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Differential marking of embryos by location and date of release reveals within-river natal and parental influence in progeny return timing in Sockeye Salmon

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Running Header: Parental control over progeny homing and return timing

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22 Abstract.—The tendencies of salmon and trout to spawn in proximity to their natal site and
23 follow the parental timing of breeding are fundamental to their population structure, and also
24 affect the performance of enhancement facilities. Specifically, understanding how parental
25 spawning date and offspring release location affect the timing and place of breeding by returning
26 adults is important to the evaluation of hatchery supplementation programs and their integration
27 with sympatric naturally spawning populations. We collected Sockeye Salmon *Oncorhynchus*
28 *nerka* carcasses over three spawning seasons to evaluate spawn timing and distribution. Thermal
29 marks on the otoliths of hatchery-origin carcasses allowed assignment of fish to parents that
30 spawned in the early, middle, and late parts of the season, and to release locations in the lower,
31 middle, and upper parts of the river. The early portion of the spawning run was composed of a
32 higher proportion of hatchery-origin fish than was the case later in the season. Hatchery-origin
33 adults that were released early in the spring as fry (from early spawning parents) were recovered
34 early in the season, and those released later in the spring as fry were recovered later in the
35 season. The natural-origin spawn timing most closely matched middle and late hatchery fry
36 release groups in all years. Our data also demonstrated a correspondence between hatchery fry
37 release location and adult recovery location; fry released at rkm 1.0 were recovered a median 7.0
38 km lower in the river than fry released at rkm 21.7, and 10.0 km lower than fry released at rkm
39 35.1. These data contribute to the substantial body of evidence that population characteristics of
40 anadromous salmonids are sensitive to influence from cultural practices even under benign
41 regimes because of the strong connections between parental and progeny timing, and the fine-
42 scale homing of salmon to release sites within a river.

43 Introduction

44 Salmonids (salmon, trout, and char of the genera *Oncorhynchus*, *Salmo*, and *Salvelinus*) are an
45 exceptionally important group of fishes, owing to their value in commercial, recreational, and
46 subsistence fisheries, aquaculture, and ecosystem services (Shearer 1992; NRC 1996). The
47 structuring of discrete populations (Utter 2004; Garcia de Leaniz et al. 2007) arises from the
48 strong tendency for adults to return to their natal stream for spawning (i.e., homing). Although it
49 is clear from many studies that the vast majority of salmonids surviving to maturity return to
50 their natal river, the extent to which they return to specific natal locations within a given river
51 has not been resolved (Quinn 1993; Keefer and Caudill 2014). Most homing studies have

52 examined the distribution of Chinook Salmon, *Oncorhynchus tshawytscha*, and Coho Salmon, *O.*
53 *kisutch*, and to a lesser extent steelhead, the anadromous form of *O. mykiss*, among the Pacific
54 Salmon species, that were released as smolts from hatcheries (e.g., Quinn and Fresh 1984;
55 Labelle 1992; Candy and Beacham 2000; Westley et al. 2013). In these species, juveniles feed in
56 streams or they are reared in hatcheries for months or years, until they are ready for seaward
57 migration (i.e., at the parr-smolt transformation: Hoar 1976; McCormick and Saunders 1987),
58 when olfactory imprinting to permit subsequent homing is generally thought to occur (Hasler and
59 Scholz 1983). The life history of Pink, *O. gorbuscha*, Chum, *O. keta*, and Sockeye Salmon, *O.*
60 *nerka*, contrasts with this pattern; fry of these species emerge from gravel nests and immediately
61 migrate away from their natal site (Quinn 2018). Sockeye Salmon fry must imprint prior to or
62 during emergence because they leave the natal stream so early in their lives, some moving
63 immediately to sea, but more typically migrating to a lake, where they feed for a year or two
64 before leaving as smolts from the lake's outlet. The rich life history variation (e.g., Blair et al.
65 1993; Quinn et al. 1999; Quinn et al. 2001) and genetic population structure (e.g., Gomez-
66 Uchida et al. 2011; Larson et al. 2014) within lake systems that characterize Sockeye Salmon are
67 consistent with homing fidelity to the breeding site rather than the smolt transformation site.
68 Experimental work provided evidence of olfactory imprinting by fry (Havey et al. 2017), but the
69 extent to which they express this ability in natural systems is unclear.

70 Imprinting by salmon fry prior to or during emergence is important because it may affect
71 the spatial scale of homing; how near to the natal site do salmon return, and how does homing
72 interface with selection of spawning sites by females? The release locations of steelhead trout
73 smolts in the Alsea and Wilson rivers in Oregon (Wagner 1969), and the Chilliwack River in
74 British Columbia (Slaney et al. 1993) influenced their spatial distribution in recreational fisheries
75 as returning adults, indicating homing to locations within a single river. Moreover, Sockeye
76 Salmon returned as adults to a spring-fed pond within a single small stream where they had
77 emerged as fry (Quinn et al. 2006). In contrast, Dittman et al. (2010) reported that Chinook
78 Salmon released as smolts after acclimation in different parts of the Yakima River system
79 showed distribution patterns as returning adults that largely mirrored those of naturally spawning
80 conspecifics, suggesting that habitat selection and social factors may have influenced spawning
81 site choice. Thus, the spatial scale of homing, relative to the site of emergence, is poorly known

82 yet, such homing fidelity will strongly affect population structuring within river systems through
83 the distribution patterns of spawning adults.

84 In addition to the importance of homing, perennial differences in timing of migration and
85 spawning have long been recognized as key features defining salmonid populations, and play an
86 important role in their conservation and management (Killick 1955; Ricker 1972). Populations
87 spawning in colder streams tend to spawn earlier in the year than those in warmer streams, to
88 synchronize emergence at appropriate times of the year for juvenile feeding (Sheridan 1962;
89 Brannon 1987; Brannon et al. 2004). There is also a heritable component to timing variation
90 within populations, as evidenced by responses to deliberate selection in aquaculture (e.g.
91 Siitonen and Gall 1989; Neira et al. 2006), inadvertent selection in hatchery programs (Flagg et
92 al. 1995; Quinn et al. 2002; Ford et al. 2006), and the evolution of transplanted populations
93 (Quinn et al. 2000). Indeed, a review of heritability values in salmonids concluded that traits
94 related to timing are under stronger genetic control than any other group of traits (Carlson and
95 Seamons 2008).

96 Thus, the spatial scale of homing (almost entirely a learned response) and the temporal
97 scale of spawning date (to a greater extent a heritable trait) are key features in the population
98 structure of salmonids. Moreover, the two traits may be linked in natural populations. For
99 example, earlier arriving salmon may spawn farther upstream than later fish (Doctor and Quinn
100 2009). In recent decades, it has become widely understood that the deliberate and inadvertent
101 practices in hatchery programs including breeding, rearing, and release strategies, can affect not
102 only the hatchery program but also nearby wild populations (e.g., NRC 1996; Utter 2004; Naish
103 et al. 2007). Cognizant of these concerns, hatchery programs may employ practices designed to
104 reduce differences from local wild populations to optimize the full use of the habitat by the
105 naturally spawning fish while maintaining benefits from the hatchery program (Mobrand et al.
106 2005).

107 The present study, on Sockeye Salmon, was designed to answer two questions derived
108 from the features of salmonid biology outlined previously. First, if Sockeye Salmon fry are
109 released in different locations in a single river, will they return preferentially as adults to breed
110 near those locations, or will they match the spatial distribution of naturally spawned
111 conspecifics? Second, will the progeny of adults spawned in the hatchery in early-, mid-, and late

112 fall display this same timing upon their return as adults, and do their timing patterns differ from
113 those of naturally spawned Sockeye Salmon? We addressed these questions in the Cedar River,
114 located in Western Washington State, where the otoliths of all hatchery-origin Sockeye Salmon
115 fry are marked using exposure to thermal shifts during incubation (Volk et al. 1994). Marks are
116 specifically applied to distinguish fry released at different sites (rkm 1.0, rkm 21.7, and rkm
117 35.1) and at different times in the spring (early, middle, and late), and to distinguish hatchery-
118 produced from naturally-spawned Sockeye Salmon, from which the hatchery population was
119 derived.

