstream of WNFH. Mature male residuals were also susceptible to bird predation, with 3 (0.5%) detected at avian colonies in the Columbia River. Residual S1 and S2 steelhead experienced positive growth after release from the hatchery. Instantaneous growth rates did not differ among residual S1, residual S2 and resident *O. mykiss* (ANOVA, $F_{2, 17}$ = 2.18, $P = 0.14$,). There was only one mature male in the sample of 18 recaptured residuals with growth rate data, and it was the only fish that lost weight.

<A>Discussion

This 6-year study is the first to investigate the effects of age at release on the characteristics and rate of residualism in hatchery steelhead. Steelhead from both the S1 and S2 treatments residualized in the vicinity of the hatchery in nearly equal proportions. Residuals from both treatments were comprised of small male and female immature parr and maturing or mature males. However, age at release significantly affected the predominant residual phenotype, with more parr present in the S1 treatment and more mature males present in the S2 treatment. Evidence from PIT tag recoveries in the Methow and Columbia River basins further substantiated these findings. Residual male behavior indicates they may be responding to the presence of females and may mate with them, and parr appear to grow at levels similar to natural origin *O. mykiss* and may compete with them for resources and habitat.

The great majority of hatchery steelhead programs have historically reared S1 smolts, and precociously mature male residuals have been documented in several studies of such programs (Schmidt and House 1979; Viola and Schuck 1995; Tipping 2003; Sharpe et al. 2007, Hausch and Melnychuk 2012; Sloat and Reeves 2014). There are two reports characterizing hatchery steelhead reared to age-2 smolts (Schmidt and House 1979; Bjornn and Ringe 1984), both of which mention that precociously mature male steelhead were prevalent (ranging from 6.5% to 10% of males) when sampled in March prior to release. The duration of hatchery culture, rearing environment (i.e., temperature), and ration determine the growth of hatchery steelhead. Previous assessments of residualism in hatchery steelhead determined that residual steelhead are often smaller or larger than the modal smolt size (Hausch and Melnychuk 2012). Steelhead in the lower size range tend to residualize as immature parr, and many researchers have reported that precociously mature males were larger than average size (Tipping 2003; Sharpe et al. 2007; Hausch and Melnychuk 2012). Consistent with previous reports, residuals expressing the parr phenotype prior to release were smaller than steelhead with the visual appearance of smolts. Contrary to previous studies (Tipping 2003; Sharpe et al. 2007; Hausch and Melnychuk 2012), we found that mature male residuals were not larger than steelhead classified as ‘transitional’ or smolts. Both S1 and S2 steelhead with visual characteristics of parr and fork lengths < 146 mm had a probability of less than 5% of being detected as migrants, but there were fewer S2 steelhead in this category presumably due to their greater opportunity for growth afforded by an additional year in the hatchery. Age at release also affected the percentage of mature male residuals, which were more prevalent in the S2 rearing strategy. We found that the mature male residuals were even less likely to migrate than the parr phenotype, presumably because they remained near the hatchery to attempt spawning with anadromous females present on the spawning grounds at the time of release.

<B>Estimated and actual residual phenotypes

Male residuals in Spring Creek were disproportionately abundant compared to our prerelease assessment, and many males were mature or maturing. The percentage of recaptured mature male S1 residuals was more than 17 times higher than our pre-release assessment, but the percentage of recaptured S2 mature males was similar to our pre-release assessment. It is most likely that the maturation process progressed between the pre-release assessment and recapture to a greater degree in the S1 fish than the S2 fish. The S2 mature males may have been at a more advanced stage of maturation from the additional year of rearing and were more easily visually identifiable during pre-release sampling. During the warm summer months in Spring Creek these S1 maturing males may have experienced rapid advancement of the maturation process in preparation for completion of maturation the following spring at age-2.

<B>Migrant sex ratios

The present study confirms that residualism in hatchery steelhead is male biased and adds that age at release affects the magnitude of male bias. Previous studies found that the sex ratio of juvenile steelhead approximate a 50:50 male:female ratio prior to migration (Hausch and Melnychuk 2012; Ohms et al. 2014; Thompson et al. 2015) while outmigrating smolts are frequently female biased (Peven et al. 1994; Ohms et al. 2014) in steelhead and other salmonid species (Jonsson and Jonsson 1993; Jonsson et al. 1998; Paez et al. 2011; Hendry et al. 2004). Among returning anadromous adults, studies have found sex ratios vary considerably among years, systems and between hatchery and natural fish, being 50:50 among some systems and female biased in others (Shapovalov and Taft 1954; Ward and Slaney 1988; Savvaitova et al. 2002; Rundio et al. 2012; Thompson et al. 2015). In the current investigation, the percentage of males was lower in the fish detected migrating than in the prerelease sample for both S1 and S2 treatments. Female bias in outmigrating smolt populations is typically attributed to the predominance of precociously maturing males among residuals (Hausch and Melnychuk et al. 2012; Ohms et al. 2014; Thompson et al. 2015).

The estimated rates of total residualism from the prerelease sampling indicated that age at release did not affect the percentage of total residuals produced, but did affect phenotype composition of residuals. The annual residualism index in Spring Creek showed patterns congruent with the different phenotypic characteristics of S1 and S2 steelhead in the prerelease sample, and served as a representative surrogate for residual production in the Methow River at large. There was a positive but not statistically significant correlation between the annual residual index and the percentage of estimated parr in the prerelease sample; the slope of the correlation was larger for S1 than for S2 steelhead, which is consistent with the higher percentage of parr phenotype in the S1 rearing treatment. The correlation between the estimated percentage of mature male phenotype residuals and the annual residual index was also not statistically significant, with no directional trend for the S1 rearing treatment and a positive trend for the S2 rearing treatment. This was consistent with the higher percentage of mature male phenotype residuals seen in the S2 rearing treatment and the relative scarcity of precociously mature males in the S1 steelhead.

<B>Fate and distribution of residuals

Mature male residuals had higher rates of PIT tag detection than parr after release, and the majority of mature male detections occurred in Spring Creek near the hatchery. Of the relatively few residuals detected in the Methow River, a greater percentage of mature male detections occurred upstream of the WNFH, while more parr were detected downstream of the hatchery. Residual steelhead commonly reside in close proximity to their release site (summarized in Hausch and Melnychuk 2012). In the present study, the highest percentage of PIT tag detections for both residual phenotypes also occurred in Spring Creek near the hatchery suggesting that the majority of residuals did not migrate very far from their release site at the hatchery. However, this conclusion should be tempered by the fact that this survey effort was heavily biased by the close proximity of Spring Creek to the hatchery and the associated ease of fish capture. Additionally, year-round hatchery discharges to Spring Creek and dense riparian cover provided a cooler thermal refugia from the warmer mainstem Methow River. Nevertheless, a low percentage of both residual phenotypes were detected in the Methow River upstream and downstream of the hatchery, indicating that some residuals distribute widely within the

Methow River Basin. The residual S1 and S2 steelhead had positive growth rates between their release and time of recapture, but it was not significantly different from growth rates of natural-origin *O. mykiss* from the Methow River, and there were no significant effects of age-at-release on growth rate. A similar result was observed for hatchery steelhead intentionally released as subyearling fry (Tatara et al. 2009); growth rates of hatchery fry were positive but not significantly different from those of naturally produced steelhead fry. The results indicate that residual steelhead are growing and possibly competing with natural-origin *O. mykiss* (McMichael et al 1999).

