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Factors influencing density, distribution, and mesohabitat selection of juvenile wild salmonids and residual hatchery winter steelhead

William R. Brignon [a,b,*], Douglas E. Olson [a], Howard A. Schaller [a], Carl B. Schreck [b]

[a] United States Fish and Wildlife Service, Columbia River Fisheries Program Office, 1211 SE Cardinal Court, Suite 100, Vancouver, WA 98683, USA
[b] Oregon Cooperative Fish and Wildlife Research Unit, United States Geological Survey, Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331-3803, USA

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ABSTRACT

To best manage Eagle Creek National Fish Hatchery, negative interactions between hatchery salmonids and Endangered Species Act listed wild salmonids in the Eagle Creek Basin need to be minimized. Our objectives were: 1) to compare summer rearing densities in two similar streams, where one stream received a release of hatchery salmonids and one stream did not receive a release of hatchery salmonids, 2) to determine if residual hatchery winter steelhead were present in the Eagle Creek Basin, and 3) if so, determine how their presence and density relates to mesohabitat selection and distribution of naturally produced salmonids. A comprehensive snorkel survey identified significantly higher densities of juvenile coho salmon rearing in North Fork Eagle Creek, compared to upper and lower Eagle Creek. We found age 0 winter steelhead in significantly higher densities in upper Eagle Creek as opposed to lower Eagle Creek and North Fork Eagle Creek. Residual hatchery steelhead were located only in Eagle Creek and were rearing in the same 15 mesohabitat units that contained the estimated majority of wild fish populations. In Eagle Creek, the probability of occurrence for all species, regardless of origin, was highest in the vicinity of the hatchery. Residual hatchery winter steelhead density indicated a negative relationship with age 0 winter steelhead density. Due to residual hatchery winter steelhead being present in only 15 sampled habitat units we recommend future sampling effort be focused in areas with known populations of residual hatchery winter steelhead to determine if a distinct relationship between these population densities exists. From these data it is unclear if residual hatchery steelhead are affecting densities, distributions, and mesohabitat selection of wild salmonids in the basin. However, while we were unable to detect any direct impacts of residual hatchery fish on the wild population, these results do suggest the potential exists for competitive ecological interactions between hatchery and wild populations.

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1. Introduction

Hatcheries have come under increased scrutiny in the last 20 years with regards to negative ecological interactions between hatchery and natural origin (wild) salmonids. These interactions are thought to be one reason for the current decline in abundance of Pacific salmon *Oncorhynchus* spp. in the Columbia River Basin (Levin et al., 2001; Meffe, 1992). Hatcheries in the Pacific Northwest were initially constructed, and are still operated, to mitigate for the loss of spawner abundance, spawning habitat, and degradation of rearing habitat caused by overharvest, logging, irrigation, and construction of the hydropower system (Olson et al., 2004). These hatcheries release millions of juvenile salmonids into river systems where they may interact and compete with wild salmonids, some of which are listed as threatened and endangered under the Endangered Species Act. Understanding interactions that occur between populations of hatchery and wild salmonids is vital to the management and preservation of Pacific salmon.

Large releases of juvenile hatchery salmonids increase the density of fish in streams at various times of the year, potentially increasing competition for limited resources (Bohlin et al., 2002; Glova, 1987; Kennedy and Strange, 1986; Kostow and Zhou, 2006; Li and Brocksen, 1977). Hatchery reared salmonids have the potential to interact with wild salmonids through a variety of mechanisms, including competition for food and habitat (Bachman, 1984; Jacobs, 1981), predation (Cannamela, 1993), spread of disease (Goede, 1986; Ratliff, 1981), and behavioral disturbances (McMichael et al., 1999). The considerable numbers of hatchery salmonids released, combined with their generally larger size, provides them with a competitive advantage over wild salmonids of the same year class (McMichael et al., 2000; Nickelson et al., 1986) and later year classes. This places wild fish at a distinct disadvantage at both the community and individual levels.

Hatcheries release salmonids in the spring as presumptive smolts with the assumption that they will directly migrate to the ocean, thereby

* Corresponding author. Tel.: +1 360 604 2576.
E-mail address: bill_brignon@fws.gov (W.R. Brignon).

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minimizing any negative effects on wild rearing fish. However, hatchery releases have lowered densities of wild fish rearing in the vicinity of the hatchery release (Vincent, 1987) and in the path of their out-migration (Hillman and Mullan, 1989). Predation (Cannamela, 1993) and early migration (Hillman and Mullan, 1989; McMichael et al., 1999) are two mechanisms by which hatchery fish lower the density of wild rearing salmonids. Wild fish are typically smaller and less developed than hatchery fish of the same brood year (Nickelson et al., 1986; Rhodes and Quinn, 1998), which makes them more prone to predation and less ready to emigrate at the same time as larger hatchery fish. Hillman and Mullan (1989) reported substantial redistribution in wild spring Chinook salmon *O. tshawytscha* and wild steelhead *O. mykiss* after releases of hatchery spring Chinook salmon in the Wenatchee River, Washington. When wild salmonid abundance is reduced by interactions with spring releases of hatchery fish, valuable rearing habitat is left underutilized throughout the summer months, effectively lowering stream productivity.

Determining if wild fish are being displaced by the "swamping effect" caused during hatchery releases is important for hatchery managers. McMichael et al. (1999) documented dominant agonistic behaviors of hatchery steelhead which resulted in wild *O. mykiss* being displaced from preferred habitats. They theorized that the larger size of hatchery steelhead placed the smaller wild fish at a distinct competitive disadvantage. When hatchery fish displace juvenile wild salmonids, summer rearing densities may be lower in streams that experience a hatchery effect than in streams that do not.

Ecological impacts from releases of hatchery steelhead on populations of wild salmonids are highest when hatchery fish fail to emigrate quickly (McMichael et al., 2000). Delayed migration by hatchery steelhead (i.e., residual hatchery steelhead) and their impacts on wild salmonids have been well documented (e.g., Brostrom, 2003; McMichael et al., 1997, 1999; Viola and Schuck, 1995). In the North Fork Teanaway River, a tributary to the Yakima River in Washington, residual hatchery steelhead were shown to reduce the growth of wild resident *O. mykiss* during the summer (McMichael et al., 1997). The same study documented no effect of residual hatchery steelhead on spring Chinook salmon half their size. McMichael et al. (1997) concluded that there was no effect on spring Chinook because this species resides in different habitats in the river, therefore minimizing any competitive effects. This indicates that displacement caused by hatchery fish may have different impacts among species as it does within species (Jacobs, 1981).

Eagle Creek, a tributary to the Clackamas River, receives annual releases of winter steelhead and coho salmon *O. kisutch* from Eagle Creek National Fish Hatchery (NFH). In 2007 the Columbia Basin Hatchery Review Team completed its review of Eagle Creek NFH (USFWS, 2007). They listed delayed hatchery fish migration and residual hatchery winter steelhead in Eagle Creek (Kavanagh et al., 2006) as ecological conflicts and risks to Endangered Species Act listed natural populations of winter steelhead in the Clackamas River Basin. Therefore, the objectives of this study were: 1) to compare summer rearing densities in two similar streams, where one stream received a release of hatchery salmonids and one stream did not receive a release of hatchery salmonids, 2) to determine if residual hatchery winter steelhead were present in the Eagle Creek Basin, and 3) if so, determine how their presence and density relates to mesohabitat selection and distribution of naturally produced salmonids.