120 Methods

121 *Study Site.*—The Cedar River, a tributary to Lake Washington, supports a population of naturally
122 spawning Sockeye Salmon. Adults return and spend several months in the lake (Newell et al.
123 2007), before spawning in the Cedar River up to river kilometer (rkm) 35.1, where they are
124 blocked by Landsburg Diversion Dam. The Cedar River downstream of the dam is a single
125 thread river system flowing through semi-rural, suburban, and urban habitat (from upstream to
126 downstream; Figure 1), with most of the water coming from the upper watershed. During spring
127 when fry migrate, flow at the mouth of the Cedar River is approximately 30% greater than at the
128 Landsburg Diversion Dam. At the peak of fall spawning, flow is approximately 20% greater at
129 the mouth than at Landsburg (data source: USGS real-time gages 12117600 and 12119000). The
130 lower reaches are channelized from Lake Washington to approximately 5 km upstream, above
131 which private residences dominate the river banks.

132
133 *Cedar River Hatchery.*—Hatchery supplementation began in the Cedar River in 1991 in an effort
134 to enhance harvest opportunities. The hatchery, located at rkm 35.1 has been managed under the
135 Cedar River Adaptive Management Plan (City of Seattle 2006) since 2011 with the goal of
136 retaining similar characteristics in the hatchery- and natural-origin components of the run for
137 traits such as size and age at maturity, and timing and spatial distribution of spawning. Adults
138 were collected at rkm 2.7 at a resistance board weir and, to a lesser extent (< 20%), at the
139 Landsburg Diversion Dam, transported to the hatchery, and held until spawning. The fertilized
140 eggs were incubated in water piped from a spring on the south side of the Cedar River at rkm
141 35.1 that was the same for all incubating groups.

142 After emergence, Sockeye Salmon fry volitionally moved to troughs where they
143 remained for 0 - 22 days before they were transported to one of three locations in the Cedar
144 River and immediately released at an average total length of 28 - 35 mm. Prior to release, the fry
145 were exposed to distinct thermal shifts in the hatchery holding water to induce visible marks on
146 their otoliths (Volk et al. 1994). These unique otolith marks provided a reliable method to
147 identify batches of fry when other tagging methods could not be applied due to the small size and
148 abundance of the fish, and linked individuals to a release location and time category. The annual
149 production of fry was divided into thirds and given categorical early, middle, or late release
150 identities, in combination with lower, middle, and upper location release identities. Time
151 categories differed in the exact median date among brood years but provided adequate
152 assessment of sequential timing within cohorts (Table 1). These early, middle, and late fry
153 groups were produced by parents that spawned relatively early, middle, and late in the previous
154 fall. Sockeye Salmon fry were not acclimated in river water but were transported from the
155 hatchery directly to one of three release locations in the Cedar River; (1) lower: near the mouth
156 where it enters Lake Washington at rkm 1.0, (2) middle: mid-river at rkm 21.7, and (3) upper: at
157 the hatchery and upper extent of accessible spawning habitat at rkm 35.1. For brood years 2009-
158 2012, the proportion of fry released at each release location varied, but the proportion of fry
159 released in each time category remained similar (Table 1).

160
161 *Carcass Sampling.*—Carcasses were sampled in the Cedar River in 2014, 2015, and 2016
162 beginning in late September over the 35.1 km reach accessible to Sockeye Salmon. Establishing
163 visual criteria for surveyors to distinguish fresh dead carcasses (< 7 days old) from older
164 carcasses was central to the sampling methodology. A carcass deterioration study was conducted
165 by tethering carcasses with a known mortality date, and then inspecting and photographing them
166 daily to document the progressive deterioration in the Cedar River. Three carcass condition
167 categories were established from these data. Condition 1 included freshly dead individuals with
168 at least one clear eye, firm body texture, and pink gills. Condition 2 included carcasses with
169 cloudy eyes, gills that had lost their pink coloration, and softening body texture. Condition 3
170 carcasses were in advanced state of decay as evidenced by soft flesh, heavy fungal and bacterial
171 matting of the carcass, and putrid odor. All carcasses encountered on the river were visually
172 categorized, but only otoliths from carcasses in conditions 1 and 2 were sampled. Thus, on each

173 survey we sampled only fish that had expired within the last week to assign carcasses to discrete
174 time and space strata.

175 In all years, the location of each fresh carcass (condition 1 or 2) was marked with a GPS
176 waypoint to define carcass distributions and calculate sampling rates. The sex of each carcass
177 was identified and both sagittal otoliths were removed and later examined by an experienced
178 technician, providing a relatively error free method to distinguish between groups (Volk et al.
179 1999, Wilson 2013). The ages of natural-origin Sockeye Salmon were determined by
180 examination of otoliths, whereas the ages of hatchery-origin fish were determined by identifying
181 the unique thermal mark. Hatchery-origin carcasses were assigned to a fry release time category
182 and location based on thermal marks, read blind with respect to the recovery location to prevent
183 bias.

184

185 *Data Analysis.*— To ensure statistical validity of our tests regarding the proportion of hatchery-
186 origin fish and spawn timing and location, the number of hatchery-origin carcasses collected by
187 reach (j) and sampling week (i) was adjusted to account for sampling rate (Skalski 2002).
188 Specifically, the total number of hatchery-origin carcasses in a particular week \times area stratum
189 was estimated by dividing the number of hatchery-origin carcasses collected by the fraction of
190 fresh carcasses sampled:

$$\hat{H}_{ij} = \frac{h_{ij}}{f_{ij}} \quad (1)$$

191 where \hat{H}_{ij} = estimate of the total hatchery-origin carcasses in the i th week ($i = 1, 2, \dots, t$) and j th
192 river stratum ($j = 1, 2, \dots, t$); h_{ij} = number of hatchery-origin otoliths collected; f_{ij} = fraction of
193 carcasses (conditions 1 and 2) sampled. \hat{N}_{ij} = the number of natural-origin otoliths, was
194 determined analogously. The proportion of hatchery-origin carcasses in the i th week ($i = 1, 2, \dots,$
195 t) and j th river stratum ($j = 1, 2, \dots, t$) was estimated by dividing the estimated number of
196 hatchery-origin carcasses by the total estimated carcasses. Equation 1 was applied to raw carcass
197 counts to estimate the number of carcasses for other groups including age (3, 4, 5, 6, and
198 unknown), temporal fry release categories (early, middle, and late), and fry release locations
199 (lower, middle, and upper). This mathematical adjustment prevented bias in our spatial and
200 temporal data by accounting for sampling rate of all visible carcasses.

201 The spatial distribution of recovered female hatchery- and natural-origin carcasses was
 202 evaluated using a Kruskal-Wallis test (KW test) by brood year (Sokal and Rohlf 1981). When
 203 statistical differences were observed, we tested the hypothesis of no difference in spawning
 204 distribution for hatchery- and natural-origin adults for age-4 and age-5 using Kolmogorov-
 205 Smirnov cumulative distribution test (KS test) (Sokal and Rohlf 1981). Only female spawning
 206 distributions are presented to simplify graphical presentation, and because female carcass
 207 distribution provides the best representation of spawning distribution due to sex-specific
 208 movement patterns (Murdoch et al. 2009). Next, a KW test was used to determine if adult
 209 spawning distribution differed among the three fry release locations and natural-origin carcasses.
 210 The spawning distribution of each release group was plotted, and KS tests (on female
 211 distributions adjusted for sample rate) were conducted. The median spawn location from each
 212 group's distribution was used as a descriptor of the midpoint of spawning.

213 Each Sockeye Salmon carcass was associated with a sample week and allowed us to
 214 compare the difference in recovery timing of hatchery- and natural-origin carcasses by year.
 215 First, the proportion of hatchery-origin carcasses in each sample week was calculated to identify
 216 the general trend in spawn timing. The proportion of hatchery-origin carcasses in the i th week (i
 217 = 1, 2, ..., t) and j th river stratum ($j = 1, 2, \dots, t$) was estimated as follows where n_{ij} = the
 218 number of natural origin otoliths.

$$\hat{\theta}_{ij} = \frac{h_{ij}}{h_{ij} + n_{ij}} \quad (2)$$

219 The hypothesis that hatchery- and natural-origin spawn timing differed was tested using a KS
 220 test comparing the temporal distribution of carcass recoveries each year (Sokal and Rohlf 1981).
 221 Both female and male carcasses were included in the analysis of spawn timing. Finally, the
 222 distribution of adult carcass recoveries by sample week was compared among the fry release
 223 time categories (surrogates for parental spawn timing) for early, middle, and late fry release
 224 groups to the natural-origin group with a KW test and subsequent KS tests when significance
 225 was determined for each year. The significance level α was set at 0.05 for all tests.

