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ARTICLE

Within-river straying: sex and size influence recovery location of hatchery Chinook salmon (*Oncorhynchus tshawytscha*)

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Abstract: Salmon straying is often defined as the failure of adults to return to their natal river system. However, straying within a river basin can be problematic if hatchery salmon do not return to their hatchery of origin and subsequently spawn in the wild with natural-origin salmon. We examined within-river straying patterns from 34 years of coded-wire tag data, representing 29 941 hatchery fall Chinook salmon (*Oncorhynchus tshawytscha*) in the Elk River, Oregon, USA. Using classification tree analysis, we found that females and larger salmon were more likely to be recovered on the spawning grounds than males and smaller fish. Females larger than 980 mm had a 51.6% likelihood of recovery on the spawning grounds rather than at the Elk River Hatchery. Our findings raise questions about the behavior of straying adults and implications for management of these stocks, with a focus on methods to reduce within-river straying. We recommend further studies to determine whether carcass recoveries are fully representative of hatchery salmon that stray within the Elk River basin.

Résumé : L'errance de saumons est souvent définie comme le défaut d'adultes de retourner à leur réseau hydrographique natal. L'errance au sein d'un bassin hydrographique peut toutefois être problématique si des saumons d'écloserie ne retournent pas à leur écloserie d'origine et frayent subséquemment en liberté avec des saumons d'origine naturelle. Nous examinons les motifs d'errance au sein de rivières à la lumière de 34 années de données de micromarques codées représentant 29 941 saumons quinnats (*Oncorhynchus tshawytscha*) d'automne issus d'une écloserie dans la rivière Elk (Oregon, États-Unis). En utilisant l'analyse d'arbre de classification, nous constatons que les femelles et les saumons plus gros étaient plus susceptibles d'être récupérés dans les frayères que les mâles et les poissons plus petits. Les femelles de plus de 980 mm avaient une probabilité de 51,6 % d'être récupérées dans les frayères plutôt qu'à l'écloserie de la rivière Elk. Nos constatations soulèvent des questions quant au comportement des adultes errants et sont importantes pour la gestion de ces stocks, notamment en ce qui concerne les méthodes employées pour réduire l'errance au sein de rivières. Nous recommandons que soient réalisées d'autres études pour déterminer si les carcasses récupérées sont entièrement représentatives de saumons d'écloserie qui errent dans le bassin de la rivière Elk. [Traduit par la Rédaction]

Introduction

Anadromous Pacific salmon (*Oncorhynchus* spp.) typically spawn in their natal streams after returning from the ocean, relying on navigation and homing behavior guided by geomagnetic (Putman et al. 2013) and olfactory (Hasler and Scholz 1983) cues. However, straying from the natal site is also a natural component of salmonid life histories (Quinn 2005), which may provide benefits such as reduced competition, increased gene flow among wild populations, and colonization of novel habitats (Kaitala 1990; Hendry et al. 2004). The term "straying" has typically been applied to larger spatial scales when individuals return to non-natal river basins to reproduce (Quinn 1993; Keefer and Caudill 2014). However, because salmon are capable of homing with extraordinary precision to their natal site within a river system (Varnavskaya et al. 1994; Quinn 1999; Neville et al. 2006), straying may also occur within natal river basins. Natal homing can be thought of as a hierarchical process (Neville et al. 2006), wherein the degree of straying or natal site homing represents points on a spatial continuum. At one end of the spectrum, spawning in a different river basin represents straying to a novel, potentially nonancestral area. Conversely, returning to the specific natal reach within a river system is an example of fine-scale homing. This highlights the range of straying or homing behaviors that individuals may exhibit during their reproductive migrations. In this study, we explicitly examine the phenomenon of within-river straying by hatchery-produced salmon.

Straying may reflect a salmon's inability to locate its natal site or may represent a fish's decision to spawn elsewhere owing to social and environmental factors (Quinn 2005). Salmon make decisions at fine spatial scales, which may lead to less precise homing within their natal river basin. Spawning site selection is one such decision involving complex tradeoffs between site-specific homing, spawning habitat selection, competition, and mate choice (Hendry et al. 2004; Dittman et al. 2010; Cram et al. 2013). Challenges associated with finding the natal site and tradeoffs between natal site homing and spawning habitat selection may be exacerbated in hatchery-reared salmon. While hatchery salmon are not inherently more likely to stray (Quinn and Dittman 1992), many hatchery rearing and release practices can dramatically increase the rate of straying (Quinn 1993; Pascual et al. 1995). Using

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brood stock that is not native to the watershed, transporting juveniles before release, and releasing juveniles at inappropriate times can all increase adult straying behavior (Quinn 1993; Pascual et al. 1995). Straying by hatchery-origin salmon can present genetic and ecological risks to wild populations through competition, disease transmission, genetic introgression, and associated fitness reductions (Jonsson and Jonsson 2006; Araki et al. 2008; Christie et al. 2012; Rand et al. 2012). Indeed, straying by hatchery-origin salmon is a major challenge for fisheries managers as they balance production and conservation mandates (Grant 2012; Flagg 2015). Many salmon hatcheries are managed to enhance harvest while simultaneously attempting to minimize interactions between hatchery-raised and wild fish. These programs capitalize on the philopatric behavior of salmon by trapping adults that return volitionally to the hatchery from which they were released.

However, not all hatchery-produced salmon return to their natal hatcheries, and they may instead spawn in the wild with natural-origin adults. In this regard, hatchery salmon may be considered "strays" if they spawn in the wild, even if it is within the same river system as their hatchery of origin. Although this occurs at a smaller spatial scale than typically used to describe straying, it can be a useful concept when considering salmon genetic and management goals. Studies have demonstrated a negative relationship between the productivity of wild spawning salmon populations and the proportion of hatchery-origin fish among spawners, or pHOS (McGinnity et al. 2009; Chilcote et al. 2011). As a result, common management objectives include maintaining low pHOS values in locations containing both production hatcheries and wild salmon populations (Paquet et al. 2011). While pHOS is often used for management purposes, it is actually a measure of hatchery fish straying into the wild population rather than a representation of the hatchery fish that stray from the natal hatchery (Keefer and Caudill 2014). Hence, the issue of hatchery salmon spawning in the natal river basin rather than returning to their hatchery of origin is a known concern, but one that has rarely been examined in the context of straying from the hatchery. To differentiate this fine-scale version of straying by hatchery fish from the usual definition of straying among river basins, we refer to this phenomenon as "within-river straying". Specifically, we define within-river strays as hatchery salmon that return to their natal river but spawn on the natural spawning grounds rather than return to their hatchery of origin within that basin. This definition reflects the management goals of production hatcheries — whose aim is to produce salmon for fisheries while simultaneously attempting to minimize impacts on wild populations — as opposed to those of conservation programs, which intend to supplement wild populations.