<B>Residual contribution to adult returns

Residuals had a very low probability of seaward migration in subsequent year(s) and negligible contribution to anadromous production. Only 7 of the 1,783 (0.4%) PIT tagged residuals were detected migrating from the Methow River is a subsequent migration period, suggesting extremely poor overwinter survival, despite the fact that residual steelhead had similar growth rates as resident *O. mykiss*. All steelhead in subsequent migration periods were of the parr phenotype at release, and the majority were S1 steelhead. Snow et al. (2013) found a similar result; A greater number (791) of PIT tagged residuals were captured in the Twisp River (a tributary to the Methow River), but only 87 (0.07%) of 125,256 PIT tagged steelhead released into the Twisp River were detected as migrants in the Columbia River in a subsequent year. Snow et al. (2013) also attributed this finding to poor overwinter survival. The most striking finding was that neither residual phenotype contributed substantially to the production of anadromous adults. No precocious males and only one parr phenotype were detected returning from the ocean as an anadromous adult over the course of the 6 year study. The combined smolt-to-adult return rate for all PIT tagged residuals (both residual phenotypes) over five release years was 0.06%. Snow et al. (2013) also found that S1 steelhead that did not volitionally leave a hatchery raceway and were subsequently forced out had higher levels of residualism and produced fewer returning anadromous adults than steelhead exiting hatchery raceways volitionally.

<B>Ecological interactions

The production of residual hatchery steelhead may pose significant negative ecological and genetic consequences to native stocks and reduce the production of more desirable anadromous adults (Naish et al. 2007; Pearsons 2008; Snow et al. 2013). Residuals may compete for food and habitat with conspecifics and other native species (McMichael et al. 1997, 1999; McMichael and Pearsons 2001; Huntingford 2004; Tatara and Berejikian 2012) and may prey on natural stocks (Hawkins and Tipping 1999; Naman and Sharpe 2012). Related to predation, large releases of hatchery steelhead and concomitant residuals may tend to increase and concentrate piscivorous fish, birds and mammals in and around headwater rearing areas (Berejikian 1995; Collis et al. 1995; Johnsson et al. 2001; Nickleson 2003;). Since residuals may be concentrated in large numbers near spawning areas they may present a potential pathway for transfer of disease to native stocks (see review in Naish et al. 2007). But, with the exception of a few exotic pathogens like whirling disease (Bartholomew and Reno 2002), the diseases that infect wild and hatchery fish, are typically endemic to a given watershed (Naish et al. 2007). To date there are few documented cases of hatchery salmonids directly infecting natural stocks (McVicar 1997), thus, this topic remains a significant area of uncertainty and worthy of further research (Naish et al. 2007). Finally, precociously mature residual steelhead (Araki et al. 2007) and spring Chinook salmon (Ford et al. 2012) have been found to interbreed with natural fish presenting a potential genetic risk to native stocks as well.

In the current investigation, both the S1 and S2 regimes produced a similar percentage of residuals; however, the ecological and genetic consequences of the S1 and S2 residuals are likely to differ. The higher proportion of mature males produced from the S2 rearing regime may pose greater competition and genetic risks than the S1 regime. Precociously mature hatchery males collected in Spring Creek were significantly larger than the S1 and S2 hatchery parr and are likely much larger than natural-origin salmonid parr as well. In addition to their size advantage, precociously mature males are likely more aggressive than hatchery and natural-origin parr. During final maturation they have elevated reproductive steroid levels including 11-ketotestosterone, the major androgen in teleost fish (Larsen et al. 2017), and experience enhanced pheromone signaling (Stacey et al. 2003) associated with competition for both resource acquisition and mating opportunity (Sørensen et la. 2007; Conrad et al. 2011). These factors may increase aggression and risk-taking behavior in mature males relative to immature fish. The greater proportion of precocious males produced by the S2 rearing regime also presents a greater opportunity for genetic introgression with native stocks than the S1 regime. A greater percentage of precocious males were detected upstream than parr during the steelhead spawning season, suggesting that precocious males were seeking mating opportunities with anadromous females. Males that are mature when released may only need to survive for a short time to spawn with returning steelhead. Immature parr would need to survive an additional year or more to potentially breed or outmigrate and return as an anadromous adult. Based on our detection and adult returns of PIT tagged parr each of these scenarios is highly improbable. Taken together, based on residual production, if management circumstances dictate the need for an S2 rearing regime for hatchery steelhead programs, emphasis should be placed on minimizing the production and release of precociously mature males wherever possible.

<B>Controlling residualism rates

There are three primary methods that can be used individually or in some combination to control residualism rates in hatchery steelhead programs. (1) Volitional release has been implemented with variable success as a method for sequestering the residuals in the hatchery raceways while the true smolts exit the facility (Viola and Schuck 1995; Gale et al. 2009; Snow et al. 2013; Tatara et al. 2017). After a period of volitional emigration the raceway gates are closed and non-migrants can either be euthanized or released into closed bodies of water where they won't present risk to native stocks. At the Winthrop National Fish Hatchery this strategy has been employed with limited success as the mature males appeared to exit the facility in relatively large numbers along with the smolts. (2) Sorting of potential residuals based on size and appearance could be employed to remove fish less than a predetermined size indicative of immature parr (i.e. < 146 mm in the current study) and mature males expressing secondary sex characteristics. However, this strategy is labor intensive and involves significant handling near the time of release when most fish are undergoing the stressful physiological process of smoltification (Hoar 1988). (3) Rearing regimes can be designed to limit the number of residuals produced (Sharpe et al. 2007; Berejikian et al. 2012). From the current investigation, the S1 rearing regime limited the number of precociously mature males, but increased the likelihood of producing immature parr.

Modulating growth to increase the number of fish exceeding the size threshold necessary to achieve maximum smolt development in all fish is recommended. Similarly, growth modulation can be implemented to limit growth rate in the first year of rearing to reduce the number of fish that initiate precocious male maturation the following year (Sharpe et al. 2007). Well-designed rearing strategies that achieve both objectives (inducing smoltification and limiting precocial male maturation) may hold the most promise for decreasing residualism while increasing the smolt-to-adult return rates of steelhead hatchery programs.

<B>Management implications

A primary management objective at the WNFH was to develop a localized broodstock that specifically returned to the Methow River. The later return date of adult salmon to the headwaters of the Methow River basin necessitated the need to develop an S2 rearing regime. Results have demonstrated that an S2 regime can be successfully implemented in a production hatchery steelhead program while providing equivalent or better juvenile survival through the Columbia River basin (Tatara et al. 2017). However, from a hatchery operations perspective this approach requires the hatchery to produce one brood class every two years from the same rearing space rather than two brood classes in an S1 program. As it pertains to residualism, our results suggest a cautionary note is warranted. The S1 and S2 regimes produced similar numbers of residual steelhead, but the S2 regime produced a greater proportion of precociously mature males that may pose a greater ecological and genetic risk to natural stocks than an S1 regime. Furthermore, rearing for an additional year in the hatchery environment compared with an S1 strategy may increase the potential for domestication selection (Fraser 2008; Berejikian et al. 2011). These risks may be outweighed, to some degree, by successful localization of the broodstock and equivalent or better smolt to adult return rates in an S2 program (Tatara et al. 2017). Additionally, the risks may be minimized by properly designed growth regimes that effectively manage the tradeoffs between rearing small and large smolts (see Larsen et al. 2013 for Spring Chinook salmon). Rearing smaller smolts may reduce smolt survival and produce more parr residuals, but also reduce precocious male residuals. Alternatively, rearing larger smolts may increase smolt survival and produce less parr residuals, but increase production of precocious males. Ultimately, the success of an S2 regime must be judged by comparing the relative reproductive success of S1 and S2 returning adults. This research is currently underway and will hopefully provide for a comprehensive understanding of the costs and benefits of this approach for the WNFH and others facilities considering the production of age-2 steelhead smolts.

