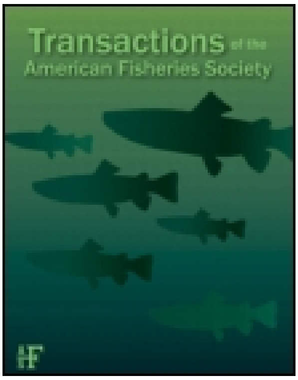

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Homing and Spawning Site Selection by Supplemented Hatchery- and Natural-Origin Yakima River Spring Chinook Salmon

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[Article]

Homing and Spawning Site Selection by Supplemented Hatchery- and Natural-Origin Yakima River Spring Chinook Salmon

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Abstract.—It is well known that salmon home to their natal rivers for spawning, but the spatial scale of homing within a river basin is poorly understood and the interaction between natal site fidelity and habitat-based spawning site selection has not been elucidated. Understanding the complex trade-offs among homing to the natal site, spawning site selection, competition for sites, and mate choice is especially important in the context of hatchery supplementation efforts to reestablish self-sustaining natural spawning populations. To address these questions, we examined the homing patterns of supplemented Yakima River spring Chinook salmon *Oncorhynchus tshawytscha* released from satellite acclimation facilities after common initial rearing at a central facility. Final spawning location depended strongly on where fish were released as smolts within the upper Yakima River basin, but many fish also spawned in the vicinity of the central rearing hatchery, suggesting that some fish imprinted to this site. While homing was clearly evident, the majority (55.1%) of the hatchery fish were recovered more than 25 km from their release sites, often in spawning areas used by wild conspecifics. Hatchery and wild fish displayed remarkably similar spawning distributions despite very different imprinting histories, and the highest spawning densities of both hatchery and wild fish occurred in the same river sections. These results suggest that genetics, environmental and social factors, or requirements for specific spawning habitat may ultimately override the instinct to home to the site of rearing or release.

Philopatry is a fundamental aspect of salmon biology, and homing to the river of origin for reproduction has been extensively documented. Homing to the natal river, or homing to the natal tributary in large river systems, is generally very precise (Dittman and Quinn 1996). Different species and even particular populations may demonstrate different rates of straying, but in general salmon return to the river basin from which they originated (Hendry et al. 2004). On a finer spatial scale, as fish enter the specific river or river reach from which they originated, the relative precision of homing to the natal site is poorly understood. There is considerable genetic and demographic evidence indicating that within a metapopulation, many salmon "stray" from their natal site (Rieman and Dunham 2000; Schtickzelle and Quinn 2007). At the same time, fine-scale homing has also been extensively documented using both genetic analysis (Bentzen et al. 2001; Neville et al. 2006; Kitanishi et al. 2009) and mark–recapture studies (Quinn et al. 2006). The process that ultimately dictates a salmon's fidelity to its natal site presumably involves a complex trade-off among selective pressures to home, spawning habitat selection, competition, and mate choice (Dittman and Quinn 1996; Hendry et al. 2004).

Homing by adult salmon is governed by the olfactory discrimination of and attraction to their natal waters (Dittman and Quinn 1996). Before their seaward

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migration, juvenile salmon learn to identify (imprint on) site-specific odors associated with their home stream and later use these retained odor memories to guide the final phases of their spawning migration (Hasler and Scholz 1983). This imprinting process is critical for the successful completion of the spawning migration, and salmon that do not experience their natal waters during appropriate juvenile stages are more likely to stray to nonnatal sites (Lister et al. 1981; Quinn 1993; Dittman and Quinn 1996). Many studies have identified the parr–smolt transformation as an especially important period for olfactory imprinting (Hasler and Scholz 1983; Dittman et al. 1996). However, in the wild, many species display complex juvenile migration patterns, indicating that imprinting must occur at earlier developmental periods as well (e.g., Beckman et al. 2000; Habicht et al. 2007).

Understanding the relationship between early rearing experience and ultimate homing success has become increasingly important in managing artificial propagation programs as they shift from segregated production hatcheries to integrated supplementation hatcheries, which are designed to enhance wild populations by integrating hatchery- and natural-origin fish on the spawning grounds (Flagg et al. 2000; Mobrand et al. 2005). Typically, supplementation hatcheries artificially spawn naturally produced adults, rear the embryos and juveniles at the central hatchery, and then release juveniles from satellite acclimation facilities so that the fish will ultimately return to those locations to spawn (Bugert 1998; Flagg and Nash 1999; Flagg et al. 2000). Salmon generally return to the site from which they were released (Donaldson and Allen 1958; Ricker 1972), but fish that are transported and released off-site tend to stray more than fish that are released directly from the rearing site (Lister et al. 1981; reviewed by Quinn 1993).

Straying may reflect a salmon's inability to locate the natal site (due to improper juvenile imprinting or adult orientation) or could represent the fish's decision not to use the natal site due to environmental and demographic factors. For example, if habitat quality is degraded at the natal site, salmon might be expected to stray in search of appropriate spawning habitat (e.g., Leider 1989). Even subtle differences in environmental quality and habitat (e.g., gravel type, temperature, flow, groundwater influences, water chemistry, biological productivity, and olfactory cues) might influence spawning site selection, thereby affecting the decision to home or stray (e.g., Baxter and Hauer 2000; Geist 2000). Decision-based straying is a special concern for supplementation programs where acclimation sites may be developed in areas that do not have appropriate spawning habitat, and homing salmon may therefore choose not to spawn near the release site.

In this study, we examined the patterns of homing and spawning site selection by spring Chinook salmon *Oncorhynchus tshawytscha* in relation to a supplementation hatchery's rearing and release locations to examine the efficacy of satellite acclimation sites in facilitating successful imprinting and colonization of targeted habitat. Specifically, we hypothesized that the distribution of spawners within the Yakima River, Washington, would reflect homing to and spawning in the vicinity of the acclimation–imprinting release site or early rearing site. To test these hypotheses, we mapped and analyzed the spawning distribution of wild Yakima River spring Chinook salmon and hatchery-reared Chinook salmon released from three acclimation facilities in the upper Yakima River basin as part of a supplementation program.

Methods

Study site and population.—The Yakima River is a major tributary of the Columbia River system in central Washington (Figure 1). The upper Yakima River spring Chinook salmon population spawns in an area encompassing approximately 200 river kilometers (rkm) throughout the main-stem Yakima River and its major tributaries (Cle Elum and Teanaway rivers) upstream from Roza Dam (located at rkm 208; rkm 0 = confluence with the Columbia River). The highest densities of spawning occur upstream from the city of Ellensburg (Figure 1). Maturing adults migrate into the Yakima River basin in the spring (May–June) and spawn from mid-September to early October. Juveniles spend a year in freshwater before migrating to the ocean in their second spring. Most adults (80–90%) return at age 4 (after 2 years in the ocean), although small percentages of both males and females return at age 5 (1–5%) and 10–20% of males return at age 3 (Knudsen et al. 2006).

The Yakima–Klickitat Fishery Project (YKFP) supplementation program began artificial production of upper Yakima River spring Chinook salmon at the Cle Elum Supplementation and Research Facility (hereafter, Cle Elum Hatchery) in 1997. The YKFP is an integrated hatchery program specifically designed to increase natural production by promoting natural spawning between wild and supplemented fish. An additional goal of the program is to re-establish natural spawning in underused habitat by imprinting juvenile salmon at satellite acclimation facilities located throughout the upper Yakima River basin. Broodstock collection, rearing, and marking protocols for the YKFP supplementation program have been described earlier (Knudsen et al. 2006; Fast et al. 2008). Briefly,