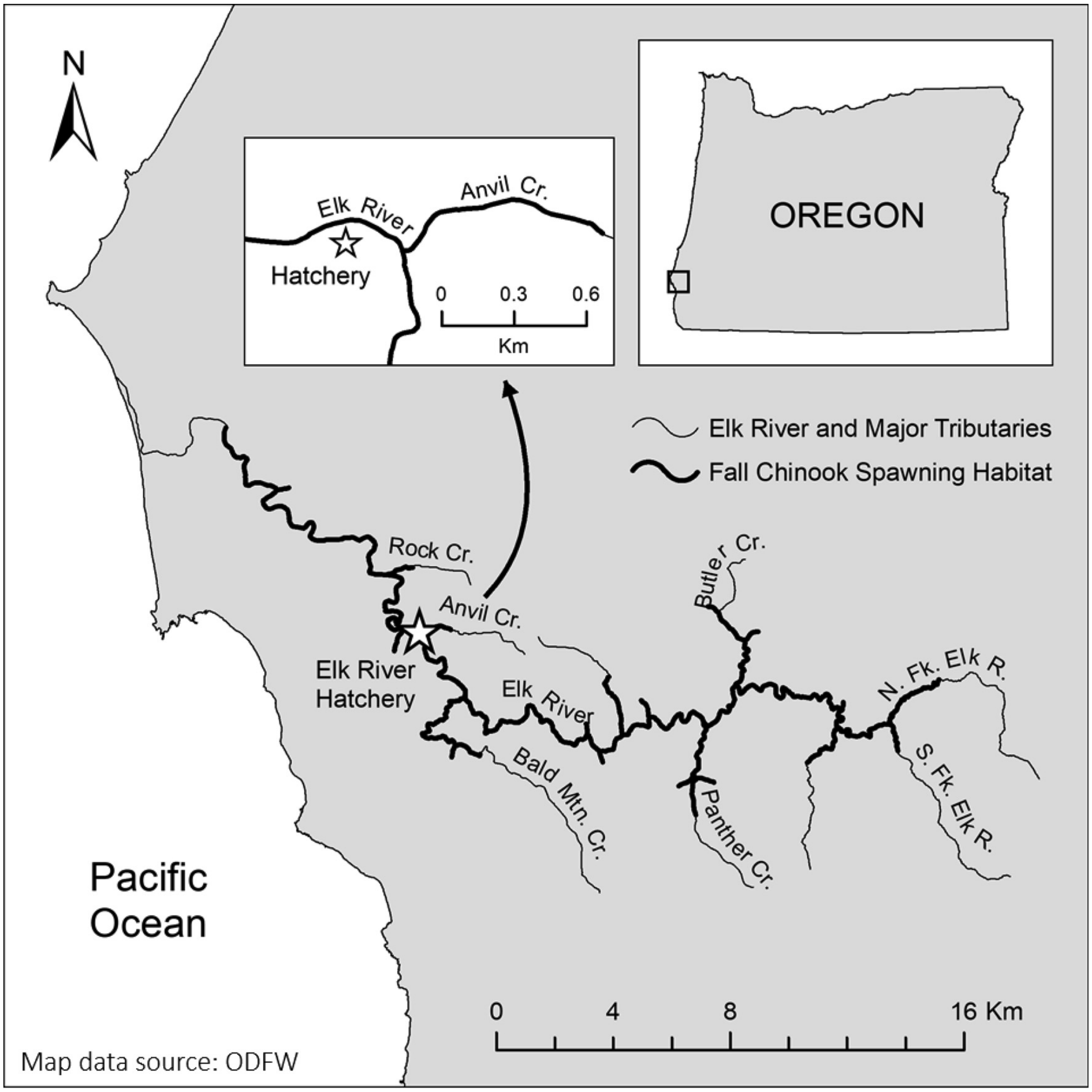
While factors that contribute to out-of-basin straying have been extensively studied (Keefer and Caudill 2014), the mechanisms underlying within-river straying by hatchery salmon are less clear. Several studies have found that spawning habitat and sex of the individual can influence adult movements within the natal river basin (Neville et al. 2006; Anderson and Quinn 2007; Peterson et al. 2016; Marklevitz and Morbey 2017). In the majority of studies, male salmon exhibited greater movement and exploratory behavior (Neville et al. 2006; Anderson and Quinn 2007; Marklevitz and Morbey 2017), although a difference between sexes is not always observed (Øklamd et al. 2001; Peterson et al. 2016). Spawning habitat can also influence sex-biased movements. For instance, Neville et al. (2006) found that female Chinook salmon genotypes had stronger spatial autocorrelation in patchier spawning habitats. Available spawning habitat or wild conspecifics in nearby locations can contribute to salmon failing to spawn at their natal site (Quinn 1993; Dittman et al. 2010; Bett et al. 2017; Hughes and Murdoch 2017). In addition, hatchery fish tend to choose similar spawning sites as wild or naturalized individuals (Dittman et al. 2010; Marklevitz and Morbey 2017). Neville et al. (2006) suggested that little is known about the transition between fine-scale homing and reproductive decisions such as spawning site selection. However, hatchery populations may be useful in studying this transition point, as characteristics of within-river strays can be compared to those of hatchery adults that return to their hatchery.

Within-river straying may also be influenced by the imprinting process. During the freshwater phase of their spawning migrations, adult salmon rely on olfactory cues associated with their natal site that they imprinted upon as juveniles (Hasler and Scholz 1983; Dittman and Quinn 1996). Hasler and Scholz (1983) hypothesized that each river, tributary, and perhaps even reach within a river has a unique chemical odor that provides an olfactory signature that salmon can use to identify their natal site. According to sequential imprinting theory, juvenile salmon imprint at multiple points during their seaward migration (Harden Jones 1968; Brannon 1982). Juveniles learn olfactory waypoints at several different locations and times, and then identify these odors in reverse order when they return to spawn as adults. Imprinting to specific odors associated with the natal site enables the fine-scale homing abilities displayed by adult salmon, including the ability of hatchery fish to locate their hatchery of origin. However, this fine-scale homing ability may be limited in a hatchery setting if juveniles do not have a unique water source on which to imprint.

The use of mainstem river water during rearing may lead to imprecise homing by returning hatchery salmon. Although the presence of conspecifics and food odors at the hatchery would likely alter the water chemistry, preliminary studies suggest that the chemical signatures of odor cues may not be dramatically altered simply by passage through a hatchery (Lemanski 2015). The lack of a distinct chemical signature at such a hatchery may limit the olfactory imprinting and homing process, whereby fine-scale homing becomes challenging and can be overridden by other environmental or social cues. In this scenario, within-river straying would result from the impaired imprinting process and absence of a unique chemical cue associated with the hatchery rather than a fish's impaired ability to detect olfactory cues. If the hatchery lacks a unique odor signature that distinguishes it from mainstem river water, then returning hatchery adults may be limited in their fine-scale homing abilities and need to increase searching behaviors to locate the natal hatchery. This may, in combination with available spawning resources, accelerate the transition from homing to reproductive decisions and contribute to an increased likelihood of spawning in the river.

To investigate the transition between fine-scale homing and reproductive decisions in hatchery salmon, we explored demographic factors that may contribute to within-river straying of hatchery-origin fall Chinook salmon (*Oncorhynchus tshawytscha*). We examined recovery location and biometric data for adult Chinook salmon that were produced, tagged, and released as juveniles from the Oregon Department of Fish and Wildlife (ODFW) Elk River Hatchery, Oregon, USA. As a harvest program, the Elk River Hatchery's goal is to produce salmon for the commercial and recreational fisheries while minimizing impacts to the wild population (ODFW 2016). Juvenile Chinook salmon are released directly from the hatchery in early fall. However, the Elk River Hatchery's rearing water is sourced from the mainstem Elk River surface water after fish are ponded (ODFW 2016), which may contribute to within-river straying. To address the issue of within-river straying in the Elk River, the ODFW implemented several actions beginning in 2015, including altering the hatchery fish ladder, physically removing hatchery fish from tributaries, and reducing the number of hatchery juveniles released. In addition, beginning in 1994, the hatchery retained some juveniles throughout the adult run to act as a conspecific attractant to the Elk River Hatchery. Hatchery personnel also began operating the trap during set timeframes starting in 2012 to ensure it was consistently operational throughout the entire run.

Fig. 1. Map indicating the location of the Oregon Department of Fish and Wildlife (ODFW) Elk River Fish Hatchery (star) and spawning habitat within the Elk River, Oregon, USA. Spawning habitat data were provided by ODFW.



