Breeding Success Of Wild and First Generation Hatchery Female Spring Chinook Spawning In An Artificial Stream

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This report covers one of many topics under the Yakima/Klickitat Fisheries Project's Monitoring and Evaluation Program (YKFPME). The YKFPME is funded under two BPA contracts, one for the Yakama Nation and the other for the Washington Department of Fish and Wildlife (Contract number 00027871, Project Number 1995-063-25). A comprehensive summary report for all of the monitoring and evaluation topics will be submitted after all of the topical reports are completed. This approach to reporting enhances the ability of people to get the information they want, enhances timely reporting of results, and provides a condensed synthesis of the whole YKFPME. The current report was completed by the Washington Department of Fish and Wildlife.

Executive Summary
In 2001 we began comparing the relative reproductive success of first generation and wild spring Chinook native to the upper Yakima River. The work was done in an artificial stream that was built on the grounds of the Cle Elum Supplementation Research Facility. Our approach was to place mixtures of adult hatchery and wild spring Chinook salmon into the artificial stream and allow them to reproduce under quasi-natural conditions. Their reproductive success was evaluated by estimating the number of offspring each fish produced. This was accomplished by performing pedigree assessments based on microsatellite DNA. Altogether seven test groups of adults were placed into the artificial stream. While the fish reproduced their activities were recorded on audiotape by up to eight individuals who used focused animal observation techniques. During this past contract period, two milestones were completed. First, the pedigree assessments in each of the seven test groups were completed. Altogether over 13,000 fry were analyzed and assigned to parental fish. Second, over 500 hours of audiotapes were transcribed and data from those records were placed into electronic spreadsheets for analysis.

These data were used to compare the relative breeding success of first generation hatchery and wild female spring Chinook salmon. No differences were detected in the egg deposition rates of wild and hatchery females ($P = 0.228$). Pedigree assignments based on microsatellite DNA, however, showed that the eggs deposited by wild females survived to the fry stage at a 7% higher rate ($P = 0.01$) 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 have disclosed similar low-level effects on adult and juvenile traits. The cumulative impact of such differences will need to be considered when hatcheries are used to restore depressed populations of salmon.

All findings in this report should be considered preliminary and subject to further revision unless they have been published in a peer-reviewed technical journal.

Abstract

First generation hatchery and wild spring Chinook salmon from the upper Yakima River, Washington State 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 (P = 0.228). Pedigree assignments based on microsatellite DNA, however, showed that the eggs deposited by wild females survived to the fry stage at a 7% higher rate (P = 0.01) 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 have disclosed similar low-level effects on adult and juvenile traits. The cumulative impact of such differences will need to be considered when hatcheries are used to restore depressed populations of salmon.

Introduction

Using hatcheries to conserve depressed salmonid populations is a common management strategy in North America. In some cases, naturally produced local origin fish (wild brood stock) are brought into a hatchery for breeding and their progeny are reared for varying periods of time prior to being released into natural habitat. 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), 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 in natural conditions (Peterssson and Järvi 1997; Fleming and Petersson 2001; McLean et al. 2004). However, many of these studies compared the reproductive success of non-local 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). None have been done on conservation programs where attempts have been made to minimize domestication, and none have been done at the very beginning of a hatchery program, when domestication has not yet occurred. In this paper we report on a study that compared the breeding success of wild and first generation hatchery spring Chinook

(*Oncorhynchus tshawyscha*). The hatchery fish originated from wild parents and were produced from a 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 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 non-territorial, 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. Comparisons between hatchery and wild males will be presented in the future.

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 State. The Yakima-Klickitat Fishery Project is using the CESRF to monitor the effects of a supplementation program on upper Yakima River spring Chinook. Prior to 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. In Press). 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 (rkm 206 measured from the confluence with the Columbia River). All upper Yakima River salmon must pass through this structure. Every Chinook salmon produced from the CESRF was adipose fin clipped and may also possess a Passive Integrated Tag, Coded Wire Tag, or 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 by Knudsen et al. (2006). All females were either four or five years old and males were two, three, four or five years old. Collected fish were transported 81 km to CESRF and held in a 30.5 m x 4.6 m x 3 m holding pond.