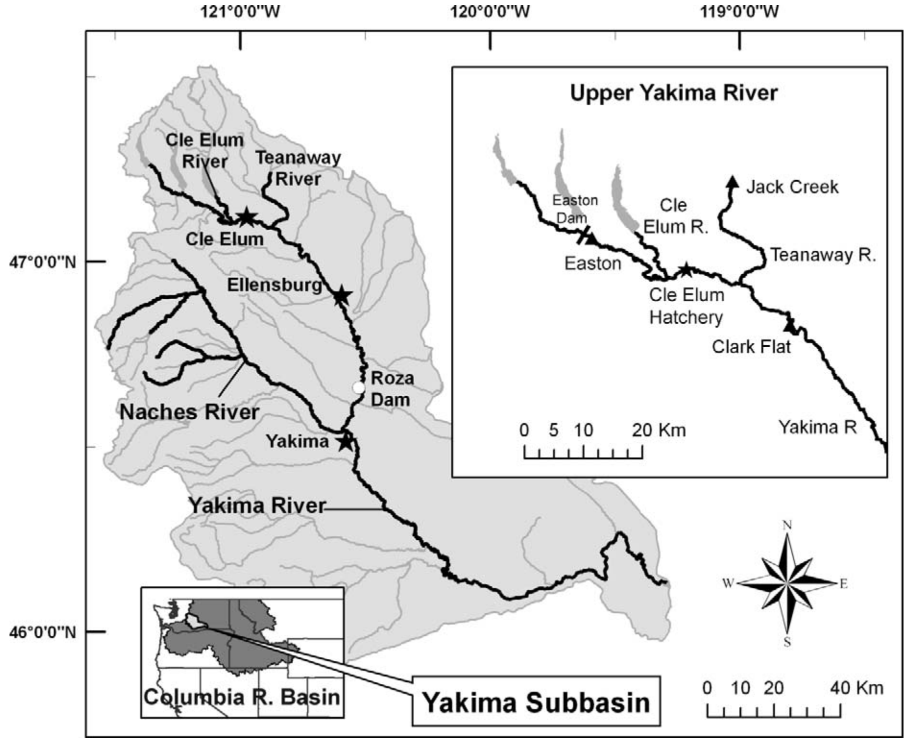

FIGURE 1.—The Yakima River basin, Washington, including the Cle Elum and Teanaway rivers. All upper Yakima River spring Chinook salmon are enumerated as homing adults at Roza Dam, and broodstock for the supplementation program are collected there. Fertilization and initial juvenile rearing occur at the Cle Elum Hatchery (Cle Elum Supplementation and Research Facility; star in upper inset). In their second spring, the fish are transferred to one of three acclimation sites (Easton, Jack Creek, and Clark Flat; black triangles in upper inset) for final rearing and release. The lower inset shows the location of the Yakima River subbasin within the Columbia River basin.

eggs were fertilized and incubated at the Cle Elum Hatchery during September through April, and juveniles were transferred to outdoor raceways for approximately 10 additional months of rearing. The water source for incubation and rearing was a combination of well water and Yakima River water taken just upstream from the hatchery; the proportion of volume from each water supply was adjusted seasonally to maintain appropriate rearing temperatures. In February of their second year (before the parr–smolt transformation), fish were transferred to one of three satellite facilities used for acclimation, imprinting, and release (Easton, Clark Flat, and Jack Creek; Figure 1). The water source for each facility was river water pumped from just upstream of each site. After 2–8 weeks of acclimation (typically from April to early June), smolts were allowed to volitionally migrate from the facilities over the next 2 months. After this period, all remaining fish were forced out of the acclimation sites. All fish were marked with release-site-specific coded wire tags, color-coded elastomer eye tags (Northwest Marine Technology, Inc.), and adipose fin clips. Upon return as adults, all hatchery-reared fish were allowed to spawn naturally within the basin. At the time these adult fish were returning to the spawning areas of the upper Yakima River basin, no fish were present and no water was running at any of the acclimation sites. However, the Cle Elum Hatchery facility had juvenile spring Chinook salmon rearing at the site, and water released from its outflow (rkm 290) would have contained conspecific odors.

Spawning ground surveys.—To assess the spatial distribution of hatchery-origin and naturally produced adults, we conducted comprehensive annual carcass surveys of the upper Yakima River basin from 2002 to 2005. Beginning in late September, the entire upper Yakima River and its Chinook salmon-bearing tributaries (Cle Elum and Teanaway rivers) from the Keechelus Dam to Ellensburg were surveyed once (Figure 1). We did not survey for carcasses in the main-stem Yakima River above Easton Dam during 2002 or 2003 or in the 15.1-km section immediately above Ellensburg during

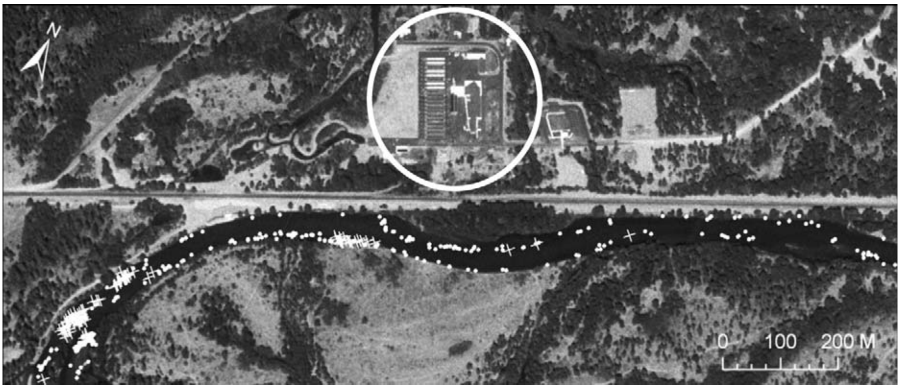

FIGURE 2.—An example of data plotted on an aerial photograph of a 1.0-km section of the Yakima River, Washington, at the Cle Elum Hatchery (within the circle), showing the Chinook salmon carcass recovery locations (white dots) and redd locations (white × symbols) during 2002–2005.

2002. Retrospective analysis of redd counts from 2002 and 2003 suggested that less than 4% of the upper Yakima River population spawned in these areas during those years (YKFP 2008). Surveys in the Cle Elum River and the main-stem Yakima River below Easton Dam were staggered to avoid temporal bias in any one area. This was accomplished by initially surveying approximately one-half of each 10-km reach from Easton Dam to Ellensburg (Figure 1). After completing this first pass, the rest of each reach was surveyed during a second pass through the entire spawning area. The Teanaway River and main-stem Yakima River above Easton Dam were surveyed only once in each year (Figure 1). Surveyors identified and recovered as many carcasses as possible, recording the location with a hand-held Global Positioning System (GPS) data logger (Geoexplorer 3 or Geo-XT, Trimble; Figure 2). For each recovered carcass, the following data were collected: (1) date, (2) origin of the fish (i.e., hatchery versus naturally spawned), (3) gender and age-class (adult or jack), (4) length (fork length and mid-eye to hypural plate), and (5) location and color of elastomer tags. Tissue containing coded wire tags was collected for later tag recovery and analysis to determine site of release. After sampling, the tail of each carcass was removed to avoid resampling and the carcass was returned to the river. During these same periods, Yakama Nation tribal biologists conducted weekly surveys for spring Chinook salmon redds throughout the upper Yakima River and its tributaries until spawning was completed. Each redd was flagged with color-coded ribbons indicating the date when the redd was identified, and the location of each redd was subsequently mapped with a GPS data logger (Figure 2).

We assumed that the site of carcass recovery within the upper Yakima River approximated the site of spawning. If Chinook salmon spawned in multiple locations or migrated long distances after spawning, our results might be confounded by these movements. Chinook salmon typically build only one redd and defend it until they are near death (Healey 1991; Bentzen et al. 2001; Murdoch et al. 2009a). Female spring Chinook salmon carcasses in another upper Columbia River tributary were closely associated with their redds (Murdoch et al. 2009b). Furthermore, unlike rivers where flooding can move carcasses considerable distances (Zhou 2002), flow throughout most of the Yakima River basin is tightly regulated by dams and early fall floods did not occur during the years in which our studies were carried out.

Geographical information systems analysis.—To calculate the location of each carcass and redd, we used the linear referencing features of ArcView version 9.1 (Environmental Systems Research Institute, Inc.). River routes for the Yakima River and appropriate tributaries were created from the StreamNet Pacific Northwest hydrology data set (StreamNet 2001), and these shape files were used to calculate river distances upstream from an arbitrary starting point near Ellensburg. Sites of carcass recovery were located along the appropriate linear river route in the ArcGIS Desktop program using a snap tolerance of 1,000 m to ensure that all points were included, even in areas of extensive river braiding. Carcass densities were calculated using the ArcView Spatial Analyst extension with a search radius of 50 m and an output cell size of 100 m.

Statistical analysis.—We first assessed spawning site selection using a log-linear regression model with a Poisson distribution to test for effects of several categorical factors (acclimation site, gender, age at return, return year, and brood year) on the distribution of spawners in the main-stem Yakima River and its

TABLE 1.—Total number of spring Chinook salmon migrating past Roza Dam into the upper Yakima River basin, Washington, 2002–2005 (total run), and number of carcasses recovered and mapped from each hatchery release group (Easton, Clark Flat, and Jack Creek) or from wild fish.