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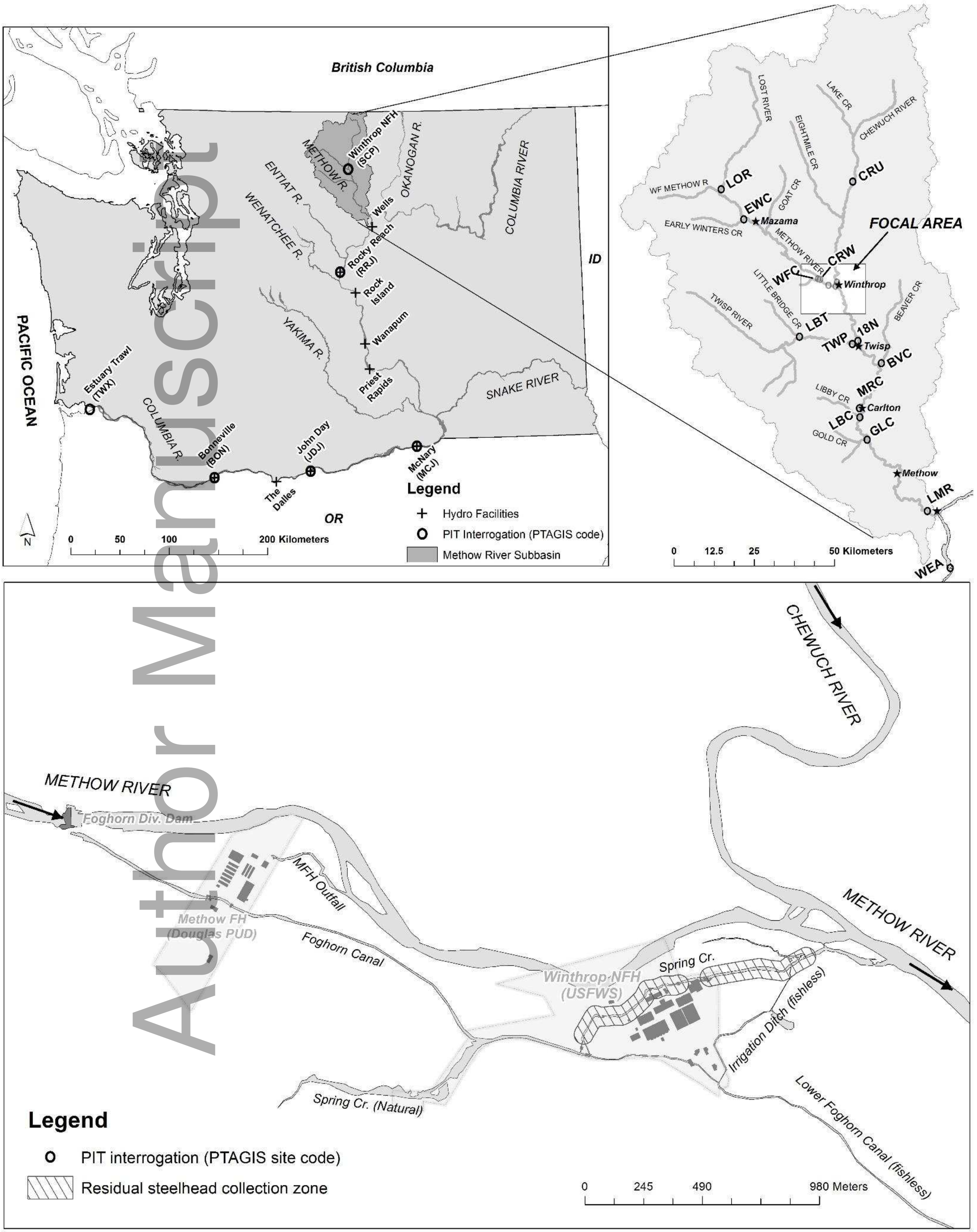
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Priest Rapids
YAKIMA R.
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WFC
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TWISP RIVER
LBT
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PIT interrogation (PTAGIS site code)
Residual steelhead collection zone
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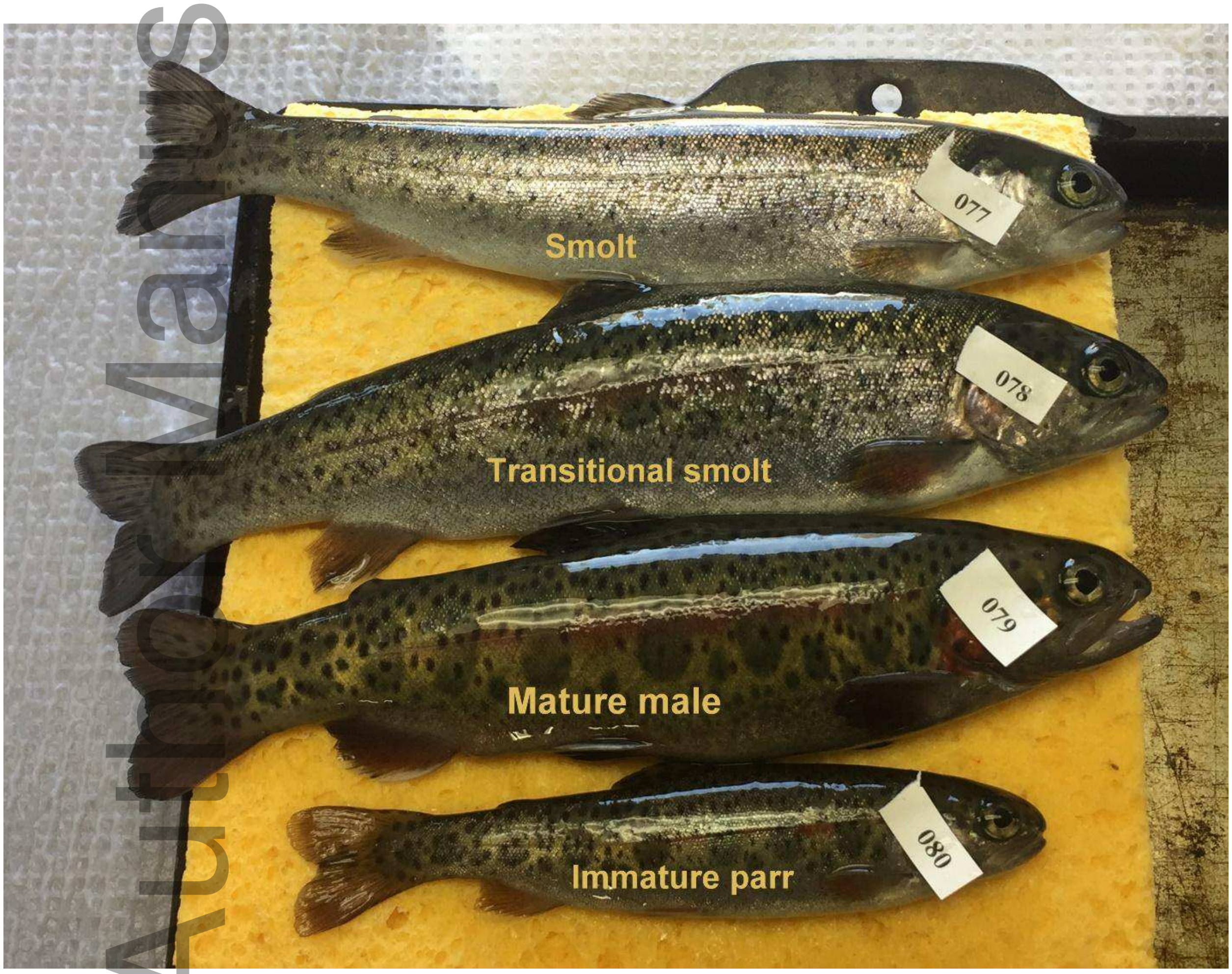