226

227 Results

228 The locations of 4,915 fresh carcasses were mapped and 3,760 were identified as hatchery- or
 229 natural-origin over three spawning seasons in 2014, 2015, and 2016 (Table 2). An estimated 9%,

230 22%, and 31% of the overall Sockeye Salmon run in the Cedar River was sampled in each year,
231 respectively, after accounting for fish removed in the broodstock. The annual sample of otoliths
232 averaged 72 - 81% of all visible carcasses for temporal and spatial strata across the study (Table
233 2). The sex ratio of the carcasses (expressed as percentage of sampled females) varied among
234 years: 48% in 2014, 52% in 2015, and 57% in 2016. The age of 3,732 hatchery- and natural-
235 origin carcasses was assigned, and the fry release location ($n = 1,847$) and time category ($n =$
236 1,930) was designated to hatchery-origin carcasses when otolith marks were readable.

237
238 *Age Composition of Carcasses.*—Carcass age-classes were used to associate spawning
239 distribution with the corresponding fry release brood year, and in each sampling year, most of
240 the female hatchery-origin Sockeye Salmon were age-4 (2014 - 75%, 2015 - 89%, and 2016 -
241 89%) (Table 3). However, in 2014, only 44% of female natural-origin carcass samples were age-
242 4, but in 2015 and 2016, most female natural-origin carcasses were age-4 (2015 - 88%, 2016 -
243 80%). Age-3 and age-6 carcasses were collected but composed <5% of female carcasses.

244
245 *Spatial Distribution of Carcasses.*— In 2014, the median spawning locations of hatchery- and
246 natural-origin females were similar with a median 1.6 km difference, but in 2015 and 2016, age-
247 4 hatchery-origin fish spawned a median 12.5 and 8.0 km farther upriver, respectively, than
248 natural-origin females of the same age (Figure 2). The recovery locations of hatchery-origin fish
249 corresponded to their release location as fry in all years. For all brood years, female hatchery fry
250 released near the mouth of the Cedar River (rkm 1.0) were recovered significantly lower in the
251 river than fry released at the middle or upper release sites (Figure 3, $H = 310.0$, $P < 0.0001$). The
252 female hatchery fry released at the upper site spawned at a median distance >10.0 km upstream
253 of the lower release group ($D = 0.48$, $P < 0.0001$). Female natural-origin carcasses were most
254 similar in distribution to female hatchery-origin carcasses that were released as fry at the mouth
255 of the Cedar River. Their median spawning locations were both at rkm 5.0 with no difference
256 between them ($D = 0.05$, $P = 0.24$).

257 The hatchery-origin spawning distribution was related to the corresponding brood year
258 fry release distribution. For example, in 2014, the median recovery location for age-5 hatchery-
259 origin Sockeye Salmon was the lowest observed in the study at < 3 rkm, representing a brood
260 year where all hatchery fry were released at rkm 1.0 (Figure 4, Table 4). In 2014, hatchery-origin

261 age-4 females were recovered significantly farther upstream than age-5 females (Table 4, $D =$
262 0.31 , $P < 0.02$). A significant difference in the distribution of age-4 and age-5 hatchery-origin
263 carcasses was also detected in 2015, when the younger age-class spawned a median 7.6 km
264 farther upstream (Table 4, $D = 0.28$, $P < 0.01$). The age-5 spawners in 2015 originated from a
265 hatchery brood in which 69% of fry were released at the lowest site, while only 35% of age-4
266 spawners had been released at the lower site. No difference was detected between age-4 and age-
267 5 hatchery-origin females in 2016 when nearly identical proportions of fry were released at each
268 of the sites (Figure 4).

269
270 *Temporal Distribution of Carcass Recoveries.*—Hatchery-origin carcasses comprised a greater
271 portion of the spawning run early in the season, whereas later in the run, most individuals were
272 natural-origin (Figure 5). In 2016, 83% of carcasses recovered during the initial sampling in late
273 September were of hatchery-origin and in 2015, 73% were of hatchery-origin. In 2016, the
274 percentage of hatchery-origin individuals in the carcass samples did not fall below 50% until late
275 October, when more than three-quarters of the total carcasses had been sampled for the year. In
276 all years, 90% of recovered carcasses were natural-origin fish in early December, but the peak in
277 carcass abundance for both brood origins occurred early in the sampling period, when hatchery-
278 origin fish predominated. While natural-origin fish numerically dominated the carcass samples in
279 November and December, the proportional contribution to the naturally spawning population
280 was small. In all years, <3% of the carcasses were collected in late December (Figure 6).

281 Hatchery-origin Sockeye Salmon, as a whole, spawned earlier than natural-origin
282 conspecifics in all years (Figure 6, 2014: $D = 0.13$, $P = 0.004$; 2015: $D = 0.17$, $P < 0.0001$; 2016:
283 $D = 0.29$, $P < 0.0001$), with differences in median spawn dates of 6 d in 2014, 5 d in 2015, and
284 11 d in 2016. Among the hatchery-origin fish, the fry release time category affected carcass
285 recovery timing ($H = 561.5$, $P < 0.0001$). In all but one pair-wise comparison (2016 late fry
286 release group), the spawn timing distribution for hatchery-origin female and male carcasses did
287 not differ statistically, and sexes were pooled in subsequent analysis (Table 5). Carcasses
288 associated with the early fry release group (produced by parents that spawned earlier) were
289 recovered earlier than middle or late fry release groups, and recovery time was ordered by
290 release group (Figure 7). In 2014, the natural-origin spawn timing curve fell between the middle
291 and late fry release groups, and the temporal distribution was not significantly different than the

292 middle fry release group ($D = 0.12$, $P = 0.23$). A similar pattern was observed in 2015, but the
293 natural-origin spawn timing distribution differed from all fry release groups (Table 5). In 2016,
294 the natural-origin fish spawned significantly later than all hatchery-origin fry release groups
295 (Table 5).

296

297 Discussion

298 *Spatial Distribution of Spawning*

299 The spawning distribution of adult Sockeye Salmon was strongly affected by fry release location
300 (regardless of age at maturity) varying markedly between hatchery fry release groups in all years.
301 Adult hatchery-origin fish spawned at greater median distances upstream of Lake Washington in
302 sample years when the corresponding fry had been released at the upper end of the potential
303 spawning habitat. Similarly, when hatchery fry releases were confined to the mouth of the river,
304 the spawning distribution of hatchery-origin Sockeye Salmon shifted downstream. Meanwhile,
305 the spawn distribution of natural-origin fish remained similar among brood years, and most
306 closely matched the lowest fry release group. Thus, hatchery fry release location apparently
307 played a pivotal role in the link between homing and breeding site selection by adults. Cedar
308 River Hatchery Sockeye Salmon fry were incubated and reared in water from a natural spring
309 near the hatchery facility. As a result, they might be expected to return to the upper end of
310 suitable spawning habitat (rkm 35.1) near the hatchery if they imprinted prior to release or were
311 searching for the spring water in which they were incubated (Quinn 1993). It therefore appears
312 that they may not have imprinted during their period at the hatchery, only doing so upon release
313 and initiation of downstream migration. This is consistent with experiments on Coho Salmon
314 smolts that did not seem to imprint while at hatcheries prior to release, but only after they
315 commenced migration (Vreeland et al. 1975; Dittman et al. 1996).