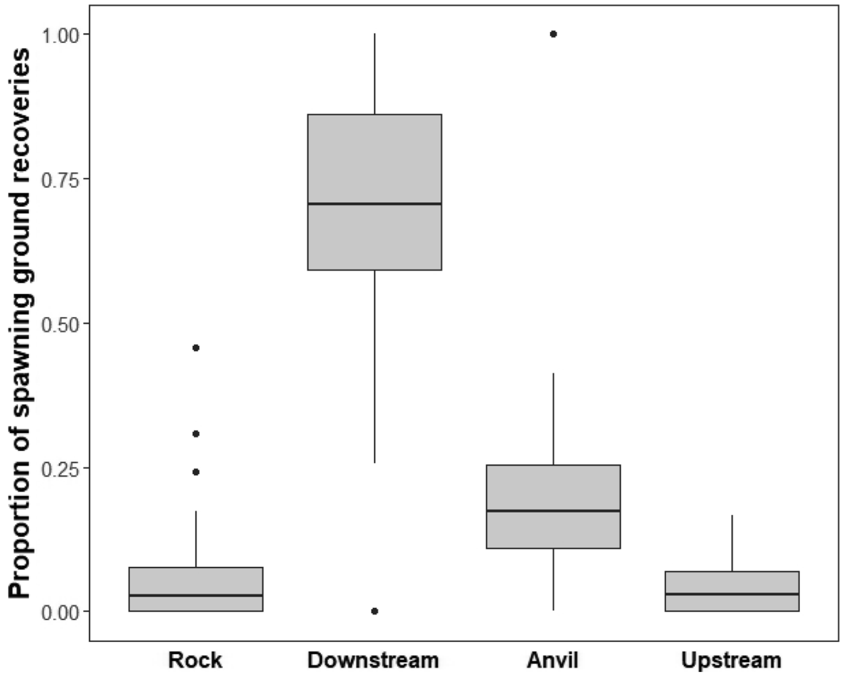
We analyzed a coded-wire tag (CWT) data set that spans a period of 34 years. This large data set allowed us to evaluate patterns of homing and straying within the Elk River basin over time and examine relationships between recovery location and individual characteristics of hatchery adults. We hypothesized that the sex of hatchery Chinook salmon would influence within-river straying in the Elk River Basin. Owing to fine-scale movement differences between the sexes, female and male hatchery fish will have different likelihoods of recovery on the spawning grounds within the Elk River Basin compared with recovery at the Elk River Hatchery. Males show increased exploratory movement behaviors, so they may be more likely to encounter and enter the Elk River Hatchery trap. Alternatively, their increased movement may lead to males exploring other tributaries within the basin and result in greater recoveries on the spawning grounds. Since female and male fall Chinook salmon can return at different ages and sizes, we included age and fork length in our analysis to account for these variables. Size of adult salmon can influence the probability of recovery (Zhou 2002; Murdoch et al. 2010) and also play a role in competition for spawning resources (van den Berghe and Gross 1989; Foote 1990; Fleming and Gross 1994). In addition, Healey and Prince (1998) found support for differences in male coho salmon movements based on body size, but Rich et al. (2006) found little support for these differences in male sockeye salmon. However, the influence of body size on Chinook salmon within-river straying is unknown. Here, we use the Elk River Basin as a case study for examining within-river straying and its potential mechanisms.

Methods

Location, hatchery practices, and data collection

The Elk River Hatchery is located at river kilometre 22.5 on the Elk River in Oregon, USA (42.7387°N, 124.4032°W), and adult collection occurs at the hatchery's on-site return ladder (Fig. 1). Brood stock for this integrated hatchery program are taken primarily from hatchery adults, but wild adults that volitionally enter the hatchery return ladder are also incorporated as brood stock (ODFW 2016). Fish are incubated in well water as embryos, ponded and reared as juveniles in water pumped from the Elk River, and released directly into the river as subyearlings. Adult fall Chinook salmon enter the Elk River beginning in October, and spawning occurs from November to February (Burck and Reimers 1978). The Elk River Hatchery stock contains fish from 2 to 7 years of age,

Fig. 2. Box and whisker plots depicting the annual proportions of coded-wire tags recovered from hatchery Chinook salmon carcasses on spawning grounds within the Elk River. Proportions were calculated as the number of salmon recovered on the spawning grounds for a given location and run year divided by the total number of spawning ground recoveries for the run year. Data set encompasses run years 1983–2016. The box represents the interquartile range, and the horizontal line represents the median for each recovery location. Lines or "whiskers" extending from each box represent the data within 1.5 times the interquartile range. Values outside this range are outliers indicated by solid points. "Rock" is recoveries in Rock Creek, "Downstream" is recoveries in the mainstem Elk River downstream of the Elk River Hatchery, "Anvil" is recoveries in Anvil Creek, and "Upstream" refers to recoveries upstream of the Elk River Hatchery, both in the mainstem Elk River and its tributaries.



although the majority of hatchery adults return between 2 and 4 years of age (Nicholas and Hankin 1989; Hankin et al. 1993). The majority of natural-origin fish spawn in the mainstem Elk River, downstream of the hatchery, and in the Anvil or Rock Creek tributaries (Fig. 1). Hatchery-origin Chinook salmon that do not return to the hatchery typically spawn in these same locations of the Elk River basin (Fig. 2), often among natural-origin individuals (S. Richardson, ODFW, Corvallis, Oregon, personal communication, 2017). From 2000 to 2015, the mean percentage of hatchery-origin Chinook salmon found on the spawning grounds (pHOS) was 51.3% based on carcass recoveries (ODFW 2016).

Many hatchery rearing practices can influence straying behavior, such as using brood stock not native to the watershed, transporting juveniles before release, or releasing juveniles at different times, resulting in interannual variation of release dates (Pascual et al. 1995; Candy and Beacham 2000). For our analysis, we first examined rearing practices at Elk River Hatchery to determine whether any of these activities might confound our analyses of in-river straying. The original brood stock for the Elk River fall Chinook hatchery program were collected by dip netting wild adults from the Anvil and Rock Creek tributaries of the Elk River during the 1969–1970 run year (Reimers and Bender 1979), ensuring that the Elk River Hatchery stock was native to the basin. Fall Chinook salmon for this program were reared exclusively at the Elk River Hatchery and, except as noted below, were released directly from the hatchery. In 2007, an experimental group of juvenile fish marked with a unique CWT code were transported downstream prior to release. However, these fish were excluded from our analysis, since transporting juvenile fish can increase the likelihood of subsequent adult straying (Solazzi et al. 1991). Finally, juveniles were consistently released in the autumn to coincide with the first freshet, after rearing for ~8–10 months at the hatchery. While autumn release might affect imprinting success (Unwin and Quinn 1993; Pascual et al. 1995), interannual variability was assumed to not be a confounding factor for the analysis, as fish were consistently released at similar times in early fall.

Commencing with the release of fall Chinook juveniles from the Elk River Hatchery in 1978, a portion of the production each year was implanted with a CWT (Northwest Marine Technology, Inc., Shaw Island, Washington, USA). Adult Chinook salmon returning to the Elk River were scanned for CWTs at the hatchery during artificial spawning events and on the spawning grounds from carcasses. Spawning ground surveys were conducted annually by ODFW personnel during the late fall and winter, coinciding with the run timing for this stock. Surveys covered 38.7 km of salmon spawning habitat in the Elk River basin and were conducted regularly throughout the season with fairly consistent effort among years, but with some influence from weather conditions (S. Richardson, ODFW, Corvallis, Oregon, personal communication, 2017). Survey protocols prioritized stream reaches and emphasized areas that typically had a greater abundance of spawning adults. Sites with the highest percentage of spawners, representing the majority of suitable spawning habitat, were surveyed every 7–10 days when weather conditions permitted. In general, reaches with moderate abundance were surveyed every 2–3 weeks, while reaches with few fish were surveyed twice per season. Surveyors recorded the survey reach in which a carcass was found.

Coded-wire tag records

For this study, we obtained CWT data from the Regional Mark Information System (RMIS) database, maintained by the Regional Mark Processing Center of the Pacific States Marine Fisheries Commission (http://www.rmpc.org). These data include the tag code, sex, fork length (mm), brood year, run year, and geographic recovery location for each recovered adult fish. Age for each fish was calculated by subtracting the brood year from the run year. We downloaded CWT records for the Elk River fall Chinook stock reared and released at the ODFW Elk River Hatchery and recovered as adults within the Elk River basin. For our analysis, we only examined the records of adults that were recovered at the hatchery or on the natural spawning grounds within the Elk River basin, since these records reflect individuals that likely had an opportunity to spawn. We excluded salmon harvested in fisheries, as the final destinations of these fish were unknown. The recovery of carcasses on spawning grounds is consistent with permanent straying, as defined by Keefer and Caudill (2014), rather than temporary straying or exploratory behavior. In total, we examined records from 34 run years, spanning 1983–2016 (see online Supplementary material, Table S2[1]). When analyzing biometric data, we excluded records that had missing information for the sex or length of the fish. In addition, we removed 10 records of individuals that were older than 2 years of age but were listed with a fork length < 280 mm, since these fish were anomalously small for their age and the lengths were assumed to be data entry errors. This filtering resulted in 29 941 records suitable for analysis.

Data analysis

We did not use expansion factors available in the RMIS database, but instead analyzed records of individual hatchery fish recovered in the Elk River basin. Expansion factors are estimates provided from the RMIS database to account for sampling effort, calculated by dividing the total sample by the number of fish examined for CWTs (Nandor et al. 2010). We used the raw records rather than the expansion factors, since we were interested in the biological characteristics of individual hatchery fish. This allowed us to investigate recovery patterns that might be explained by sex, age, or size of the individual salmon. We classified fish either as recovered at the Elk River Hatchery or as within-river strays recovered on the spawning grounds in the Elk River.