Figure 2. Four phenotypes of hatchery steelhead trout observed prior to release from Winthrop National Fish Hatchery: from top to bottom, smolt, transitional smolt, mature male, immature parr.

Table 1: Summary of pre-release sampling effort and characterizations of age-1 (S1) and age-2 (S2) steelhead released from Winthrop National Fish Hatchery over release years (RY) 2011 through 2015.

RY	Group-Brood year	Fork length mean ± SD (mm)	Pre-release sample (n)	"parr" (n)	"transitional" (n)	"smolt" (n)	"mature" (n)	Genetic sex determined (n)	Sex ratio F:M
2011	S1 - 2010	158.3 ± 35.1	955	305	251	399	0	920	45:55 z
	S2 - 2009	186.6 ± 25.7	918[a]	47	236	258	37	548	41:59 z
2012	S1 - 2011	172.2 ± 28.4	953	134	438	372	9	937	56:44 z
	S2 - 2010	185.5 ± 21.7	1,000	89	575	264	72	929	57:43 z
2013	S1 - 2012	195.1 ± 21.6	2,930	106	1,948	874	2	1912	46:54 z
	S2 - 2011	193.7 ± 22.0	2,925	247	1,672	903	209	1912	44:56 z
2014	S1 - 2013	177.2 ± 23.4	3,185	228	1,368	1,589	0	N/A	N/A
	S2 - 2012	190.6 ± 18.6	2,906	108	1,442	1,276	80	N/A	N/A
2015	S1 - 2014	172.5 ± 26.3	2,865	254	1,903	707	1	N/A	N/A
	S2 - 2013	198.5 ± 21.4	2,961	94	1,914	805	148	N/A	N/A

[a] Smolt index data values for 340 S2 fish were lost in 2011

z Sex ratio significantly different from 50:50 ($\alpha < 0.001$, G-test)

Table 2: Summary of Winthrop National Fish Hatchery residual sampling efforts in the hatchery outfall channel (Spring Creek) from release years (RYs) 2010 - 2015.

RY	Sample month(s)	Method(s)	S1 residuals (n, %)	S2 residuals (n, %)	Unknown residuals (n, %)	Total residuals (n)	Total effort (h)	Catch per unit effort
2010	August	Angling, Dipnet	113, 88.3%	7, 5.5%	8, 6.2%	128	28	4.6
2011	August, September	Electrofish, Angling	204, 77.0%	51, 19.2%	10, 3.8%	266	50	5.3
2012	August, September	Electrofish, Angling, Dipnet	72, 32.9%	141, 64.4%	6, 2.7%	219	36.8	6.0
2013	August, September	Electrofish, Angling, Dipnet	45, 33.6%	83, 61.9%	6, 4.5%	134	43.5	3.1
2014	September	Electrofish	21, 63.7%	11, 33.3%	1, 3.0%	33	17.3	1.9
2015	July	Electrofish, Angling	11, 5.9%	150, 80.6%	25, 13.4%	186	23.7	7.6
Grand Total			467, 48.3%	443, 45.9%	56, 5.8%	966		
Mean						160.8	33.2	4.7
SD						74.8	11.3	1.9

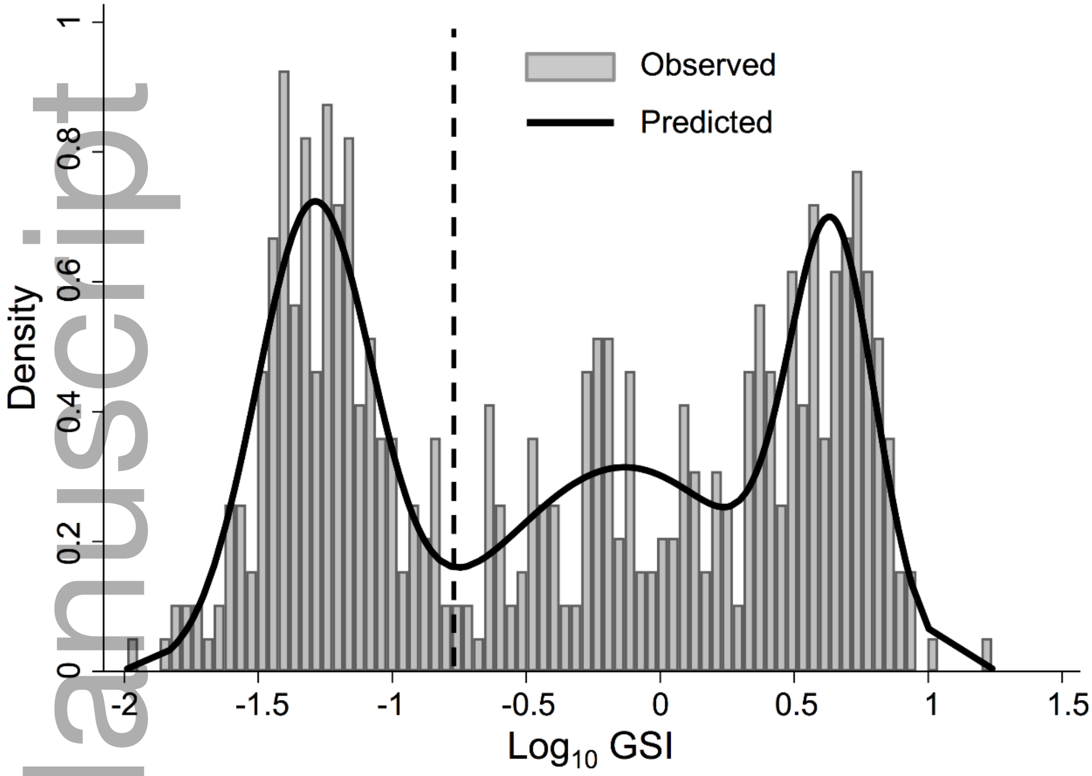


Figure 3. Histogram of observed $\log_{10}$ gonadosomatic index (GSI) values and predicted values (based on a finite mixture model with a mixture of three normal distributions) for all male residual S1 and S2 steelhead captured in Spring Creek between 2011 and 2015. Males with $\log_{10}$ GSI values below -0.86 (dashed vertical reference line) were classified as immature and those above as maturing males.

