

Breeding Success of Wild and First-Generation Hatchery Female Spring Chinook Salmon Spawning in an Artificial Stream

STEVEN L. SCHRODER*

Washington Department of Fish and Wildlife, 600 Capitol Way North, Olympia, Washington 98501, USA

CURTIS M. KNUDSEN

Oncorh Consulting, 2623 Galloway SE, Olympia, Washington 98501, USA

TODD N. PEARSONS, TODD W. KASSLER, SEWALL F. YOUNG, AND CRAIG A. BUSACK

Washington Department of Fish and Wildlife, 600 Capitol Way North, Olympia, Washington 98501, USA

DAVID E. FAST

Yakama Nation, Post Office Box 151, Toppenish, Washington 98948, USA

Abstract.—First-generation hatchery and wild spring Chinook salmon *Oncorhynchus tshawytscha* from the upper Yakima River, Washington, were placed into an artificial stream and allowed to spawn. Seven independent test groups were placed into the stream from 2001 through 2005. No differences were detected in the egg deposition rates of wild and hatchery females. Pedigree assignments based on microsatellite DNA, however, showed that the eggs deposited by wild females survived to the fry stage at a 5.6% higher rate than those spawned by hatchery females. Subtle differences between hatchery and wild females in redd abandonment, egg burial, and redd location choice may have been responsible for the difference observed. Body size did not affect the ability of females to spawn or the survival of their deposited eggs. How long a female lived was positively related to her breeding success, but female origin did not affect longevity. The density of females spawning in portions of the stream affected both egg deposition and egg-to-fry survival. No difference, however, was found in the overall distribution patterns of the two types of females. Other studies that have examined the effects of a single generation of hatchery culture on upper Yakima River Chinook salmon have disclosed similar low-level effects on adult and juvenile traits. The cumulative effect of such differences will need to be considered when hatcheries are used to restore depressed populations of Chinook salmon.

Using hatcheries to conserve depressed salmonid populations is a common management strategy in North America. In some cases, naturally produced local origin fish (wild broodstock) are brought into a hatchery for breeding and their progeny are reared for varying periods of time before being released into natural habitats. The concept of using native broodstock and cycling progeny through artificial culture until abundance increases or becomes stabilized has been referred to as supportive breeding (Ryman and Laikre 1991; Laikre and Ryman 1996) or supplementation (Cuenco et al. 1993; Goodman 2004). However, behavioral (Fleming and Gross 1992; Lura et al. 1993; Fleming et al. 2000), morphological (Fleming and Gross 1992; Petersson et al. 1996; Busack et al. 2007), and physiological (Petersson and Järvi 1993; Fleming and Petersson 2001; Knudsen et al. 2006) divergences

have been observed between hatchery and wild salmonids, making supplementation a controversial strategy.

Moreover, previous studies have shown that salmonids produced by artificial culture are not as reproductively successful as wild fish when they spawn under natural conditions (Petersson and Järvi 1997; Fleming and Petersson 2001; McLean et al. 2004; Araki et al. 2007). However, many of these studies compared the reproductive success of nonlocal hatchery fish with native salmonids or with fish that had experienced multiple generations of hatchery exposure. Few efforts have compared reproductive success when both hatchery and wild fish possess a common genetic history (Dannewitz et al. 2004), and none have been done on conservation programs where attempts have been made to minimize domestication. In this paper we report on a study that compared the breeding success of wild and first generation hatchery spring Chinook salmon *Oncorhynchus tshawytscha*. The hatchery fish originated from wild parents and were produced from a

* Corresponding author: schrosls@wdf.wa.gov

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TABLE 1.—Number and size of hatchery and wild female spring Chinook salmon placed into the observation stream at the Cle Elum Supplementation Research Facility from 2001 to 2005. The females in the 2001 and 2002 test groups had 221 m² of area available for spawning, while those in the 2003–2005 test groups had 550 m².

Test group	Sex	Origin	Number	Weight range	Mean weight (kg)
2001A	Female	Hatchery	8	3.07–4.76	4.08
		Wild	8	2.10–6.57	4.55
	Male ^a	Hatchery	9	2.14–4.95	3.09
		Wild	12	2.03–7.46	4.69
2001B	Female	Hatchery	8	2.87–4.28	3.61
		Wild	9	3.18–4.88	4.04
	Male	Hatchery	7	2.60–5.25	3.54
		Wild	11	1.78–4.90	3.56
2002A	Female	Hatchery	11	2.93–5.70	4.50
		Wild	11	3.78–6.16	4.78
	Male	Hatchery	11	2.80–4.43	3.48
		Wild	11	2.99–5.56	4.20
2002B	Female	Hatchery	9	3.27–5.10	3.90
		Wild	8	3.37–4.72	4.23
	Male	Hatchery	7	3.03–6.40	4.16
		Wild	9	2.72–5.64	4.12
2003	Female	Hatchery	13	3.00–6.58	4.67
		Wild	11	3.52–7.83	4.89
	Male	Hatchery	10	1.77–6.51	4.67
		Wild	14	2.33–7.14	4.36
2004	Female	Hatchery	10	2.54–5.00	3.92
		Wild	10	3.12–4.57	3.73
	Male	Hatchery	19	1.76–5.81	3.49
		Wild	10	3.00–6.62	4.26
2005	Female	Hatchery	11	2.47–4.24	3.40
		Wild	12	3.06–5.20	3.98
	Male	Hatchery	13	3.05–7.01	4.42
		Wild	12	3.51–6.42	4.23

^a Hatchery and wild age-0 and 1-year-old males (precocious males) and 3-year-old anadromous males (jacks) were also placed in the test groups

conservation hatchery where measures were taken to minimize inadvertent domestication (Fast 2002; Knudsen et al. 2006). We assessed breeding success directly by means of pedigree analysis and, because the study was done in an artificial stream, were also able to observe behaviors correlated with reproductive success.

The reproductive behaviors of male and female salmon are distinct. Breeding success in female spring Chinook salmon is influenced by their ability to acquire and defend territories, construct nests, attract males, spawn, and protect their nests from re-excavation by neighboring females. Males, on the other hand, are nonterritorial and must find, defend, court, and spawn with receptive females to achieve breeding success. Because the behavior and challenges faced by each sex are dissimilar, different traits and abilities need to be measured when assessing breeding success. Consequently, for clarity we have separated the results of our analyses by sex. Here we compare the ability of wild and hatchery females to produce newly emerged fry.