We examined recovery reach in relation to the Elk River Hatchery by grouping survey reaches into four categories: mainstem Elk River downstream of the hatchery, Rock Creek, Anvil Creek, and upstream of the Elk River Hatchery, including both the mainstem Elk River and its tributaries (Fig. 2). Although Rock Creek is downstream of the Elk River Hatchery (Fig. 1), because it is a tributary, hatchery adults would need to make a choice to enter Rock Creek. Anvil Creek also represents a special case, since it is located across the mainstem Elk River from the hatchery (Fig. 1). All surveys upstream of the Elk River Hatchery were grouped together because hatchery salmon recovered in these locations completely bypassed the hatchery ladder and overshot their natal site. We calculated the annual proportions for each of these four categories as the number of salmon recovered on the spawning grounds for a given category and run year divided by the total number of spawning ground recoveries for the run year (Fig. 2). This allowed us to determine which locations have the highest proportion of within-river strays in relation to the Elk River Hatchery throughout the 34 run years in the CWT data set.

To examine within-river straying from the Elk River Hatchery over time, we calculated recovery rates on the spawning grounds by run year and sex. Recovery rates on the spawning grounds were calculated as the number of hatchery adults for a given sex and run year that were recovered on spawning grounds in the Elk River basin, divided by the total number of hatchery adults of the given sex recovered in the Elk River basin, both on the spawning grounds and at the hatchery. Recovery rates on the spawning grounds were the minimum stray rate for hatchery Chinook salmon, as not all fish that spawned in the wild were recovered during surveys. We used these calculations of recovery on the spawning grounds to examine potential variation in sex-biased within-river straying over time. To evaluate a difference in recovery location by sex, a one-sample Student's t test was performed on the difference between male and female recovery rates by run year. All analyses were conducted using the statistical software R, version 3.4.2 (R Core Team 2017).

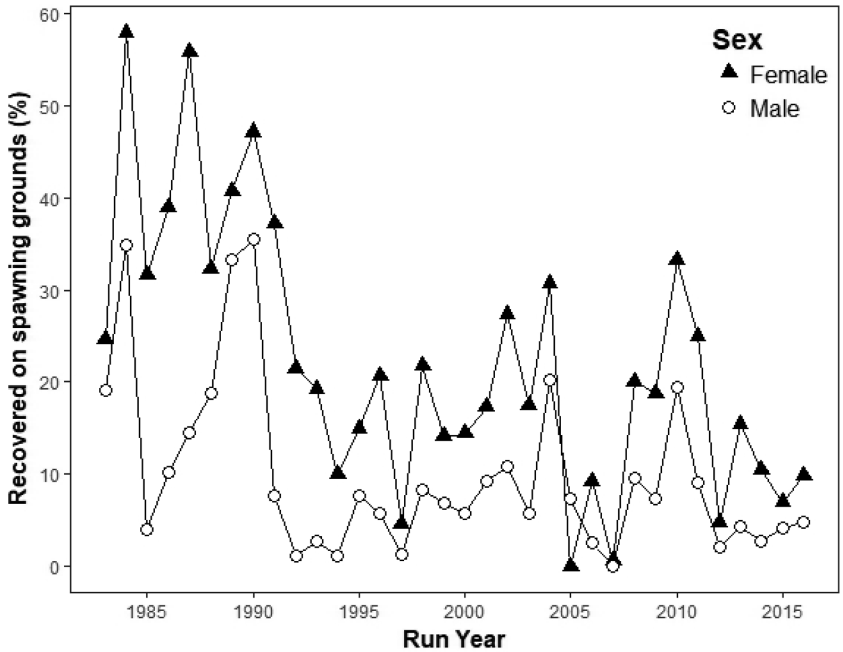
The standard method for evaluating a binary response such as straying based on multiple predictor variables is to perform a logistic regression. However, an examination of the residuals suggested that logistic regression and random effects logistic regression models provided a poor fit for the Elk River data set. Consequently, we used nonparametric methods of analysis to evaluate the relationships between sex, fork length, age, and recovery location of hatchery fall Chinook salmon within the Elk River basin. We performed a conditional random forest permutation and constructed a conditional inference tree using the partykit package (Hothorn and Zeileis 2015) for R. A benefit of using the conditional random forest is the ability to evaluate the relative importance of highly correlated predictors. The variables sex, age, and length can be highly correlated in salmon, because a fish's length generally increases with age and male salmon may be larger at maturity than females for a given age (Quinn 2005). For instance, in the Elk River Hatchery data set, males typically mature at a younger age than females (Supplementary Table S1[1]). As a result, males returning to the Elk River were overall more likely to be smaller than females (Supplementary Fig. S1[1]), although they are slightly larger at maturity for most age classes (Supplementary Fig. S2[1]).

To evaluate these correlated variables, we first performed a conditional random forest permutation on the data set using the cforest function (Hothorn and Zeileis 2015). We used fork length, sex, and age as input variables for predicting the recovery location of an individual salmon. The conditional random forest operates by creating multiple conditional inference trees from samples of the data set. We generated 1000 trees and used the default for the number of variables randomly sampled, which is the suggested square root of the number of input variables (Strobl et al. 2009). As recommended by Strobl et al. (2009), we performed several random forest runs using different seeds to verify that the results were stable and robust. Conditional variable importance was assessed by the varimp function, which uses a conditional permutation-importance measure capable of evaluating correlated predictors (Strobl et al. 2008). The ordered ranking of the variables determines their relative importance from the random forest (Strobl et al. 2009).

Since irrelevant variables in the conditional variable importance can randomly vary near zero (Strobl et al. 2009), we selected the two variables with the greatest importance scores to construct a conditional inference tree using the ctree function (Hothorn et al. 2006). The predictor variables under consideration were age, fork length, and sex. This allowed us to further examine the relationships between the highest-ranking input variables and the recovery location of individual hatchery salmon. The ctree function uses a permutation-based significance test to select the optimal predictor variable and point for splitting the data, represented by internal nodes. The data are split into groups with the goal of creating final groups, or terminal nodes, that contain statistically significant differences in the response variable given the predictors. The minimum statistical level for applying a stepwise split was set at 0.99, which is analogous to $p \leq 0.01$, the value required for a split to be performed. A Bonferroni correction was applied to account for several statistical tests performed simultaneously on the dataset. This resulted in a classification tree describing relationships between the variables along with a set of

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2018-0384.

Fig. 3. Hatchery fall Chinook salmon recovery within the Elk River basin, by sex, for fish containing a coded-wire tag. Recovery rates were calculated as the number of adults recovered on spawning grounds in the Elk River basin divided by the total number of adults recovered in the Elk River basin, both on the spawning grounds and at the Elk River Hatchery.



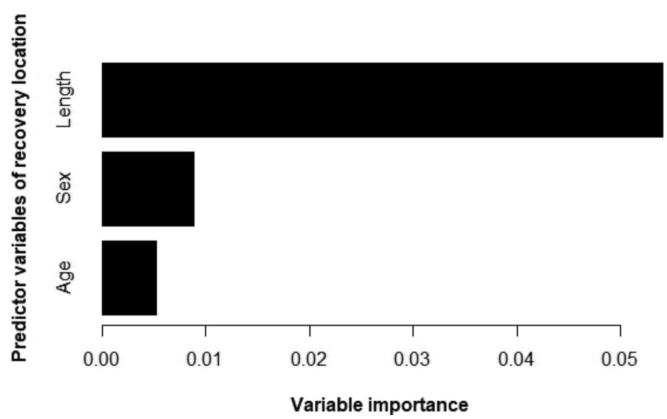
rules for splitting the data into groups with different likelihoods of recovery by location.

Results

Of the 29 941 CWT Chinook salmon records analyzed, 17 598 were male, predominantly age 2 (25.3%), age 3 (36.9%), and age 4 (30.3%), and 12 343 were female, predominantly age 3 (14.3%), age 4 (63.2%), and age 5 (20.6%) (Supplementary Table S1[1]). The majority of fish (26 413, 88.2%) were recovered at the Elk River Hatchery trap, and 3528 (11.8%) were recovered on the spawning grounds in the Elk River basin. The majority of within-river strays were recovered on the spawning grounds in the mainstem Elk River, downstream of the Elk River Hatchery (Fig. 2). In general, a larger proportion of females from each run year was found on the spawning grounds than males for the same year (Fig. 3). Although the proportion of each sex recovered on the spawning grounds appears to have decreased since the 1980s, the pattern of females having greater recovery proportions on the spawning grounds remains apparent. This pattern was consistent in 33 of the 34 run years analyzed, with a significant difference between the recovery rates for males and females on the spawning grounds (Student one-sample t test, $p < 0.01$). On average, the proportion of females recovered on the spawning grounds was 0.12 greater than the proportion of males for the same run year (95% confidence interval: 0.09–0.15).