	Year			
Group	2002	2003	2004	2005
Total run (*n*)	8,091	3,258	10,187	5,717
Carcasses sampled (*n*)				
Wild	395	162	1,982	1,348
Easton	404	96	177	52
Clark Flat	608	192	397	47
Jack Creek	324	138	298	187
Total number sampled (% of total run)	1,731 (21.4%)	588 (18.1%)	2,854 (28.0%)	1,634 (28.6%)

tributaries. We assessed brood year as a surrogate for imprinting history because fish from the same brood year experienced the same environmental conditions during out-migration, and hatchery fish experienced the same acclimation procedures. We selected the most parsimonious model using Akaike's information criterion (Crawley 2002) and then developed subsequent models to examine interactions between significant main effects and other categorical factors. Significant effects were further characterized by pairwise comparisons between treatments using Pearson's chi-square contingency analysis.

Within-tributary distribution was assessed using carcass location (rkm) as the dependent variable. These data did not satisfy tests for normality, so all subsequent analyses of rkm data used nonparametric statistical tests. To test for the effects of acclimation site, gender, return year, brood year, and age at return on within-tributary distribution, we first used Kruskal–Wallis tests, which were then followed by pairwise comparisons between treatments using Wilcoxon's signed rank tests. To determine whether supplementation influenced the overall spatial distribution of spawning within the upper Yakima River subbasin, we used Wilcoxon's signed rank tests to assess whether hatchery fish collectively demonstrated different spawning patterns from wild fish. The test statistic presented represents the chi-square approximation for these tests.

We used similar nonparametric Kruskal–Wallis tests to examine whether fidelity to the release site or to Cle Elum Hatchery (defined as the distance carcasses were recovered from these sites) depended on release site or origin. We first tested actual distance from the acclimation site or from Cle Elum Hatchery as a direct measure of fidelity. To account for any bias related to tributary length, we conducted the analysis of distance from the acclimation site a second time by assigning all tributary spawners to the point on the main-stem Yakima River at the tributary's confluence and measuring the distance to the acclimation site (or tributary mouth in the case of Jack Creek fish). To determine whether early rearing at Cle Elum Hatchery influenced the spawning location within the main-stem Yakima River, we also conducted a secondary analysis of distance from the hatchery using only those fish recovered in the main stem of the Yakima River below Easton Dam. Log-linear models were developed and tested using S-plus version 8.0 (Insightful Corp., Seattle, Washington). All other statistical analyses used JMP software (SAS Institute, Inc., Cary, North Carolina). The significance level α was set at 0.05 for all tests.

Results

During the 4 years of this study (2002–2005), 27,524 spring Chinook salmon returned to the upper Yakima River basin to spawn naturally (Table 1). The percentage of hatchery-reared fish each year ranged from 20.3% to 76.4%. We recovered and mapped the location of 6,807 carcasses (24.7%) that could be definitively assigned as wild or to specific acclimation sites. Recovery rates were similar for wild (26.4%) and hatchery-reared fish (25.6%) but were higher for 4- and 5-year-old adults (28.6%) than for 3-year-old fish (8.8%).

Distribution among Rivers

The recovery location of hatchery fish depended strongly on the site of release. Our initial log-linear regression analysis of potential factors affecting the distribution of salmon among rivers (the Cle Elum, Teanaway, and main-stem Yakima rivers) identified acclimation site as the only significant main effect. Subsequent year-by-year pairwise comparisons between wild fish and the hatchery fish from the different acclimation sites indicated that wild fish and fish released from the Jack Creek facility on the Teanaway River each had different distributions from all other groups in all years ($P \leq 0.05$) except 2005 (Jack Creek versus Clark Flat: $P = 0.29$; wild fish versus Clark Flat: $P = 0.58$). Most fish within each group spawned in the main-stem Yakima River (Figures 3, 4), but this tendency was greater for fish released from the two main-stem acclimation sites (Easton: 95.5%; Clark Flat: 91.9%) than for wild fish (83.4%) or fish released from the Jack Creek site (61.2%). Fish released from the Jack Creek facility were the only group with a substantial proportion of spawners in the Teanaway River (Figure 3). Few of the other groups spawned in the Teanaway River. On a proportional basis, the Cle Elum River was used most frequently by wild fish, but a significant percentage of hatchery fish also spawned in this tributary even though none of these fish had been released there (Figure 3). Few of the fish released from main-stem acclimation facilities were recovered in the Cle Elum River, whereas 14.9% of the Jack Creek fish (the only hatchery group released from a tributary) were recovered in the Cle Elum River, the other major tributary in the upper Yakima River basin (Figure 3).

For each group, the distribution of fish among the Cle Elum, Teanaway, and main-stem Yakima rivers did not differ among years ($P \leq 0.22$); the exception was Jack Creek fish ($\chi^2 = 91.49$, $P < 0.001$; Figure 3). The annual variation for Jack Creek fish was driven primarily by the percentage of Jack Creek fish spawning in the Teanaway River, which varied from a high of 37.7% in 2002 to a low of 2.7% in 2005. We observed no significant differences in tributary distribution based on gender, age at return, or release year.

Distribution within Rivers

The distribution of fish within the Yakima River and its two major tributaries also depended strongly on juvenile rearing history (main-stem Yakima River: $\chi^2 = 453.4$, $P \leq 0.001$; Teanaway River: $\chi^2 = 14.4$, $P \leq 0.001$; Cle Elum River: $\chi^2 = 40.3$, $P \leq 0.001$; Figure 4). We hypothesized that the distribution of spawners within the Yakima River would reflect homing to and spawning in the vicinity of the acclimation–imprinting release site. Consistent with this hypothesis, fish released from the Easton acclimation site (the farthest upstream in the basin) spawned farthest upstream in the main-stem Yakima River (mean rkm = 58.82), whereas fish released at the Clark Flat site spawned farther downriver (mean rkm = 46.67; Kruskal–Wallis test: $\chi^2 = 413.0$, $P \leq 0.001$). The distribution of Jack Creek fish in the main-stem Yakima River (mean rkm = 46.5) was similar to that of Clark Flat fish (Wilcoxon's signed rank test: $\chi^2 = 0.2$, $P = 0.646$). The distribution of wild fish in the main-stem Yakima River was distinct from and intermediate between the distributions of all other groups (mean rkm = 52.8, $\chi^2 \geq 82.5$, $P \leq 0.001$; Figure 4). Although the absolute distribution of fish in the main-stem Yakima River varied between years ($\chi^2 = 137.8$, $P \leq 0.001$), the relative location of carcasses within the main-stem Yakima River consistently followed a pattern in which Easton fish spawned the farthest upstream, Jack Creek and Clark Flat fish spawned the farthest downstream, and wild fish spawned in an intermediate reach. Gender and age had significant effects on carcass distribution within the Yakima River ($\chi^2 = 88.8$, $P \leq 0.001$). Adult females (4 or 5 years old) were recovered higher in the watershed (mean rkm = 53.96) than were adult males (mean rkm = 50.72). Three-year-old males (jacks) were recovered farther downstream than either adult males or females (mean rkm = 46.64).

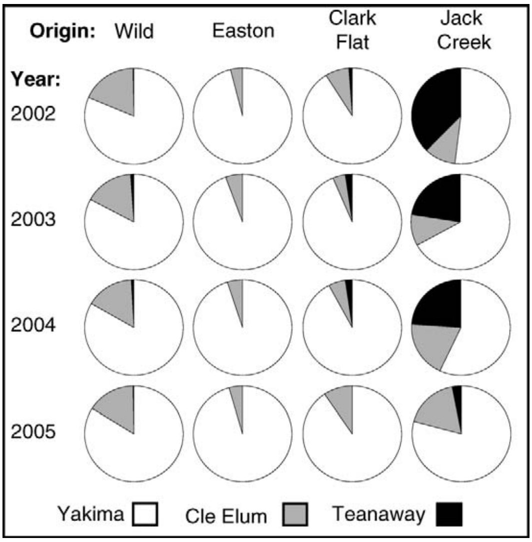

FIGURE 3.—Relative distribution of Chinook salmon carcasses recovered in the Cle Elum, Teanaway, and main-stem Yakima rivers, Washington. Pie charts represent the proportion of hatchery fish (released from three acclimation sites) or wild fish that were recovered in each river during each year (2002–2005).

Distributions within the two tributaries also depended on release site ($\chi^2 \geq 14.4$, $P \leq 0.001$). Within the Teanaway River, fish released from the Jack Creek acclimation site at rkm 27.6 tended to spawn below the acclimation site (mean rkm = 10.8), but fish from the other two groups recovered from the Teanaway River spawned even farther downstream ($\chi^2 \geq 4.2$, $P \leq 0.04$; Figure 4). There was no difference in the distribution of wild fish (mean rkm = 8.2) and Clark Flat fish (mean rkm = 5.9) within the Teanaway River ($\chi^2 = 2.6$, $P = 0.11$). Comparisons between years were not possible due to small sample sizes. In the Cle Elum River, wild fish spawned farthest upstream (mean rkm = 10.1), followed by fish released from Jack Creek (mean rkm = 9.4), Clark Flat (mean rkm = 8.1), and Easton (mean rkm = 7.5; $P \leq 0.05$). We observed no significant differences in distribution within the tributaries based on gender, age at return, or release year.