316 Our results are broadly consistent with previous studies showing that hatchery-origin
317 salmon tend to return and spawn near or at the site of release (Quinn 1993). However, most
318 previous studies involved releasing the salmon as smolts, the period when olfactory imprinting
319 for subsequent homing is generally thought to occur (Hasler and Scholz 1983). For example, the
320 linkage between the locations of smolt release and adult spawning has been documented for
321 Chinook Salmon (Hoffnagle et al. 2008) and steelhead trout (Mackey et al. 2001), but in these
322 species, juveniles have extensive periods of time in freshwater for olfactory learning. The

323 experiments with steelhead smolts reported by Wagner (1969) were unusual in that the fish were
324 released at different points along the same river rather than in a tributary (e.g., Gorsky et al.
325 2009) or specific acclimation facility (e.g., Garcia et al. 2004; Dittman et al. 2010). Even the
326 previous field study on Sockeye Salmon fry imprinting allowed the fish to emerge in a side
327 channel of the main stream to which they returned (Quinn et al. 2006). Therefore, our results
328 were especially notable from the standpoint of homing because all the Sockeye Salmon fry were
329 held at the same hatchery, were not placed in acclimation facilities, and only differed in the
330 release locations in the mainstem, from which point they commenced downstream migration.
331 Indeed, trapping of fry at the lower part of the Cedar River revealed that hatchery fry tended to
332 be recovered on the same night that they were released or the next night (Seiler et al. 2005),
333 implying that they left the release site more or less immediately upon release into the Cedar
334 River. The Cedar River has a single main channel and few tributaries between the release sites.
335 Nevertheless, the Sockeye Salmon fry rapidly imprinted on chemical traces that were sufficiently
336 distinct to support differential distribution along the main river channel when they returned three
337 or four years later. Havey et al. (2017) found that Sockeye Salmon imprinted to odors at both the
338 alevin and smolt stages in laboratory conditions, and our work showed that fry released in the
339 Cedar River imprinted at the initiation of downstream migration.

340 Despite the obvious role of imprinting in guiding adult salmon to their natal sites for
341 spawning, habitat selection can also affect spawning distributions. Notably, Dittman et al. (2010)
342 found significant straying of Chinook Salmon from acclimation facilities where smolts were
343 released. The distributions of those hatchery-reared fish were similar (though not identical) to
344 those of naturally-reared fish, implying that habitat quality (or perhaps social interactions with
345 other fish) affected breeding site selection (see also Cram et al. 2013). There are widespread
346 efforts to induce homing to particular locations in hatchery-reared salmon through the use of
347 acclimation facilities where juveniles are held for variable periods of time prior to volitional
348 release (e.g., Garcia et al. 2004, Dittman et al. 2010). In the present study, the spawning
349 distribution of hatchery-reared Sockeye Salmon overlapped with that of the naturally spawning
350 population, but was strongly linked to hatchery fry release sites.

351 The spawning distribution of natural-origin Sockeye Salmon was similar in the three
352 study years. Past hatchery fry release patterns (notably, most fry releases were at the mouth
353 between 2007 – 2009) may have influenced the distribution of the naturally spawning population

354 and contributed to the steadily increasing number of fish spawning in the lower river (Timm and
355 Wissmar 2014). Nevertheless, salmonid populations do not spawn uniformly or randomly in a
356 river system, but characteristically spawn in certain core areas perennially (e.g., Klett et al. 2013;
357 Cram et al. 2017), though they may expand into other habitats when density is high (Isaak and
358 Thurow 2006). A wide variety of physical factors affect this spawning site selection, including
359 interactions among water velocity, depth, gravel size, and groundwater (Beechie et al. 2008).
360 There can also be interannual variability in salmon spawning distribution due to the effects of
361 environmental factors such as flow levels, floods, and landslides. We therefore conclude that the
362 naturally-produced adult spawning distribution in this system largely reflects habitat suitability
363 and spawning site fidelity, and that of the hatchery-produced fish largely reflects fry release sites,
364 in combination with habitat suitability.

365

366 *Temporal Distribution*

367 The spawn timing of hatchery-origin Sockeye Salmon was earlier than natural-origin spawning
368 timing in all years. Recovery of adult carcasses allowed us to explore the linkage between timing
369 of hatchery fry release (itself a function of parental breeding date) and the timing of hatchery-
370 origin Sockeye Salmon in the naturally spawning population. For all sample years, our data
371 demonstrated that the distribution of spawn timing of hatchery-origin adults corresponded with
372 their timing of release as fry (hence the timing of spawning by their parents). In all years, the
373 median recovery date of hatchery-origin carcasses was earliest for early released fry, mid-timed
374 for the middle release groups, and latest for the late releases, a pattern also observed over a
375 decade earlier in Cedar River carcass surveys (WDFW 2003). These results imply a genetic
376 control over spawning timing, consistent with the high heritability of the trait as shown by a
377 number of experiments (e.g., Siitonen and Gall 1989; Sato et al. 2000; Neira et al. 2006).

378 Over multiple decades, spawning times of hatchery populations can become
379 progressively earlier (Flagg et al. 1995; Quinn et al. 2002; Ford et al. 2006), apparently from
380 inadvertent selection, and as shown by purposeful hatchery selection for the earliest returning
381 broodstock, become earlier within a single generation (Clarke et al. 2017). As our results
382 demonstrate, these early spawned fish returned earlier as adult spawners. Hatchery managers
383 may tend to spawn the early arriving fish because the total abundance of returning adult salmon
384 is uncertain and the priority is to fully utilize the hatchery's capacity. Furthermore, the eggs from

385 fish returning towards the end of the season may exceed the capacity of the facility, in which
386 case the fish might be sacrificed unspawned or returned to the river. Lastly, as is regularly
387 observed in the Cedar River, conditions in the river might be more conducive to trapping salmon
388 earlier in the season, providing another source of selection on timing. The practice of collecting
389 broodstock as soon as fish become available is understandable, but overrepresentation of early
390 returning fish may incrementally advance spawn timing. Even relatively small annual biases
391 towards earlier collection may accumulate over years to advance run timing, and this seems to be
392 happening with Cedar River Sockeye Salmon (Tillotson et al. 2018).

393

394 *Carcass Sampling*

395 The systematic sampling and categorization of all visible carcasses was important for accurately
396 describing the spatial and temporal distribution of spawning in the Cedar River. In this way, only
397 freshly dead individuals were sampled, ensuring a consistent temporal sample and limiting the
398 potential for carcass drift to < 7 days. The potential for carcass drift or biased recovery rates
399 (Zhou 2002) to obscure patterns in spatial distribution was addressed in multiple ways in our
400 study. Carcass drift alone cannot explain the clear and consistent differences in distributions of
401 carcass recoveries from the marked and unmarked groups. Data were analyzed separately for
402 male and female carcasses to account for sex-specific behavior (i.e., females tend to defend their
403 nest site and remain nearer spawning locations: Murdoch et al. 2010). Finally, and fortuitously in
404 this study, high river discharges that might increase the rate and magnitude of drift (Zhou 2002),
405 did not occur during the primary carcass collection period. In 2014 and 2015, 88% and 99% of
406 the run was complete by November 1 when higher flows occurred. In 2016, flow increased
407 earlier, on October 19, but 90% of the run was complete by that date. In all years, carcass
408 recoveries continued using the established temporally stratified approach to sample the tail end
409 of the spawning run through December.

410

411 *Hatchery Program Implications*

412 Comparing the spawning distribution and timing of hatchery- and natural-origin salmon is a
413 critical component in evaluating the effectiveness of an integrated hatchery program (Mobrand et
414 al. 2005), especially as it relates to fry release strategies. In an integrated stock (i.e., one in which
415 it is assumed all individuals have some hatchery ancestry but also experience selection in the

416 river), the spawning distribution of natural-origin generations will be influenced in some degree
417 by hatchery ancestors. As demonstrated in this study, parental spawn timing and homing fidelity
418 to fry release sites can strongly affect the distribution of the subsequent generation in Sockeye
419 Salmon. It may therefore be possible to adjust hatchery fry release strategies to promote adult
420 returns to habitats where higher survival could be expected. Such sites may be recently restored
421 reaches or high quality naturally occurring reaches where populations have been depleted due to
422 other causes. High habitat quality (i.e., sites that afford higher egg-fry survival) would be a better
423 basis for choosing release sites than simply offering convenience such as ease of river access for
424 releases. On the other hand, the strong parent-offspring links that influence the timing of
425 breeding constitute further evidence that this trait is under genetic control, and so very
426 susceptible to deliberate and inadvertent selection. Such selection might move the distribution of
427 timing in the population away from the optimal period for reproduction, given current and likely
428 future conditions.

429

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440

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640 Figure 1.—Map showing the Cedar River and locations of the Cedar River Hatchery, the
641 broodstock collection weir, and the hatchery fry release sites.