The age and fork length of adult Chinook salmon were strongly correlated, making it difficult to separate effects from these two variables. The Pearson correlation for age and fork length was 0.85 in our data set, a positive correlation indicating that smaller fish were predominantly younger individuals and larger salmon were generally older. In addition, males tended to mature at a younger age than females, meaning they were smaller on average. However, by using conditional random forests, we were able to evaluate variable importance for different types of predictors without the misleading preference for correlated predictors (Strobl et al. 2008). Conditional variable importance revealed that the most relevant variable for predicting recovery location was the fork length of the fish, followed by sex and then age (Fig. 4). Since

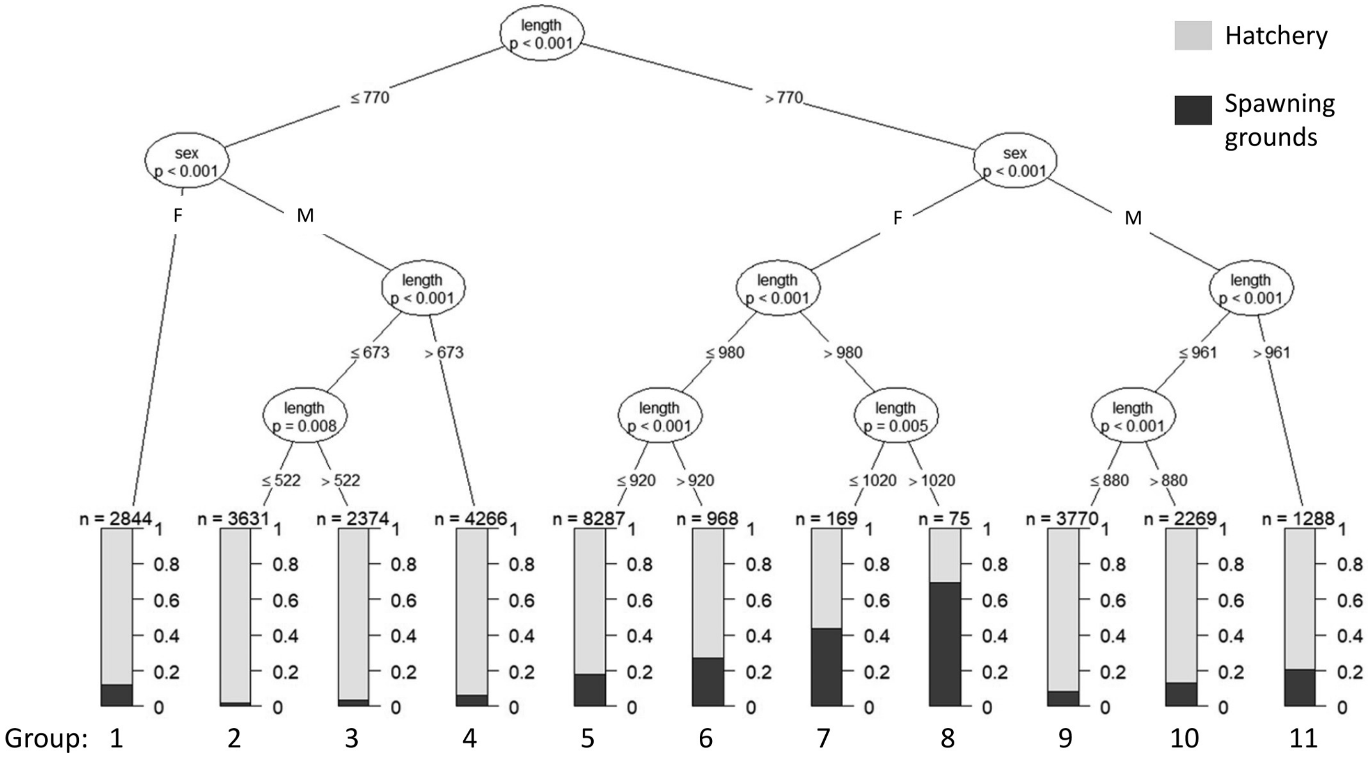
Fig. 4. Random forest predictor variables ranked by conditional variable importance score. The ordered ranking of the variables, rather than the absolute value of the importance score, determines importance (Strobl et al. 2009).



irrelevant variables randomly vary near zero and the order of the variables describes their relative importance (Strobl et al. 2009), age is unlikely to be an informative predictor of recovery location when accounting for length.

Since fork length and sex were the two top-ranked variables identified by conditional variable importance, we used both variables as inputs in the conditional inference tree. This analysis allowed us to determine whether the differences we observed in recovery rates between males and females (Fig. 3) were primarily due to size, as has been documented in previous studies (Zhou 2002; Murdoch et al. 2010). The resulting classification tree produced 10 node splits, with both sex and size identified as significant variables ($p < 0.01$) for predicting the recovery location of adult hatchery Chinook salmon (Fig. 5). This generated 11 terminal nodes, or final groups, characterized by different sex and size criteria with significantly different proportions of Chinook salmon that were recovered on the spawning grounds. The pro-

Fig. 5. Conditional inference tree depicting recovery location of adult hatchery fall Chinook salmon in the Elk River basin. Terminal nodes show proportions of adults with a coded-wire tag that fall into the group, which is defined by the set of rules for splitting at each internal node. The characteristic used and level of significance for each split is shown in the internal nodes. Length is fork length (in mm).



portion of recovered within-river strays varied from a high of 0.693 for very large females (group 8) to a low of 0.021 for small males (group 2). Overall, these results indicate that a greater percentage of females and larger fish of both sexes were recovered on the spawning grounds when compared with males or smaller fish (Fig. 5).

In particular, fish size was a primary factor contributing to recovery location. The best predictor from the root node split in the classification tree analysis was a 770 mm size threshold and, within a specific sex, fork length continued to drive branch separation (Fig. 5). This was especially apparent for female branches of the classification tree (groups 1, 5–8): spawning ground recovery proportions increased dramatically with increasing size over the five groups, from a low of 0.119 for the smallest females (group 1) to 0.693 for the largest females (group 8). Similarly, spawning ground recovery proportions increased for males over the six increasing size groups in the classification tree (groups 2–4, 9–11), with the largest males (group 11) straying at a rate of 0.205. This corresponds with the conditional random forest ranking fork length as the most relevant variable for predicting recovery location of the fish (Fig. 4).

Overall, females had a higher probability of recovery on the spawning grounds compared with males of similar size groups, suggesting that sex was also a major factor influencing recovery location (Fig. 5). This is consistent with the observed pattern by run year demonstrating that females were consistently recovered in higher proportions on the spawning grounds compared with males (Fig. 3). While length criteria used for splitting in the classification tree were not identical for both sexes, recovery proportions on the spawning grounds for fish of approximately equal size were significantly higher for females than for males. For example, recovered females >980 mm (groups 7 and 8) had a stray proportion of 0.516, while recovered males of a similar size (>961 mm, group 11) had a stray proportion of 0.205 (Fig. 5). A proportion > 0.5 indicates that an individual in the specified group is more likely to be recovered on the spawning grounds rather than at the hatchery, since recovery location has only two possible states. In the classification tree, the proportion of large females (group 8) found on the spawning grounds exceeded 0.5. These results suggest that large female Chinook salmon may be choosing to remain in the Elk River rather than enter the hatchery. In contrast, large males of a similar size tended to be recovered at the hatchery rather than on the Elk River spawning grounds.

Discussion

Our analyses of the CWT data set suggest that Elk River Hatchery Chinook salmon recovered on the Elk River spawning grounds differed from those recovered at the hatchery. In particular, females and larger fish were more likely to be recovered on the spawning grounds, suggesting that biological factors contribute to within-river straying. Our initial hypothesis for a difference between within-river straying based on sex of the individual was supported. However, sex does not appear to be the most important variable driving recovery location in the Elk River basin, as fork length was the top-ranked variable (Fig. 4). Since age was the lowest-ranking variable of importance and had a value near zero (Fig. 4), it is unlikely to be a highly relevant predictor when length and sex are already considered as predictors of recovery location. Given that fork length and age were highly correlated, the ranking of fork length as the most important predictor and age as the least suggests that the pattern of larger fish having greater probability of recovery on spawning grounds is not an artifact of age.