Distribution Relative to Acclimation Sites

Site of acclimation and release influenced the general distribution of hatchery spawners, but most fish were not recovered near their respective release sites. Overall, the mean distance carcasses were found from their acclimation–release sites was 29.3 rkm, and several fish were recovered 80 rkm away from their

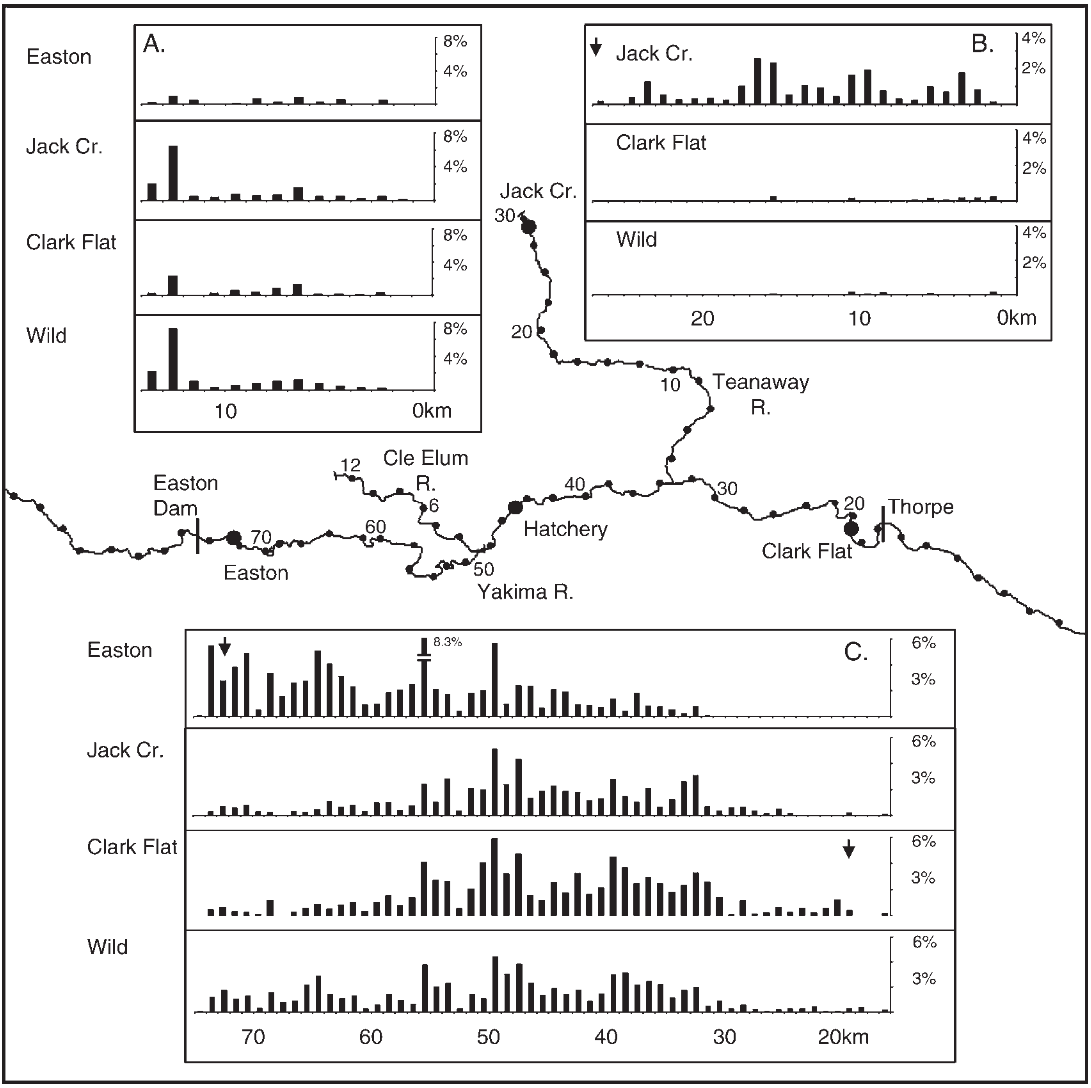

FIGURE 4.—Distribution of Chinook salmon carcasses from each of the hatchery release groups (Easton, Jack Creek, and Clark Flat) or from wild fish within the **(A)** Cle Elum River, **(B)** Teanaway River, and **(C)** main-stem Yakima River, Washington. The data represent the number of carcasses recovered in each 1-km segment of river expressed as a percentage of the total number of carcasses recovered from that group in the entire upper Yakima River basin (except the areas above Easton Dam and below Thorpe; see text for explanation). The river kilometer (rkm) values on the map correspond to the same rkm values on the graphs. Data were pooled for all years of the study (2002–2005). Large black circles on the map and arrows on the graphs indicate the locations of the acclimation–release sites.

acclimation–release sites (Figure 5). The distance from release to recovery locations depended strongly on the site ($\chi^2 = 968.8$, $P \leq 0.001$). Easton fish demonstrated the highest fidelity (mean distance from the release site = 13.8 rkm) in comparison with fish from the Clark Flat facility (mean distance = 29.6 rkm) and the Jack Creek facility (mean distance = 40.8 rkm).

The especially poor homing fidelity of Jack Creek fish, as suggested by the mean distance of nearly 41 rkm from the release site, partly reflects the acclimation site's location high in the Teanaway River system (27.6 rkm from the mouth); thus, any Jack Creek fish that spawned outside the Teanaway River automatically had 27.6 km added to its fidelity measure. Therefore, we reanalyzed the data after assigning all tributary spawners to the point on the main-stem Yakima River at the confluence with the tributary and assessed distance to the acclimation site (or the tributary mouth

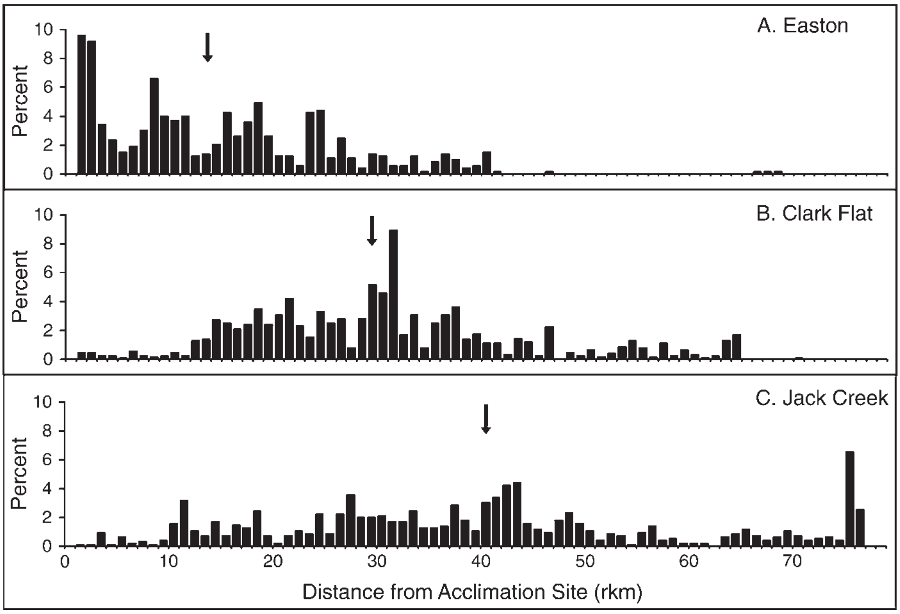

FIGURE 5.—Percentage of hatchery Chinook salmon carcasses (from three release groups) that were recovered within each 1-km bin of distance (river kilometers [rkm]) from the acclimation–release site: **(A)** Easton; **(B)** Clark Flat; and **(C)** Jack Creek, Washington. Arrows indicate the mean carcass distance from the acclimation site.

in the case of Jack Creek fish). Using this measure, fish released from the Easton facility still demonstrated the highest fidelity to their acclimation site (mean distance from the release site = 13.5 rkm) and Clark Flat fish still showed relatively poor site fidelity (mean distance from the release site = 29.0 rkm). As expected under these criteria, Jack Creek fish demonstrated higher fidelity to the area around the confluence with the Teanaway River (mean distance from the Teanaway River = 14.4 rkm). Using this distance as a measure of homing, Jack Creek fish showed significantly higher fidelity to their release tributary than Clark Flat fish did to their acclimation site ($\chi^2 = 491.2$, $P \leq 0.001$) but less fidelity than was exhibited by Easton fish ($\chi^2 = 3.85$, $P = 0.049$).