2. Methods

2.1. Study location description

The Eagle Creek basin (23,313 ha) is located in northwest Oregon where it originates in the Mount Hood National Forest and flows northwest 42.4 km to the Clackamas River at river kilometer (rkm) 25.6. The three major tributaries to Eagle Creek are South Fork Eagle Creek (rkm 20.6), Delph Creek (rkm 14.4) and North Fork Eagle Creek (rkm 10.4). Three natural waterfalls are located within the mainstem of Eagle Creek. The lower (rkm 8) and middle falls (rkm 14.9) allow for adult salmonid passage via manmade fish ladders, and the upper falls (rkm 21.8) is a block to anadromy. Eagle Creek and North Fork Eagle Creek flow through a combination of private and public lands including forests dominated by old growth stands and commercial stands of timber. Tree species include true firs (*Abies* spp.), Douglas fir (*Pseudotsuga menziesii*), western red cedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*). The lower watershed is comprised of agricultural lands and suburban areas. This study included 21.8 rkm of Eagle Creek from the mouth to the upper falls and the lower 14.8 rkm of North Fork Eagle Creek.

Eagle Creek NFH is located at rkm 21.3, 0.5 km below the upper falls on Eagle Creek. At the time of this study, Eagle Creek NFH annually released 150,000 winter steelhead smolts and 500,000 coho salmon smolts into Eagle Creek. In 2008, these releases were lowered to 100,000 winter steelhead smolts and 350,000 coho salmon smolts due to reductions in funding and to reduce potential impacts on wild fish. These releases typically occur in mid-April. The hatchery operates a segregated program where hatchery winter steelhead return between December and April and the wild population between February and May. Hatchery coho salmon spawn in October and November (USFWS, 2007) followed by the wild population. In 2003, Oregon Department of Fish and Wildlife (ODFW) began stocking Eagle Creek with 60,000 spring Chinook salmon smolts at rkm 12.2. The spring Chinook salmon originated from broodstock spawned at the ODFW Clackamas River Hatchery. Eagle Creek and North Fork Eagle Creek support naturally reproducing populations of winter steelhead and coho salmon, however successful natural reproduction primarily occurs in North Fork Eagle Creek (USFWS, 2007). The Endangered Species Act lists these naturally reproducing populations of winter steelhead and coho salmon as Threatened. Cutthroat trout *O. clarki* are also present in the North Fork Eagle Creek and primarily occur above the upper falls in Eagle Creek.

2.2. Habitat survey

We enumerated total area and total number of mesohabitat units (riffles, pools, and glides) in Eagle Creek and North Fork Eagle Creek between June and August 2007. These mesohabitat units make up the sample frame for this study. Traveling upstream, a two-person survey crew classified habitat units using definitions found in Herger et al. (1996) and recorded unit length and width to the nearest 0.5 m using a laser rangefinder (Nikon Monarch Laser 800). Surveyed units were sequentially numbered for future identification by the snorkel crew. Three Hobo Water Temp Pros (Onset Computer Corporation, Bourne, MA.) were secured to the stream bottom and water temperature (°C) was recorded every 4 h.

2.3. Snorkel survey

A two phase sampling design modified from Hankin and Reeves (1988) was conducted to determine the distribution and density of juvenile salmonids from hatchery and natural origins. The surveys took place between July 10 and September 14, 2007 at summer base flow. In the first phase of sampling, habitat units were stratified by type and chosen at random from the sample frame. Two divers working in tandem conducted single pass snorkel counts of juvenile salmonids in selected habitat units. The surveys began at the mouth of Eagle Creek and proceeded upstream past Eagle Creek NFH to the upper falls. North Fork Eagle Creek was sampled from the mouth to the upstream limit (rkm 14.8) of steelhead and coho salmon distribution. Snorkel surveys were only conducted on days when weather conditions permitted a high degree of underwater visibility (i.e., little or no rain on the previous day). A total of three snorkelers in two pairings (W. R. Brignon/J. S. Hogle and W. R. Brignon/T. E. Conder) conducted the surveys. Snorkel crews followed the protocol described by Thurow (1994). Each snorkeler visually estimated abundance of salmonids by species, age (estimated by size), and origin (hatchery vs. wild, absence or presence of adipose fin). All hatchery fish were adipose fin marked and any hatchery fish residing in the stream after July 1 were considered residual.

In the second phase of sampling, a smaller subset of habitat units was randomly selected from the sample frame. The second phase sample units were selected at a rate of approximately 1/10 the first phase units, as suggested by Dolloff et al. (1993). The upper and lower limits of selected habitat units were block netted to minimize immigration and emigration. Observers conducted single pass snorkel counts using identical methodology as in the first phase of sampling. To account for individual snorkeler biases the unit was sampled by both pairs of snorkelers. We then used multiple-pass removal (Zippin, 1958) or mark recapture (Engle et al., 2006) to determine the "true" abundance of fish within the selected habitat unit. The multiple-pass depletion was conducted using two Smith-Root backpack electroshockers (Model LR-24, Smith-Root Inc., Vancouver, WA.). Electroshocking passes continued until fish sampled during a pass were less than or equal to 25% of the fish sampled during the previous pass. Captured fish were enumerated by species and age, fork lengths were recorded, and scale samples were collected from 50 winter steelhead juveniles. Multiple-pass depletion electrofishing was conducted on all calibration units with the exception of a pool habitat unit that was too deep to accurately conduct electrofishing. Therefore, a mark-recapture was conducted as described by Engle et al. (2006) to account for snorkeler bias associated with deep pool habitats. Using equations in Dolloff et al. (1993), calibration ratios were then calculated and applied to first phase diver counts to correct for snorkeler bias.

2.4. Statistical analyses

To address our first objective, we divided Eagle Creek into two reaches, upper Eagle Creek and lower Eagle Creek, with the line of demarcation being the confluence with North Fork Eagle Creek, which was considered its own reach. We compared habitat characteristics among the three reaches. Daily water temperatures were compared between reaches using one-way analysis of variance (ANOVA). The post-hoc Student Newman–Keuls multiple range test was used to identify pairwise differences among the three reaches (Zar, 1984). We used a 3×3 contingency table to test for independence of habitat type by stream reach. Density estimates for all species were compared between stream reaches with a Kruskal–Wallis non-parametric ANOVA. A non-parametric analog to the Student Newman–Keuls multiple range test was used (Dunn, 1964) to test for pairwise differences in density estimates between study reaches. Population estimates with 95% confidence intervals were calculated for all species in each habitat type and stream reach (Dolloff et al., 1993). The percent of the estimated wild fish populations rearing in the same mesohabitat units in which residual hatchery winter steelhead were located are reported. All statistical comparisons were conducted at the $\alpha = 0.05$ significance level using S-PLUS 8.0 software (Insightful Corp., 2007).

To describe the factors affecting the density and distribution of wild salmonids and residual hatchery winter steelhead we used an approach promoted by Fletcher et al. (2005). This approach uses two separate statistical models to best describe the data and consists of a three-step process. In the first step we created two sets of data, one data set identifies the presence and absence of a particular species and the other data set identifies the density of a particular species given that the species is present (i.e., the presence data). Second, we constructed two models; a logistic regression model to describe the variables affecting the presence and absence of a species, and a generalized linear model (GLM) to describe species density given that species is present. In the final step, the results of both models were used to make inferences regarding which variables best explain the distribution and density of a species. A total of six explanatory variables were used to construct the logistic regression models and the GLMs. Variables were selected based on biological plausibility and to describe potential broad scale displacement of wild salmonids in the presence of hatchery salmonids. The variables were: 1) mesohabitat type (i.e., riffle, pool, glide), 2) distance (m) from the mouth of Eagle Creek, 3) age 0 winter steelhead density (fish/m^2), 4) age 1 winter steelhead density (fish/m^2), 5) coho salmon density (fish/m^2), and 6) residual hatchery winter steelhead density (fish/m^2). We initially included a categorical variable for stream (i.e., Eagle Creek or North Fork Eagle Creek); however data collected in North Fork Eagle Creek were omitted because; 1) preliminary analyses suggested this variable negatively affected the validity of the model and 2) residual hatchery winter steelhead, the focus of this analysis, were only observed in the mainstem of Eagle Creek. For each species (age 0, age 1, and residual hatchery winter steelhead were considered separate species for this analysis) we modeled all combinations of explanatory variables. A correlation matrix of all continuous variables suggested a potential interaction between age 0 winter steelhead density and distance from the mouth of Eagle Creek ($r = 0.60$). Therefore, this interaction term was included in the construction of GLMs describing age 1 winter steelhead density, coho salmon density, and residual hatchery winter steelhead density.