Beginning in September, fish were examined weekly to determine if they had reached maturation. Ripe fish without abnormalities were selected for the artificial stream. No effort was made to size match the fish. Prior to being placed into the stream the fish were anesthetized in a 1:19 000 part solution of tricaine methane sulphonate (Bell 1964), weighed to the nearest g, measured (fork length to nearest mm), and were tagged with 3.8 cm diameter Petersen disks. Each sex received different colored tags and the tags within a sex had unique numbers. In addition, a tissue sample from the ventral 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. In 2001 and 2002 hatchery and wild fish were placed in two separate parts of the stream while in

2003, 2004, and 2005 the entire stream was made available to all the fish. Table 1 shows the number and origin of the females that were present in each group and the range and mean of their body sizes. T-tests were used to compare the body weights of the hatchery and wild females placed into each test group.

Artificial Stream. In 2000, a 127 m x 7.9 m artificial stream was built on the grounds of the CESRF. The U-shaped structure is subdivided by concrete cross weirs into seven sections; a 21 m x 7.9 m curved elbow and six straight sections each measuring 15.2 m x 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 to 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 cm to 10.0 cm in diameter, was used as spawning substrate. The wetted width of the stream ranged between 4.3 m to 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 per second and total discharge averaged 0.37 m^{-3}·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 utilize (Healey 1991; Bjornn and Reiser 1991). A 2.1 m high wall of camouflage netting was installed on both banks with observation openings at eye level cut into this material every 2 meters along its length.

Table 1. The number and size of hatchery and wild female spring Chinook placed into the observation stream from 2001 – 2005. Females used in test groups placed into the stream in 2001 and 2002 had 221 m^2 while those used in 2003 – 2005 had 550 m^2 of area available for spawning.

Population	Sex	Origin	Number	Weight Range	Mean Weight[1]
	Female	Hatchery	9	3.07 – 4.76	4.08
		Wild	9	2.10 – 6.57	4.55
2001 A	Male[2]	Hatchery	10	2.14 – 4.95	3.09
		Wild	12	2.03 – 7.46	4.69
	Female	Hatchery	9	2.87 – 4.28	3.61
		Wild	10	3.18 – 4.88	3.99
2001 B	Male	Hatchery	7	2.60 – 5.25	3.54
		Wild	11	1.78 – 4.90	3.56
	Female	Hatchery	11	2.93 – 5.70	4.50
		Wild	11	3.78 – 6.16	4.78
2002 A	Male	Hatchery	11	2.80 – 4.43	3.48
		Wild	11	2.99 – 5.56	4.20
	Female	Hatchery	11	3.27 – 5.10	3.90
		Wild	8	3.37 – 4.72	4.23
2002 B	Male	Hatchery	7	3.03 – 6.40	4.16
		Wild	9	2.72 – 5.64	4.12
	Female	Hatchery	13	3.00 – 6.58	4.67
		Wild	13	3.52 – 7.83	4.89
2003	Male	Hatchery	11	1.77 – 6.51	4.67
		Wild	14	2.33 – 7.14	4.36
	Female	Hatchery	10	2.54 – 5.00	3.92
		Wild	11	3.12 – 4.57	3.73
2004	Male	Hatchery	19	1.76 – 5.81	3.49
		Wild	10	3.00 – 6.62	4.26
	Female	Hatchery	12	2.47 – 4.24	3.40
		Wild	14	3.06 – 5.20	3.98
2005	Male	Hatchery	13	3.05 – 7.01	4.42
		Wild	12	3.51 – 6.42	4.23

[1] Body weights are in kilograms

[2] Hatchery and wild age 0- and 1-yr-old males ("precocious males") and 3-yr-old anadromous males ("jacks") were also placed into the test groups.