642

643 Figure 2.—Box and whisker plots of carcass recoveries (upstream of the mouth) for female
644 hatchery- and natural-origin Sockeye Salmon in the Cedar River, 2014-2016. The boundaries of
645 each box display the 25th and 75th percentiles, the horizontal bar displays the median carcass
646 recovery distance, and dots depict the 5th and 95th percentile values. (HOR=hatchery-origin,
647 NOR=natural-origin).

648

649 Figure 3.—Cumulative spawning distribution of female natural- and hatchery-origin Sockeye
650 Salmon released at the lower (rkm 1.0), middle (rkm 21.7), and upper (rkm 35.1) fry release
651 locations, 2014-2016.

652

653 Figure 4.—Cumulative spawning distribution of age-4 and age-5 female hatchery-origin Sockeye
654 Salmon in the Cedar River, 2014-2016.

655

656 Figure 5.—Proportion of hatchery-origin Sockeye Salmon carcasses collected in the Cedar River
657 by sample week, 2014-2016.

658

659 Figure 6.—Estimated hatchery- and natural-origin carcasses counted in the Cedar River
660 corrected for sampling rate, 2014-2016. (H=hatchery-origin, N=natural-origin).

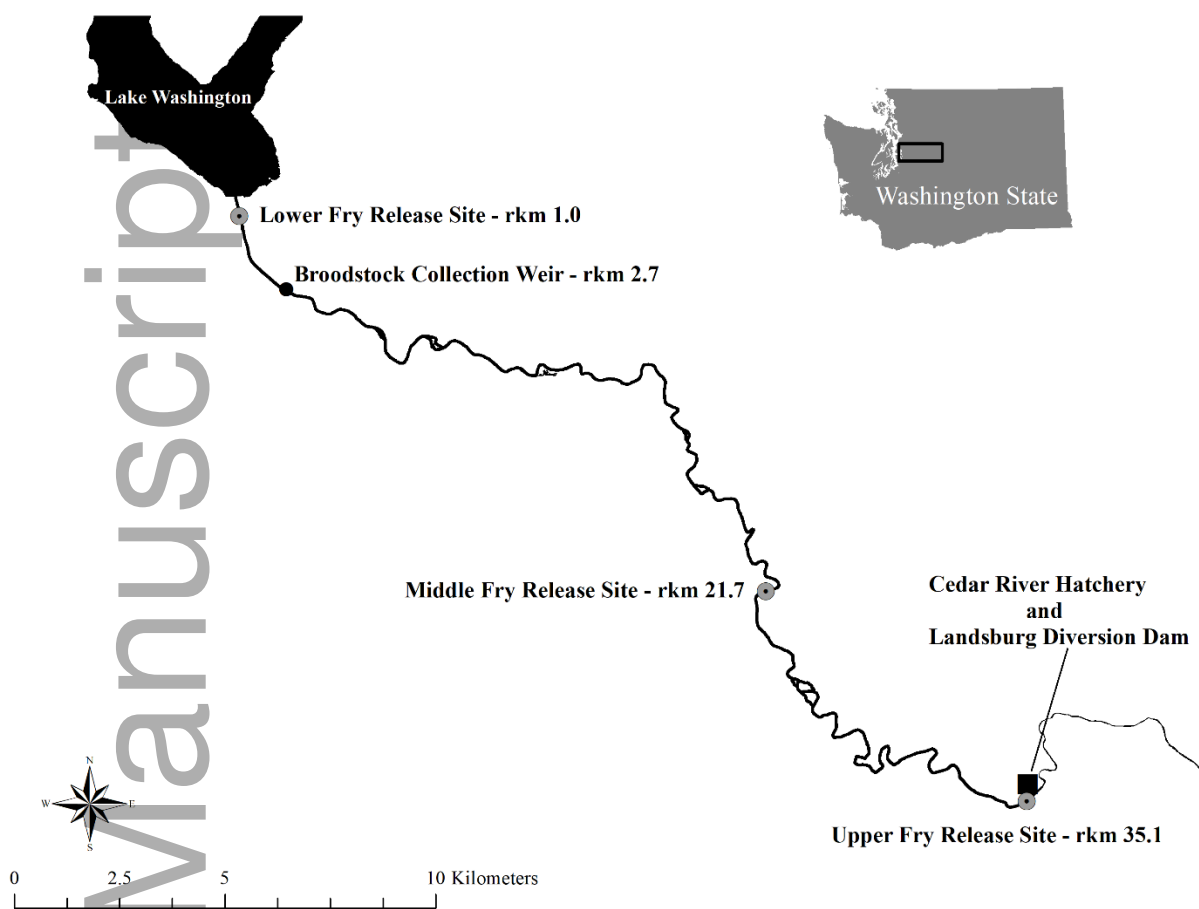
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662 Figure 7.—Cumulative temporal distribution of Sockeye Salmon carcasses for each fry release
663 time category (early, middle, late) and for natural-origin carcasses, 2014-2016.

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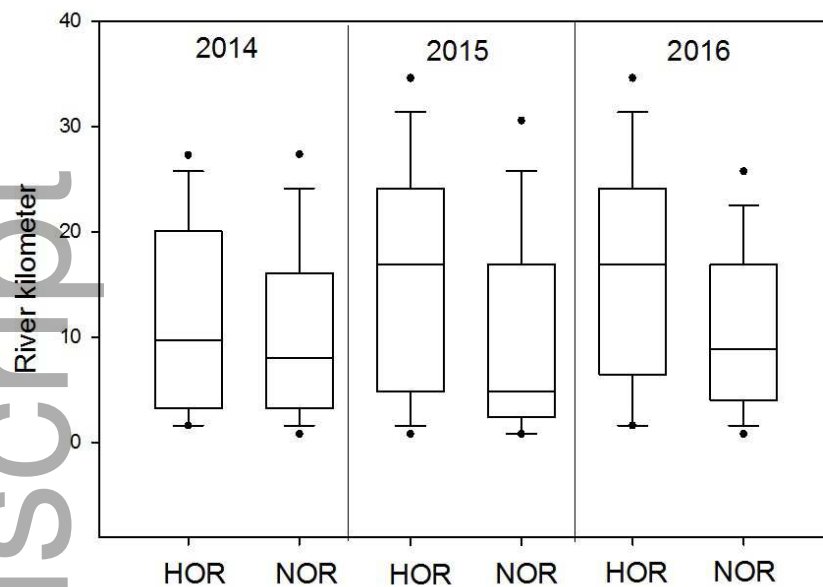
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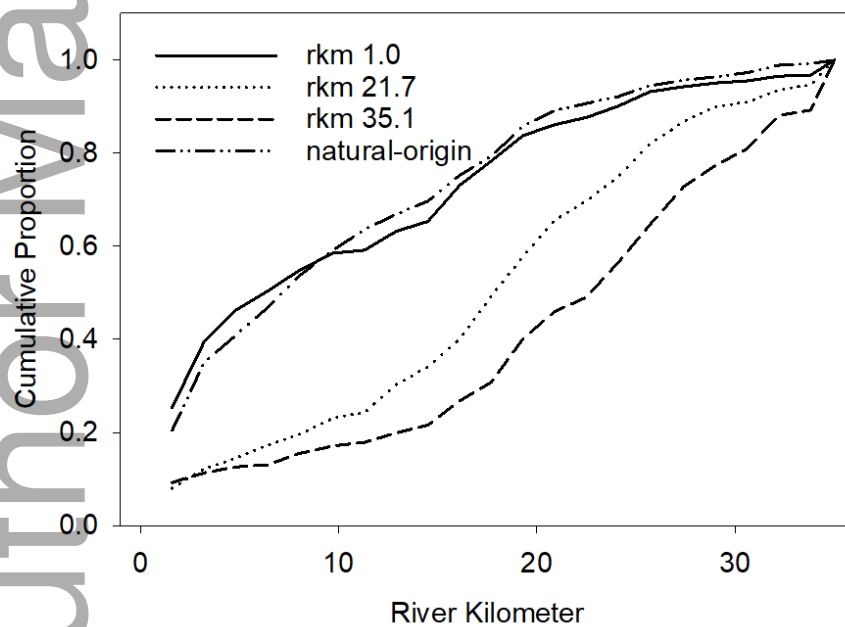
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667 Figure 1.