Logistic regression models were constructed for coho salmon, age 1 winter steelhead, and residual hatchery winter steelhead. We did not construct a logistic regression model for age 0 winter steelhead because they were present in all but two sites and therefore these data lacked the necessary contrast between presence and absence to construct a valid logistic regression model. Generalized linear models were constructed for all species.

2.5. Logistic regression modeling

Logistic regression models were fit with SAS 9.1 software (SAS Institute, 2004) using all possible combinations of explanatory variables. Akaike's Information Criterion (AIC), corrected for small sample bias (AIC_c) and AIC_c weights (w_i) were used for model selection. The AIC_c values were calculated as

$$AIC_c = -2\log_e(L) + 2(K) + \frac{[2K(K+1)]}{(n-K-1)},$$

where $\log_e(L)$ is the log-likelihood, K is the number of model parameters and n is the sample size. The AIC_c weights (w_i) were calculated as

$$w_i = \frac{e^{\left(-\frac{1}{2}\cdot\Delta i\right)}}{\sum e^{\left(-\frac{1}{2}\cdot\Delta i\right)}},$$

where Δ_i equals the AIC_c of model i minus lowest AIC_c of all possible models. The model with the lowest AIC_c and highest w_i was considered the most parsimonious and models within 2 ΔAIC_c values best explain the data and therefore were considered competing. To account for model selection uncertainty we used multi-model averaging to calculate model-averaged estimates and standard errors of the parameter coefficients for the competing models. In addition, we determined the relative variable importance (0.00–1.00) of the model-averaged variables to give a weight of evidence for the significance of the explanatory variables (Burnham and Anderson, 2002). Adjusted r^2 values were calculated for the competing models to provide a casual assessment of model fit (Ramsey and Schafer, 2002).

We used the results of the averaged logistic regression model to construct probability plots that display the influence of explanatory variables on a species occurrence. These were calculated with the equation

$$\text{probability of occurence} = \frac{e^{\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_k X_k}}{\left(1 + e^{\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_k X_k}\right)},$$

where β_0 is the regression intercept, β_k are the regression coefficients of the explanatory variables, and X_k are the explanatory variables (Hosmer and Lemeshow, 2000). Plots were constructed for each species and explanatory variable by holding the averaged variable coefficients of the other model parameters constant.

2.6. Generalized linear modeling

The presence only data (i.e., data associated with a species considering that species is present), for each species best followed a gamma distribution. These data were then fit to a series of gamma GLMs using all possible combinations of explanatory variables. The model is in the form

$$\text{Log}(\mu) = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_k X_k,$$

where β_0 is the regression intercept, β_k are the regression coefficients of the explanatory variables, X_k are the explanatory variables, and Log(μ) is the link function for the mean of the gamma distribution (Lindsey, 1997) describing species density. The shape and scale parameters of the fitted gamma distributions were input into the "extract AIC" function in SPLUS 8.0 and the resulting AIC values were used to calculate the AIC_c for the model. We used the same model selection processes described for the logistic regression portion of this analysis.

The results of the averaged gamma GLM were used to construct plots that display the influence of explanatory variables on a particular species' density. These were calculated with the equation

$$\text{species density} = e^{\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_k X_k},$$

where β_0 is the regression intercept, β_k are the regression coefficients of the explanatory variables, and X_k are the explanatory variables. Plots were constructed for each species and explanatory variable by holding the averaged variable coefficients of the other model parameters constant.

3. Results

3.1. Habitat survey

The habitat characteristics of North Fork Eagle Creek and upper Eagle Creek are more closely related than those of lower Eagle Creek. Mean daily water temperature in all reaches was significantly different ($F_{2,1047}$ = 184.8; P<001, Student–Newman–Keuls tests, P<0.05). North Fork Eagle Creek and upper Eagle Creek experience cooler average water temperatures (15.3 and 15.6 °C, respectively) with lower Eagle Creek experiencing the highest average water temperature (17.4 °C). Habitat data collected from the three stream reaches are summarized in Table 1. The Chi-square contingency table test suggested that habitat unit composition is independent of stream reach (χ^2 = 7.85, df = 4, P = 0.097). On average, lower Eagle Creek is the widest stream reach (17.8 ± 0.69 m) followed by upper Eagle Creek (14.6 ± 0.57 m) and North Fork Eagle Creek (7.48 ± 0.25 m).

3.2. Fish distribution and density

Fish densities and abundances in North Fork Eagle Creek were more evenly distributed than in Eagle Creek (Fig. 1). Residual hatchery winter steelhead were first observed in lower Eagle Creek and distributed above the hatchery to the upper falls. No residual hatchery winter steelhead were observed in North Fork Eagle Creek and no residual hatchery coho salmon were found in Eagle Creek or North Fork Eagle Creek. Densities for all species were unevenly distributed between the three reaches (Kruskal–Wallis, P<0.001, Fig. 2), with the exception of age 1 winter steelhead, which were evenly distributed between all reaches (Kruskal–Wallis, P = 0.40, Fig. 2b).

Population estimates varied among species, reaches and habitat units (Table 2).

Table 1
Summary of mesohabitat characteristics of lower Eagle Creek, upper Eagle Creek and North Fork Eagle Creek.

Stream reach	Riffles	Pools	Glides	Total
Lower Eagle Creek				
Number of habitat units	81	31	53	165
Percent of total habitat	49	19	32	100
Length of habitat units (m)	5630	1380	3407	10,417
Percent of total stream length	54	13	33	100
Area of habitat units (m^2)	106,997	25,122	60,318	192,437
Percent of total area	56	13	31	100
Upper Eagle Creek				
Number of habitat units	106	64	49	219
Percent of total habitat	48	29	23	100
Length of habitat units (m)	6584	2659	2214	11,457
Percent of total stream length	58	23	19	100
Area of habitat units (m^2)	107,869	37,417	33,016	178,302
Percent of total area	60	21	19	100
North Fork Eagle Creek				
Number of habitat units	212	121	118	451
Percent of total habitat	47	27	26	100
Length of habitat units (m)	9839	2535	2474	14,848
Percent of total stream length	66	17	17	100
Area of habitat units (m^2)	77,125	20,399	18,140	115,664
Percent of total area	67	17	16	100

3.3. Wild fish rearing in the presence of residual hatchery winter steelhead

Residual hatchery winter steelhead were observed in 15 of the 63 mesohabitat units sampled in Eagle Creek. These 15 habitat units were composed of two riffles in lower Eagle Creek and seven pools, three riffles, and three glides in upper Eagle Creek. The percentage of the estimated population of age 0 winter steelhead, age 1 winter steelhead, and coho salmon rearing in those same 15 units was 55%, 59%, and 55%, respectively.