Methods

Origin and collection of wild and hatchery fish.—In 1997 the Cle Elum Supplementation Research Facility

(CESRF) was built on the upper Yakima River, Washington. The Yakima–Klickitat Fishery Project is using the CESRF to monitor the effects of a supplementation program on upper Yakima River spring Chinook salmon. Before 1997, negligible introductions of hatchery Chinook salmon had occurred in the upper Yakima River, making this a native population with little hatchery influence (Knudsen et al. 2006; Busack et al. 2007). The hatchery fish in our study were the progeny of the first wild spring Chinook salmon used as broodstock in the CESRF and are, thus, first-generation hatchery fish. Both hatchery and wild adults were collected in the upper Yakima River from April through August at the Roza Adult Monitoring Facility (river kilometer 206, measuring from the confluence with the Columbia River). All upper Yakima River salmon must pass through this structure before they reach their spawning grounds. Every Chinook salmon produced at the CESRF had its adipose fin clipped and may also possess a passive integrated transponder tag, a coded wire tag, or an elastomer mark. The clips and tags made it possible to identify the origin of each Chinook salmon captured at the Roza facility. A representative sample of hatchery and wild adults was collected using methods described

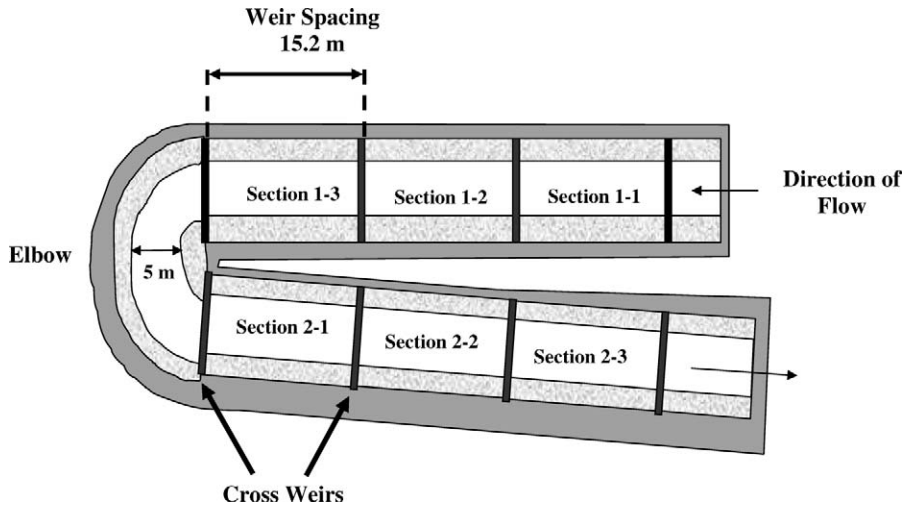


FIGURE 1.—Configuration of the artificial stream at the Cle Elum Supplementation Research Facility that was used to evaluate the breeding success of female spring Chinook salmon (not to scale).

by Knudsen et al. (2006). All females were either 4 or 5 years old and males were 2, 3, 4, or 5 years old. Collected fish were transported 81 km to CESRF and held in a pond 30.5 m long \times 4.6 m wide \times 3 m deep.

Beginning in September, fish were examined weekly to determine whether they had reached maturation. Ripe fish without abnormalities were selected for the artificial stream. No effort was made to size match the fish. Before being placed into the stream the fish were anesthetized in a 1:19,000 solution of tricaine methanesulfonate (Bell 1964), weighed to the nearest gram, measured (fork length to the nearest millimeter), and tagged with 3.8-cm-diameter Petersen discs. Each sex received a differently colored tag, and within sexes the tags had unique numbers. In addition, a tissue sample from the posterior edge of the dorsal fin was placed into 100% ethanol for later microsatellite DNA extraction. Fish were then transported 200 m and released into the artificial stream. The number and origin of females present in each group and the range and mean of their body sizes are shown in Table 1. Comparisons between the body weights of hatchery and wild females placed in each test group were made using *t*-tests.

Artificial stream.—In 2000, an artificial stream 127 m long \times 7.9 m wide was built on the grounds of the CESRF. The U-shaped structure is subdivided by concrete cross weirs into seven sections; a curved elbow 21 m long \times 7.9 m wide and six straight sections each measuring 15.2 m \times 7.9 m. Each section had a level gradient and 30-cm drops separated one section from another (Figure 1). The banks of the stream had 2:1 slopes that were armored with river rock 10–30 cm

in diameter. The streambed was lined with geotextile to prevent water loss. Gravel depth was 90 cm and river rock with a Fredle index (Lotspeich and Everest 1981) of 7 consisting of material ranging from 0.71 to 10.0 cm in diameter was used as spawning substrate. The wetted width of the stream ranged between 4.3 and 5.5 m. Discharge water from hatchery raceways at CESRF was pumped into the stream from September through May. Flows were adjusted so velocities varied from 0.1 to 2.0 m/s and total discharge averaged 0.37 m³/s. Depth was maintained by stop logs and averaged 0.4 m. The velocity and depth criteria were patterned after conditions that naturally spawning Chinook salmon typically use (Bjornn and Reiser 1991; Healey 1991). A 2.1-m-high wall of camouflage netting was installed on both banks with observation openings at eye level located every 2 m along its length.

In 2001 and 2002, the artificial stream was subdivided into two parts, each consisting of three straight sections (total length, 45.6 m). Test groups consisting of hatchery and wild fish were placed into each part. In 2003, 2004, and 2005, the entire stream was made available to single test groups of fish. Fish were introduced into the uppermost section of the stream and allowed to move freely within the sections allotted to their test group. Every section had a grid system made of 0.6-cm nylon cord that was stretched 30 cm above the water surface. The grid consisted of 3.0-m-long \times 1.5-m-wide rectangles, and each was given a unique alphanumeric designation so that fish locations and movements could be recorded.

Measures of female breeding success.—Three statistics were used to assess female breeding success. The

TABLE 2.—Regression equations used to estimate the fecundity of wild and hatchery female Chinook salmon in the test groups in the artificial stream from 2001 to 2005. Independent variables are as follows: BW = body weight (g), FL = fork length (cm), and EW = egg weight (mg). All regressions had *P* values <0.001.

Return year	Age	Equation	R ²	Regression SE
2001	4	2552.2 + (BW × 1003.9) – (EW × 12,038.2)	0.728	414.9
	4	–2012.4 + (BW × 602.4) – (FL × 48.87)	0.547	542.1
2002	4	5701.2 + (BW × 1352.9) – (FL × 58.04) – (EW × 12,563.5)	0.642	495.4
	4	1204.6 + (BW × 1019.7) – (FL × 14.55)	0.505	590.0
2003	4	4198.3 + (BW × 1172.2) – (FL × 27.93) – (EW × 13,219.0)	0.674	436.8
	4	–423.4 + (BW × 643.6) + (FL × 25.60)	0.513	532.2
2004	4	7697.0 + (BW × 1645.3) – (FL × 98.11) – (EW × 13,106.1)	0.765	356.3
	4	–91.83 + (BW × 1447.5) + (FL × 91.83)	0.605	460.9
2005	4	3300.4 + (BW × 1256.3) – (FL × 26.29) – (EW × 10,100.5)	0.757	416.0
	4	–893.8 + (BW × 758.5) + (FL × 91.83)	0.657	493.6
All years ^a	5	958.6 + (BW × 711.7)	0.436	805.9
	5	6486.4 + (BW × 1027.6) – (FL × 37.18) – (EW × 17,658.1)	0.747	522.4