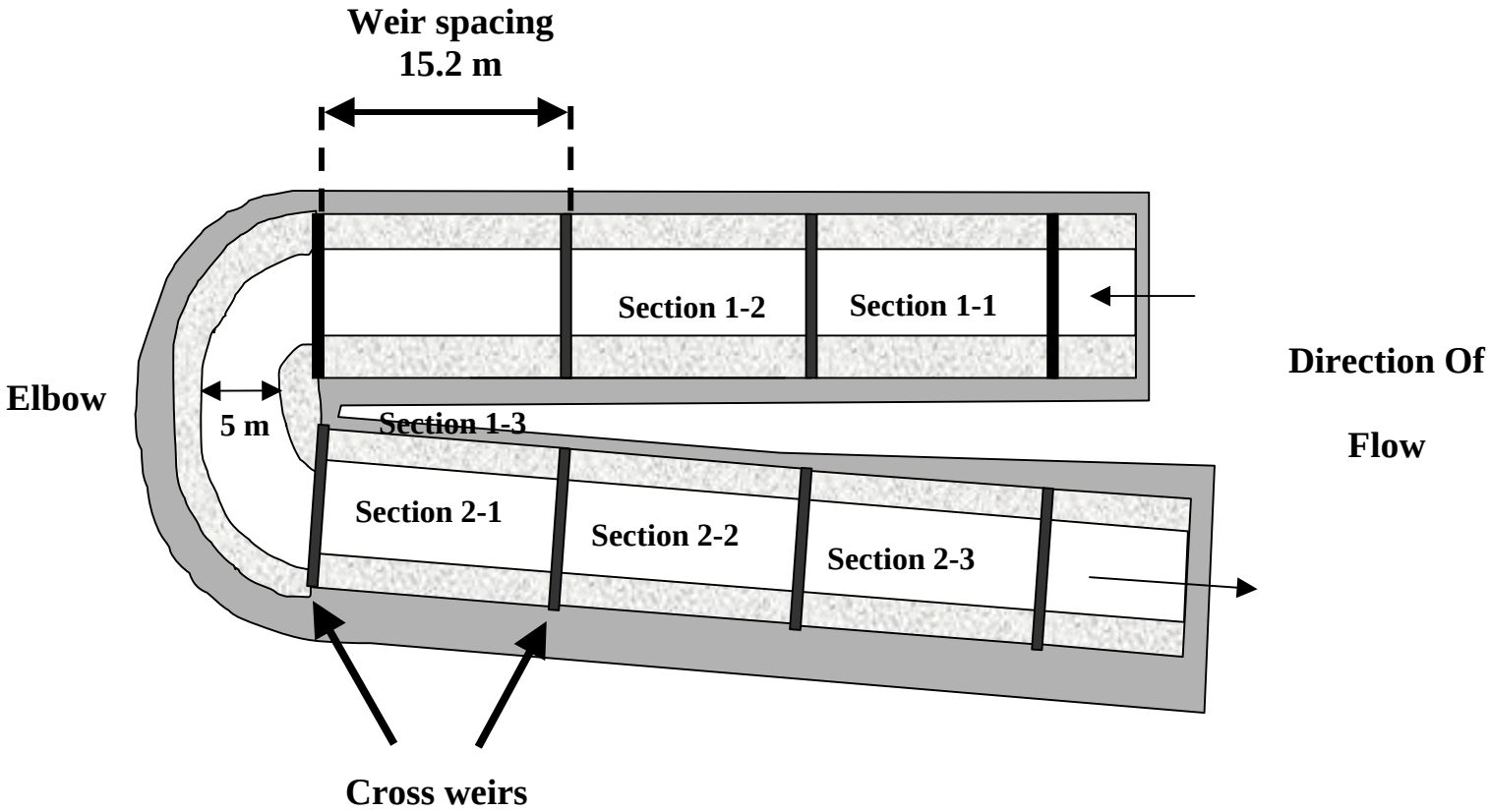


Figure 1. The dimensions of the artificial stream located at the Cle Elum Supplementation Research Facility that was used to valuate the breeding success of female spring Chinook salmon. Not drawn to scale.