3.4. Factors influencing the probability of a species' occurrence

Age 0 winter steelhead were located in 61 of the 63 (96.8%) habitat units sampled in Eagle Creek. The lack of contrast between presence and absence for this species makes it impractical to accurately model the probability of occurrence for this species/age-class. However, their presence in 96.8% of the units sampled suggests that they had a high probability of occurrence anywhere in Eagle Creek regardless of the explanatory variables. For all other species model-averaged estimates and standard errors of parameter coefficients for competing logistic regression models were calculated along with the relative variable importance of all explanatory variables contained in competing models (Table 3).

Age 1 winter steelhead were located in 47 of the 63 (74.6%) habitat units sampled in Eagle Creek. Of the 32 logistic regression models containing all possible combinations of explanatory variables, four models were within 2 ΔAIC_c values and therefore considered competing (Table 4). Coho salmon density had the highest relative variable importance (1.00), followed by age 0 winter steelhead density (0.46), distance from the mouth of Eagle Creek (0.19), and

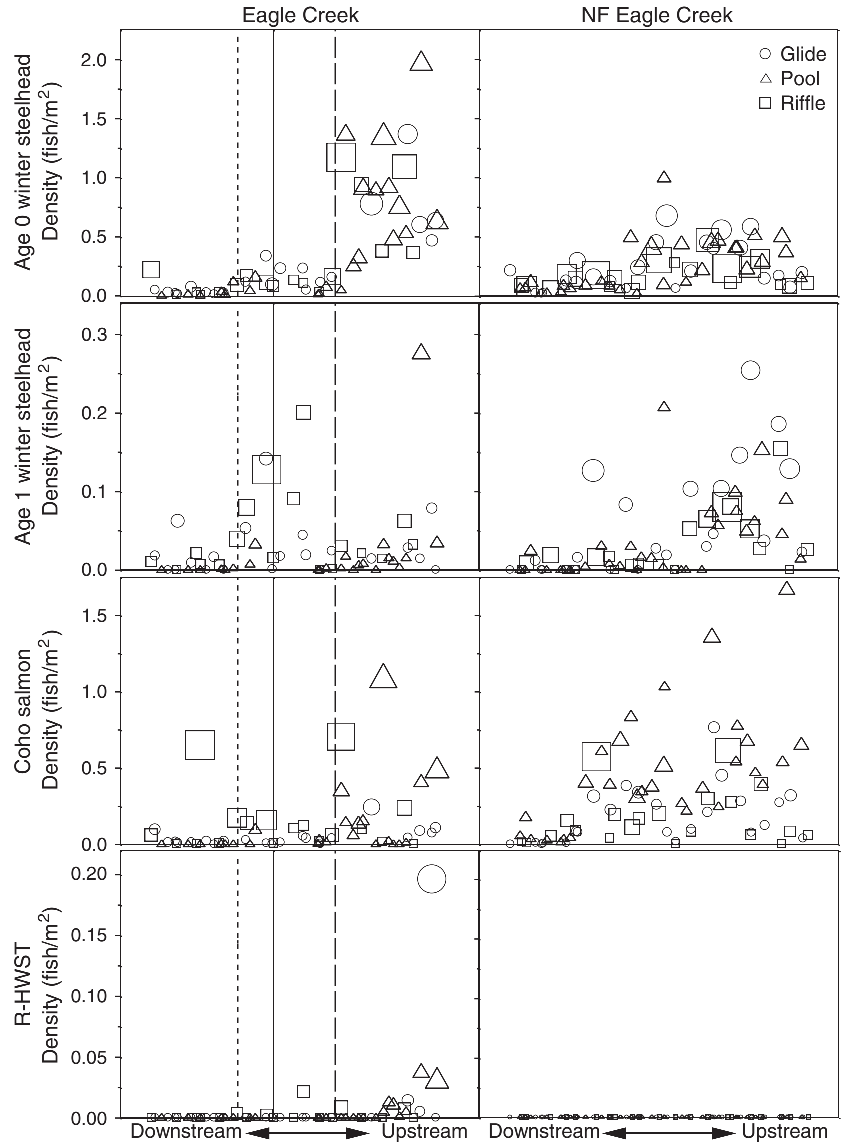

Fig. 1. Distributions of estimated densities in Eagle Creek and North Fork (NF) Eagle Creek. The size of the symbol represents the abundance of fish in the habitat unit relative to other points on the plot. Three points of reference are labeled in the Eagle Creek plot: first detection of residual hatchery winter steelhead (R-HWST, dotted line), the confluence with North Fork Eagle Creek (solid line), and the middle ladder (dashed line).

mesohabitat type (0.13). The probability of age 1 winter steelhead occurring in Eagle Creek increased with distance from the mouth of Eagle Creek, along with an increase in age 0 winter steelhead density and coho salmon density. Riffles had the highest probability of occurrence followed closely by glides and then pools (Fig. 3a).

Coho salmon were located in 48 of the 63 (76.2%) habitat units sampled in Eagle Creek. Three logistic regression models were within 2 AIC_c values and therefore considered competing (Table 4). Age 1 winter steelhead density had a relative variable importance of 1.00, followed by distance from the mouth of Eagle Creek (0.24) and age 0 winter steelhead density (0.22). There was a higher probability of coho salmon occurrence with an increase in each explanatory variable (Fig. 3b).

Residual hatchery winter steelhead were located in 15 of the 63 (23.8%) habitat units sampled in Eagle Creek. Of the 32 logistic regression models containing all possible combinations of explanatory variables, four models were within 2 AIC_c values and therefore are considered competing (Table 4). Distance from the mouth of Eagle Creek and age 1 winter steelhead density each had a relative variable importance of 1.00, followed by coho salmon density (0.53) and age 0 winter steelhead density (0.47), respectively. There was a higher probability of residual hatchery winter steelhead with an increase in each explanatory variable (Fig. 3c).

3.5. Factors influencing a species' density given the presence of that species

For all species the model-averaged estimates and standard errors of parameter coefficients were calculated along with the relative variable importance of all explanatory variables contained in the competing GLMs (Table 5).

For habitat units where age 0 winter steelhead were present, their density is best explained by three GLMs that were within 2 AIC_c values and therefore considered competing (Table 6). Distance from the mouth of Eagle Creek and coho salmon density had a relative variable importance of 1.00, followed by mesohabitat type (0.70), and age 1 winter steelhead density (0.20). Age 0 winter steelhead density was highest in riffles, followed by pools and then glides. There was a