^a Five-year-old females were rare, so data from all years were combined to create single multiple-regression equations.

first estimated the percentage of a female’s fecundity that had been spawned (percent spawned). The second estimated the survival of eggs a female spawned up to the fry stage (survival of deposited eggs). The last one estimated the percentage of a female’s absolute fecundity that had been converted to fry (fecundity to fry). To calculate these measures, we used fecundity, egg retention, and offspring production estimates from each female. Fecundities were estimated by multiple regressions using body weight, fork length, and egg weight as independent variables. Body size, mean egg weight, age, and fecundity data came from females that were artificially spawned at the CESRF (Knudsen et al. 2006, in press). Brood year and age-specific regressions were developed to estimate fecundity. Length and weight data were collected on each female placed into the artificial stream. Egg samples were either collected while a fish was being tagged or were obtained soon after a female died. Mean egg weights were determined by averaging the weights of five eggs weighed to the nearest milligram. In 18% of cases, egg weight information was not available. When that occurred multiple regressions using body size information were used to estimate fecundity (Table 2).

The number of eggs a female deposited was estimated by the equation

$$\text{egg deposition} = \text{fecundity} - \text{eggs retained.}$$

Egg retention data were obtained by hand-counting all eggs retained within a female at the time of death. Our first measure of female breeding success, percent spawned, was determined by dividing the number of eggs a female deposited by her estimated fecundity:

$$\text{percent spawned} = (\text{egg deposition}/\text{fecundity}) \times 100.$$

Our second measure of female breeding success, the survival of deposited eggs, was calculated as

survival of deposited eggs

$$= \frac{\text{number of fry produced}}{\text{eggs deposited}} \times 100.$$

To estimate the number of fry generated by each female, we first determined how many fry had been produced from her test group. This was accomplished by installing fyke nets with floating live boxes in the artificial stream. The traps were put in place before emergence and were fished continuously until fry migration ceased; then seines and electrofishing gear were used to recover any remaining fry. Next, 10% of each day’s catch was preserved in 100% ethanol and used in microsatellite DNA pedigree assessments.

The pedigree analyses disclosed the number of fry each female had contributed to the 10% sample obtained from her test group. Those values were converted to percentages by dividing them by the total number of fry that had been used in each pedigree analysis. These percentages were multiplied by the number of fry produced by a test group to estimate the total number of juvenile fish produced by each female. Once the number of fry produced by each female was estimated it was possible to generate our third measure of female breeding success, the ability to convert absolute fecundity into fry. This value was obtained by the equation

$$\text{fecundity to fry} = \frac{\text{number of fry produced}}{\text{fecundity} - \text{eggs lost at tagging}}.$$

Pedigree analysis.—For test groups 1 and 2, genomic DNA was extracted from the fry and adult samples by digesting their tissues in a 5% chelex solution containing 0.4 mg proteinase *K* per sample. Following digestion the samples were heated to denature proteins and the DNA extracts were stored at 5°C until all analyses were completed. Spin column extraction kits from Machery-Nagel were used to

TABLE 3.—Microsatellite loci and number of alleles scored for the pedigree analyses of hatchery and wild spring Chinook salmon spawning in the artificial stream.

Locus and totals	Population							Reference
	2001A	2001B	2002A	2002B	2003	2004	2005	
<i>Ots-101</i>	24	24	24	24				Small et al. (1998)
<i>One-8</i>	13	13	16	16				Scribner et al. (1996)
<i>Ots-1</i>	5	5	5	5				Banks et al. (1999)
<i>Ocl-1</i>	7	7	6	6				Condrey and Bentzen (1998)
<i>Ots-100</i>	40	40						Small et al. (1998)
<i>Ots-2M</i>	8	8	11	11				Banks et al. (1999)
<i>Ots-107</i>	21	21						Nelson and Beacham (1999)
<i>Omm-1135</i>			7	7				Rexroad et al. (2001)
<i>Omm-1142</i>			12	12				Rexroad et al. (2001)
<i>Ogo-2</i>	10	10	9	9				Olsen et al. (1998)
<i>Ssa-197</i>	21	21	20	20				O'Reilly et al. (1996)
<i>Oki-100</i>					19	21	20	K. Miller, unpublished data
<i>Ots-201b</i>					21	21	21	M. Banks, unpublished data
<i>Ots-208b</i>					25	25	29	Greig et al. (2003)
<i>Ssa-408</i>					20	18	20	Cairney et al. (2000)
<i>Ogo-4</i>	11	11	9	9	10	11	11	Olsen et al. (1998)
<i>Omm-1080</i>					36	35	35	Rexroad et al. (2001)
<i>Ots-213</i>					21	23	25	Greig et al. (2003)
<i>Ots-G474</i>					7	10	12	Williamson et al. (2002)
<i>Ots-3M</i>	8	8	7	7			9	Banks et al. (1999)
<i>Ots-9</i>							5	Banks et al. (1999)
<i>Ots-211</i>					24	23	24	Greig et al. (2003)
<i>Ots-212</i>					20	18	23	Greig et al. (2003)
Loci genotyped	11	11	11	11	10	10	12	
Fry assigned	991	780	1,566	1,264	2,750	2,892	2,973	

purify genomic DNA from fish in test groups 3–7. Adults and fry were genotyped at 10 or more loci (Table 3). The number of alleles per locus ranged from 5 at *Ots-1* to 40 at *Ots-100*. Microsatellite DNA loci were amplified via polymerase chain reaction (PCR) using fluorescent-labeled primers obtained from Applied Biosystems or Integrated DNA Technologies. Data were collected using an ABI-3100 Genetic Analyzer. Applied Biosystems Genemapper 3.0 software was used to collect, analyze and determine genotypes at each locus. Allele identification on sampled fry was attempted on all loci. In some instances, allele identification was not possible. However, fry had to be genotyped at six or more loci before they were assigned to a parent fish. A maximum likelihood procedure in Cervus 2.0 (Marshall et al. 1998) was used to infer parent–offspring relationships. The procedure uses allele frequency data to assign likelihoods to parent–offspring combinations and allows mismatching genotypic data to be evaluated concurrently with matching genotype data.

Behavioral observations.—Once fish were in the artificial stream, up to eight observers recorded fish activities during daylight hours. These observations were continued until spawning ceased, typically within 72 h or less. Focused fish observations were made, the observers dictating the activities of individual fish onto audiotapes in 4–10-min segments before proceeding to

another fish. If a female was watched, her location in the stream, whether she was territorial or wandering, and any redd construction activities were recorded.