In general, fish released from acclimation sites high in the watershed tended to spawn below the acclimation site, whereas fish released lower in the basin were recovered above the acclimation site (Figure 4). For example, the Jack Creek acclimation facility is located high in the Teanaway River system (27.6 rkm from the mouth), and of the 226 Jack Creek fish recovered in this system none were recovered above the acclimation site and less than 5% were recovered within 5 rkm downstream from the site. Similarly, 90.9% of the fish from the Easton acclimation site located in the upper reaches of the main-stem Yakima River (rkm 72.60) were recovered below the acclimation site. On the other hand, 99.4% of the fish released from the Clark Flat facility, which was located relatively low on the main-stem Yakima River (rkm 19.2), were recovered upstream from that facility. These patterns largely reflect the distribution of available spawning habitat as indicated by historical redd distributions (Major and Mighell 1969; YKFP 2008).

Distribution Relative to the Cle Elum Hatchery

To assess whether spawning site selection by supplemented fish was influenced by imprinting and homing to the early rearing site at the Cle Elum Hatchery, we also examined the distance that hatchery carcasses were recovered from the Cle Elum Hatchery as a function of rearing history (Figure 6). Hatchery fish spawned closer to the hatchery than did wild fish ($\chi^2 = 83.6$, $P \leq 0.001$), but the distance from the hatchery varied among acclimation site groups (Kruskal–Wallis test: $\chi^2 = 247.2$, $P \leq 0.001$). Within the Yakima River, fish released from the Clark Flat and Jack Creek facilities tended to spawn near the Cle Elum Hatchery (Clark Flat: 8.64 rkm from the hatchery; Jack Creek: 8.60 rkm from the hatchery), whereas Easton fish spawned farther from the hatchery site (14.27 rkm from the hatchery; Kruskal–Wallis test: $P \leq 0.001$; Figure 6). Both the Clark Flat and Jack Creek groups tended to spawn closer to the hatchery site than did

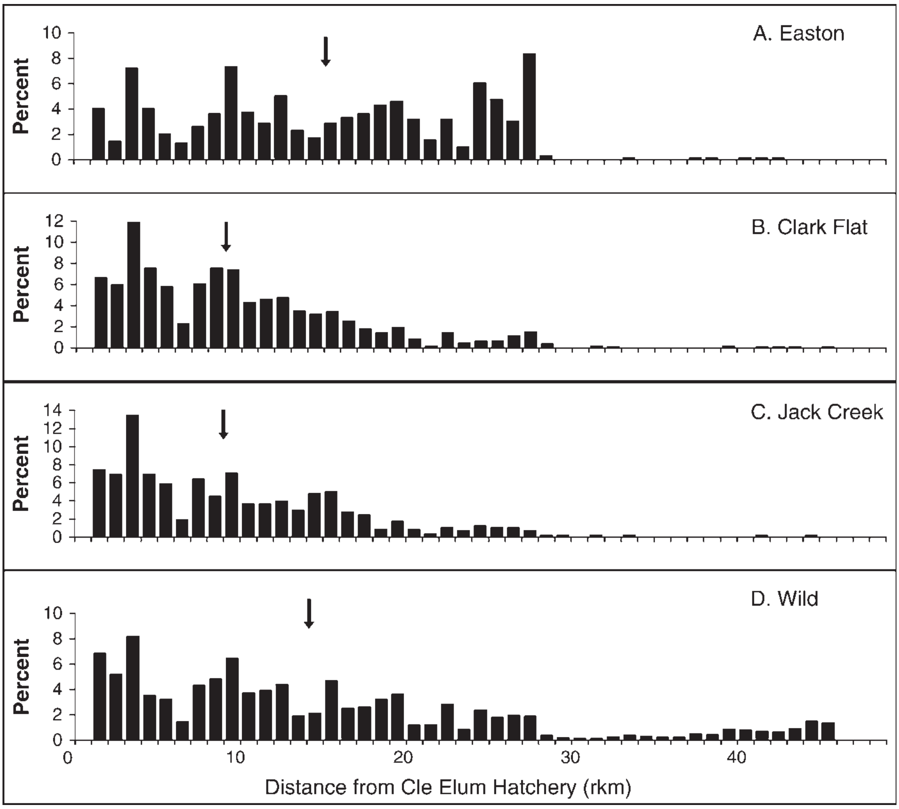

FIGURE 6.—Percentage of hatchery or wild Chinook salmon carcasses that were recovered in the main-stem Yakima River, Washington, within each 1-km bin of distance (river kilometers [rkm]) from the inlet of Cle Elum Hatchery: **(A)** Easton release group; **(B)** Clark Flat release group; **(C)** Jack Creek release group; and **(D)** wild fish. Arrows indicate the mean carcass distance from the hatchery.

wild fish (13.34 rkm from the hatchery; $\chi^2 \geq 43.2$, $P \leq 0.001$; Figure 6).

Relative Distributions of Hatchery and Wild Fish

At the spatial scale we analyzed, wild and hatchery fish (all acclimation sites collectively) displayed similar spawning distributions within the upper Yakima River basin (Figure 7). Density analysis showed considerable overlap of the two groups in terms of which sections of the river were used for spawning and which areas had the highest densities of spawners (Figure 7). Indeed, if the entire upper Yakima River basin is divided into 1-km segments, six of the eight highest density segments for wild spawners were also the highest density segments for hatchery spawners. The closest acclimation site to these high-density segments was over 18 rkm away. Within the main-stem Yakima River below Easton Dam, the spawning locations of hatchery and wild fish were remarkably similar ($\chi^2 = 0.68$, $P = 0.41$; Figure 8A). In this area, both groups had median spawning locations of 50.1 rkm that were within 71 m of each other and had similar interquartile ranges (Figure 8A). However, the spawning distributions of hatchery and wild fish diverged for the Cle Elum River, the Teanaway River, and the main-stem Yakima River above Easton Dam. In the Cle Elum River, both groups had high densities of spawners in the uppermost reach (Figure 7), but on average wild fish spawned higher in the river than did hatchery fish (wild fish: mean rkm = 10.1; hatchery fish: mean rkm = 8.76; $\chi^2 = 26.7$, $P \leq 0.001$) and the distribution of carcasses differed between groups (Figure 8B). Spawning in the Teanaway River was dominated (91.7% of recoveries) by hatchery fish (Figure 7). The distributions of hatchery and wild fish tended to differ within the Teanaway River (Figure 8C), but the low number of wild fish reduced the statistical power and the mean spawning locations were not significantly different. The 14.7-rkm stretch of the Yakima River above Easton Dam (Figure 1) was used almost exclusively (98.3% of 241 fish recovered) by wild fish (Figure 7).

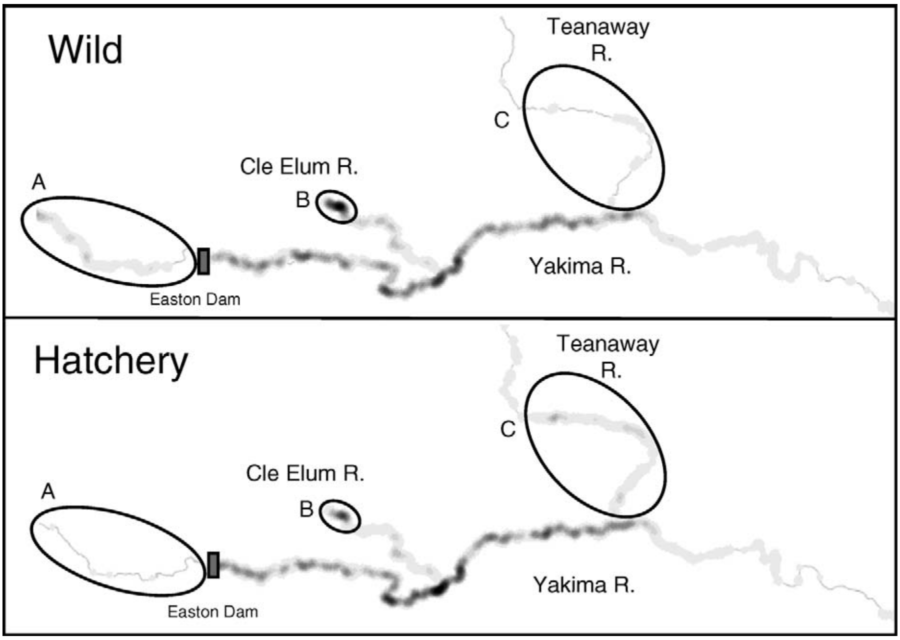

FIGURE 7.—Relative density (number of carcasses/river kilometer) of hatchery (all acclimation sites pooled) and wild Chinook salmon carcasses recovered in the upper Yakima River basin, Washington. The distribution and density of hatchery and wild spawners were similar except in the main-stem Yakima River above Easton Dam (A), at the base of the Cle Elum Dam on the Cle Elum River (B), and in the Teanaway River (C). The absolute densities of wild fish were higher than those of hatchery fish, but the density scales were standardized so that relative differences in abundance within groups could be compared.

