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30 During the development of this manuscript, our esteemed colleague and co-author, David

31 Noakes, passed away. His contributions to fisheries science were innumerable, and we deeply

32 appreciate the energy he devoted to this project. The broad community of people touched by

33 his work will feel this loss keenly. Author Manuscript

Abstract

 Many adult hatchery-origin Pacific salmon return to their natal river but do not enter the hatchery, instead spawning in the river, where they can have detrimental genetic and ecological effects on naturally reproducing wild populations. This phenomenon is especially well documented in Elk River, Oregon Chinook Salmon, based on previous analyses of coded wire tag recoveries. Here, we used radio tags to compare the movements of natural- and hatchery– origin (n = 11 and 15, respectively) Chinook Salmon to determine if their behavior could explain 42 the in-river straying patterns of hatchery salmon. Most tagged hatchery-origin (87%) and natural-origin (73%) adults initially moved upriver, to the vicinity of the hatchery. Most natural- origin adults then moved downstream of the hatchery entrance to spawn but the movements of hatchery-origin adults were different. Hatchery-origin males and females had the highest and lowest variation in total distance moved, respectively. Our results are consistent with the hypothesis that while most hatchery origin salmon return to the vicinity of the Elk River 48 Hatchery, some fail to enter, perhaps because the hatchery's odors were not perceived as distinct from those of the river, or (in the case of hatchery-origin males) they stopped short of the hatchery after encountering spawning conspecifics. Thus, spawning distributions may not always reflect in-river movements of Chinook Salmon, and we encourage fisheries managers to continue investigating methods that reduce potentially harmful interactions between hatchery- and natural-origin fish. States on naturally reproducing wild populative
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Introduction

 The homing of salmonid fishes (*Salmo*, *Oncorhynchus*, and *Salvelinus* species) to their natal breeding site reduces gene flow between groups breeding in different rivers. This reproductive isolation allows natural selection to operate on adaptive traits, resulting in the population-specific patterns of productivity and local adaptations that necessitate management of discrete populations (Quinn 2018). Individuals that spawn at sites other than natal streams are said to have strayed, and this occurs at low but variable levels among species and populations (Quinn 1993; Keefer and Caudill 2014; Westley et al. 2013).

 In addition to the extensive network of naturally reproducing salmonid populations, many rivers entering the Atlantic and Pacific oceans also have hatcheries, where mature adults are artificially spawned and their progeny are incubated as embryos, fed as juveniles, and then released to grow at sea, support fisheries, and replenish the population (Naish et al. 2007). When spawning in the wild, hatchery-origin salmon often have lower reproductive success than natural-origin counterparts and can reduce the reproductive success of natural-origin spawners (Araki et al. 2009; Seamons et al. 2012). To avoid deleterious effects on the natural-origin population's fitness, managers often try to minimize genetic interactions between natural- and hatchery-origin fish on spawning grounds; therefore, hatchery-origin salmon spawning in the river may generate concern (Bett et al. 2017). 84 reproducions are the states and an education to operate on adaptive trans, resulting in the populations, or eventually enter than because the necessite management of Local deploted to the state of the state of the state

 Hatchery-origin salmon might spawn in the river rather than enter their natal hatchery for several reasons, but two candidate explanations might be assessed by the movement patterns of adults in the river. First, adult salmon might encounter suitable breeding habitat and aggregations of mature conspecifics in the river before reaching their natal hatchery, and 79 spawn there (i.e., "stop short") rather than continuing upriver to enter the hatchery (Bett and Hinch 2015). Alternatively, salmon might reach the hatchery, but "bypass" it because they fail 81 to recognize the chemical signature of the water flowing from the hatchery or are dissuaded from entering by some physical features of the site such as fishway design (Thorstad et al. 2008). Such salmon might return downstream or continue past the hatchery to spawn in the

 enter a particular hatchery could inform changes to management practices and facilities to reduce in-river straying.