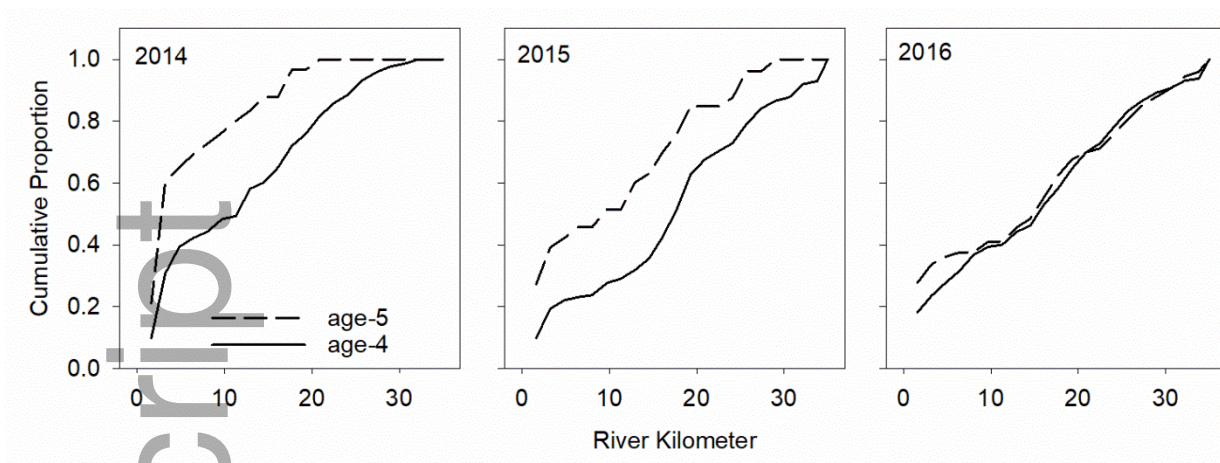
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669 Figure 2.



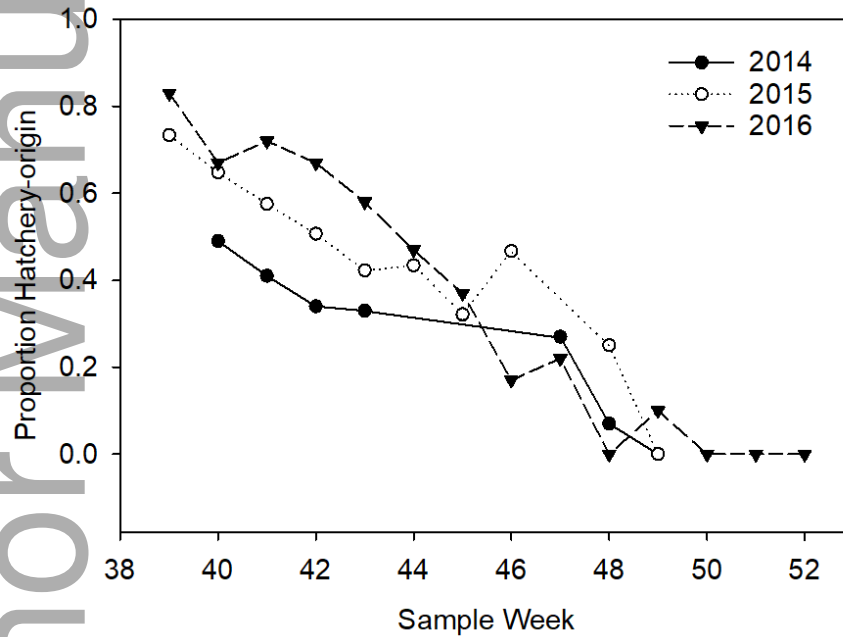
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671 Figure 3.



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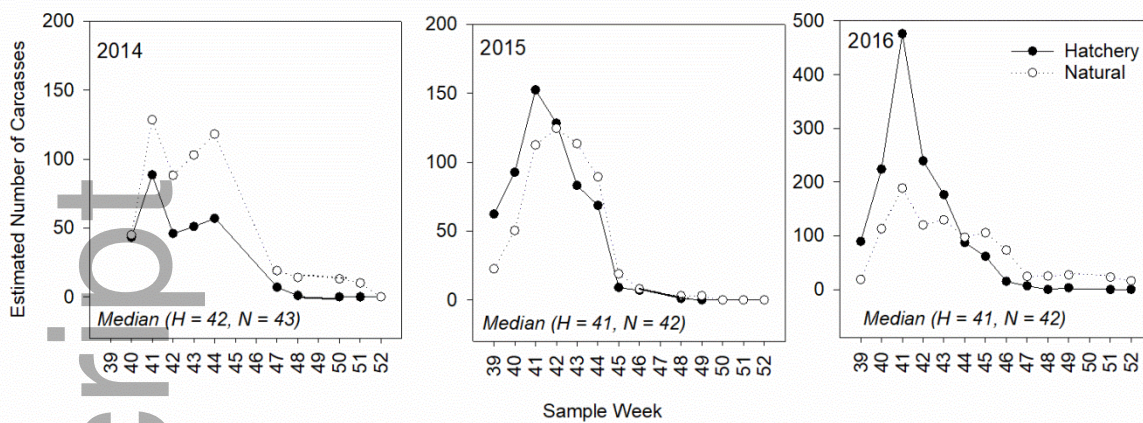
673 Figure 4.



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675 Figure 5.

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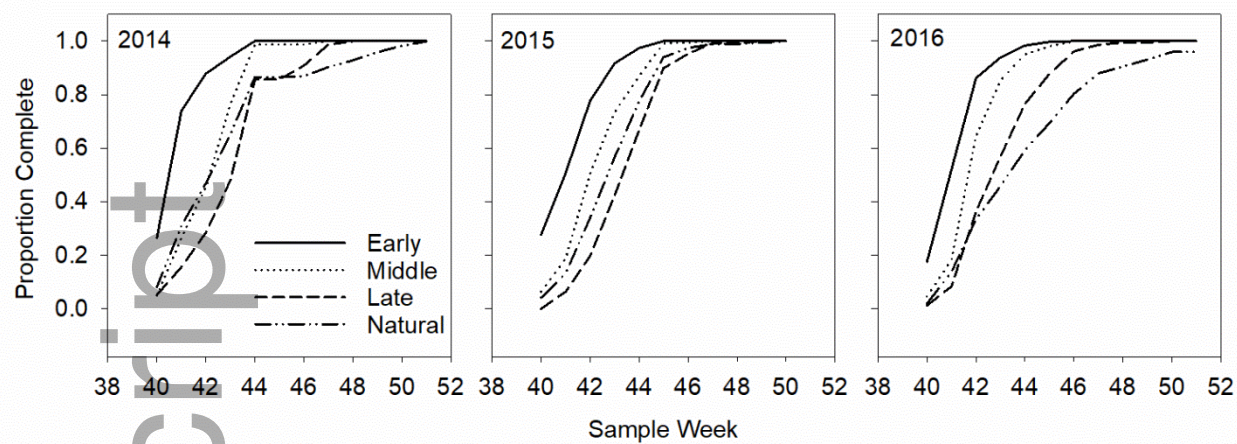


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678 Figure 6.

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681 Figure 7.