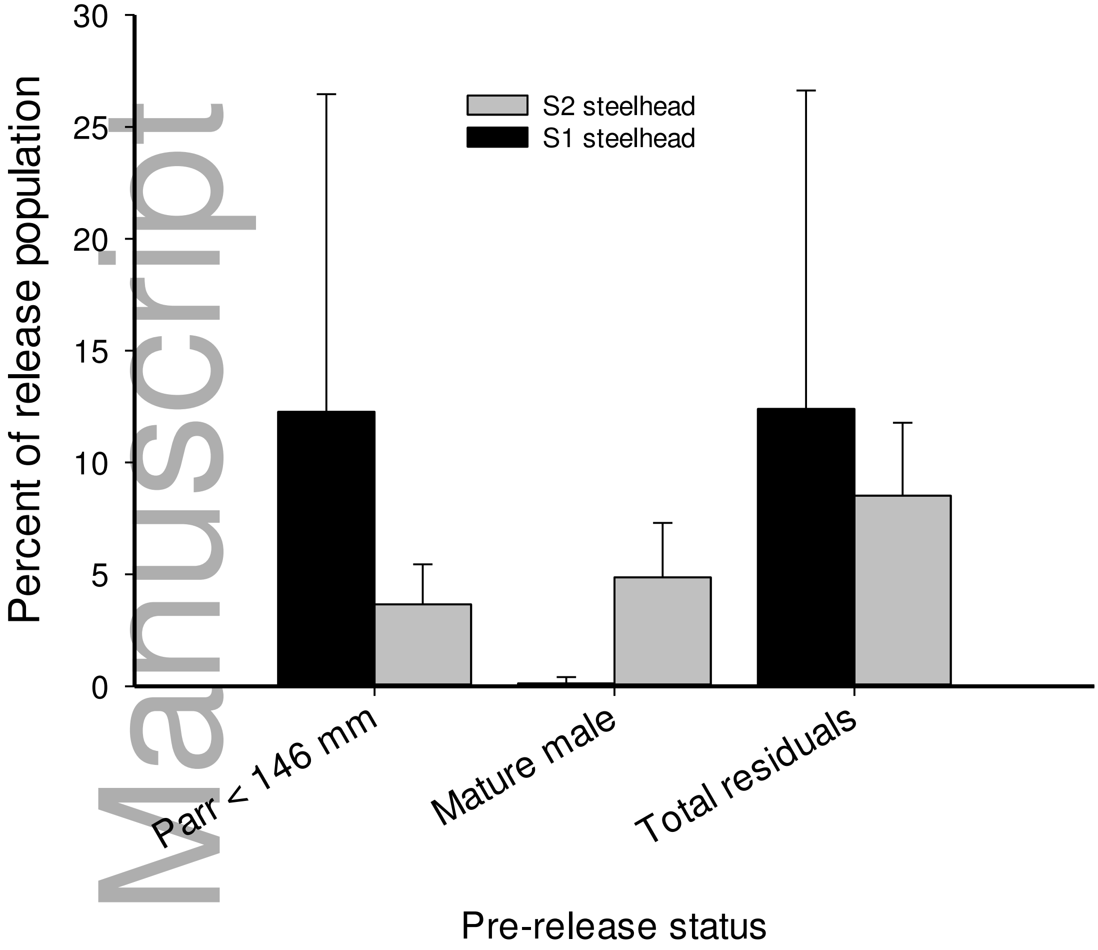


Figure 4. Mean percentages and 95% confidence intervals of S1 (black bars) and S2 (grey bars) parr, mature males, and total residual steelhead (sum of parr and mature males) released from WNFH in 2011 – 2015. Characterizations are based on phenotype assigned during pre-release sampling with parr < 146 mm post-hoc categorized as putative residuals.

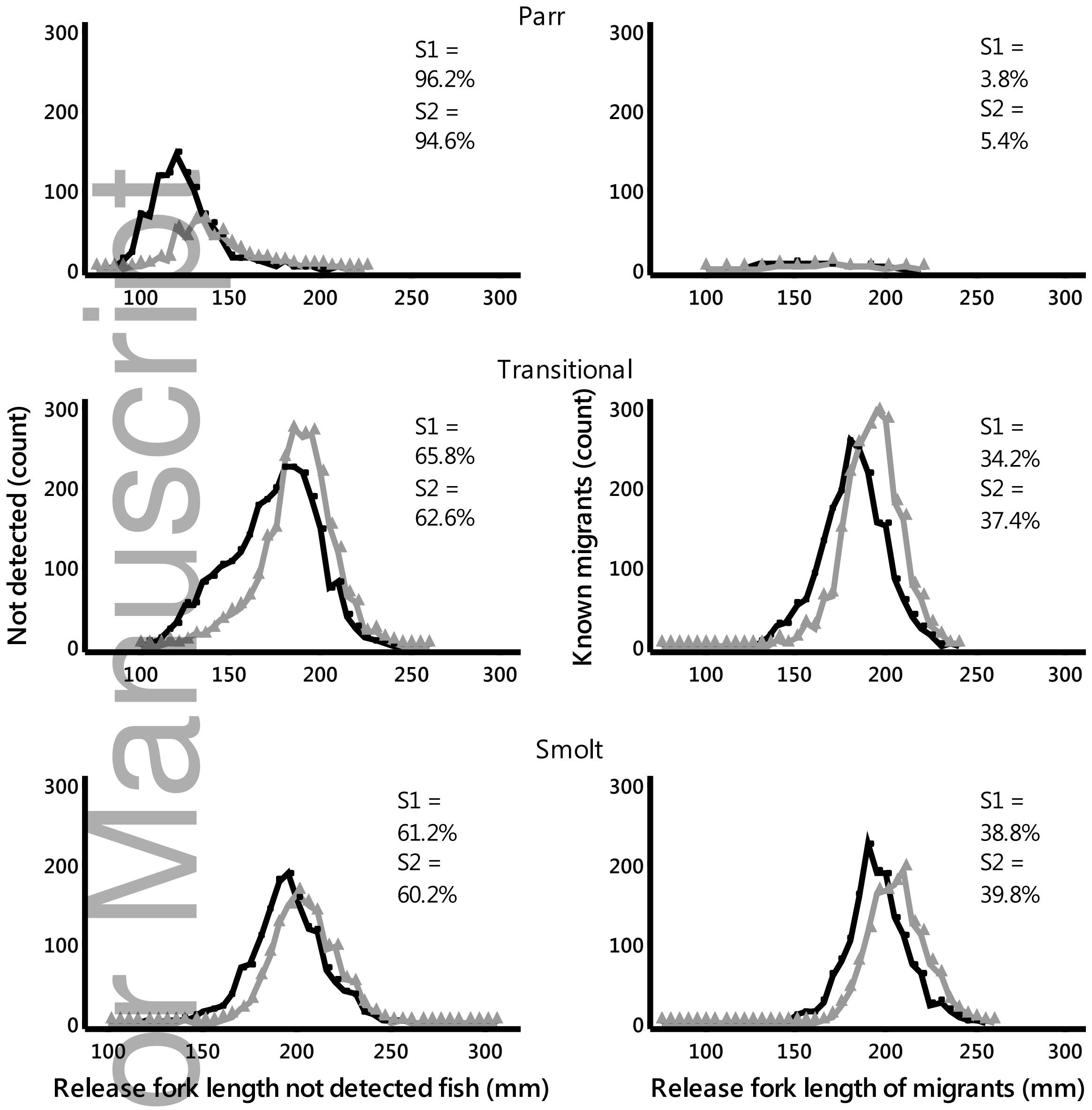


Figure 5. Fork length distributions and percentages for 21,958 PIT-tagged S1 (black line) and S2 (grey line) hatchery steelhead released from Winthrop National Fish Hatchery between 2011 and 2015 by pre-release phenotype (parr top row, transitional smolts middle row, and smolts bottom row). PIT-tagged fish that were not detected as migrants in the Columbia River are on the left column and known migrant steelhead are on the right.