 In-river straying has been documented in fall-run Chinook Salmon, *O. tshawytscha*, in the Elk River (Figure 1), on the coast of Oregon, USA (Nicholas and Downey 1983; data summarized in Quinn 1993). These salmon are coded wire tagged (CWT), and intensively monitored by the Oregon Department of Fish and Wildlife (ODFW) to estimate catch, escapement and other metrics. Analysis of over three decades of Elk River Hatchery Chinook Salmon CWT data revealed that hatchery-origin fish spawning in the river tended to be larger 93 fish and more often females, relative to those entering the hatchery, and that most tagged strays were recovered on spawning grounds downstream from the hatchery (Pollock et al. 2020). However, the movements of hatchery- and natural- origin fish prior to death and recovery were unknown. In this study we used radio telemetry to determine which of two possible migration patterns was more prevalent among Elk River Hatchery Chinook Salmon in the river: stop short of the hatchery, or bypass it, as described above. We then placed the data in the context of the long-term distributions of spawning by natural- and hatchery-origin 100 salmon in the basin, based on carcass surveys. 188 the like hyrer (Highre 1), and the coast of Oregon, U.SA (Nicholas and Downy 1985; dast

189 sommarized by the Oregon Department of Fish and Wildlife (ODFW) and intensively

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METHODS

 Field Methods. - During October–December 2018 we captured adult Chinook Salmon in seine and tangle nets just upstream from the mouth of the Elk River, which empties into the Pacific Ocean (Figure 1). Netting was conducted at night, when fish tend to enter the river, allowing recovery time between handling and possible encounters with anglers. Nets were monitored and retrieved as soon as any fish was detected. Each fish was removed from the net and held in an insulated tank containing ambient temperature river water, circulated and oxygenated with a pump, and a chemical additive to reduce physical handling effects on the fish (Harnish et al. 2011). Water was replaced when it warmed or cooled to a difference of 1 C° relative to river water. Each fish was identified to sex and origin (natural or hatchery), based on the presence or absence of an adipose fin. Fish > 600 mm fork length and in good health received gastric

 antennas, pulse rates of 45.8 ppm and pulse width of 34 ms, and a maximum battery life expectancy of 222 days. Esophageal tagging is considered to be the least invasive tagging method when regurgitation does not occur (Smith et al. 2009). A distinct punch mark on the 117 operculum of each tagged fish indicated capture location and date.

 We used receivers (ATS R4500C) to determine the positions and movements of tagged fish during the spawning season. We deployed five fixed receivers in the Elk River basin to 120 optimize detections of fish relative to spawning grounds and the hatchery outflow (Figure 1). Their locations were selected to optimize signal detection from different river sections, and also for access via private land. Receivers were housed in watertight boxes, connected to a power source (solar panel and/or deep-cell battery), with two antennas to determine directionality of 124 tag detections. Receivers scanned the frequencies of the transmitters, with 3 sec timeout, 10 125 sec scan time, and 10 min store time settings. Data were downloaded every few days. A sixth 126 receiver was used for mobile tracking to search for tagged fish upstream of the Elk River Hatchery, and locate tagged salmon carcasses at the end of the spawning season. 117 operculum of each tagge

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 Mobile tracking was conducted weekly in the Elk River basin using a receiver with a 3- element Yagi antenna. Where the road ran parallel to the river, tracking was done from a truck 130 but otherwise it was done on foot, and from pontoon boats. When tags were detected, the 131 surveyor adjusted the gain and monitored signal strength to locate the transmitter, then recorded the site on a GPS. When tags were detected in the same location over multiple tracking events, and the site showed no signs of spawning activity or live fish, surveyors endeavored to retrieve the tag and determine final disposition.