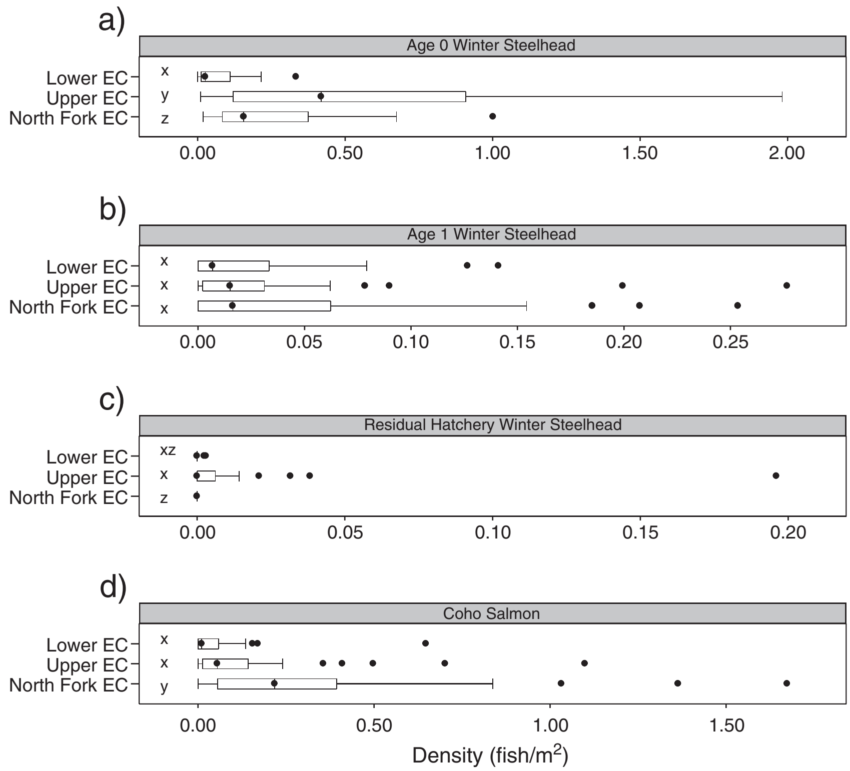

Fig. 2. Estimated salmonid densities in lower Eagle Creek (EC), upper Eagle Creek, and North Fork Eagle Creek. The ends of each box are the 25th and 75th quartile range and the horizontal line within the box is the median. The whisker ends are all data points that fall within the distance calculated as 1.5 times the interquartile range. A dot that lies beyond the whiskers represents an outlier. Lower case letters to the right of the y-axis represent significant differences ($P>0.05$) in pairwise comparisons.

positive relationship between age 0 winter steelhead density and distance from the mouth of Eagle Creek, coho salmon density, and age 1 winter steelhead density (Fig. 4a).

For habitat units where age 1 winter steelhead were present, their density is best explained by two GLMs that were within 2 AIC_c values and therefore considered competing (Table 6). Age 0 winter steelhead density and mesohabitat type had a relative variable importance of 1.00, followed by residual hatchery winter steelhead (0.54). Age 1 winter steelhead density was highest in riffles, followed by glides then pools. There was a positive relationship between age 1 winter steelhead density and both age 0 and residual hatchery winter steelhead densities (Fig. 4b).

For habitat units where coho salmon were present, their density is best explained by one GLM. The difference between this model and the next closest model was 2.24 AIC_c values and therefore not considered a competing model (Table 6). Mesohabitat type and age 0 winter steelhead density were included in model. The highest densities of coho salmon were found in riffles, followed by pools and then glides. There is a positive relationship between coho salmon density and age 0 winter steelhead density (Fig. 4c).

For habitat units where residual hatchery winter steelhead were present, their density was best explained by one GLM. The difference between this model and the next closest model was 2.84 AIC_c values and therefore not considered a competing model (Table 6). Distance from the mouth of Eagle Creek, age 0 winter steelhead density and age 1 winter steelhead density were included in model. There is a positive relationship between residual hatchery winter steelhead density and both distance from the mouth of Eagle Creek and age 1 winter steelhead density. However, there was a negative relationship between residual hatchery winter steelhead density and age 0 winter steelhead density (Fig. 4d).

4. Discussion

Residual hatchery winter steelhead were found rearing in Eagle Creek in the presence of Endangered Species Act listed wild salmonids,

Table 2
Population estimates of juvenile fish in lower Eagle Creek (LEC), upper Eagle Creek (UEC), and North Fork Eagle Creek (NFEC) calculated from two phase snorkel surveys conducted during the summer of 2007. Confidence intervals (95%) are in parentheses.

Species	Age 0 winter steelhead			Age 1 winter steelhead			Residual hatchery winter steelhead			Coho salmon		
Habitat type	LEC	UEC	NFEC	LEC	UEC	NFEC	LEC	UEC	NFEC	LEC	UEC	NFEC
Glides	2949 (±2160)	10,708 (±2124)	3162 (±3157)	712 (±263)	454 (±250)	677 (±167)	0	282 (±250)	0	958 (±908)	1975 (±887)	2460 (±1429)
Pools	948 (±2957)	18,421 (±4046)	2581 (±5664)	112 (±49)	637 (±85)	247 (±150)	0	215 (±85)	0	255 (±762)	6283 (±1079)	5397 (±1582)
Riffles	9255 (±885)	30,015 (±1318)	10,870 (±3080)	4491 (±283)	2030 (±500)	1501 (±1315)	102 (±283)	187 (±500)	0	15,626 (±784)	11,090 (±1215)	14,471 (±2940)
Totals	13,152 (±3342)	59,143 (±4459)	16,613 (±6954)	5315 (±348)	3121 (±508)	2425 (±1254)	102 (±348)	685 (±508)	0	16,839 (±1267)	19,348 (±1697)	22,328 (±3486)

Table 3
Relative variable importance and estimated model coefficients (±SE) for a logistic regression model averaged among competing models used to describe the factors influencing the probability of a species occurrence.

Model variable[a]	Relative importance	Averaged coefficient (±SE)
Age 1 winter steelhead		
Intercept	na	0.10 (0.47)
Coho.den	1.00	17.11 (9.32)
Age0.den	0.46	1.96 (1.45)
Dist.EC	0.19	0.000048 (0.000050)
HABTYPE (glide)	0.13	−0.07 (0.47)
HABTYPE (pool)	0.13	−0.72 (0.48)
Coho salmon		
Intercept	na	0.24 (0.48)
Age1.den	1.00	60.77 (30.89)
Age0.den	0.22	0.07 (1.03)
Dist.EC	0.24	0.000039 (0.000049)
Residual hatchery winter steelhead		
Intercept	Na	−7.63 (2.40)
Dist.EC	1.00	0.000331 (0.00014)
Age1.den	1.00	29.11 (11.83)
Age0.den	0.47	1.79 (1.31)
Coho.den	0.53	3.91 (3.01)

[a] Variable definitions: Dist.EC = distance from the mouth of Eagle Creek(m), HABTYPE = mesohabitat type (riffles, pools, glides), Age0.den = age 0 winter steelhead density (fish/m^2), Age1.den = age 1 winter steelhead density (fish/m^2), Coho.den = coho salmon density (fish/m^2).

therefore the potential exists for competitive ecological interactions. This potential for competition is magnified by the fact that the majority of wild salmonids in Eagle Creek were observed in the same 15 mesohabitat units as residual hatchery winter steelhead. However, because the hatchery and wild populations were not segregated at the mesohabitat scale, any competitive interactions are occurring at a smaller scale. Grant et al. (1998) suggests that studies observing density and distribution of fishes should be conducted at smaller scales than our study to best understand how individual territory size changes in response to habitat and food availability, and ultimately determines the carrying capacity for a stream.

Table 4
Competing logistic regression models used to describe a species presence and absence in Eagle Creek. Age 0 winter steelhead are not included in this table because they were present in 61 of the 63 habitat units sampled and therefore lacked the appropriate contrast to accurately model the probability of occurrence for this species. Competing models are ranked by Akaike's information criterion weights (w_i) which are calculated using the number of estimated parameters (K), log likelihood ($\log_e L$), Akaike's information criterion (AIC) corrected for small sample size (AIC_c) and the differences in AIC_c (Δ_i). The proportion of variability (adjusted r^2) in the data that is accounted for by the model is reported.