Although little is known about how levels of within-river straying observed in the Elk River compare with other systems, a number of factors may contribute to the high rates of hatchery Chinook straying from the Elk River Hatchery. Management practices for returning adults have changed over the past several decades, which likely influenced the interannual variation of within-river straying levels (Fig. 3). One example, which was implemented during several years in the 1980s, is the practice of "recycling" returning hatchery adults from the Elk River Hatchery back into the river prior to the spawning period. The apparent decline in spawning ground recoveries over time (Fig. 3) may be attributed in part to the discontinuation of this practice. However, current pHOS levels remain high (ODFW 2016).

Based on the biological characteristics of fish recovered on the spawning grounds, within-river straying in the Elk River basin is consistent with the combined effects from inadequate imprinting and the availability of spawning resources downstream of the hatchery. This results in a decision process whereby spawning site selection overrides site-specific homing, leading hatchery salmon to spawn in the river. Despite variable environmental conditions and interannual variation, our analyses demonstrated that female hatchery Chinook salmon were consistently found in greater proportions on the Elk River basin spawning grounds (Fig. 3). Since the majority of optimal spawning habitat and the highest density of wild spawners is located below the Elk River Hatchery (Burck and Reimers 1978), mature hatchery fish encounter abundant spawning habitat and potential mates (Fig. 2) before reaching the hatchery facility. Bett and Hinch (2015) suggested that salmon homing involves a hierarchical process wherein homing adults first seek imprinted olfactory cues associated with their natal site (i.e., Elk River Hatchery). In the absence of recognized cues, they secondarily seek conspecifics and appropriate spawning habitat. Owing to the lack of a unique water source, water in the Elk River Hatchery ladder may not be distinctly different from mainstem Elk River water. Under this scenario, returning hatchery salmon may not be able to home directly to the Elk River Hatchery. Consequently, hatchery adults must search more extensively to locate their natal site, which increases the tendency of hatchery fish choosing to spawn in the river. This is a likely possibility given that the majority of within-river strays are recovered in the mainstem Elk River, downstream of the hatchery (Fig. 2). Thus, the combination of extensive searching to locate the natal site and the biological characteristics of the returning adults may lead to the differences we observed between sexes and sizes of within-river strays.

The random forest analysis suggests that fork length is the most important variable for predicting recovery location of hatchery Chinook salmon in the Elk River basin, followed by sex of the fish (Fig. 4). Passage at the Elk River Hatchery ladder does not exclude large salmon, as several fish >1020 mm were recovered at the hatchery. While it is possible that the return ladder may have some size selectivity, this demonstrates that very large fish are capable of ascending the ladder and entering the hatchery trap if they choose. In the classification tree, large females (Fig. 5; group 8) were more likely to be recovered on the spawning grounds than at the Elk River Hatchery. Given that not all naturally spawning salmon are recovered during surveys, this finding indicates that large females may be choosing to spawn in the river, as their true proportion of within-river straying could be even greater than that inferred from recoveries. This pattern differs from studies of between-basin straying, wherein males tended to stray more (Hard and Heard 1999; Hamann and Kennedy 2012) or no differences in stray rates between sexes were observed (Unwin and Quinn 1993; Thedinga et al. 2000). However, our results are consistent with those of other studies demonstrating that males display greater exploratory behavior within the natal basin (Neville et al. 2006; Anderson and Quinn 2007; Marklevitz and Morbey 2017). Within the natal river basin, hatchery males may explore more widely than hatchery females, resulting in males being more likely to discover and return to the Elk River Hatchery. This is a hypothesis that can be tested with a telemetry study, to determine whether behavioral differences based on sex could drive the likelihood of returning to the hatchery.

Large hatchery salmon may be more likely to be recovered on the spawning grounds, since larger fish are generally more capable of defending spawning resources (Foote 1990). Larger females may spawn in the river because they are better able to defend spawning sites (van den Berghe and Gross 1989), whereas smaller females may lose these resource competitions and instead continue travelling upstream and ultimately enter the hatchery. Similarly, larger males may be more successful at competing for access to females on the spawning grounds (Fleming and Gross 1994). Migration timing could also differentially influence within-river straying behavior. For example, jacks (i.e., smaller males) enter the Elk River earlier in the season than females or older, larger males (Burck and Reimers 1978). Therefore, small males may have a greater tendency to move past the unoccupied spawning grounds and enter the hatchery as they search for the natal site and potential mates. The lack of a unique odor at the Elk River Hatchery may amplify these differences between sexes and sizes of fish by necessitating an increase in searching behavior to locate the hatchery.

Our analysis relied on the recovery of carcasses on spawning grounds as an indicator of within-river straying. This assumed that fish of different sexes and lengths had an equal probability of being recovered during annual spawning ground surveys. However, it is unlikely that this assumption is valid for smaller adults, as several studies have demonstrated that recovery probability during such surveys is strongly linked to fish size (Zhou 2002; Murdoch et al. 2010). Recovery of smaller fish may be less likely because they are harder to find during surveys (Zhou 2002). In addition, stream flows or scavengers could remove salmon carcasses from streams, which may lead to biases during surveys (Cederholm et al. 1989; Reimchen 2000; Zhou 2002). However, it is unclear whether smaller fish are affected disproportionately by streamflow (Zhou 2002). Nonetheless, fish with a fork length > 770 mm (Fig. 5; groups 5–11) had a relatively similar likelihood of recovery (Zhou 2002), and the general pattern of larger fish and females being more likely to stray was extremely robust for these groups as well. In addition, studies in similar systems found no significant difference between male and female recovery rates of fall Chinook salmon, after accounting for length (Zhou 2002). However, to address the uncertainty regarding carcass recovery, we recommend that a telemetry study be conducted on hatchery Chinook salmon returning to the Elk River to determine the effect of size and sex on recovery probability. Such a study would aid in evaluating the movements and final locations of adults. It could answer the question of whether smaller individuals are more likely to return to the Elk River Hatchery or remain on the spawning grounds and therefore simply not be recovered during surveys.

Identifying effective methods to reduce in-river stray rates can be a challenge in locations where pHOS exceeds management goals. Effective management actions might include altering the hatchery fish ladder, physically removing hatchery fish from the river, retaining a few juvenile smolts as a conspecific attractant, or reducing the number of hatchery juveniles released. In the Elk River, all these approaches have been employed in an effort to reduce the level of within-river straying. In 2015, the ODFW began to remove returning hatchery adults from the spawning grounds on Anvil and Rock Creeks through the use of weirs. During August 2015, the Elk River Hatchery altered the adult ladder opening to increase attraction flow at the trap. Although hatchery personnel typically operated the ladder for at least 2–3 months during the run, in 2012 the ODFW set trap operation dates from the beginning of November to the end of February in an effort to collect more hatchery salmon. Starting in 1994, the Elk River Hatchery retained a small subset of the brood as juvenile smolts. These juveniles were kept in a raceway at the hatchery throughout the adult run as a potential attraction to the hatchery. Beginning in fall 2015, the ODFW also reduced the number of fish released from the Elk River Hatchery from 325 000 to 275 000 juveniles to decrease the number of hatchery salmon that spawn in the river. However, if the number of hatchery adults spawning in the Elk River remains high, the number of juveniles released from the Elk River Hatchery may need to be further reduced (ODFW 2016). However, this may lead to negative social and economic consequences for the fishery.

One method to reduce within-river straying may be to add a unique chemical odor to the Elk River Hatchery water during critical imprinting periods, allowing juveniles to imprint upon a scent associated only with the hatchery. This odor could then be metered into the Elk River Hatchery ladder during the adult run, providing a unique olfactory cue to enable fine-scale homing to the hatchery. Earlier tests of this approach produced mixed results (Rehnberg et al. 1985; Hassler and Kutchins 1990), but it was successful in increasing the return rate of coho salmon to a California hatchery (Hassler and Kucas 1988). Using this approach in the Elk River may provide a more robust signature for imprinting and homing that will reinforce natal site homing as the primary migratory driver and override social and environmental cues that may encourage within-river spawning.

Straying between river basins plays a fundamental role in salmon population dynamics and has been extensively studied to identify factors contributing to elevated rates of straying (Keefer and Caudill 2014). However, far less is known about the mechanistic causes of within-river straying, though it is a widespread phenomenon affecting most salmon-bearing streams that contain both hatchery and wild populations. The Elk River Hatchery program provides an extensive time series of CWT recoveries that serves as an ideal case study for within-river straying. In the Elk River Hatchery program, we identified fork length and sex as demographic factors influencing within-river straying, suggesting that a reproductive decision process contributed to a tendency for hatchery fish to spawn in the wild. We also discussed the possibility of adding a unique odor to the hatchery water as a method that may reduce within-river straying for locations where the hatchery lacks a distinct water source. Further study of within-river straying for other salmon species and hatchery programs is warranted to better assess and develop management strategies to address this issue.