 Lastly, we wanted to relate the tracking data to information on the distribution of spawning in the basin. From 2005 - 2018, ODFW personnel conducted annual Chinook Salmon carcass surveys of all available salmon spawning habitat in the Elk River basin by boat or on foot. Reaches that typically have many spawning adults were surveyed every 7-10 days, reaches with fewer adults were surveyed every 2-3 weeks, and those that typically have few or none were surveyed twice. For each recovered carcass, the recovery location by stream reach, sex, and origin (hatchery- or natural-origin, later confirmed by coded wire tag extraction or scale

 Analyses. - Fish that were captured by anglers and those that did not move from the first receiver station were removed from the dataset. All data were then collated and filtered to 146 remove false detections resulting from detections of tags already removed from fish, and 147 duplicate detections on two adjacent receivers. Duplicate detections occurred when a fish was within the detection radius of more than one receiver. In these instances, the detection with the highest signal strength was retained as the best estimator of fish location (Skalski et al. 2001). Given the average distance between receivers (4.5 river kilometers (rkm)) and the sinuosity of the river channel, most duplicate detections were on the two upriver receivers (stations 4 and 5). These receivers were only 0.34 rkm apart and their proximity resulted in numerous duplicate detections. Therefore, data from these receivers were combined to eliminate effects that redundant detections from fish moving between them would otherwise have on our results.

 The filtered data were used to calculate metrics describing coarse-scale movement 157 patterns. Metrics were then compared among groups based on all combinations of fish origin x 158 sex. The number of paths was defined as the number of movements by each fish between each receiver station, and was used as a measure of the extent of movement within the Elk River. For example, a fish moving directly from the tagging location to the hatchery would have a path value of 3 (Path 1: Receiver 1 to Receiver 2; Path 2: Receiver 2 to Receiver 3; Path 3: Receiver 3 to Receiver 4 [at the hatchery]). Mean movement rate (rkm/h) was calculated by dividing the 163 rkm between sequential receiver pairs by the time between detections closest to the receiver site. Closest detections were defined as those with the strongest signals during an uninterrupted series of detections. Mean rate was then calculated from all paths between receiver pairs for each fish, and total movement was the sum of rkm of all paths for each fish. The coefficient of variation (CV) of total rkm travelled was a measure of individual variation in movement patterns within a group (e.g., hatchery-origin females, natural-origin males). Total rkm CV was calculated by dividing the standard deviation by the mean for each group. We compared movement patterns among groups using nonmetric multidimensional 141 scaling for the veganity of the veganitation of the vectors and the veganitation of the highest synthe and show the hi

172 2013; Jari et al. 2019). Metrics were standardized and fourth-root transformed prior to creating matrices of Euclidean distance to reduce the effect of extreme values on results (Legendre and Legendre 2013). NMDS allows for the visualization of differences among groups by compressing 175 complex data into two-dimensions. The proximity of points on the resulting ordination illustrates the similarities among groups (Kruskal 1964). We used analysis of similarities (ANOSIM) to test for differences in movement pattern among groups and to identify interactions (Clarke 1993; Meyer et al. 2010; Whitmore and Litvak 2018). ANOSIM calculates 179 the overlap among groups and compares it to overlap simulated from 999 random starts, with statistical significance (p < 0.05) indicating little overlap, or greater differences among groups. To test for differences in upstream movement time, we calculated the time from receiver 1 to 182 receiver 4/5 (the hatchery). We used a two-way fixed factor ANOVA to test for differences in 183 movement rate by origin and sex and post-hoc testing to compare differences among groups. Because the carcass survey reaches did not align exactly with the reaches between the fixed site receivers, we grouped the spawning distribution data into four bins encompassing the entire spawning area of the Elk River basin: 1) river mouth (rkm 0.0) to a boat ramp (rkm 7.1) 5.3 rkm above Receiver 1 (rkm 2.8) and 1.4 rkm below Receiver 2 (rkm 8.4); 2) boat ramp (rkm 7.1) to receiver 3 (rkm 14.0); 3) Receiver 3 to Receiver 4 (rkm19.9)/ Receiver 5 (rkm 20.2) including Rock Creek tributary; and 4) all areas above Receiver 5, including Anvil Creek. We then calculated the annual proportion of hatchery- and natural-origin fish in each bin by dividing the number of hatchery- or natural-origin salmon recovered in that bin by the total number recovered in the study area that year. 21%

2008 1200 87%) moved upstream to the hatchery and of these, 85% (11 of 13 fish) and the hatchery.