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683 Table 1.—Proportion of Cedar River Hatchery Sockeye Salmon fry by release location (lower,
 684 middle, and upper river) and release time category (early, middle, and late) groups for BY2009 -
 685 BY2012.

| Brood Year | Fry Release Location | Fry Release Time Category | | |
|------------|----------------------|---------------------------|--------|------|
| | | Early | Middle | Late |
| 2009 | Lower - rkm 1.0 | 0.31 | 0.38 | 0.31 |
| | Middle - rkm 21.7 | 0.00 | 0.00 | 0.00 |
| | Upper - rkm 35.1 | 0.00 | 0.00 | 0.00 |
| 2010 | Lower - rkm 1.0 | 0.20 | 0.26 | 0.22 |
| | Middle - rkm 21.7 | 0.17 | 0.06 | 0.09 |
| | Upper - rkm 35.1 | 0.00 | 0.00 | 0.00 |
| 2011 | Lower - rkm 1.0 | 0.12 | 0.11 | 0.12 |
| | Middle - rkm 21.7 | 0.12 | 0.14 | 0.13 |
| | Upper - rkm 35.1 | 0.11 | 0.09 | 0.06 |
| 2012 | Lower - rkm 1.0 | 0.13 | 0.13 | 0.16 |
| | Middle - rkm 21.7 | 0.09 | 0.08 | 0.12 |
| | Upper - rkm 35.1 | 0.12 | 0.11 | 0.06 |

686

687

688 Table 2.—Summary of Sockeye Salmon carcass sampling statistics including total number of
 689 otoliths recovered and observed, average annual sample rate, estimated Cedar River escapement
 690 (data source: Washington Department of Fish and Wildlife), number of broodstock collected, and
 691 percent of the estimated spawning run sampled.

| Category | 2014 | 2015 | 2016 |
|---|---------------|--------------------|-------------------|
| Number of otoliths collected (Hatchery/Natural) | 790 (272/518) | 1,136 (542/594) | 1,834 (1,059/775) |
| Number of fresh carcasses counted | 981 | 1,587 | 2,347 |
| Average annual carcass sampling rate | 80.5% | 71.6% | 78.1% |
| Estimated escapement | 16,791 | 10,648 | 11,777 |
| Number of broodstock fish collected | 6,341 | 3,286 | 4,204 |
| Percent of the estimated run sampled | 9% | 22% | 31% |

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694 Table 3.—Age composition of hatchery- and natural-origin Sockeye Salmon carcasses collected
 695 in the Cedar River (2014-2016). Age-class was determined by otolith annuli for all natural-origin
 696 carcasses, and from unique brood year marks for all hatchery-origin carcasses.

| Age-class | <u>2014 (% by age)</u> | | <u>2015 (% by age)</u> | | <u>2016 (% by age)</u> | |
|-----------|------------------------|---------|------------------------|---------|------------------------|---------|
| | Hatchery | Natural | Hatchery | Natural | Hatchery | Natural |
| 3 | 0.4 | 0.9 | 0.3 | 2.3 | 1.0 | 4.7 |
| 4 | 75.4 | 44.0 | 89.1 | 87.9 | 88.6 | 80.4 |
| 5 | 20.6 | 55.2 | 10.6 | 9.8 | 10.4 | 14.9 |
| 6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |

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699 Table 4.—Median carcass recovery distance (rkm) and Kolmogorov-Smirnov test results
 700 evaluating brood year differences in the spawning distribution of female Sockeye Salmon
 701 carcasses collected in the Cedar River, 2014-2016.

| Sample Year | Origin | Median distance (rkm) | | <i>D</i> -stat | <i>P</i> -value |
|-------------|----------|-----------------------|-------|----------------|-----------------|
| | | Age-4 | Age-5 | | |
| 2014 | Hatchery | 9.7 | 2.8 | 0.31 | 0.02 |
| | Natural | 11.3 | 6.4 | 0.23 | 0.002 |
| 2015 | Hatchery | 17.3 | 9.7 | 0.28 | 0.01 |
| | Natural | 4.8 | 6.0 | 0.12 | 0.80 |
| 2016 | Hatchery | 16.9 | 16.9 | 0.10 | 0.40 |
| | Natural | 8.9 | 8.0 | 0.12 | 0.25 |

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703 Table 5.—Kolmogorov-Smirnov test results evaluating differences in the spawn timing
 704 distribution of Sockeye Salmon carcasses from early, middle, late, and natural-origin groups and
 705 between female and males within a fry release time category that were collected in the Cedar
 706 River, 2014-2016.

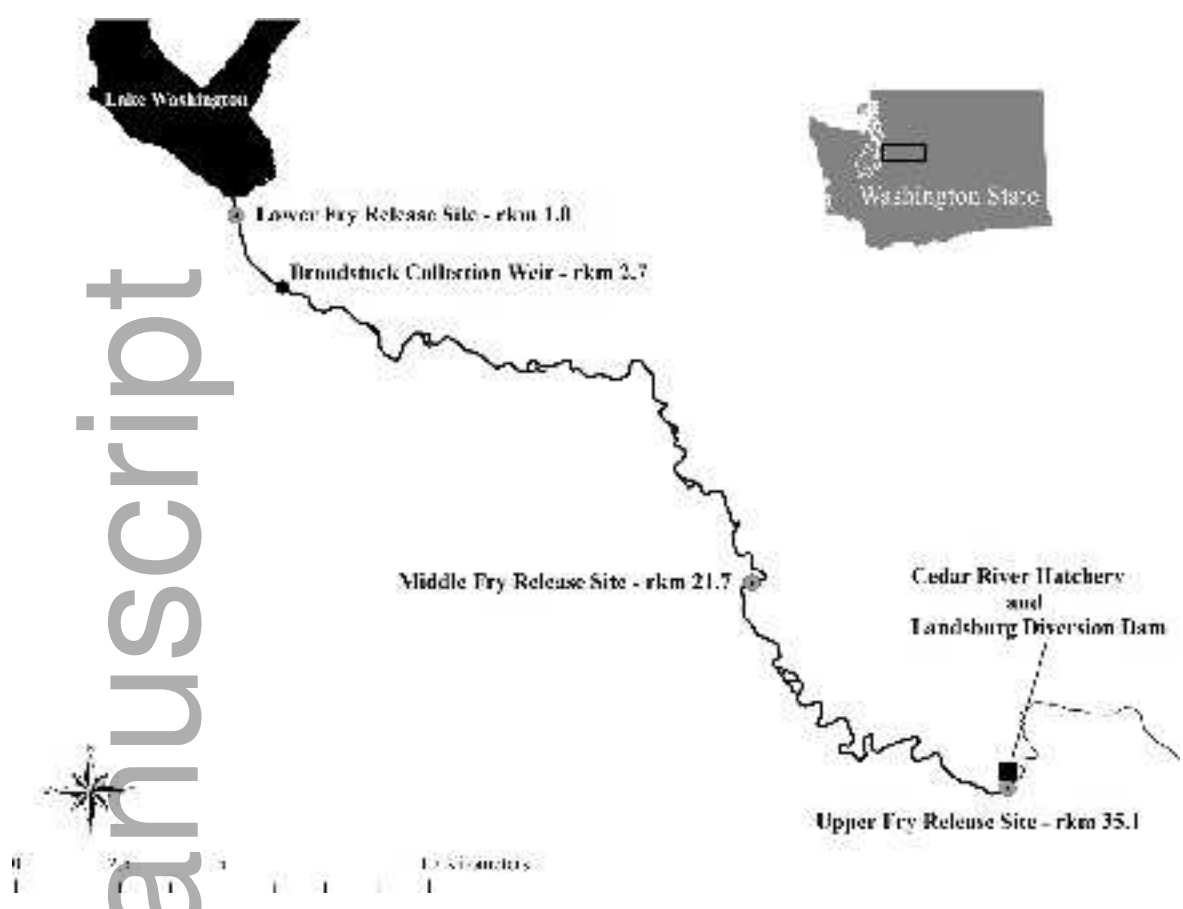
| Comparison | 2014 | | 2015 | | 2016 | |
|--|----------------|-----------------|----------------|-----------------|----------------|-----------------|
| | <i>D</i> -stat | <i>P</i> -value | <i>D</i> -stat | <i>P</i> -value | <i>D</i> -stat | <i>P</i> -value |
| Fry Release Time Category (Female and Male pooled) | | | | | | |
| Early to Natural | 0.43 | <0.0001 | 0.44 | <0.0001 | 0.53 | <0.0001 |
| Middle to Natural | 0.12 | 0.23 | 0.17 | 0.0002 | 0.40 | <0.0001 |
| Late to Natural | 0.18 | 0.02 | 0.14 | 0.02 | 0.18 | <0.0001 |
| Early to Middle | 0.48 | <0.0001 | 0.32 | <0.0001 | 0.34 | <0.0001 |
| Middle to Late | 0.29 | 0.002 | 0.31 | <0.0001 | 0.28 | <0.0001 |
| Early to Late | 0.59 | <0.0001 | 0.58 | <0.0001 | 0.50 | <0.0001 |
| Female-Male within a Fry Release Time Category | | | | | | |
| Early | 0.06 | 1.00 | 0.09 | 0.69 | 0.13 | 0.09 |
| Middle | 0.17 | 0.59 | 0.15 | 0.12 | 0.11 | 0.19 |
| Late | 0.15 | 0.77 | 0.18 | 0.15 | 0.13 | 0.01 |

| | | | | | | |
|----------------|------|------|------|------|------|---------|
| Natural-origin | 0.04 | 0.95 | 0.12 | 0.03 | 0.15 | <0.0001 |
|----------------|------|------|------|------|------|---------|