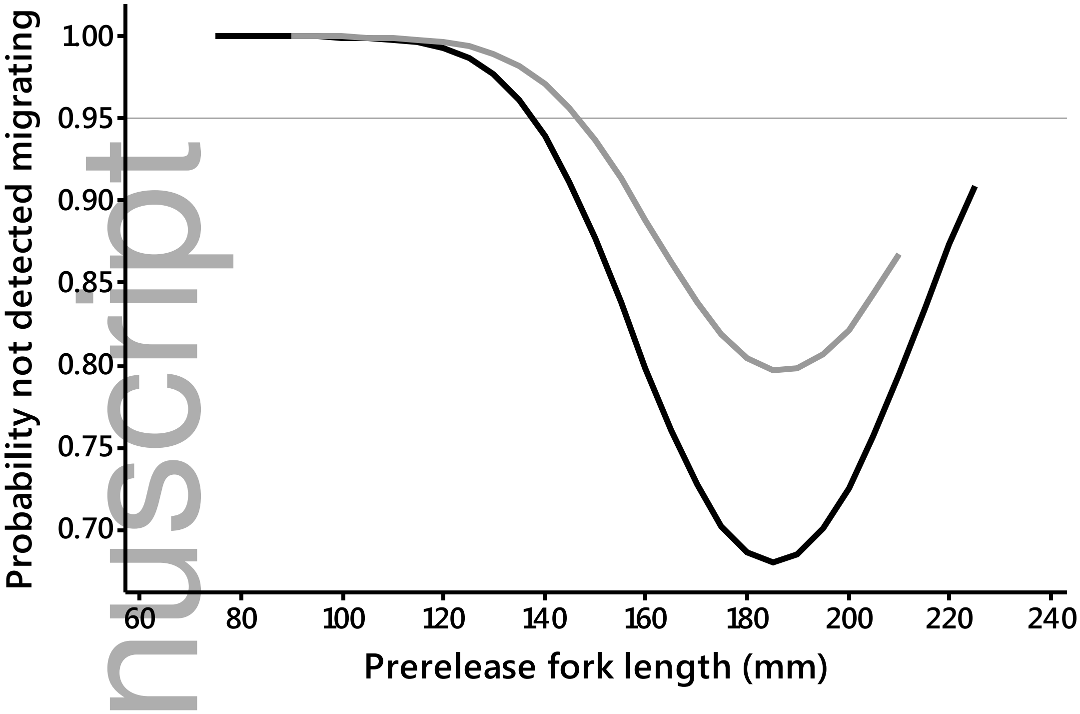


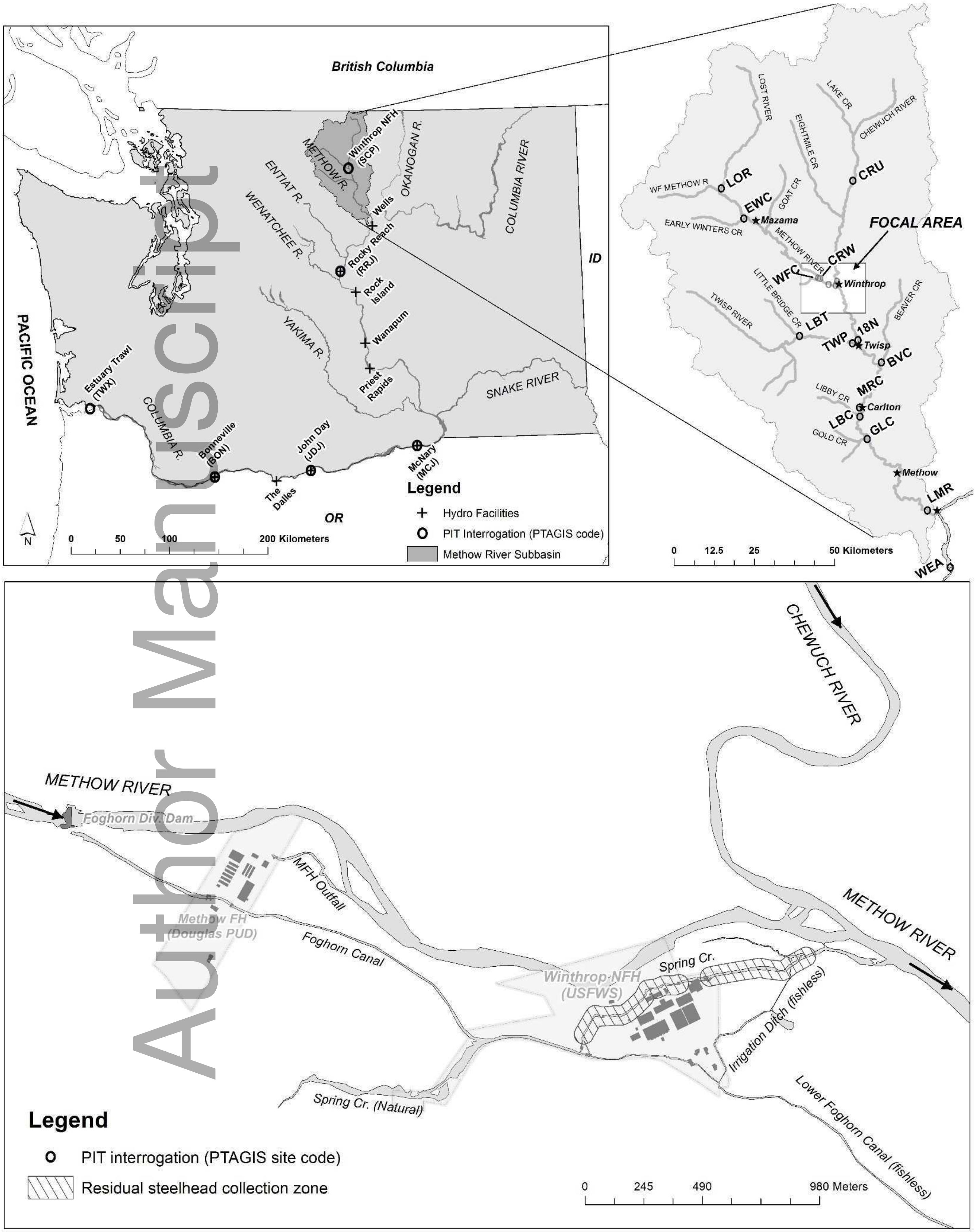
Figure 6. Predicted probability of not being detected migrating in the Columbia River for age-1 (black line) and age-2 steelhead parr (grey line) released from WNFH between 2011 through 2015 (combined). Parr with ≥ 0.95 probability of not being detected while migrating were considered residuals.