Rank	Model[a]	K	$\log_e L$	AIC	AIC_c	Δ_i	w_i	Adjusted r^2
Age 1 winter steelhead								
1	Coho.den	2	−30.17	64.34	64.54	0.00	0.35	0.18
2	Coho.den, Age0.den	3	−29.12	64.23	64.63	0.09	0.33	0.15
3	Coho.den, Age0.den, HABTYPE	5	−27.73	65.46	66.51	1.97	0.13	0.17
4	Coho.den, Dist.EC	3	−29.70	65.40	65.80	1.26	0.19	0.22
Coho salmon								
1	Age1.den	2	−29.64	63.28	63.48	0.00	0.53	0.14
2	Age1.den, Dist.EC	3	−29.31	64.62	65.03	1.55	0.24	0.15
3	Age1.den, Age0.den	3	−29.41	64.81	65.22	1.74	0.22	0.15
Residual hatchery winter steelhead								
1	Dist.EC, Age1.den, Coho.den	4	−17.24	42.48	43.17	0.00	0.34	0.50
2	Dist.EC, Age1.den, Age0.den	4	−17.42	42.83	43.52	0.35	0.29	0.50
3	Dist.EC, Age1.den	3	−18.94	43.88	44.29	1.12	0.19	0.45
4	Dist.EC, Age1.den, Age0.den, Coho.den	5	−16.71	43.41	44.46	1.29	0.18	0.52

[a] Variable definitions: Dist.EC = distance from the mouth of Eagle Creek (m), HABTYPE = mesohabitat type (riffles, pools, glides), Age0.den = age 0 winter steelhead density (fish/m^2), Age1.den = age 1 winter steelhead density (fish/m^2), Coho.den = coho salmon density (fish/m^2).

McMichael and Pearsons (2001) documented that residual hatchery steelhead had migrated over 12 km upstream from a release site on the Teanaway River, WA into areas containing Endangered Species Act listed fish populations. Considering that North Fork Eagle Creek is thought to be the primary area for successful natural production of Endangered Species Act listed species in the Eagle Creek Basin (USFWS, 2007), there was a concern that residual hatchery winter steelhead from Eagle Creek National Fish Hatchery would make a similar migration up the North Fork Eagle Creek. Our results suggest that residual hatchery winter steelhead did not migrate up North Fork Eagle Creek, however similar to McMichael and Pearsons (2001) we did document an upstream migration in Eagle Creek. Due to the impassible upper falls located above the hatchery, fish were only able to migrate upstream less than 0.5 km, a fraction of what McMichael and Pearsons (2001) observed.

As referenced earlier, North Fork Eagle Creek is considered the main site for successful reproduction of winter steelhead (USFWS, 2007), therefore it was unexpected to find the highest abundance and densities of age 0 winter steelhead in upper Eagle Creek. There are many possibilities for this outcome. Matala et al. (2008) found that genetic samples collected from naturally produced juvenile winter steelhead in upper Eagle Creek were most similar to samples collected from Eagle Creek National Fish Hatchery. Therefore, it is possible the high abundance and density of age 0 winter steelhead in upper Eagle Creek is the result of adult hatchery fish spawning in the stream. Juvenile density can be high in the vicinity of the spawning grounds (Groot and Margolis, 1991) until density dependent emigration and dispersal takes place. Studies have shown that progeny of hatchery fish who spawn naturally in the stream can be less fit than their wild counterparts (Araki et al., 2007; Ford, 2002; Lynch and O'Hely, 2001), which translates into lower adult survival. This may be a hint as to why the North Fork Eagle Creek is the primary producer of wild adult steelhead.

Hatchery winter steelhead spawning in upper Eagle Creek may also factor in to the lower densities of juvenile coho salmon. Hayes (1987) documented a large decrease in reproductive success of early spawning trout populations after their redds were super-imposed by later spawning individuals. In the Eagle Creek Basin, hatchery coho salmon return to spawn between September and November, followed by wild coho salmon from November to December. Both coho populations are followed by hatchery winter steelhead, from December through March, and finally the wild winter steelhead population, from February through June. All coho salmon, regardless of origin, will be competing for spawning habitat with the later returning steelhead population and therefore redd superimposition may impact their reproductive success. Incidence of redd superimposition would be higher in the mainstem Eagle Creek because the large number of hatchery winter steelhead returning to the basin rarely stray into the North Fork Eagle Creek (Kavanagh et al., 2006).

There is little doubt that habitat availability plays a role in Eagle Creek and North Fork Eagle Creek. It is possible that juvenile rearing habitat in upper Eagle Creek is better suited for age 0 winter steelhead and juvenile rearing habitat in North Fork Eagle Creek is best suited for coho. Most likely there is not one specific explanation, rather a suite of reasons with variable levels of impact that explain the spatial differences in age 0 winter steelhead and coho salmon abundance and densities in Eagle Creek and North Fork Eagle Creek. To gain a definitive understanding of these types of interactions and the variables that influence them, manipulative studies are needed.

As densities increase in Eagle Creek so did the probability of a species' presence. If one species was displacing another, we would