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RESULTS

 We tagged 48 Chinook Salmon (26 natural-origin and 22 hatchery-origin). Of these, 15 were removed just above the tagging site by anglers or predators, and 6 fish were removed by anglers and 1 to predation after entering the receiver array, leaving 26 fish for analysis (Table 198 1). We recovered five loose tags from the river, but we could not determine whether regurgitation, anglers, or predators were responsible. Most hatchery-origin fish (13 of 15 fish,

201 No hatchery-origin fish were detected upstream of the hatchery during mobile tracking. All 7 202 hatchery-origin females moved to the hatchery entrance; 5 entered the hatchery and 2 were 203 later recovered downstream on or near spawning areas. Of the 8 hatchery-origin males, 6 were 204 detected near the hatchery entrance and all of these ultimately entered the hatchery. The 205 other 2 hatchery-origin males were never detected near the hatchery and were recovered 206 downstream on or near spawning areas. Most (73%) natural-origin fish also moved upstream as 207 far as the hatchery but only 25% of them entered the hatchery. Three natural-origin fish were 208 detected upstream of the hatchery during mobile tracking. Of the 7 natural-origin females, 5 209 moved upstream as far as the hatchery entrance; 2 of those entered the hatchery and the other 210 3 moved downstream to spawning areas. None of the 4 natural-origin males entered the 211 hatchery but 3 moved upstream as far as the hatchery entrance. Of these, 2 later moved 212 downstream and 1 spawned in a tributary upstream of the hatchery. Only 1 natural-origin male 213 moved directly to the downstream spawning grounds.

214 The NMDS revealed overlap in the movement patterns of natural-origin males, natural-215 origin females, and hatchery-origin males (Figure 2), but hatchery-origin females were distinct 216 from all other groups, with substantially fewer paths, and less total distance travelled and 217 variation in total movement (Table 2). The ANOSIM revealed a significant interaction between 218 origin and sex (ANOSIM, $p = 0.001$) due to the similar patterns of hatchery-origin males and 219 natural-origin females and males, precluding the interpretation of main effects. We split the 220 data and ran the ANOSIM on origin, which indicated that hatchery-origin fish had fewer paths 221 and less total movement than natural-origin fish (ANOSIM, p = 0.042). Natural-origin fish made 222 more reciprocal movements between receivers, resulting in more paths and total movement 223 (Table 2). Variation in total movement was high within all groups with the sole exception of 224 hatchery-origin females, which tended to move more directly to their ultimate location. The 225 groups also differed in time from receiver 1 to the hatchery (receiver 4), with an effect of sex 226 (ANOVA, $p = 0.024$) but not origin (ANOVA, $p = 0.672$), and no interaction (ANOVA, $p = 0.059$) 227 between origin and sex. Post-hoc testing revealed that natural-origin males reached the detected near the hatchery entrance and all of these ultimately entered the naturely.
206 obter 2 hatchery forigin males were new detected near the hatchery and were recovered to the 2 natural-origin females were recovere

 Carcass surveys indicated that hatchery- and natural-origin salmon had remarkably similar distribution within the Elk River basin, as most adults of hatchery- and natural-origin were recovered in the 5.9 km reach just below the hatchery (Figure 4). These data suggest that 232 the majority of preferred spawning habitat and naturally spawning conspecifics were in the river downstream from the hatchery. Above the hatchery, most hatchery-origin fish were recovered in Anvil Creek, the tributary immediately upstream of the hatchery entrance ladder (Figure 1), whereas natural-origin fish spawning above the hatchery tended to use areas farther upstream.