In 77 instances, female behavior 20 min before and 10 min after spawning was described. Before spawning, females create nests by performing multiple independent digging actions. During a digging episode, the body is rotated 90° and the caudal peduncle and fin are rapidly swept back and forth over the substrate. This behavior loosens the streambed, disperses stones, and purges sediments from the streambed. As a nest develops, digging actions become more focused until a circular depression in the streambed has been created. After spawning, digging acts are used to bury eggs. During our observations, female digging frequency per minute and the number of body flexures performed per digging episode were noted before and after spawning. Nest construction and egg burial activities of hatchery and wild females were graphed and compared.

Additionally, whenever spawning events were observed and visibility allowed, we recorded how long it took females to cover eggs until they were no longer visible. We felt that this was an important trait because rapid burial would protect eggs from immediate predation. A Kolmogorov–Smirnov two-sample test was used to see whether egg burial time varied because of female origin.

Data analyses.—Paired *t*-tests were performed to determine whether hatchery and wild females differed in their ability to deposit eggs and whether the eggs they spawned survived at different rates. In the first test, the variables compared were the mean percent spawned values found in hatchery and wild females in the seven test groups. In the second the mean survival of eggs deposited by hatchery and wild females was compared, while in the third test the average ability to convert absolute fecundity to fry was contrasted. Before analysis, percentages were normalized by the arcsine transformation. These were one-sided tests because hatchery fish were expected to be less competent than wild counterparts due to inadvertent domestication (Araki et al. 2007).

Additionally, relationships between percent spawned, egg survival during incubation, and the ability to convert fecundity to fry were examined within each test group by female type. We regressed percent spawned values, for example, with the percentage of absolute eggs that had been converted to fry to see how much variation in fry production could be explained by the ability to successfully deposit eggs. Similar regressions between the percent spawned and the survival of deposited eggs were performed to see whether survival during incubation was affected by how completely a female had spawned. A final set of regressions looked at the relationship between survival of eggs during incubation and the capacity to convert fecundity to fry. The overall significance of each set of regressions was evaluated by using Fisher's combined probability tests (Sokal and Rohlf 1995).

Analyses were also performed to explore the importance of seven female traits on breeding success, including female size. The importance of body weight on the ability of hatchery and wild females to deposit eggs and produce fry was examined by means of regression using \log_{10} transformed body weight. Separate regressions were performed on data from each type of female originating from the same test group. The overall importance of body weight on the ability of females to deposit eggs and on the survival of their eggs in the artificial stream was examined by using Fisher's combined probability tests.

A two-way analysis of variance (ANOVA) was performed to ascertain whether hatchery and wild females placed into the artificial stream had eggs that differed in size. In this analysis, one fixed factor was test group while the other was female origin. The importance of egg size during incubation was examined by means of regressions that evaluated the influence of egg weight (\log_{10} transformed) on egg-to-fry survival within each test group by female type.

The *P*-values from those independent tests were also used in Fisher's combined probability tests to see whether egg weight had any effect on survival during the incubation period.

The number of hours each female lived (longevity) was calculated by subtracting the median time and date her test group entered the artificial stream from the date and time she was first observed as dead. These data were regarded as ordinal because exact times of death were not always obtained. Mann-Whitney *U*-tests were used to determine whether a difference existed in the longevity of hatchery and wild females within the same test group. The relationships between longevity and the percentage of eggs spawned, egg-to-fry survival during incubation, and the ability of females to convert absolute fecundities to fry were examined by means of Kendall's tau correlation analyses. Separate analyses were done for wild and hatchery females in each test group. The overall significance of each set of correlations was examined by using Fisher's combined probability tests.

In every test group, the effect of instantaneous density on female breeding success was examined by calculating mean values for percent spawned, deposited egg survival during incubation, and ability to convert absolute fecundity to fry for females that spawned in the same section of the artificial stream. Instantaneous densities were determined by dividing the number of territorial females present in a section by the section's wetted surface area. Interactions among females spawning in different sections of the artificial stream did not occur and, therefore, data collected from an individual section were regarded as independent from one another. Regressions were performed that examined how our measures of female breeding success (dependent variables) were affected by female density.

Because females were released into the uppermost section of the artificial stream, it gave them the opportunity to choose a redd location anywhere within the stream. Interactions among females could affect where redds were established. However, the availability of numerous potential redd sites in the stream made where a female spawned a largely independent decision. Contingency chi-square tests (2×3 for the 2001 and 2002 test groups and 2×5 for the 2003, 2004, and 2005 test groups) were used to determine whether hatchery and wild females established redds in different sections of the artificial stream. Moreover, because the flow patterns in each section of the artificial stream were similar to one another, we tested whether hatchery and wild females chose different areas within sections of the stream for redd locations. A 2×4 contingency chi-square test was used in this analysis. One variable was female type, hatchery or

TABLE 4.—Mean percent spawned, survival of deposited eggs, and conversion of fecundity to fry for hatchery and wild spring Chinook salmon females placed into the artificial stream, 2001–2005.

Population	Female origin	Mean percent spawned (%)	Mean survival of deposited eggs (%)	Mean fecundity converted to fry (%)
2001A	Hatchery	87.7	20.6	16.8
	Wild	87.5	34.0	30.0
2001B	Hatchery	91.7	59.5	51.0
	Wild	99.2	72.4	71.2
2002A	Hatchery	83.0	50.7	39.7
	Wild	96.9	56.7	53.1
2002B	Hatchery	89.2	54.8	44.3
	Wild	95.3	63.1	57.0
2003	Hatchery	95.9	70.0	65.5
	Wild	89.4	65.9	50.4
2004	Hatchery	98.5	57.7	56.1
	Wild	93.6	62.4	55.2
2005	Hatchery	77.7	69.2	51.0
	Wild	90.6	67.2	56.6
Mean hatchery		89.1	54.6	46.3
Mean wild		93.2	60.2	53.4
Difference		4.1	5.6	7.0

wild, while the other variable was location. Each section was split into four 3.8-m × 4.9-m locations or subsections. The uppermost subsections had high turbulence and velocities up to 2 m/s. Conversely, flows were laminar and current velocities were between 0.1 and 0.3 m/s in the lowest subsections. The two interior subsections had intermediate turbulence and water velocity values (S. L. Schroder and C. M. Knudsen unpublished data). A final 1 × 4 contingency chi-square test was performed to see whether females, regardless of type, preferred to establish redds in one or more of the subsections.

Because some females created two or more redds, a 2 × 2 contingency chi-square test was performed to determine whether the tendency to create more than one redd was linked to female type. In addition, some females were observed abandoning their redds for one or more days before dying. Thus, a 2 × 2 contingency chi-square test was performed to determine whether female origin was related to redd abandonment.

Results

Breeding Success

No difference was seen in the ability of hatchery and wild female Chinook salmon to deposit their eggs. Average egg deposition across the test groups was 93.2% in wild and 89.1% in hatchery females (paired-*t*-test: $t = 1.16$, $P = 0.15$). There was a significant difference in the survival of eggs spawned; mean egg-to-fry survival averaged 60.2% in wild females and 54.6% in hatchery fish (paired-*t*-test: $t = 2.13$, $P = 0.04$). We also compared the ability of the two types of females to convert fecundity to fry (Table 4). On average, wild females transformed 53.4% of their eggs

into fry while 46.3% of the eggs carried by hatchery fish produced fry. This difference bordered on significance (paired-*t*-test: $t = 1.61$, $P = 0.08$).