In 2001 and 2002, the stream was subdivided into two parts, each consisting of three straight sections (total length was 45.6 m). In 2003, 2004, and 2005, the entire stream was made available to a single test group of fish. Fish were introduced into the uppermost section of the stream and were 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 by 1.5 m squares and each square was provided with 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. One 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 (Actual Egg Deposition or AED survival). The last one measured the percentage of a female's absolute fecundity that had been converted to fry (Potential Egg Deposition or PED survival). To calculate these measures, we used fecundity, egg retention, and offspring production estimates from each female. Fecundities were estimated by multiple regressions whose independent variables equaled body weight, length, and egg weight. Body size, mean egg weight, age and fecundity data used to create these relationships came from females that were artificially spawned at the CESRF (Knudsen et al. 2006; Knudsen et al. 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 water-hardened eggs weighed to the nearest mg. In a few instances (18%) egg weight information was not available. When that occurred multiple regressions using body size information were used to estimate fecundity**.**

AED was computed as PED minus eggs retained. Egg retention data were obtained by hand counting all eggs retained within a female at time of death. Our first measure of female breeding success, percent spawned, was determined by dividing a female's AED value by her estimated fecundity or PED. Before being employed in statistical analyses these percentages were normalized by using the arcsine transformation.

Our second measure of female breeding success, AED survival, was calculated by dividing the number of fry a female produced by her AED value. The arcsine transformation was also used to normalize these values. To estimate the number of fry produced 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 prior to emergence and were fished continuously until fry migration ceased, then seines and electro-shocking gear were used to remove remaining fry so they could be hand counted. Next, 10 percent of each day's catch was preserved in 100% ethanol and used in microsatellite DNA pedigree assessments.

The pedigree analyses estimated the number of fry each female had contributed to the 10 percent 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 create an estimate of the total number of juvenile fish produced by each female. Once the number of fry produced by each female was known it was also possible to generate our third measure of female breeding success, PED survival, or the ability to convert eggs into fry. This value was obtained by dividing the number of fry produced by each female by her PED or absolute fecundity. The arcsine transformation was also used to normalize these values.

Paired t-tests were employed to determine if 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 random variable compared was the mean AED survival rates of survival of hatchery and wild females. A final test compared the mean PED survival values of the two types of females. These were one-sided tests because hatchery females were expected to be less competent than wild counterparts due to inadvertent domestication (Waples 1999).

Regression analyses were used to examine whether traits in hatchery and wild females spawning in the same population had different effects on their breeding success. Female body weight (log 10), for example, was regressed on percent spawned and AED survival values to examine the importance of female size on breeding success. We also regressed percent spawned values with PED survival to see how much variation in fry production could be explained within a female type by the ability to successfully deposit eggs. Similar regressions between percent spawned and AED survival values were performed to see if survival of deposited eggs was affected by how completely a female had spawned. A final set of regressions looked at the importance of AED survival on the ability of females to convert eggs to fry.

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 proteinase K. Following digestion the samples were heated to denature proteins and the DNA extracts were stored at 5^{o}C until all analyses were completed. Spin-column extraction kits from Machery-Nagel were used to purify genomic DNA from fish in test groups 3 – 7. Adults and fry were genotyped at 10 or more loci (Table 2). The number of alleles per locus ranged from 5 in Ots-1 to 40 at Ots-100. Microsatellite DNA loci were amplified via the 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. 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 dead. These data were regarded as ordinal because exact times of death were not always obtained. Mann-Whitney U tests

Table 2. Microsatellite loci and number of alleles scored for the pedigree analyses made on hatchery and wild spring Chinook salmon spawning in the artificial stream.