Discussion

Homing Patterns

The spawning location of spring Chinook salmon depended strongly on juvenile release site. Fish released from main-stem acclimation facilities returned and spawned primarily in the main-stem Yakima River (92.7%), and almost all fish recovered in the Teanaway River had been released there as juveniles. Furthermore, the spatial patterns of adult recoveries within

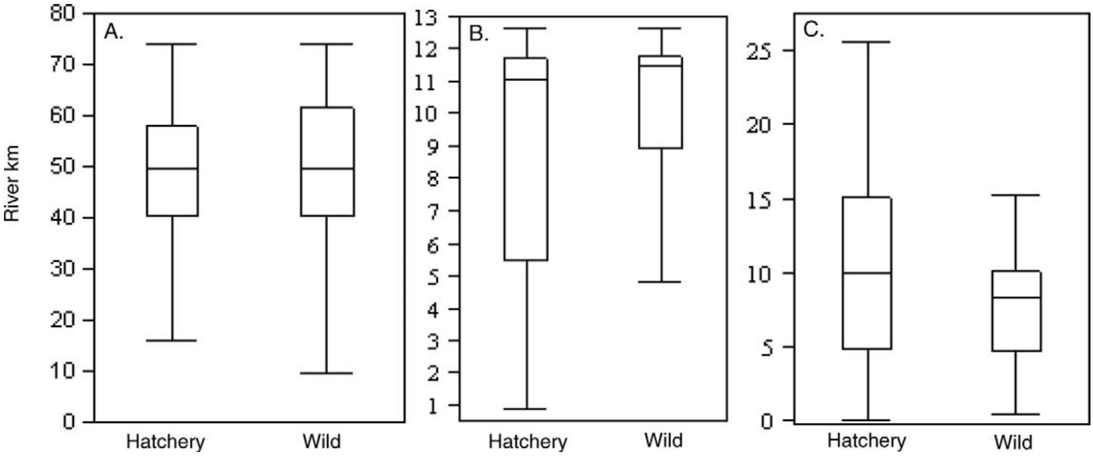

FIGURE 8.—Distribution of hatchery (all acclimation sites pooled) and wild Chinook salmon carcass recoveries within the **(A)** main-stem Yakima River, **(B)** Cle Elum River, and **(C)** Teanaway River, Washington. In each box-and-whisker plot, the horizontal line indicates the median river kilometer of carcass recovery, the box represents the interquartile range, and the whiskers show the range of the recovery locations to the outermost data points.

each river also indicated the influence of release location; Chinook salmon released from upstream acclimation sites were generally recovered farther upstream than fish released from downstream sites. These results suggest that naturally spawning hatchery Chinook salmon demonstrated homing fidelity to their release locations and that the use of satellite acclimation–release facilities can influence the spatial distribution of supplemented fish. These findings are consistent with previous studies indicating that salmon tend to imprint and return as adults to the site at which they were released and initiated their downstream migration (reviewed by Lister et al. 1981; Quinn 1993). However, our study is the first to comprehensively assess homing at a fine spatial scale to identify the ultimate spawning locations of naturally spawning hatchery fish released from multiple sites.

The parr–smolt transformation has been implicated as an important developmental window for imprinting (Hasler and Scholz 1983; Dittman et al. 1996), and our results indicated that spring Chinook salmon exposed to acclimation site waters during smolting were able to imprint to the release site. However, the recovery of many hatchery fish in the vicinity of Cle Elum Hatchery suggests that the fish also learned homing cues at earlier developmental periods as well as during smolting. In particular, many fish released from the Clark Flat (37.8%) and Jack Creek (40.5%) acclimation sites were recovered within 5 rkm of Cle Elum Hatchery even though the facility is more than 25 rkm from these acclimation sites. Returns of hatchery salmon to the rearing site instead of the release site have been observed previously (Lister et al. 1981; Johnson et al. 1990; Slaney et al. 1993), and imprinting before smolting is consistent with the life history patterns of wild spring Chinook salmon, which often display extensive seasonal downstream migrations away from the natal site before smolting (Beckman et al. 2000) but later return to their natal area to spawn.

Interestingly, a significant percentage of hatchery fish were recovered in the Cle Elum River, where no hatchery fish were released. These fish might have imprinted to Cle Elum River water while being reared at Cle Elum Hatchery. The hatchery intake is located 2 km downstream from the confluence of the Cle Elum and Yakima rivers (Figure 1), and during part of the year a large percentage of the water at the hatchery intake originates from the Cle Elum River. Salmon are able to discriminate between different mixtures of stream waters (Fretwell 1989) but can be attracted to unfamiliar nonnatal locations if imprinted odors are present (Hasler and Scholz 1983; Fretwell 1989). Interestingly, carcass recovery in the Cle Elum River was greater for fish from the Jack Creek facility than for fish released from the two closer main-stem acclimation sites. One possible explanation for this is that higher-order streams (such as the Teanaway and Cle Elum rivers) may share chemosensory properties and fish may imprint "generically" to chemicals associated with tributary water. Moreover, movement into both tributaries involves a similar "right turn" (Figure 1), and some aspect of imprinting and homing might also involve learning navigational routes as has been demonstrated in the main-stem Columbia River (Keefer et al. 2006).

Taken together, the acclimation-site-specific patterns of homing we observed are most consistent with the sequential imprinting hypothesis proposed by Harden-Jones (1968) and Brannon (1982). Those authors hypothesized that salmon learn a series of olfactory waypoints as they migrate through freshwater and then retrace this odor sequence as adults. Thus, wild Yakima River spring Chinook salmon may learn olfactory information as they emerge from the natal gravel, during subsequent seasonal downstream movements, and during their seaward migration as smolts. For hatchery fish that are transported and released off site, the sequential imprinting hypothesis predicts that fish will return to the release site where they initiated their seaward migration. At that point, if the fish can detect the odors of their rearing site, they will continue on to it. This prediction has been largely supported by transport studies indicating that if the rearing site is close enough to the release site, most fish will return as adults to the rearing site (Lister et al. 1981; Johnson et al. 1990). Interestingly, if the release site is upstream from the rearing site, returning salmon will often bypass the initial rearing site and return to the release site (Quinn et al. 1989; Brannon and Quinn 1990; but see Johnson et al. 1990).

The sequential imprinting scenario would explain the large percentage of Clark Flat and Jack Creek fish recovered upstream from their release sites in the vicinity of Cle Elum Hatchery or in the Cle Elum River. On the other hand, relatively few fish from the Easton acclimation site were recovered in the vicinity of the hatchery or in the Cle Elum River despite the proximity of this acclimation site to the hatchery and the Yakima–Cle Elum River confluence. Consistent with the sequential imprinting hypothesis, these fish may have returned to the vicinity of the acclimation site upstream from Cle Elum Hatchery and then, being unable to detect any earlier imprint signal (i.e., chemical cues emanating from the hatchery), chose to spawn in the vicinity of their last familiar homing cue.

Spawning Site Selection

While many of the Chinook salmon released as part of the YKFP demonstrated some degree of homing to their acclimation sites or to Cle Elum Hatchery, perhaps the most striking finding was that hatchery fish were frequently recovered in areas far from any juvenile rearing site. While sequential imprinting and homing could explain many of the patterns of spawning site selection that we observed, learning and homing to site-specific cues cannot explain the recovery of hatchery fish in areas they had never experienced. Interestingly, the majority of hatchery fish recovered away from juvenile rearing or release sites were found in areas that were also used extensively by wild fish for spawning (Figure 7). One possible explanation for this observation is that both hatchery and wild fish require specific spawning habitat, and at some point the need to find an appropriate spawning location ultimately supersedes the instinct to home to the site of rearing or release. We observed that fish released from the Easton acclimation site demonstrated high fidelity to spawning areas near this site, while fish released from the other acclimation facilities tended to spawn in areas far from their release sites. These patterns of straying and spawner distributions coincided with the relative distribution of spring Chinook salmon spawning habitat in the upper Yakima River basin (Snyder and Stanford 2001; Yakima Subbasin Fish and Wildlife Planning Board 2004). Thus, Chinook salmon may initially home back to their release site but then begin searching for appropriate spawning habitat if it is not available at the release site.