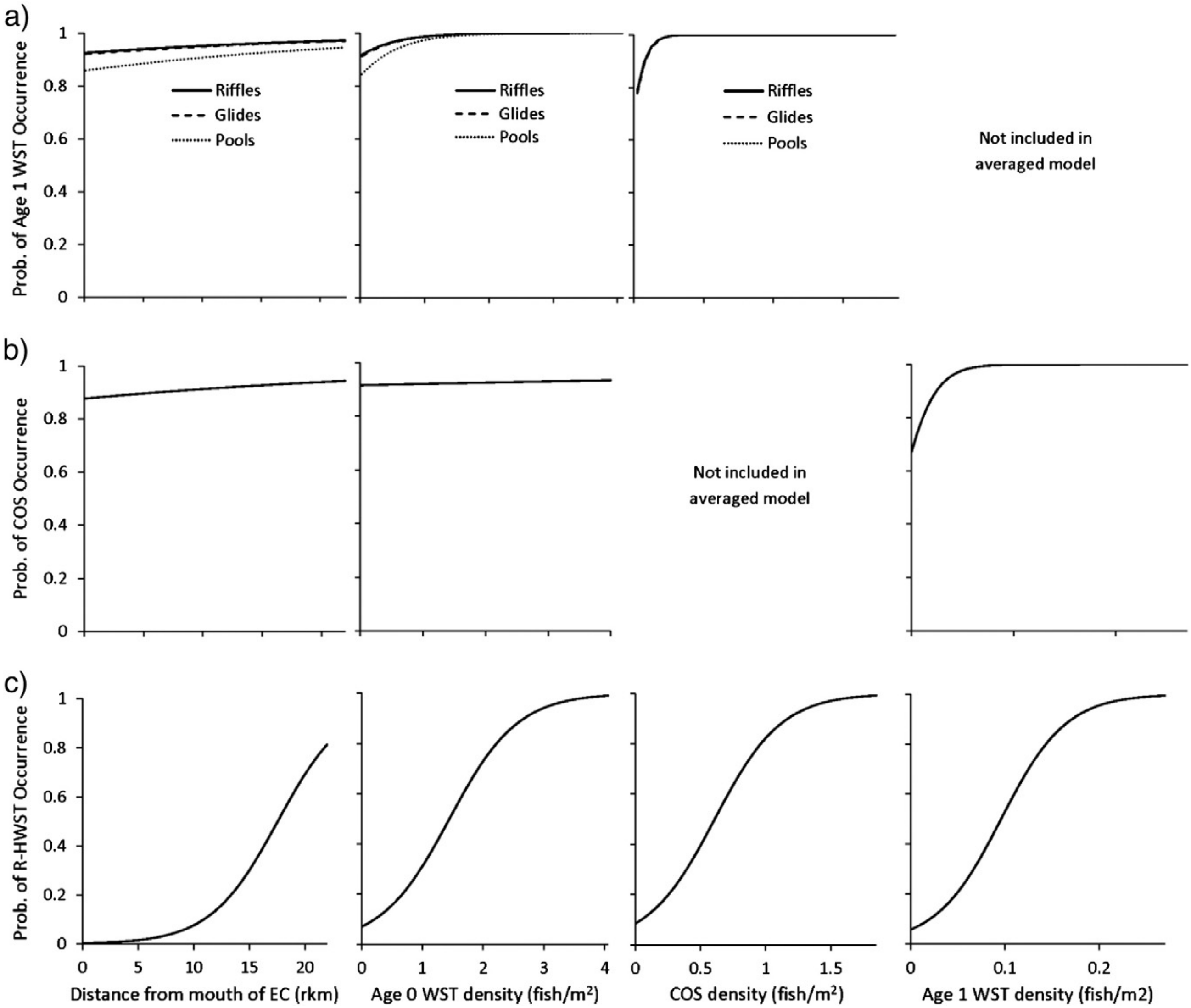

Fig. 3. Probability of a species occurence in Eagle Creek (EC). Plots were constructed with model averaged parameter estimates of competing logistic regression models. Winter steelhead (WST), coho salmon (COS), and residaul hathcery winter steelhead (R-HWST) have been abbreviated.

expect to see an inverse relationship between the probability of a species occurrence and density of the species used as an explanatory variable. Coho salmon can displace steelhead from pool mesohabitats to riffle mesohabitats (Hartman, 1965). This was not the case in Eagle Creek. Coho salmon, age 0 winter steelhead and age 1 winter steelhead were more dense in riffle mesohabitats followed by slow water habitats (i.e., pools and glides). This suggests that there was no effect on mesohabitat selection as a function of interspecific or intraspecific competition. It is possible that any displacement from preferred habitats was not occurring at the mesohabitat scale.

Another important factor in describing the probability of a species occurrence was distance from the mouth of Eagle Creek. Most likely this is a function of the adult fish spawning in the cooler water temperatures of upper Eagle Creek and therefore, on a reach scale, juvenile fish were located relatively close to where they hatched. Due to the presence of the large waterfalls located at the middle ladder of Eagle Creek, it is highly unlikely that juvenile fish were able to migrate upstream from lower Eagle Creek into this upper reach.

Densities of all species in Eagle Creek either had no relationship or a positive relationship. There is one exception to this statement. The GLM describing residual hatchery winter steelhead density indicated a negative relationship with age 0 winter steelhead density. This was most likely the result of an influential data point where the highest density (0.19 fish/m^2) of residual hatchery winter steelhead was located in a habitat unit with a relatively low density (0.46 fish/m^2) of age 0 winter steelhead. We recommend future sampling efforts be focused in areas with known populations of residual hatchery winter steelhead to determine if a distinct relationship between these population densities exists.

Given our study design, there are four scenarios that could explain our inability to explicitly document a displacement of wild salmonids from preferred mesohabitats by residual hatchery winter steelhead. First, studies suggest that hatchery fish can displace wild fish (Hillman and Mullan, 1989; McMichael et al., 1999; Vincent, 1987). We did not observe this in Eagle Creek. Second, Jonasson et al. (1996) documented the highest densities of residual hatchery steelhead were located near the release site, similar to our study. Also consider that Vincent (1987) concluded that releases of hatchery fish reduced populations of wild rearing fish in the vicinity of the release site. Therefore, any displacement of wild fish by residual hatchery winter steelhead in Eagle Creek likely would have been observed in the upper reaches near the hatchery. With the majority of both the wild salmonid population and the residual hatchery winter steelhead population located in upper Eagle Creek it

Table 5
Competing generalized linear models used to describe the density (fish/m^2) of a species given that the species is present in Eagle Creek. Competing models are ranked by Akaike's information criterion weights (w_i) which are calculated using the number of estimated parameters (K), Akaike's information criterion (AIC) corrected for small sample size (AIC$_c$) and the differences in AIC$_c$ (Δ_i). The proportion of variability (adjusted r^2) in the data that is accounted for by the model is reported.

Rank	Model[a]	K	AIC	AIC$_c$	Δ_i	w_i	Adjusted r^2
Age 0 winter steelhead							
1	Dist.EC, Coho.den, HABTYPE	5	82.01	83.06	0.00	0.50	0.46
2	Dist.EC, Coho.den	3	83.71	84.11	1.05	0.30	0.42
3	Dist.EC, Coho.den, HABTYPE, Age1.den	6	83.36	84.86	1.79	0.20	0.46
Age 1 winter steelhead							
1	Age0.den, HABTYPE, R-HWST.den	5	64.30	65.76	0.00	0.54	0.28
2	Age0.den, HABTYPE	4	65.17	66.12	0.36	0.46	0.24
Coho salmon							
1	Age0.den, HABTYPE	4	64.77	65.70	0.00	1.00	0.26
Residual hatchery winter steelhead							
1	Dist.EC, Age0.den, Age1.den	4	29.75	33.75	0.00	1.00	0.61

[a] Variable definitions: Dist.EC = distance from the mouth of Eagle Creek (m), HABTYPE = mesohabitat type (riffles, pools, glides), Age0.den = age 0 winter steelhead density (fish/m^2), Age1.den = age 1 winter steelhead density (fish/m^2), Coho.den = coho salmon density (fish/m^2), R-HWST.den = residual hatchery winter steelhead density (fish/m^2).

is difficult to detect displacement without pre-release data. Due to high spring flows and the associated turbidity we were unable to collect pre-release abundance data on wild fish rearing below the hatchery that would be required for this type of case–control comparison. Third, the studies that documented displacement of wild fish as a function of hatchery fish were conducted shortly after (≤1 month) the release of the hatchery fish (Hillman and Mullan, 1989; McMichael et al., 1999) when the abundance of hatchery fish was higher than that of the wild fish. It is possible that because we were evaluating a displacement caused by residual hatchery winter steelhead, which have resided in the stream for over 2 months; any potential large scale displacement may have occurred closer to the time of release. Lastly, scale may play a role in our findings. It is possible that the number of residual hatchery winter steelhead was not large enough to elicit a displacement response or that the elicited response is occurring at a spatial scale smaller than the mesohabitat scale. Regardless, residual hatchery winter steelhead appear to not displace wild ESA listed fish in Eagle Creek and North Fork Eagle Creek at the mesohabitat scale during the time of our study.

Table 6
Relative variable importance and estimated model coefficients (±SE) for a generalized linear model averaged among competing models used to describe the factors influencing a species density (fish/m^2) given that the species is present.

Model variable[a]	Relative importance	Averaged coefficient (±SE)
Age 0 winter steelhead		
Intercept	na	−3.20 (0.80)
Dist.EC	1.00	0.000117 (0.000052)
Coho.den	1.00	1.57 (1.67)
HABTYPE (pool)	0.70	0.11 (0.46)
HABTYPE (riffle)	0.70	0.83 (0.49)
Age1.den	0.20	2.06 (4.17)
Age 1 winter steelhead		
Intercept	na	−3.68 (0.33)
Age0.den	1.00	1.07 (0.40)
HABTYPE (pool)	1.00	−1.19 (0.44)
HABTYPE (riffle)	1.00	0.35 (0.42)
R-HWST.den	0.54	11.23 (6.07)
Coho salmon		
Intercept	na	−3.46 (0.31)
Age0.den	1.00	1.19 (0.39)
HABTYPE (pool)	1.00	0.93 (0.44)
HABTYPE (riffle)	1.00	1.25 (0.42)
Residual hatchery winter steelhead		
Intercept	na	−8.49 (1.25)
Dist.EC	1.00	0.000256 (0.000077)
Age0.den	1.00	−1.12 (0.62)
Age1.den	1.00	8.59 (3.63)

[a] Variable definitions: Dist.EC = distance from the mouth of Eagle Creek (m), HABTYPE = mesohabitat type (riffles, pools, glides), Age0.den = age 0 winter steelhead density (fish/m^2), Age1.den = age 1 winter steelhead density (fish/m^2), Coho.den = coho salmon density (fish/m^2), R-HWST.den = residual hatchery winter steelhead density (fish/m^2).