Overall, the capacity to deposit eggs (% spawn) was positively associated with the ability to convert fecundity to fry in hatchery and wild females (Fisher's combined probability tests: $P < 0.001$ for both tests). In our test groups, 25–69% of the variation in the capacity to convert eggs into fry could be explained by the ability of a female to deposit eggs. In a few of the test groups, however, no relationship between egg deposition and fecundity-to-fry conversion was found. This counterintuitive result happened because little variation in egg deposition occurred among the females. All were equally capable of spawning eggs, but their deposited eggs survived at variable rates. Survival of deposited eggs was not related to how completely a female had spawned (Fisher's combined probability tests: $P = 0.401$ for hatchery and $P = 0.418$ for wild females). Females that deposited just a portion of their eggs achieved egg-to-fry survival rates that were equivalent to individuals that had deposited most or all of their eggs. For hatchery females, survival of the eggs they deposited accounted for 47–90% of the variation in their ability to convert absolute fecundity to fry (Fisher's combined probability test: $P < 0.001$). Similarly, 70–99% of the variation in fry production in wild females was accounted for by the survival of their deposited eggs (Fisher's combined probability test: $P < 0.001$). In general, the quality of the incubation environment a female created appeared to have a stronger effect on her capacity to convert eggs to fry than her ability to deposit eggs.

Body Size

Wild females were significantly larger than hatchery fish in one test group (*t*-test: $P = 0.01$). Although not statistically significant, wild females had greater mean body weights in five of the remaining six populations. A subsequent Fisher's combined probability test indicated that wild females were slightly larger than their hatchery counterparts ($P = 0.05$). Linear regressions were used to evaluate the importance of female body weight on our measures of female breeding success. Data from hatchery and wild females from the same test group were combined in the regressions that examined the importance of body weight on the ability of females to deposit eggs. This was done because the paired *t*-test indicated that hatchery and wild females deposited eggs in an equivalent manner. In one of the test groups a positive relationship between body size and egg deposition occurred ($r^2 = 22\%$, $P = 0.03$). In all the others no relationship was seen; r^2 values ranged from 0.1% to 10% and P -values varied from 0.14 to 0.90. Additionally, no significant relationship between female weight and egg survival during incubation was seen, r^2 values ranged from 0.01% to 3.6% for hatchery and from 0.0% to 12.9% for wild females. In one test group a positive relationship between body weight of wild females and their ability to convert fecundity to fry was observed ($r^2 = 37\%$, $P = 0.05$) in all the other test groups no relationship between these two variables was seen. To increase power, the P -values from the above regressions were used in Fisher's combined probability tests. None of these tests were significant; $P = 0.28$ for the effect of body weight on the ability to deposit eggs, $P = 0.99$ in both hatchery and wild females for the effect of body weight on survival of deposited eggs, and $P = 0.99$ and 0.52 on the capacity of hatchery and wild females to convert fecundity to fry. Thus, in our experimental setting, body weight had no effect on egg deposition, egg-to-fry survival, or on the capacity to convert absolute fecundity to fry.

Egg Weight

The overall mean egg weight for wild females was 215 mg, which was 17 mg or 5.9% heavier than the average egg weight for hatchery females (ANOVA: $P = 0.033$). However, almost no variation in egg-to-fry survival could be explained by egg weight. Out of the 10 regressions that were performed by female type, six had positive slopes while four others had negative ones. Only one was significant, and in this instance there was a negative relationship between egg size and survival in hatchery females spawning in the 2004 test group ($r^2 = 60.9\%$, $P = 0.02$, $n = 8$). Yet in general, egg weight had no effect on survival during incubation

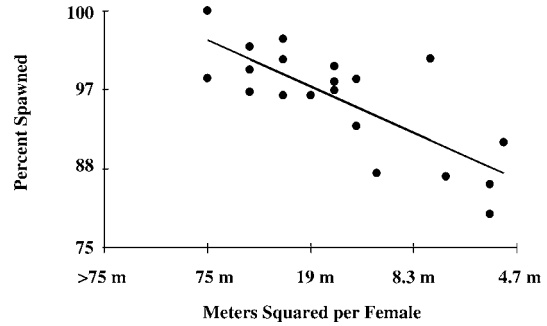


FIGURE 2.—The effect of spawner density on mean egg retention in spring Chinook salmon females in the artificial stream. Data from hatchery and wild females were combined across all seven test groups, as no difference was found in their ability to deposit eggs.

under the flow and gravel composition conditions present in the artificial stream (Fisher's combined probability test: $P = 0.26$ for hatchery and $P = 0.56$ for wild females).

Longevity

Origin had little effect on female longevity. In one test group wild females did have longer mean lifetimes (Mann-Whitney *U*-test: $P = 0.01$); however, in the remaining six test groups no difference was seen. We found positive relationships between longevity and the percentage of eggs spawned (Fisher's combined probability test: $P < 0.001$), egg-to-fry survival (Fisher's combined probability test: $P = 0.001$ for hatchery and $P = 0.037$ for wild females), and the ability to convert absolute fecundity to fry (Fisher's combined probability test: $P < 0.001$ in both types of females). Consequently, in our test groups, longevity appeared to be an important factor in determining female breeding success.

Distribution Patterns

Once released into the artificial stream females, could move freely throughout the sections that were allotted to their test group. Distribution of females within the artificial stream was not uniform. In five of the test groups, 44–66% of the females established redd territories in the lowest section available to them. Females spawning in these sections had 4.8–7.5 m² (weighted mean, 5.8 m²) of space available for redds. Conversely fish spawning elsewhere in the artificial stream had 10–74 m² (weighted mean, 21.3 m²) of space for redd locations. Quinn et al. (2007) showed that high instantaneous densities of spawning females increases egg retention and lowers survival of deposited eggs in salmonids. This trend was observed in the

artificial stream and is shown in Figure 2, which combines information on both types of females from all seven test groups. A regression analysis disclosed that approximately 60% of the variation in egg deposition could be explained by female density ($P < 0.001$). Similar analyses regressed egg survival during incubation and the ability to convert absolute fecundity to fry on density ($m^2/female$). Both were significant; 21% of the variation in egg survival ($P = 0.04$) and 48% in the ability to convert eggs to fry ($P < 0.001$) could be explained by female density. These general trends prompted us to examine whether hatchery or wild females had different distribution patterns in the artificial stream and were, therefore, subject to different instantaneous densities.