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References

Anderson, J.H., and Quinn, T.P. 2007. Movements of adult coho salmon (*Oncorhynchus kisutch*) during colonization of newly accessible habitat. Can. J. Fish. Aquat. Sci. **64**(8): 1143–1154. doi:10.1139/f07-087.

Araki, H., Berejikian, B.A., Ford, M.J., and Blouin, M.S. 2008. Fitness of hatchery-reared salmonids in the wild. Evol. Appl. **1**(2): 342–355. doi:10.1111/j.1752-4571.2008.00026.x. PMID:25567636.

Bett, N.N., and Hinch, S.G. 2015. Attraction of migrating adult sockeye salmon to conspecifics in the absence of natal chemical cues. Behav. Ecol. **26**(4): 1180–1187. doi:10.1093/beheco/arv062.

Bett, N.N., Hinch, S.G., Burnett, N.J., Donaldson, M.R., and Naman, S.M. 2017. Causes and consequences of straying into small populations of Pacific salmon. Fisheries, **42**(4): 220–230. doi:10.1080/03632415.2017.1276356.

Brannon, E. 1982. Orientation mechanisms of homing salmonids. *In* Proceedings of the Salmon and Trout Migratory Behavior Symposium. pp. 219–227.

Burck, W.A., and Reimers, P.E. 1978. Temporal and spatial distribution of fall Chinook salmon spawning in Elk River. Information Report Series Fisheries Number 78-3, Research Section, Oregon Department of Fish and Wildlife, Charleston, Oregon.

Candy, J.R., and Beacham, T.D. 2000. Patterns of homing and straying in southern British Columbia coded-wire tagged Chinook salmon (*Oncorhynchus tshawytscha*) populations. Fish. Res. **47**(1): 41–56. doi:10.1016/S0165-7836(99)00124-1.

Cederholm, C., Houston, D., Cole, D., and Scarlett, W. 1989. Fate of coho salmon (*Oncorhynchus kisutch*) carcasses in spawning streams. Can. J. Fish. Aquat. Sci. **46**(8): 1347–1355. doi:10.1139/f89-173.

Chilcote, M.W., Goodson, K.W., and Falcy, M.R. 2011. Reduced recruitment performance in natural populations of anadromous salmonids associated with hatchery-reared fish. Can. J. Fish. Aquat. Sci. **68**(3): 511–522. doi:10.1139/F10-168.

Christie, M.R., Marine, M.L., French, R.A., Waples, R.S., and Blouin, M.S. 2012. Effective size of a wild salmonid population is greatly reduced by hatchery supplementation. Heredity, **109**(4): 254–260. doi:10.1038/hdy.2012.39.

Cram, J.M., Torgersen, C.E., Klett, R.S., Pess, G.R., May, D., Pearsons, T.N., and Dittman, A.H. 2013. Tradeoffs between homing and habitat quality for spawning site selection by hatchery-origin Chinook salmon. Environ. Biol. Fishes, **96**(1): 109–122. doi:10.1007/s10641-012-0026-1.

Dittman, A.H., and Quinn, T.P. 1996. Homing in Pacific salmon: mechanisms and ecological basis. J. Exp. Biol. **199**(1): 83–91. PMID:9317381.

Dittman, A.H., May, D., Larsen, D.A., Moser, M.L., Johnston, M., and Fast, D. 2010. Homing and spawning site selection by supplemented hatchery- and natural-origin Yakima River spring Chinook salmon. Trans. Am. Fish. Soc. **139**(4): 1014–1028. doi:10.1577/T09-159.1.

Flagg, T.A. 2015. Balancing conservation and harvest objectives: a review of considerations for the management of salmon hatcheries in the US Pacific Northwest. N. Am. J. Aquacult. **77**(3): 367–376. doi:10.1080/15222055.2015.1044058.

Fleming, I.A., and Gross, M.R. 1994. Breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*): measures of natural and sexual selection. Evolution, **48**(3): 637–657. doi:10.1111/j.1558-5646.1994.tb01350.x. PMID:28568247.

Foote, C.J. 1990. An experimental comparison of male and female spawning territoriality in a Pacific salmon. Behaviour, **115**(3): 283–314. doi:10.1163/156853990X00617.

Grant, W.S. 2012. Understanding the adaptive consequences of hatchery-wild interactions in Alaska salmon. Environ. Biol. Fishes, **94**(1): 325–342. doi:10.1007/s10641-011-9929-5.

Hamann, E.J., and Kennedy, B.P. 2012. Juvenile dispersal affects straying behaviors of adults in a migratory population. Ecology, **93**(4): 733–740. doi:10.1890/11-1009.1. PMID:22690624.

Hankin, D.G., Nicholas, J.W., and Downey, T.W. 1993. Evidence for inheritance of age of maturity in chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. **50**(2): 347–358. doi:10.1139/f93-040.

Hard, J.J., and Heard, W.R. 1999. Analysis of straying variation in Alaskan hatchery Chinook salmon (*Oncorhynchus tshawytscha*) following transplantation. Can. J. Fish. Aquat. Sci. **56**(4): 578–589. doi:10.1139/cjfas-56-4-578, 10.1139/f98-199.

Harden Jones, F.R. 1968. Fish migration. Edward Arnold Ltd., London.

Hasler, A.D., and Scholz, A.T. 1983. Olfactory imprinting and homing in salmon: Investigations into the mechanism of the imprinting process. Springer-Verlag, Berlin.

Hassler, T.J., and Kucas, S.T. 1988. Returns of morpholine-imprinted coho salmon to the Mad River, California. N. Am. J. Fish. Manage. **8**(3): 356–358. doi:10.1577/1548-8675(1988)008<0356:ROMICS>2.3.CO;2.

Hassler, T.J., and Kutchins, K. 1990. Homing by Chinook salmon exposed to morpholine. Calif. Fish Game, **76**(1): 31–35. Available from https://archive.org/details/californiafishga76_1cali/page/30 [accessed 7 November 2018].

Healey, M.C., and Prince, A. 1998. Alternative tactics in the breeding behaviour of male coho salmon. Behaviour, **135**(8): 1099–1124. doi:10.1163/156853998792913564.

Hendry, A.P., Castric, V., Kinnison, M.T., Quinn, T.P., Hendry, A., and Stearns, S. 2004. The evolution of philopatry and dispersal. *In* Evolution illuminated: salmon and their relatives. *Edited by* A.P. Hendry. Oxford University Press. pp. 52–91.

Hothorn, T., and Zeileis, A. 2015. partykit: a modular toolkit for recursive partytioning in R. J. Mach. Learn. Res. **16**: 3905–3909. Available from http://www.jmlr.org/papers/volume16/hothorn15a/hothorn15a.pdf [accessed 25 June 2018].

Hothorn, T., Hornik, K., and Zeileis, A. 2006. Unbiased recursive partitioning: a conditional inference framework. J. Comput. Graph. Stat. **15**(3): 651–674. doi:10.1198/106186006X133933.

Hughes, M.S., and Murdoch, A.R. 2017. Spawning habitat of hatchery spring Chinook Salmon and possible mechanisms contributing to lower reproductive success. Trans. Am. Fish. Soc. **146**(5): 1016–1027. doi:10.1080/00028487.2017.1336114.

Jonsson, B., and Jonsson, N. 2006. Cultured Atlantic salmon in nature: a review of their ecology and interaction with wild fish. ICES J. Mar. Sci. **63**(7): 1162–1181. doi:10.1016/j.icesjms.2006.03.004.

Kaitala, V. 1990. Evolutionary stable migration in salmon: a simulation study of homing and straying. Ann. Zool. Fenn. **27**(2): 131–138. Available from http://www.jstor.org/stable/23736030 [accessed 4 September 2018].

Keefer, M.L., and Caudill, C.C. 2014. Homing and straying by anadromous salmonids: a review of mechanisms and rates. Rev. Fish Biol. Fish. **24**(1): 333–368. doi:10.1007/s11160-013-9334-6.

Lemanski, J.R. 2015. Effects of current hatchery practices on salmon odor recognition and responses. M.Sc. thesis, Department of Fisheries and Wildlife Science, Oregon State University, Corvallis, Oregon, USA.