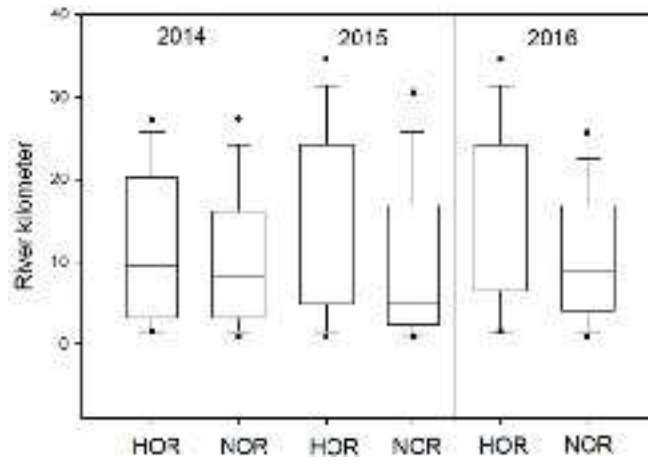
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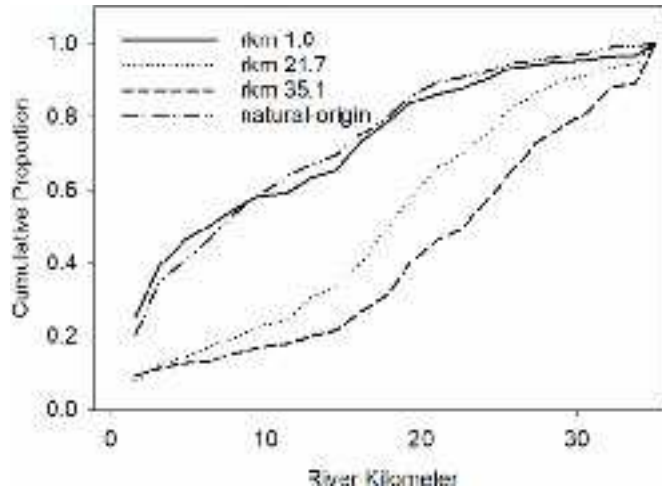
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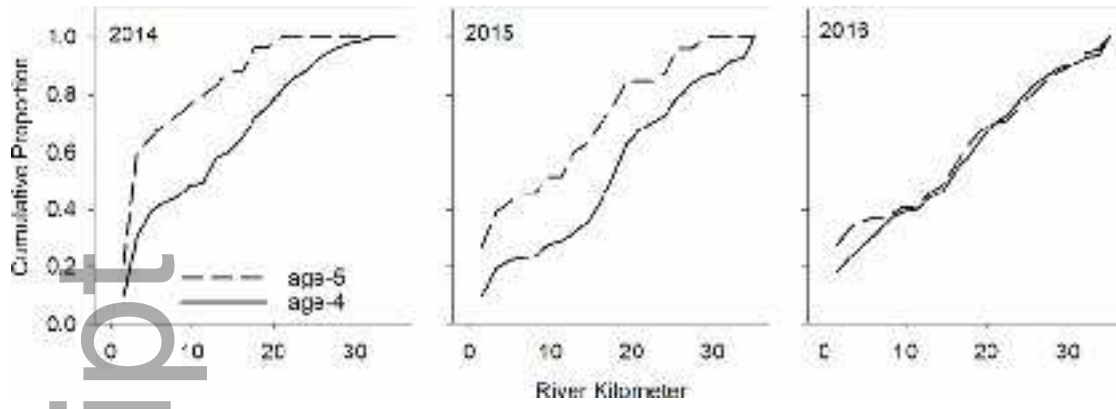
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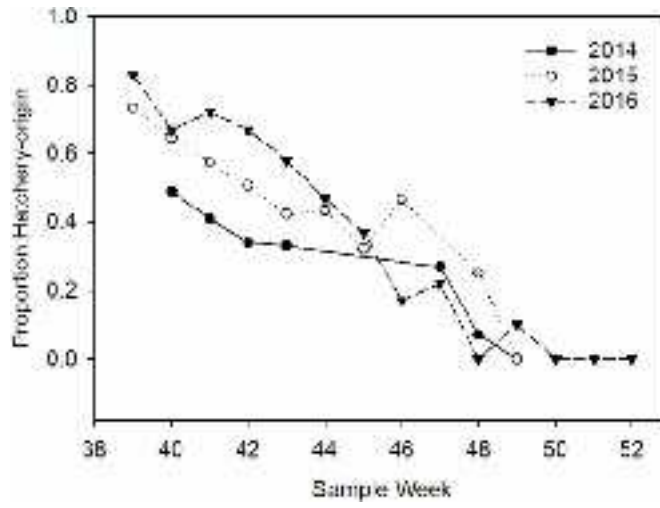


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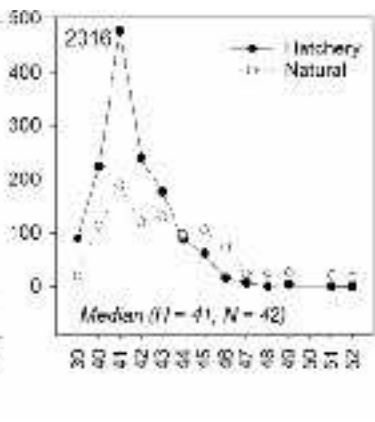
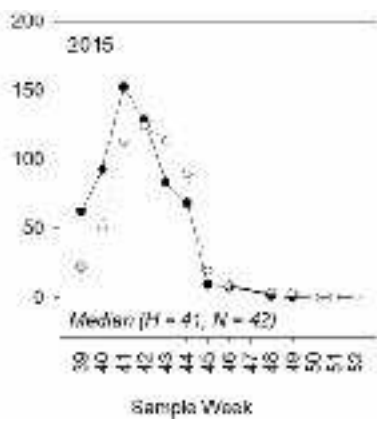
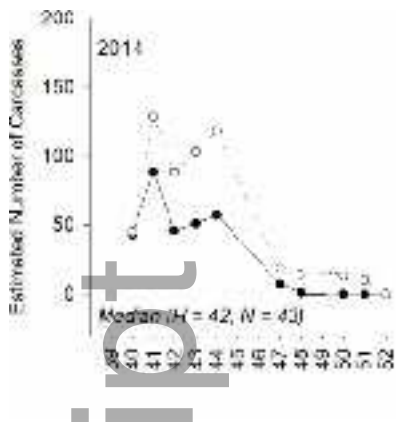


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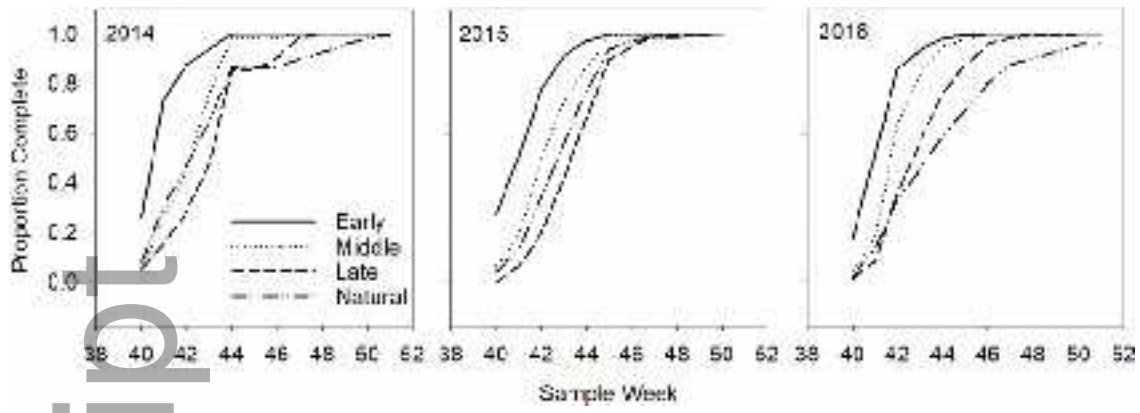


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