We examined redd distributions in the artificial stream in three ways. First, contingency chi-square tests were used to see whether hatchery and wild females created redds in different sections of the observation stream. In four test groups, females could spawn in one of three sections. In the other three test groups, females could locate themselves throughout the entire stream (Figure 3). In both instances, the null hypothesis of equivalent distribution could not be rejected ($\chi^2 = 2.81$, $P = 0.245$ for the 2×3 analysis; $\chi^2 = 2.60$, $P = 0.627$ for the 2×5 test).

Second, we examined whether female origin affected where redds were established within a section. Each section was subdivided into four equal subsections that roughly corresponded with different degrees of water velocity and turbulence. The null hypothesis of this analysis could not be rejected ($\chi^2 = 6.73$, $P = 0.081$) suggesting that both types of females distributed themselves within each section similarly. Third, we combined data from both hatchery and wild females to ascertain whether particular areas within a section were preferred for redd placement. The lowest subsection (containing laminar and slightly accelerating flows) was chosen significantly more often than the other three subsections ($\chi^2 = 55.09$, $P < 0.001$). In fact, 58% of the wild and 42% of the hatchery female salmon chose this subsection for their redds. Of all the subsections in the artificial stream these most closely resembled the transition zone between pool and riffle in natural streams. A subsequent chi-square test indicated that females used the remaining three subsections in an equivalent manner ($\chi^2 = 1.61$, $P = 0.447$).

Nest Construction and Egg Burial

We compared the digging frequency and number of body flexures used per dig by observing 35 hatchery and 42 wild female salmon 20 min before and 10 min after spawning. No differences in digging frequency were seen. Both types of females averaged one digging

act every 2.5 min before spawning. Immediately after egg deposition, digging frequency in hatchery and wild females increased by more than an order of magnitude eventually decreasing to prespawning levels 20–30 min later (Figure 4). The number of body flexures per dig before spawning was quite variable, ranging from 2 to 16, but averaged between 5 and 8 in both types of females. Immediately after spawning 4 or fewer flexures typically occurred per dig. As newly spawned eggs were buried, hatchery and wild females increased the number of body flexures per dig in a linear fashion until 10 min after spawning at which time flexures had reached 6 or more. The digging actions used to create nests and bury newly spawned eggs were comparable in hatchery and wild females.

Egg burial times were recorded for 32 hatchery and 33 wild females. There was no difference in the time it took hatchery and wild females to bury their eggs (Kolmogorov–Smirnov test: $P = 0.41$). However, more wild females covered their eggs within the first minute after spawning (70% versus 56%) than did hatchery fish. In addition, two of the hatchery fish left their eggs exposed for more than 35 min, while the longest period of egg exposure for a wild female was 13 min (Figure 5).

Redd Abandonment

Of the total number of females placed in the artificial stream, 139 established redds and 32 of those were abandoned for more than 1 d. Three causes of abandonment were seen: eviction by other females, creation of a new redd, and general weakness. Our analyses on redd abandonment did not include cases caused by general weakness where females died 24 h or sooner after leaving their redds. Evictions were rare; only two were observed and a different type of female was involved in each instance. Twelve hatchery (17%) and five wild females (6.6%) abandoned their redds and lived for more than 1 d afterward. The 2×2 contingency chi-square test used to see whether this type of abandonment was independent of female origin was marginally nonsignificant ($\chi^2 = 3.56$, $P = 0.059$). Additionally, approximately 10% of the females constructed redds and spawned in more than one location. Both types of females exhibited this strategy with the same frequency, 10% for hatchery and 11.6% for wild females (2×2 contingency $\chi^2 = 0.164$, $P = 0.320$).

Discussion

We are aware of only one other study that compared the breeding success of first-generation hatchery females with that of wild counterparts originating from the same population (Jonsson and Fleming 1993;

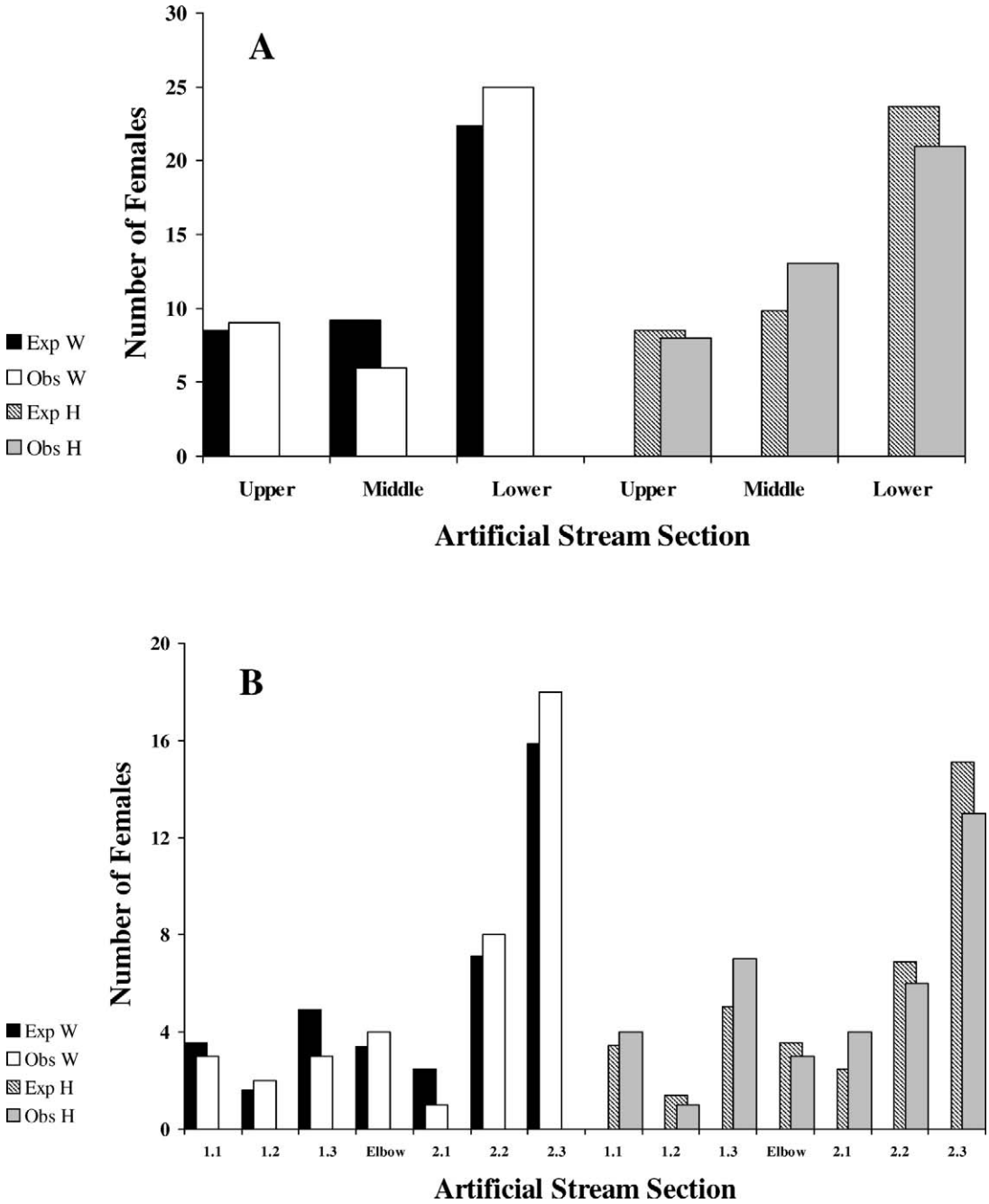


FIGURE 3.—The expected (Exp) and observed (Obs) distribution patterns of wild-origin (W) and hatchery-origin (H) spring Chinook salmon females in the artificial stream. Panel (A) shows the results when test groups were allowed to spawn in three continuous sections of the stream, panel (B) the results when test groups were allowed to use the entire stream.