An alternative explanation for the overlapping spawning distributions of hatchery and wild fish is that both groups share a genetic or phenotypic predisposition for specific spawning habitat or locations. Locally adapted salmon populations tend to demonstrate higher homing fidelity relative to transplants, which suggests a genetic component to homing and spawning site selection (Bams 1976; Candy and Beacham 2000). Furthermore, McIsaac and Quinn (1988) inferred a genetic basis for homing in Chinook salmon that were reared and released away from their ancestral spawning grounds but that returned to their ancestral sites as adults. Hatchery fish in the present study were generated from the wild population of upper Yakima River spring Chinook salmon; thus, an innate preference for certain habitat types or locations may have prompted hatchery fish to ultimately choose the same spawning sites as wild fish. Hatchery fish also display many of the same phenotypic traits as the wild fish they were derived from (Knudsen et al. 2006; Busack et al. 2007), and if salmon choose spawning sites appropriate for their phenotypes (Morbey and Hendry 2008), they may choose similar spawning sites as wild fish. Finally, the overlap in spawning distributions between hatchery and wild fish may result in part from social interactions, such as conspecific attraction and mate choice.

While the spawning distributions of hatchery and wild fish overlapped extensively throughout the upper Yakima River basin, the area above Easton Dam (Figure 1) remained largely free of hatchery fish during the 4 years of this study. One unique feature of this area is that fish must migrate through Lake Easton, the reservoir created by Easton Dam, to reach the Yakima River spawning areas located above the lake. It is possible that only fish that imprint at and migrate from this area will return to this site because migration through the lake presents too great a navigational or motivational challenge for adults that did not experience the route as juveniles. Alternatively, the reservoir may mask or buffer any olfactory cues that might be indicative of appropriate spawning habitat upstream.

Implications for Supplementation

One of the basic premises of salmon supplementation programs is that artificially produced fish will increase natural production by either (1) increasing the number of successful, naturally spawning adults in areas already occupied by wild spawners or (2) establishing self-sustaining spawning populations in habitat that is underused or that has been restored or reconnected (Flagg et al. 2000; Mobrand et al. 2005). Depending upon the primary goals of a program, the ability to rear and release hatchery fish that will return to spawn in appropriate locations is critical for supplementation success (Bugert 1998). For programs specifically designed as integrated hatchery programs, it is anticipated that wild and hatchery fish will spawn with one another and use similar spawning areas. Our results suggest that when analyzed on a basinwide scale, spatial integration of hatchery and wild spawners was largely successful. These results contrast with the few supplementation program studies that have analyzed the spatial distribution of adult hatchery and wild spring Chinook salmon and shown that hatchery fish often spawn in different areas (in many cases farther downstream) than wild fish (Hoffnagle et al. 2008; Murdoch et al. 2008).

Several factors may have contributed to the spatial overlap of hatchery and wild fish in the Yakima River (e.g., genetics, fish densities, or available spawning habitat), but one likely reason for the similar distribution of hatchery and wild fish is that hatchery juveniles were released from multiple locations throughout the Yakima River basin. The use of multiple release sites has also been successful in achieving a wide distribution of spawners in other supplementation programs (Garcia et al. 2004). If YKFP Chinook salmon had been released from only one acclimation site (as occurs in many supplementation programs; e.g., Hoffnagle et al. 2008; Murdoch et al. 2008), we might have reached different conclusions about homing patterns of hatchery-reared fish. Fish released from the three acclimation facilities displayed noticeably different patterns of dispersal relative to the release site.

One of the goals of the YKFP is to establish natural spawning in areas that are underused or where habitat has been restored. Results from our study indicate that this strategy has produced mixed results for the upper Yakima River spring Chinook salmon population. For example, some of the fish released into the Teanaway River returned to spawn in this tributary, which was rarely used before supplementation. However, most of the fish released in the Teanaway River strayed to other areas to spawn. Coincident habitat restoration efforts in the Teanaway River watershed may ultimately improve the success of the supplementation efforts in this tributary. Similarly, releases from the Clark Flat facility increased the number of fish spawning lower in the main-stem Yakima River, but few of these fish spawned in the vicinity of their release site.

Our results collectively suggest that using off-site releases to expand the range and abundance of naturally spawning salmon populations can be successful, but it must be done in close coordination with habitat and ecological assessments of appropriate release locations (Pearsons and Hopley 2001) and, where necessary, in conjunction with habitat improvements to ensure that fish will return to the target locations. Furthermore, the operation and siting of rearing hatcheries and acclimation–release sites must incorporate an understanding of the developmental periods of sensitivity for imprinting in different salmon species. Finally, even for the best release locations, it is likely that normal metapopulation dynamics and spawning site selection will result in some movement of hatchery fish to spawning areas away from the release site. Therefore, it is also important to weigh any potential negative consequences of in-basin straying (Goodman 2005) with the benefits of supplementation. If population levels are relatively healthy, it may be appropriate to allow wild fish to naturally colonize spawning areas as they are reclaimed or rehabilitated (e.g., Milner and Bailey 1989; Anderson and Quinn 2007).

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References

Anderson, J. H., and T. P. Quinn. 2007. Movements of adult coho salmon (*Oncorhynchus kisutch*) during colonization of newly accessible habitat. Canadian Journal of Fisheries and Aquatic Sciences 64:1143–1154.

Bams, R. A. 1976. Survival and propensity for homing as affected by presence or absence of locally adapted paternal genes in two transplanted populations of pink salmon (*Oncorhynchus gorbuscha*). Journal of the Fisheries Research Board of Canada 33:2716–2725.

Baxter, C. V., and F. R. Hauer. 2000. Geomorphology, hyporheic exchange, and selection of spawning habitat by bull trout (*Salvelinus confluentus*). Canadian Journal of Fisheries and Aquatic Sciences 57:1470–1481.

Beckman, B. R., D. A. Larsen, C. Sharpe, B. Lee-Pawlak, C. B. Schreck, and W. W. Dickhoff. 2000. Physiological status of naturally reared juvenile spring Chinook salmon in the Yakima River: seasonal dynamics and changes associated with smolting. Transactions of the American Fisheries Society 129:727–753.

Bentzen, P., J. B. Olsen, J. E. McLean, and T. P. Quinn. 2001. Kinship analysis of Pacific salmon: insights into mating, homing, and timing of reproduction. Journal of Heredity 92:127–136.

Brannon, E. L. 1982. Orientation mechanisms of homing salmonids. Pages 219 –227 *in* E. L. Brannon and E. O. Salo, editors. Salmon and trout migratory behavior symposium. University of Washington, Seattle.

Brannon, E. L., and T. P. Quinn. 1990. A field test of the pheromone hypothesis for homing by Pacific salmon. Journal of Chemical Ecology 16:603–609.

Bugert, R. M. 1998. Mechanics of supplementation in the Columbia River. Fisheries 23(1):11–20.

Busack, C., C. M. Knudsen, G. Hart, and P. Huffman. 2007. Morphological differences between adult wild and first-generation hatchery upper Yakima River spring Chinook salmon. Transactions of the American Fisheries Society 136:1076–1087.

Candy, J. R., and T. D. Beacham. 2000. Patterns of homing and straying in southern British Columbia coded-wire tagged Chinook salmon (*Oncorhynchus tshawytscha*) populations. Fisheries Research 47:41–56.

Crawley, M. J. 2002. Statistical computing: an introduction to data analysis using S-Plus. Wiley, London.

Dittman, A. H., and T. P. Quinn. 1996. Homing in Pacific salmon: mechanisms and ecological basis. Journal of Experimental Biology 199:83–91.

Dittman, A. H., T. P. Quinn, and G. A. Nevitt. 1996. Timing of imprinting to natural and artificial odors by coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 53:434–442.

Donaldson, L. R., and G. H. Allen. 1958. Return of silver salmon, *Oncorhynchus kisutch* (Walbaum) to point of release. Transactions of the American Fisheries Society 87:13–22.

Fast, D. E., D. Neeley, D. T. Lind, M. V. Johnston, C. R. Strom, W. J. Bosch, C. M. Knudsen, S. L. Schroder, and B. D. Watson. 2008. Survival comparison of spring Chinook salmon reared in a production hatchery under optimum conventional and seminatural conditions. Transactions of the American Fisheries Society 137:1507–1518.