Due to potential hybridization and similar phenotypic characteristics (Baker et al., 2002; Brown et al., 2004; Weigel et al., 2002) it is difficult to differentiate juvenile O. *mykiss* from juvenile cutthroat trout, especially during underwater observation. Therefore, the trend of increasing age 1 winter steelhead density in the upper reaches of North Fork Eagle Creek could be a product of species misidentification. Rosenfeld et al. (2000) found that stream width was a significant predictor of cutthroat trout presence and were able to predict cutthroat trout presence to a high degree in streams less than 7 m wide. North Fork Eagle Creek is 7.48 m wide on average with the smallest widths recorded in upper reaches.

The findings in this manuscript are an important component to assessing ecological interactions in the Eagle Creek Basin, however it is important to recognize that this is one year of data. In determining the potential impact of the hatchery on juvenile fish abundance and density a multiyear data set is preferred and could help explain potential stochastic environmental factors occurring in the basin that can confound the results of a 1 year data set. The uncertainty with snorkeler bias, particularly in riffle habitat units, may have impacted the results of this study. To correct for this bias, our calibration ratio for coho salmon in riffle habitats was 5.78 fish for each fish observed. Two calibration units weighed heavily on this calibration ratio. In two riffle calibration units we observed only one coho salmon, yet our population estimates documented more than 20 coho salmon were present. This is most likely a function of riffle habitat complexity and suggests that this type of habitat may be more utilized by coho than expected. Also, population estimates of age 1 winter steelhead in lower Eagle Creek riffle habitats may be inflated due to an influential data point where 260 fish were estimated to be rearing in a riffle habitat unit directly below the North Fork Eagle Creek confluence. It is possible that this data point is highly influenced by fish migrating from North Fork Eagle Creek. This data point inflates the lower Eagle Creek age 1 winter steelhead population estimate by more than 2000 fish, or 40%.

Eagle Creek NFH provides an important fishery for commercial, sport and tribal harvest, as well as assisting with tribal reintroduction projects upstream of Bonneville Dam. It is important to maximize these benefits while minimizing the risks to the ESA listed wild populations in Eagle Creek Basin. This study provides a basis of information regarding juvenile population sizes, densities, and rearing distribution in the basin. As a result of limited funding and biological concerns regarding Eagle Creek NFH, the USFWS Hatchery Review Team has recommended that the hatchery lower its release of 150,000 steelhead smolts to 100,000 and the release of coho salmon from 500,000 smolts to 350,000. These lower release numbers were implemented in 2008, one year after we conducted this study. Therefore, we expect that the incidence of residual hatchery winter steelhead would be lower in subsequent years. Sampling effort for any future monitoring and evaluation on the effect of residual hatchery winter steelhead on the wild population should be focused in upper Eagle Creek, where the majority of residual hatchery winter steelhead and wild salmonids are rearing.

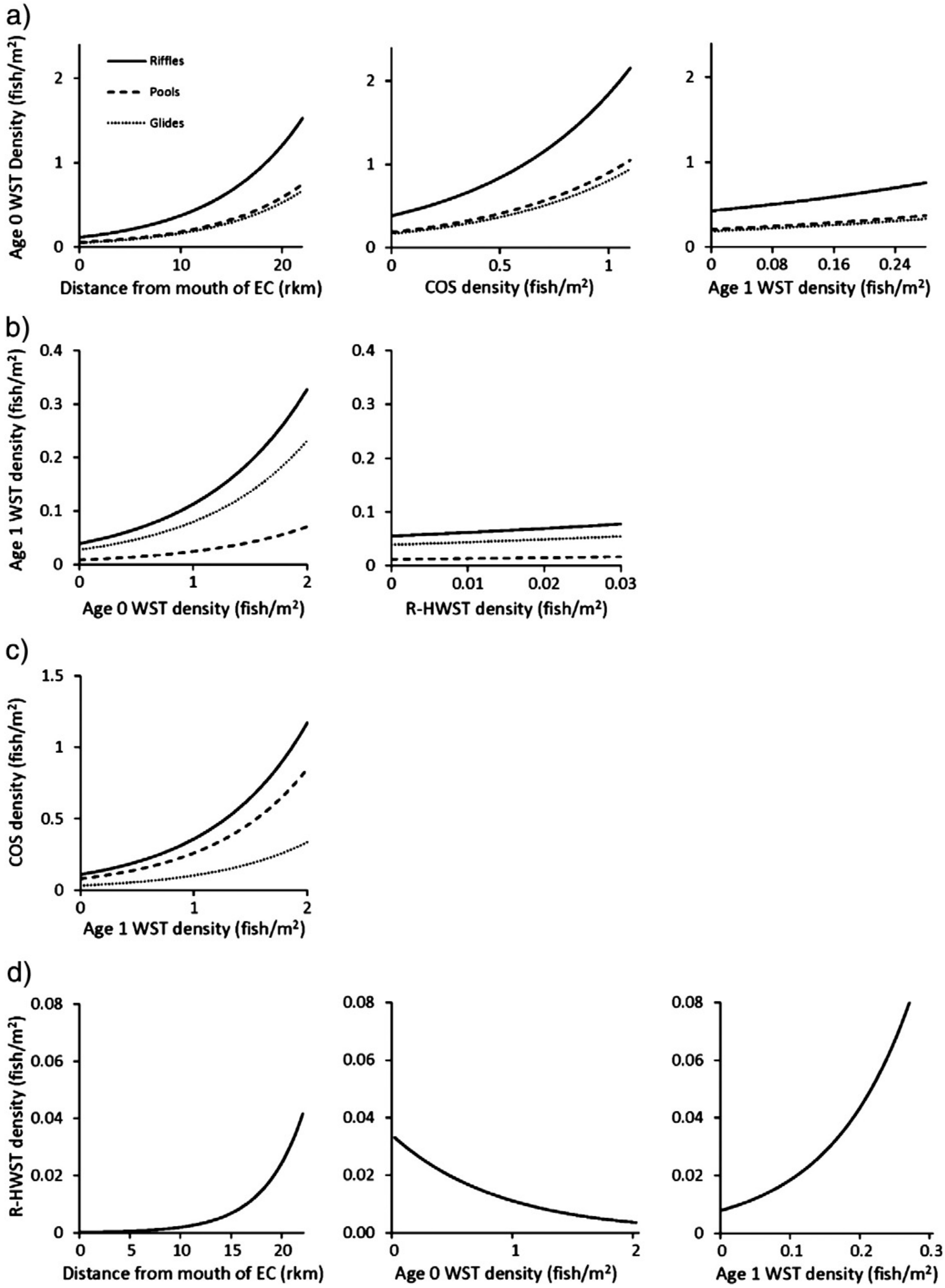

Fig. 4. Factors influencing a species density given their presence. Plots were constructed using model averaged parameter estimates from competing generalized linear models. Eagle Creek (EC), winter steelhead (WST), coho salmon (COS), and residual hatchery winter steelhead (R-HWST) have been abbreviated.

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