Fleming et al. 1997). In this study the breeding success of size-matched female Atlantic salmon *Salmo salar* spawning in artificial arenas were examined. Those investigators also compared a suite of female traits

including the onset and duration of spawning, number of nests constructed, time needed to cover eggs following spawning, nest depth, gravel composition within nests, egg retention, and incidence of redd

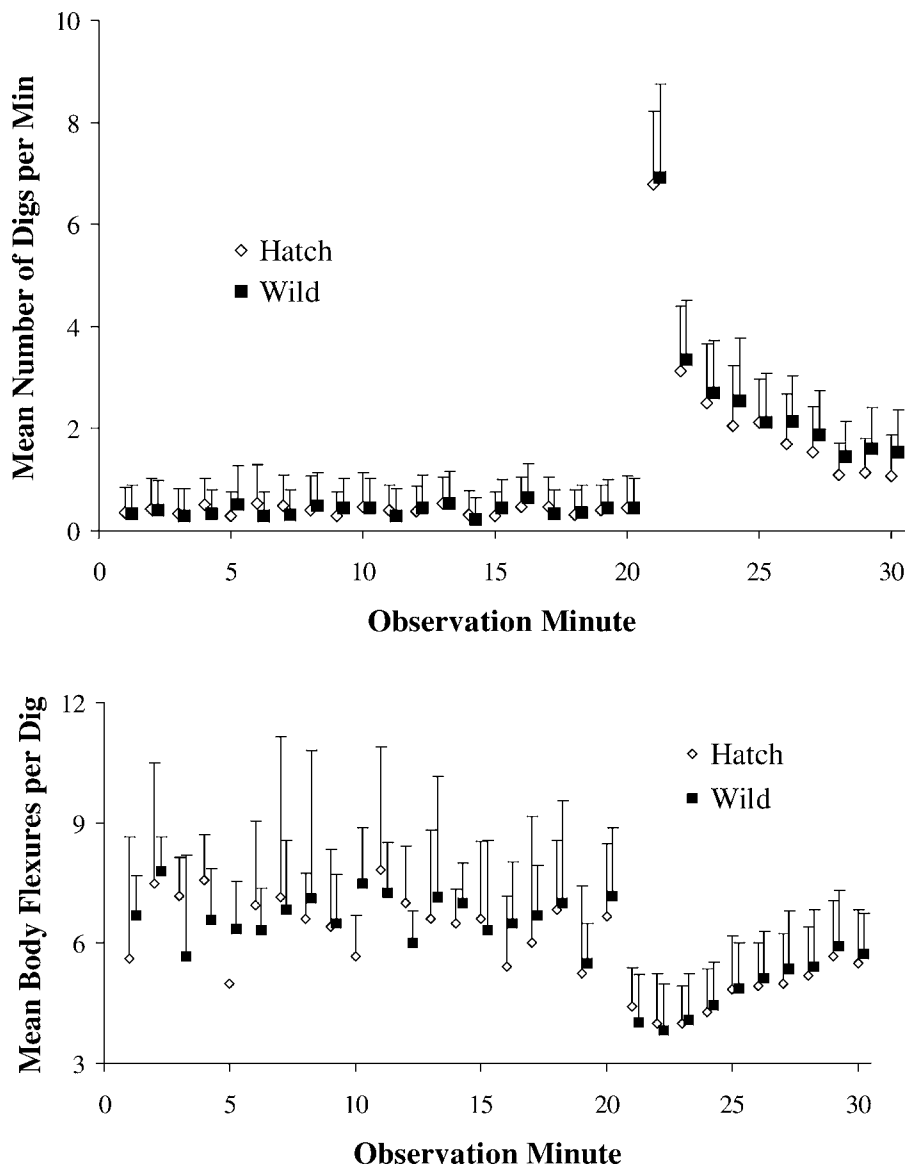


FIGURE 4.—The digging frequency and average number of body flexures used per digging episode in hatchery and wild females 20 min before and 10 min after spawning. Each error bar represents one SD from the mean. Spawning occurred at minute 20.

superimposition. No differences were found. Yet eggs deposited by hatchery fish survived about 80% as well as those spawned by wild fish (Jonsson and Fleming 1993). Our results are consistent with those studies. In our study both hatchery and wild females deposited eggs at comparable rates and no significant differences were seen between longevity, in-stream distribution, nest construction, egg burial, and redd tenure. Yet the eggs spawned by wild females had 5.6% greater egg-to-fry survival rates.

One possible cause for the difference in egg-to-fry survival that we observed is gamete quality. Yet when we compared egg viability in wild and first-generation hatchery Chinook salmon artificially spawned at the CESRF, no difference was found (Knudsen et al., in press). Instead, we speculate that subtle inequalities in three of the female traits measured in our study may have been responsible for the difference seen in survival of deposited eggs. One of these is redd abandonment. Newly fertilized salmon eggs are

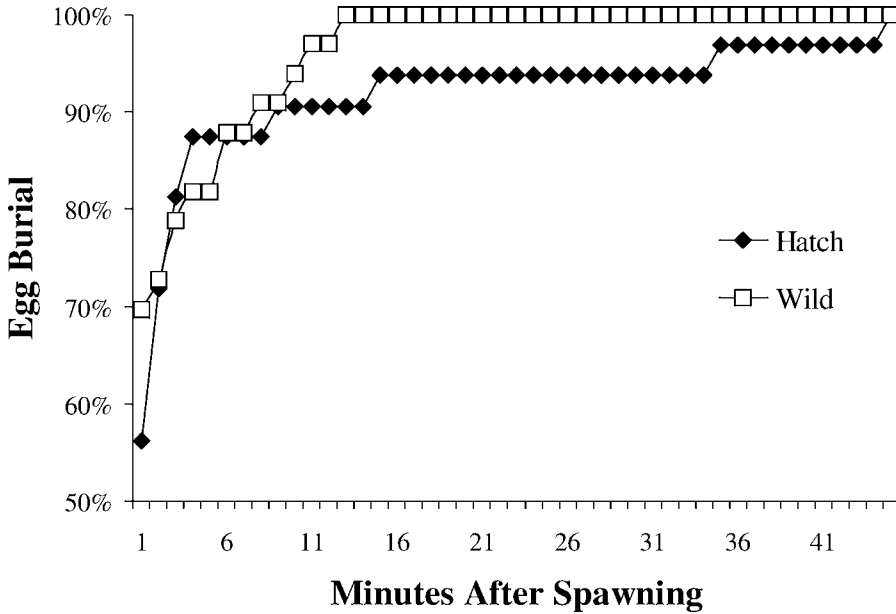


FIGURE 5.—Cumulative frequency distributions comparing the length of time that hatchery and wild female spring Chinook salmon took to cover their eggs after a spawning event in the artificial stream.