Table 3: Annual and total percentage of female and male residual hatchery steelhead recaptured from Spring Creek in release years (RYs) 2010-2015 by rearing strategy. Sample refers to the number of residuals dissected; not all recaptured residuals were dissected.

RY	S1 residuals Sample (n)	Female (%)	Male (%)	S2 residuals Sample (n)	Female (%)	Male (%)
2010	113	36.3	63.7	7	0	100
2011	160	35.6	64.4	33	21.2	78.8
2012	35	34.3	65.7	100	25.0	75.0
2013	45	22.2	77.8	83	9.6	90.4
2014	21	33.3	66.7	11	18.2	81.8
2015	11	54.5	45.5	149	15.4	84.6
Total	385	36.0	64.0	383	14.9	85.1

Table 4: Breakdown of the 1,783 PIT-tagged residual steelhead identified in the pre-release sampling at Winthrop National Fish Hatchery by residual phenotype and rearing type. Parr residuals was predicted using the decision rule from the logistic regression (≤ 146 mm fork length = 0.95 probability of not migrating). Mature male residuals were identified visually. Total residuals are the sum of the parr and mature male residual phenotypes.

Rearing type	Parr residuals		Mature male residuals		Total residuals	
	n	%	n	%	n	%
S1	916,	75%	12	2%	928	52%
S2	312	25%	543	98%	855	48%
Total	1,228	100%	555	100%	1,783	100%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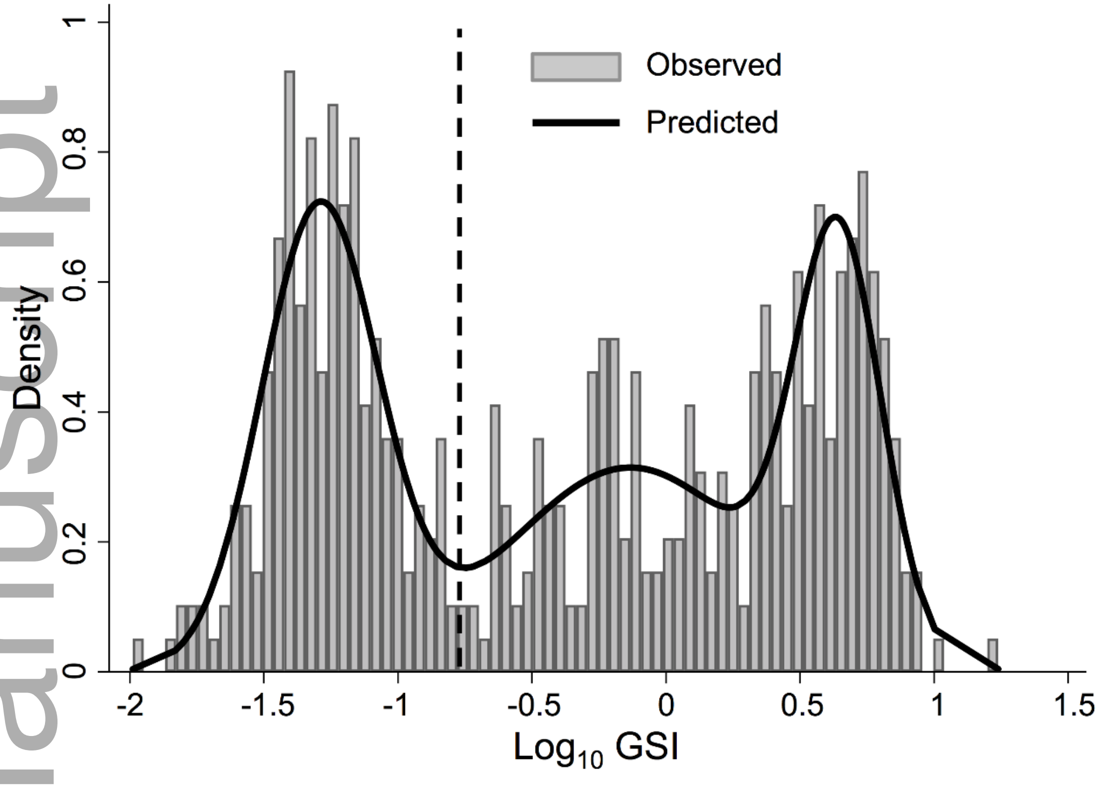

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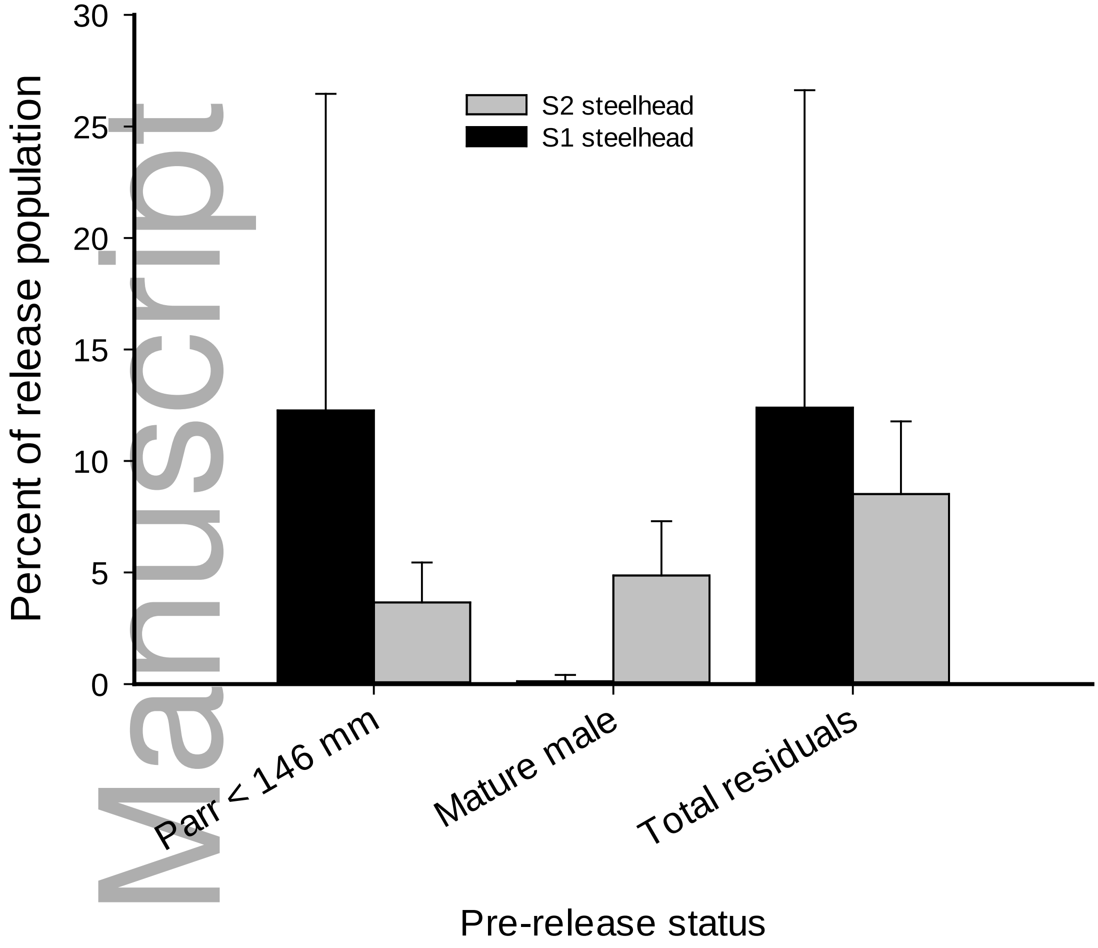