237

238 **DISCUSSION**

239 Our study was designed to evaluate two hypotheses related to the migration dynamics of 240 hatchery- and natural-origin Chinook Salmon in the Elk River basin. Hatchery-origin adult 241 salmon might stop short, prior to reaching the hatchery, owing to the availability of suitable 242 spawning habitat and aggregations of spawning adults downstream of the hatchery. 243 Alternatively, they might reach the hatchery but not enter, perhaps because some physical or 244 hydraulic feature discouraged them, or the hatchery entrance lacked a distinct olfactory 245 signature. Most (73%) hatchery-origin salmon migrated directly to the vicinity of the hatchery 246 and then entered, indicating that the hatchery was largely accessible and identifiable. However, 247 27% of the tagged hatchery-origin fish did not enter the hatchery, consistent with in-river stray 248 rates inferred from CWT analysis (Pollock et al. 2020). There is no apparent structural feature or 249 operation at the entrance to the hatchery to prevent fish from entering, and some females and 250 males of all sizes did so. In the absence of olfactory clues to lead them into the hatchery, those 251 fish might have remained in the river and possibly spawned there (Bett and Hinch 2015). The 252 hatchery uses river water and thus the discharge is similar (though presumably not identical) in 253 chemistry and temperature to that of the river itself. Fall run (ocean-type) Chinook Salmon 254 straying rates are often quite high (Quinn et al. 1991; Pascual and Quinn 1994; Westley et al. 255 2012), so the expected level of straying is somewhat uncertain at these spatial scales. That is, 256 had there been spawning in a tributary rather than the hatchery, what fraction of the salmon 232 the majority of preterred spawning nabitat and naturally space to return of the matchery. Above the hatchery, necovered in Anwil Creek, the tributary immediately upstread (Figure 1), whereas natural-origin fish spawnin

 Previous coded wire tag analysis indicated that Elk River females were less likely to enter the hatchery than males (Pollock et al. 2020). All hatchery-origin females in our study returned to the vicinity of the hatchery but took longer than males to do so. Two of the four 261 hatchery-origin fish that did not enter the hatchery were males that were never detected in the 262 vicinity of the hatchery and were recovered near spawning areas farther downstream (Figure 263 4), suggesting that attraction to conspecifics might influence in-river straying. Interestingly, males migrated more quickly to the vicinity of the hatchery than females, consistent with 265 behavior observed in other Chinook Salmon populations (Bass et al. 2019). The movements of natural- and hatchery-origin fish were significantly different, but most natural-origin salmon also reached the vicinity of the hatchery or beyond before returning to lower river spawning 268 sites. Natural-origin salmon moved more within the river, perhaps reflecting greater exploratory behavior as they sought spawning sites and mates, but the reason(s) for the difference are uncertain.

271 The data for this study are limited to one year and relatively few fish, so we interpret 272 them with caution. Environmental conditions (e.g., rainfall, river flow, and temperature) and 273 density of adults vary from year to year and could affect movement patterns, and they can also 274 vary within each season, so fish often experience different conditions (e.g., Anderson and 275 Quinn 2007; LovellFord et al. 2020). In addition to the environmental variation, we 276 acknowledge that the fish themselves are not truly replicates, as they may differ in a number of 277 traits (e.g., state of maturation, social dominance, etc.) affecting movements (e.g., Healey and 278 Prince 1998). Moreover, any given river will have its own distribution of spawning (e.g., 279 downstream or upstream of the hatchery, near or far from the tagging site and river mouth, 280 etc.). Consequently, the patterns of in-river movements and exchange between the natural 281 spawning and hatchery populations are inevitably somewhat idiosyncratic. These problems 282 (temporal variation in environmental conditions, variation among individuals, and lack of 283 genuine spatial replication) are common to many telemetry studies but any interpretation of 284 specific findings should bear them in mind. and the strate of the matter of the matter in when the matter of studying reads that were newer detected in the studying of the intervel and the term consent spare represent from strain (Figure 26)
26 4), suggesting the tr