sensitive to mechanical shock until blastopore closure (Jensen and Alderdice 1983), which will occur about 12 d after fertilization depending upon water temperatures. By leaving a redd unguarded a female’s developing eggs could be destroyed by the digging activities of other fish. Since hatchery females had a slightly higher tendency to exhibit this behavior ($P = 0.059$) their eggs may have been at greater risk of being destroyed.

Secondly, slightly more wild (58%) than hatchery fish (43%) established redds at the tail ends of sections in the observation stream (chi-square test: $P = 0.08$). These locations were often the first ones chosen by females and they possessed flow and turbulence characteristics that were similar to those occurring in natural pool-riffle transition zones. Spawning salmonids often prefer such sites because of accelerating velocities, coarse gravels, and downwelling or upwelling flows, which tend to promote the survival of developing eggs (Crisp and Carling 1989; Fleming 1996). Perhaps because more wild females spawned in these areas, their egg-to-fry survival rates relative to hatchery females was enhanced.

The third female trait that might have influenced the survival of deposited eggs was the length of time it took to cover newly spawned eggs. Few eggs were exposed in nests for longer than 1 min. In a majority of cases (56% for hatchery and 70% for wild), eggs were immediately buried by the first covering digs per-

formed by a female. Hatchery females did not appear to be as effective in covering eggs as wild fish (Figure 5). In two cases, eggs deposited by hatchery females were exposed for over 30 min. In the artificial stream these eggs would have been available to precocious males and other potential predators and therefore subsequently lost.

We also observed that approximately 10% of the wild and hatchery females placed into the artificial stream created redds in two or more separate sections of the stream. Chinook salmon females are expected to create a single redd and guard it until they are close to death (Healey 1991). It is possible that the physical environment in our stream enhanced the establishment of multiple redds. Because females often spawned in the lowermost portion of a section they could be caught by currents and swept downstream. Perhaps the 30-cm-high falls separating the sections were a migration challenge for females that had already expended energy on nest construction and other activities. In this case, the creation of a new redd may have occurred because it was not possible to return to an original site. On numerous occasions, however, we saw females moving back into upstream sections after having been swept downstream. Moreover, it seems likely that if a female possessed the energy to create an entirely new redd she should have had the capacity to navigate a 30-cm waterfall. Consequently, the use of multiple spawning locations in upper Yakima River spring Chinook

salmon may be a legitimate life history option, particularly since spawning densities are typically low on natural spawning grounds. Such a strategy has been observed in other Chinook salmon populations as well (Bentzen et al. 2001).

We chose to use a quasinatural spawning arena for our study rather than a natural stream for several reasons. Confounding factors like gravel composition and water flow could be controlled. The number, type, state of maturation, physical condition, and entrance timing of every fish placed into the stream could be regulated. Controlling entrance timing and maturation state was particularly important, as we wanted to avoid situations in which later-maturing females could reexcavate or superimpose their redds on sites used by earlier-maturing fish. The artificial stream also allowed us to collect DNA from the adult fish and to randomly subsample their offspring. Finally, it gave us the opportunity to track and record individual fish behavior and relate it to measures of breeding success.

The question posed by use of an artificial spawning arena is the same whenever a test arena is used for any behavioral work, that is, to what extent are these results applicable to fish in a natural setting? Two conclusions about the transfer of results from controlled environments to natural systems seem possible. One is that natural variation will often be great enough to overcome effects observed under controlled conditions. The cumulative effect of many confounding factors will simply overwhelm the ability to perceive differences like those that we detected, and their importance in natural populations could be muted. The other suggests that since the environment in the observation stream maximized survival, it is likely that under less forgiving conditions differences will be accentuated. We do not know which of these scenarios is more likely. Nevertheless, for management purposes it seems wise to assume that differences observed in controlled environments will manifest themselves in natural populations and plan accordingly.

Our study is just one part of a larger effort to examine the possible domestication effects on upper Yakima River Chinook salmon populations caused by a single generation of exposure to hatchery conditions at the CESRF. A number of differences between hatchery and wild spring Chinook salmon have been reported. Knudsen et al. (2006) found more than a two-fold increase in the proportion of age-3 males (jacks) in the hatchery population. They also observed that first-generation hatchery fish were smaller at age and that hatchery fish matured earlier than wild counterparts. Busack et al. (2007) also found significant differences in body shape between adult hatchery and wild fish that averaged 1.85% in females and 1.75% in males.

Knudsen et al. (in press) discovered that total egg mass, egg weight, and fecundity differed between the two types of females. These differences, however, were caused by the larger size of the wild fish. Behavioral differences have also been found. Fritts et al. (2007) simultaneously exposed juveniles originating from first generation hatchery and wild parents to fish predators and found that fry of wild origin had a 2.2% survival advantage over hatchery fry. Wild fry also appeared to be marginally (6%) superior to hatchery fish when both were forced to compete for territories and feeding stations in behavioral assays (Pearsons et al. 2007). The level of divergence found in these comparisons was similar to the difference we observed in female breeding success. In general, exposure to hatchery conditions for a single generation affected a variety of traits at relatively low levels. Knudsen et al. (2006; in press) and Busack et al. (2007) believe that the differences they observed were caused by both environmental and genetic factors as opposed to genetic change alone. The same is probably true for the small difference in female breeding success that we discovered. Conversely, the differences reported by Fritts et al. (2007) and Pearsons et al. (2007) are probably genetic in origin as the fish they compared had been incubated and reared in identical environments.

Our findings, plus those of the other investigations that have compared first-generation hatchery and wild Chinook salmon native to the upper Yakima River, indicate that the hatchery environment has caused subtle morphological, physiological, and behavioral alterations in first-generation hatchery fish. The cumulative outcomes of the small differences observed are not yet known. However, if each has a small effect on fitness, the total effect could be significant. Indeed, Araki et al. (2007) present persuasive evidence that artificial culture can significantly reduce fitness in steelhead *O. mykiss*. Consequently, a major challenge facing those who are involved with salmon conservation is to weigh the benefits of artificial intervention against the risks of extinction and unintentional domestication. Such decisions should be done on a case-by-case basis, as it is likely that the effect of hatchery conditions will vary depending upon the species being cultured and other idiosyncratic factors.

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