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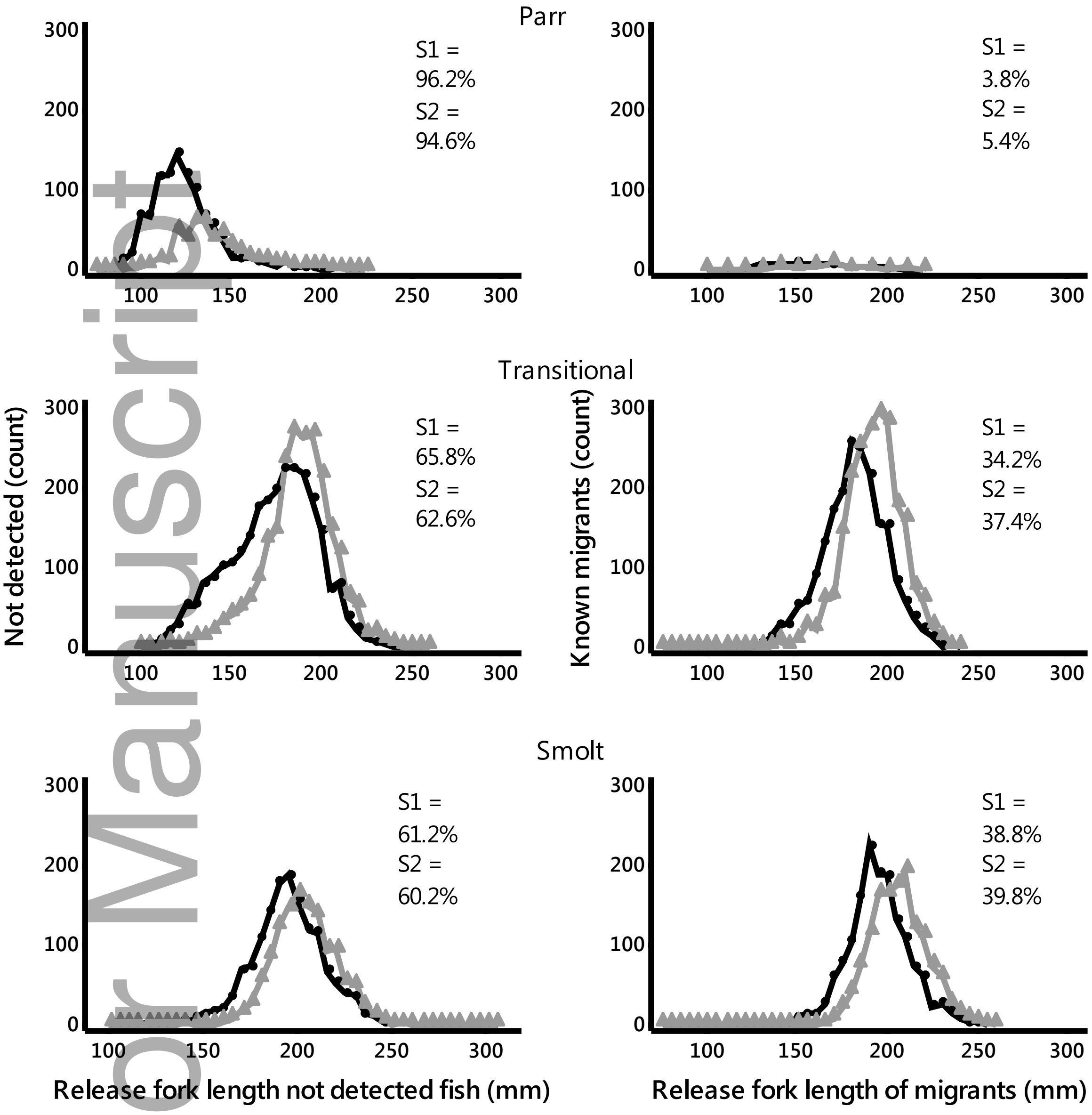

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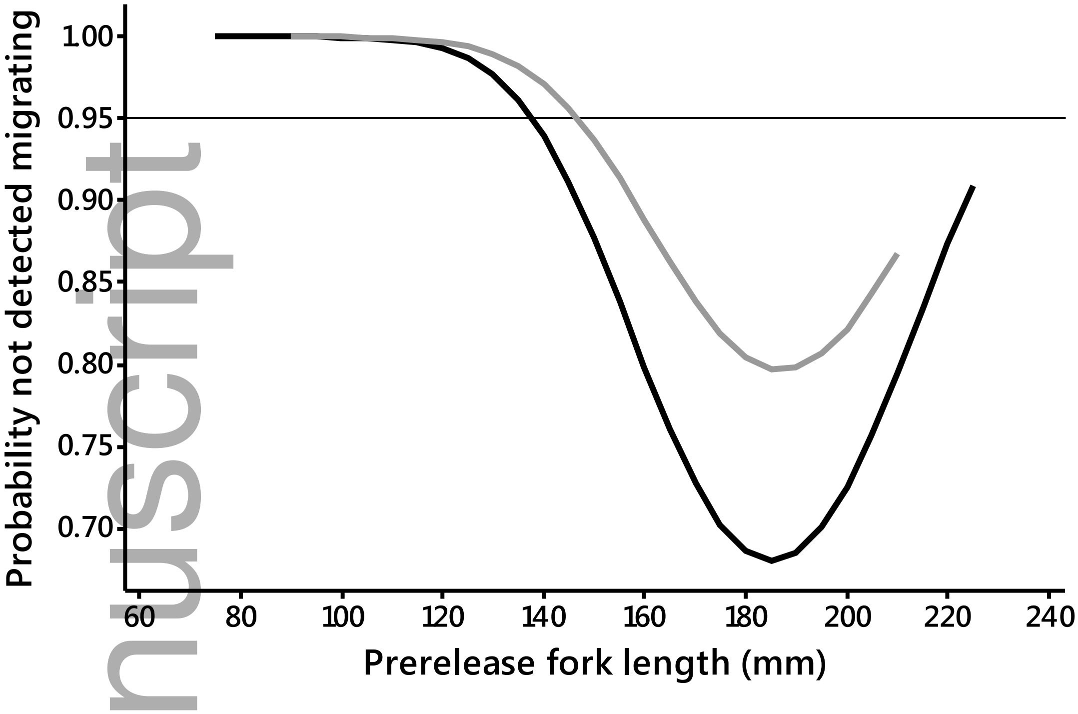

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