Marklevitz, S.A., and Morbey, Y.E. 2017. Habitat use and arrival timing of hatchery and naturalized Chinook salmon spawning in a Great Lakes tributary. Trans. Am. Fish. Soc. **146**(4): 567–583. doi:10.1080/00028487.2017.1300606.

McGinnity, P., Jennings, E., DeEyto, E., Allott, N., Samuelsson, P., Rogan, G., Whelan, K., and Cross, T. 2009. Impact of naturally spawning captive-bred Atlantic salmon on wild populations: depressed recruitment and increased risk of climate-mediated extinction. Proc. R. Soc. B: Biol. Sci. **276**(1673): 3601–3610. doi:10.1098/rspb.2009.0799.

Murdoch, A.R., Pearsons, T.N., and Maitland, T.W. 2010. Estimating the spawning escapement of hatchery- and natural-origin spring Chinook salmon using redd and carcass data. N. Am. J. Fish. Manage. **30**(2): 361–375. doi:10.1577/M09-071.1.

Nandor, G.F., Longwill, J.R., and Webb, D.L. 2010. Overview of the coded wire tag program in the greater Pacific region of North America. *In* PNAMP Special Publication: Tagging, Telemetry and Marking Measures for Monitoring Fish Populations — A compendium of new and recent science for use in informing technique and decision modalities. Pac. Northwest Aquat. Monit. Partnership Special Publ. **2**: 5–46.

Neville, H., Isaak, D., Dunham, J., Thurow, R., and Rieman, B. 2006. Fine-scale natal homing and localized movement as shaped by sex and spawning habitat in Chinook salmon: insights from spatial autocorrelation analysis of individual genotypes. Mol. Ecol. **15**(14): 4589–4602. doi:10.1111/j.1365-294X.2006.03082.x. PMID:17107485.

Nicholas, J.W., and Hankin, D.G. 1989. Chinook salmon populations in Oregon coastal river basins: description of life histories and assessment of recent trends in run strengths. Oregon State University, Ore., USA.

ODFW. 2016. Hatchery and genetic management plan for Elk River fall Chinook salmon program — updated 7 June 2016 [online]. Available from https://www.dfw.state.or.us/fish/HGMP/docs/2016/Elk%20River%20Fish%20Hatchery,%20Fall%20Chinook%20Salmon%20Program.pdf [accessed 4 October 2018].

Øklamd, F., Erkinaro, J., Moen, K., Niemelä, E., Fiske, P., McKinley, R., and Thorstad, E. 2001. Return migration of Atlantic salmon in the River Tana: phases of migratory behaviour. J. Fish Biol. **59**(4): 862–874. doi:10.1111/j.1095-8649.2001.tb00157.x.

Paquet, P., Flagg, T., Appleby, A., Barr, J., Blankenship, L., Campton, D., et al. 2011. Hatcheries, conservation, and sustainable fisheries — achieving multiple goals: results of the Hatchery Scientific Review Group's Columbia River basin review. Fisheries, **36**(11): 547–561. doi:10.1080/03632415.2011.626661.

Pascual, M.A., Quinn, T.P., and Fuss, H. 1995. Factors affecting the homing of fall Chinook salmon from Columbia River hatcheries. Trans. Am. Fish. Soc. **124**(3): 308–320. doi:10.1577/1548-8659(1995)124<0308:FATHOF>2.3.CO;2.

Peterson, D.A., Hilborn, R., and Hauser, L. 2016. Exploratory behavior of dispersers within a metapopulation of sockeye salmon. Behav. Ecol. **27**(1): 126–133. doi:10.1093/beheco/arv129.

Putman, N.F., Lohmann, K.J., Putman, E.M., Quinn, T.P., Klimley, A.P., and Noakes, D.L.G. 2013. Evidence for geomagnetic imprinting as a homing mechanism in Pacific salmon. Curr. Biol. **23**(4): 312–316. doi:10.1016/j.cub.2012.12.041. PMID:23394828.

Quinn, T.P. 1993. A review of homing and straying of wild and hatchery-produced salmon. Fish. Res. **18**(1–2): 29–44. doi:10.1016/0165-7836(93)90038-9.

Quinn, T.P. 1999. Revisiting the stock concept in Pacific salmon: Insights from Alaska and new Zealand. Northwest Sci. **73**(4): 312–324. Available from https://research.wsulibs.wsu.edu:8443/xmlui/bitstream/handle/2376/1144/v73%20p312%20Quinn.PDF [accessed 2 January 2019].

Quinn, T.P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle, Wash., U.S.A. pp. 378.

Quinn, T.P., and Dittman, A.H. 1992. Homing in Fishes. *In* Animal homing. *Edited by* F. Papi. Chapman Hall, London. pp. 145–211.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rand, P.S., Berejikian, B.A., Bidlack, A., Bottom, D., Gardner, J., Kaeriyama, M., et al. 2012. Ecological interactions between wild and hatchery salmonids and key recommendations for research and management actions in selected regions of the North Pacific. Environ. Biol. Fishes, **94**(1): 343–358. doi:10.1007/s10641-012-9988-2.

Rehnberg, B.G., Curtis, L., and Schreck, C.B. 1985. Homing of coho salmon (*Oncorhynchus kisutch*) exposed to morpholine. Aquaculture, **44**(3): 253–255. doi:10.1016/0044-8486(85)90250-9.

Reimchen, T. 2000. Some ecological and evolutionary aspects of bear–salmon interactions in coastal British Columbia. Can. J. Zool. **78**(3): 448–457. doi:10.1139/z99-232.

Reimers, P.E., and Bender, R.E. 1979. Survival and contribution of 1969-brood fall Chinook salmon from Elk River Hatchery. Information Report Series Fisheries Number 79-6, Research and Development Section, Oregon Department of Fish and Wildlife, Corvallis, Oregon.

Rich, H.B., Jr., Carlson, S.M., Chasco, B.E., Briggs, K.C., and Quinn, T.P. 2006. Movements of male sockeye salmon, *Oncorhynchus nerka*, on spawning grounds: effects of in-stream residency, density and body size. Anim. Behav. **71**(4): 971–981. doi:10.1016/j.anbehav.2005.10.004.

Solazzi, M.F., Nickelson, T.E., and Johnson, S.L. 1991. Survival, contribution, and return of hatchery coho salmon (*Oncorhynchus kisutch*) released into freshwater, estuarine, and marine environments. Can. J. Fish. Aquat. Sci. **48**(2): 248–253. doi:10.1139/f91-034.

Strobl, C., Boulesteix, A.L., Kneib, T., Augustin, T., and Zeileis, A. 2008. Conditional variable importance for random forests. BMC Bioinf. **9**(1): 11. doi:10.1186/1471-2105-9-307.

Strobl, C., Malley, J., and Tutz, G. 2009. An introduction to recursive partitioning: rationale, application, and characteristics of classification and regression trees, bagging, and random forests. Psychol. Methods, **14**(4): 323–348. doi:10.1037/a0016973. PMID:19968396.

Thedinga, J.F., Wertheimer, A.C., Heintz, R.A., Maselko, J.M., and Rice, S.D. 2000. Effects of stock, coded-wire tagging, and transplant on straying of pink salmon (*Oncorhynchus gorbuscha*) in southeastern Alaska. Can. J. Fish. Aquat. Sci. **57**(10): 2076–2085. doi:10.1139/f00-163.

Unwin, M.J., and Quinn, T.P. 1993. Homing and straying patterns of Chinook salmon (*Onchorhynchus tshawytscha*) from a New Zealand hatchery: spatial distribution of strays and effects of release date. Can. J. Fish. Aquat. Sci. **50**(6): 1168–1175. doi:10.1139/f93-133.

van den Berghe, E.P., and Gross, M.R. 1989. Natural selection resulting from female breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*). Evolution, **43**(1): 125–140. doi:10.2307/2409169. PMID:28568484.

Varnavskaya, N.V., Wood, C.C., Everett, R.J., Wilmot, R.L., Varnavsky, V.S., Midanaya, V.V., and Quinn, T. 1994. Genetic differentiation of subpopulations of sockeye salmon (*Oncorhynchus nerka*) within lakes of Alaska, British Columbia, and Kamchatka, Russia. Can. J. Fish. Aquat. Sci. **51**(S1): 147–157. doi:10.1139/f94-301.

Zhou, S.J. 2002. Size-dependent recovery of Chinook salmon in carcass surveys. Trans. Am. Fish. Soc. **131**(6): 1194–1202. doi:10.1577/1548-8659(2002)131<1194:SDROCS>2.0.CO;2.