Flagg, T. A., B. A. Berejikian, J. E. Colt, W. W. Dickhoff, L. W. Harrell, D. J. Maynard, C. E. Nash, M. S. Strom, R. N. Iwamoto, and C. V. W. Mahnken. 2000. Ecological and behavioral impacts of artificial production strategies on the abundance of wild salmon populations. A review of practices in the Pacific Northwest. NOAA Technical Memorandum NMFS-NWFSC-41.

Flagg, T. A., and C. E. Nash. 1999. A conceptual framework for conservation hatchery strategies for Pacific salmonids. NOAA Technical Memorandum NMFS-NWFSC-38.

Fretwell, M. R. 1989. Homing behavior of adult sockeye salmon in response to a hydroelectric diversion of homestream waters at Seton Creek. International Pacific Salmon Fisheries Commission, Vancouver.

Garcia, A. P., W. P. Connor, D. J. Milks, S. J. Rocklage, and R. K. Steinhorst. 2004. Movement and spawner distribution of hatchery fall Chinook salmon adults acclimated and released as yearlings at three locations in the Snake River basin. North American Journal of Fisheries Management 24:1134–1144.

Geist, D. R. 2000. Hyporheic discharge of river water into fall Chinook salmon (*Oncorhynchus tshawytscha*) spawning areas in the Hanford Reach, Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 57:1647–1656.

Goodman, D. 2005. Selection equilibrium for hatchery and wild spawning fitness in integrated breeding programs. Canadian Journal of Fisheries and Aquatic Sciences 62:374–389.

Habicht, C., L. W. Seeb, and J. E. Seeb. 2007. Genetic and ecological divergence defines population structure of sockeye salmon populations returning to Bristol Bay, Alaska, and provides a tool for admixture analysis. Transactions of the American Fisheries Society 136:82–94.

Harden-Jones, F. R. 1968. Fish migration. Arnold, London.

Hasler, A. D., and A. T. Scholz. 1983. Olfactory imprinting and homing in salmon. Springer-Verlag, Berlin.

Healey, M. C. 1991. Life history of chinook salmon. Pages 311–394 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Hendry, A. P., V. Castric, M. T. Kinnison, and T. P. Quinn. 2004. The evolution of philopatry and dispersal: homing versus straying in salmonids. Pages 52–91 *in* A. P. Hendry and S. C. Stearns, editors. Evolution illuminated: salmon and their relatives. Oxford University Press, Oxford, UK.

Hoffnagle, T. L., R. W. Carmichael, K. A. Frenyea, and P. J. Keniry. 2008. Run timing, spawn timing, and spawning distribution of hatchery- and natural-origin spring Chinook salmon in the Imnaha River, Oregon. North American Journal of Fisheries Management 28:148–164.

Johnson, S. L., M. F. Solazzi, and T. E. Nickelson. 1990. Effects on survival and homing of trucking hatchery yearling coho salmon to release sites. North American Journal of Fisheries Management 10:427–433.

Keefer, M. L., C. C. Caudill, C. A. Peery, and T. C. Bjornn. 2006. Route selection in a large river during the homing migration of Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 63:1752–1762.

Kitanishi, S., T. Yamamoto, and S. Higashi. 2009. Microsatellite variation reveals fine-scale genetic structure of masu salmon, *Oncorhynchus masou*, within the Atsuta River. Ecology of Freshwater Fish 18:65–71.

Knudsen, C. M., S. L. Schroder, C. A. Busack, M. V. Johnston, T. N. Pearsons, W. J. Bosch, and D. E. Fast. 2006. Comparison of life history traits between first-generation hatchery and wild upper Yakima River spring Chinook salmon. Transactions of the American Fisheries Society 135:1130–1144.

Leider, S. A. 1989. Increased straying by adult steelhead trout, *Salmo gairdneri*, following the 1980 eruption of Mount St Helens. Environmental Biology of Fishes 24:219–229.

Lister, D. B., D. G. Hickey, and I. Wallace. 1981. Review of the effects of enhancement strategies on the homing, straying, and survival of Pacific salmonids. Report to the Department of Fisheries and Oceans, Vancouver, British Columbia.

Major, R. L., and J. L. Mighell. 1969. Egg-to-migrant survival of spring Chinook salmon (*Oncorhynchus tshawytscha*) in the Yakima River, Washington. U.S. Fish and Wildlife Fishery Bulletin 67:347–359.

McIsaac, D. O., and T. P. Quinn. 1988. Evidence for a hereditary component in homing behavior of Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 45:2201–2205.

Milner, A. M., and R. G. Bailey. 1989. Salmonid colonization of new streams in Glacier Bay National Park, Alaska. Aquaculture and Fisheries Management 20:179–192.

Mobrand, L. E., J. Barr, L. Blankenship, D. E. Campton, T. T. P. Evelyn, T. A. Flagg, C. V. W. Mahnken, L. W. Seeb, P. R. Seidel, and W. W. Smoker. 2005. Hatchery reform in Washington state: principles and emerging issues. Fisheries 30(6):11–23.

Morbey, Y. E., and A. P. Hendry. 2008. Adaption of salmonids to spawning habitats. Pages 15–35 *in* D. Sear and P. DeVries, editors. Salmonid spawning habitat in rivers: physical controls, biological responses, and approaches to remediation. American Fisheries Society, Symposium 65, Bethesda, Maryland.

Murdoch, A. R., T. N. Pearsons, and T. W. Maitland. 2009a. The number of redds constructed per female spring Chinook salmon in the Wenatchee River basin. North American Journal of Fisheries Management 29:441–446.

Murdoch, A. R., T. N. Pearsons, and T. W. Maitland. 2009b. Use of carcass recovery data in evaluating the spawning distribution and timing of Spring Chinook Salmon in the Chiwawa River Washington. North American Journal of Fisheries Management 29:1206–1213.

Murdoch, A. R., T. N. Pearsons, T. W. Maitland, M. J. Ford, and K. Williamson. 2008. Monitoring the reproductive success of naturally spawning hatchery and natural spring Chinook salmon in the Wenatchee River. Bonneville Power Administration, Project 2003-039-00, Portland, Oregon.

Neville, H. M., D. J. Isaak, J. B. Dunham, R. F. Thurow, and B. E. Rieman. 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. Molecular Ecology 15:4589–4602.

Pearsons, T. N., and C. W. Hopley. 2001. A practical approach for assessing ecological risks associated with fish stocking programs. Fisheries 24(9):16–23.

Quinn, T. P. 1993. A review of homing and straying of wild and hatchery-produced salmon. Fisheries Research (Amsterdam) 18:29–44.

Quinn, T. P., E. L. Brannon, and A. H. Dittman. 1989. Spatial aspects of imprinting and homing in coho salmon, *Oncorhynchus kisutch*. U.S. National Marine Fisheries Service Fishery Bulletin 87:769–774.

Quinn, T. P., I. J. Stewart, and C. P. Boatright. 2006. Experimental evidence of homing to site of incubation by mature sockeye salmon, *Oncorhynchus nerka*. Animal Behaviour 72:941–949.

Ricker, W. E. 1972. Hereditary and environmental factors affecting certain salmonid populations. Pages 27–160 *in* R. C. Simon, editor. The stock concept of Pacific salmon. H. R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver.

Rieman, B. E., and J. B. Dunham. 2000. Metapopulations and salmonids: a synthesis of life history patterns and empirical observations. Ecology of Freshwater Fish 9:51–64.

Schtickzelle, N., and T. P. Quinn. 2007. A metapopulation perspective for salmon and other anadromous fish. Fish and Fisheries 8:297–314.

Slaney, P. A., L. Berg, and A. F. Tautz. 1993. Returns of hatchery steelhead relative to site of release below an upper-river hatchery. North American Journal of Fisheries Management 13:558–566.

Snyder, E. B., and J. A. Stanford. 2001. Review and synthesis of river ecological studies in the Yakima River, Washington, with emphasis on flow and salmon habitat interactions. Report of the University of Montana to the U.S. Department of the Interior, Bureau of Reclamation, Yakima, Washington.

StreamNet. 2001. Metadata for Pacific Northwest river reach data. Available: streamnet.org/pnwr/PNWNAR.html. (January 2005).

YKFP (Yakima–Klickitat Fisheries Project). 2008. Yakima–Klickitat Fisheries Project online documents and fish counts. Available: ykfp.org/docsindex.htm. (June 2008).

Yakima Subbasin Fish and Wildlife Planning Board. 2004. Yakima Subbasin plan. Northwest Power and Conservation Council. Available: nmppc.org/fw/sub-basinplanning/yakima/plan/. (June 2008).

Zhou, S. 2002. Size-dependent recovery of Chinook salmon in carcass surveys. Transactions of the American Fisheries Society 131:1194–1202.