285 Notwithstanding the likelihood that results from our tracking study may not be broadly

 which can increase the proportion of hatchery-origin fish on spawning grounds, and thus reduce the fitness of natural-origin fish (Araki et al. 2009) and the productivity of their population (Chilcote et al. 2011). These risks pose challenges for managers tasked with both fisheries enhancement and protection of natural-origin stocks. In the Elk River system, in-river 291 straying by hatchery-origin Chinook Salmon has been a long-standing concern, recently identified as a risk factor to the viability of the local natural-origin population (ODFW 2014). Efforts to reduce in-river straying in the Elk River have included altering the hatchery fish ladder and its operation, physically removing hatchery-origin fish from the river at tributary weirs, reducing the number of hatchery-origin juveniles released, and retaining juveniles in the hatchery as a conspecific attractant. Recently, managers have implemented a mark-selective fishery that is expected to increase harvest rates (removal) of hatchery-origin Chinook Salmon, while protecting natural-origin conspecifics.

 Beyond the differences in movement behavior of hatchery- and natural-origin salmon we have described, our telemetry results demonstrate that in-river movements of adult salmon cannot be confidently inferred from spawner distributions. Salmon may commonly pass and then return to their spawning site, as we found here, and move within river systems prior to final spawning site selection (Ricker and Robertson 1935). In the case of our study, this behavior could reflect some combination of sequential imprinting, homing, and redd site selection (Dittman et al. 2010), social status (e.g., Healey and Prince 1998), or evidence that initial attempts to locate the natal hatchery failed. Such exploratory movements within rivers offer multiple opportunities for collection of adult hatchery-origin fish, and we encourage managers and biologists to continue investigating methods that could reduce potentially harmful interactions between hatchery- and natural-origin fish. 329 Issenese enhancement and protection of natura-longen stocks. In the lik Nover system, in-noise
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Figure Captions

 FIGURE 1. Map of the Elk River basin, southern Oregon, USA. Locations of the five (5) stationary 326 radio receivers are indicated by the symbols $1 - 5$. The Oregon Department of Fish and Wildlife hatchery is located between receivers 4 and 5.

 FIGURE 2. NMDS ordination of movement metrics for all groups of Elk River Chinook salmon: 330 Hatchery-origin males (H_M), hatchery-origin females (H_F), natural-origin males (W_M), and natural-origin females (W_F). Circles are the axis scores of individual fish and crosses are the axis scores of the group. ed the map i
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FIGURE 3. Movement times by natural - (W) and hatchery-origin (H) female (F) and male (M)

Chinook Salmon from the tagging location to the hatchery. The horizontal lines indicate

medians, the boxes are interquartile (25-75%) ranges, the lines extending from the boxes show

minimum and maximum values, and the points are outliers.

 FIGURE 4. Distribution of hatchery- and natural-origin Chinook salmon carcasses in the Elk River Basin 2005-2018. The lines indicate medians, the boxes are interquartile (25-75%) ranges, and the whiskers the maximum and minimum values. Bins approximate locations delineated by the fixed site receivers. The hatchery is located at receiver sites 4/5.

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Figure 2.

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TABLE 1. Summary of the numbers of tagged fish by origin (H = hatchery-origin, W = natural-

origin), and sex (F or M), the direction of movement, and tag recovery location. Recovery

includes both tag and carcass recoveries outside of the hatchery.

TABLE 2. Summary of movement metrics (mean ± standard deviation) by origin (hatchery or

natural) and sex, calculated from individual tagged Chinook Salmon, and the coefficient of

variation (CoV) for total movement by each group.

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