	Population And Year							
Locus	2001 A	2001 B	2002 A	2002 B	2003 A	2004 A	2005 A	Reference
Ots-101	24	24	24	24	-	-	-	Small et al. 1998
One-8	13	13	16	16	-	-	-	Scribner et al. 1996
Ots-1	5	5	5	5	-	-	-	Banks et al. 1999
Ocl-1	7	7	6	6	-	-	-	Condrey and Bentzen 1998
Ots-100	40	40	-	-	-	-	-	Small et al. 1998
Ots-2M	8	8	11	11	-	-	-	Banks et al. 1999
Ots-107	21	21	-	-	-	-	-	Nelson and Beacham 1999
Omm-1135	-	-	7	7	-	-	-	Rexroad et al. 2001
Omm-1142	-	-	12	12	-	-	-	Rexroad et al. 2001
Ogo-2	10	10	9	9	-	-	-	Olsen et al. 1998
Ssa-197	21	21	20	20	-	-	-	O'Reilly et al. 1996
Oki-100	-	-	-	-	19	21	20	Unpublished
Ots-201b	-	-	-	-	21	21	21	Unpublished
Ots-208b	-	-	-	-	25	25	29	Greig et al. 2003
Ssa-408	-	-	-	-	20	18	20	Cairney et al. 2000
Ogo-4	11	11	9	9	10	11	11	Olsen et al. 1998
Omm-1080	-	-	-	-	36	35	35	Rexroad et al. 2001
Ots-213	-	-	-	-	21	23	25	Greig et al. 2003
Ots-G474	-	-	-	-	7	10	12	Williamson et al. 2002
Ots-3M	8	8	7	7	-	-	9	Banks et al. 1999
Ots-9	-	-	-	-	-	-	5	Banks et al. 1999
Ots-211	-	-	-	-	24	23	24	Greig et al. 2003
Ots-212	-	-	-	-	20	18	23	Greig et al. 2003
Loci Genotyped	11	11	11	11	10	10	12	
No. Of Fry Assigned	991	780	1566	1264	2750	2892	2973	

were used to determine if a difference existed in the longevity of hatchery and wild females within the same test group. Kendall's Tau correlations were used to examine the relationships between longevity and percent spawned, AED, and PED survival values in wild and hatchery females.

Once fish were in the artificial stream, up to eight observers recorded fish activities during daylight hours. These observations were continued until spawning ceased which typically took 72 hours or less. Focused animal observations were made, with observers dictating the activities of individual fish onto audiotapes in 4 to 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. Prior to spawning females create nests by performing multiple independent digging actions. During a digging episode, the body is rotated 90^{o} 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. Additionally, whenever spawnings were observed and visibility allowed we recorded how long it took females to cover eggs until they were no longer visible. We felt this was an important trait because rapid burial would protect eggs from immediate predation. The nest construction and egg burial activities of hatchery and wild females were graphed and compared. A Kolmogorov-Smirnov two-sample test was used to see if egg burial time varied because of female origin.

Contingency Chi Square tests (a 2 x 3 for the 2001 and 2002 test groups and a 2 x 5 for the 2003, 2004, and 2005 test groups) were used to determine if hatchery and wild females spawned in different sections of the artificial stream. Moreover, because 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 x 4 contingency Chi Square test was used in this analysis. One variable was female type, hatchery or wild, while the other variable was location. Each section was split into four 3.8 m x 4.9 m locations or subsections. The uppermost subsections had high turbulence and velocities up to 2 m per second. Conversely, flows were laminar and current velocities were between 0.1 to 0.3 m per second in the lowest subsections. The two interior subsections had intermediate turbulence and water velocity values (authors unpublished data). A final 1 x 4 Chi Square test was performed to see if 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 x 2 contingency Chi Square test was performed to determine if 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 prior to dying. A 2 x 2 contingency Chi Square was performed to determine if female origin was related to redd abandonment.

Results

Body Size. Wild females were significantly larger than hatchery fish in one test group (P = 0. 01). Although not statistically significant, wild females had greater mean body weights in five of the remaining six test groups. In combination, these results suggest that wild females were slightly larger than their hatchery counterparts (Knudsen et al. 2006). Linear regressions were used to evaluate the importance of female body weight (independent variable) on our measures of female breeding success (dependent variables). In one test group, wild females exhibited a positive relationship between body weight and the ability to deposit eggs (r^2 = 0.39, P = 0.024). In the other six test groups this relationship did not occur. Moreover, no significant relationships between female weight and AED and PED survival were found. Consequently, female body weight did not appear to be an important factor affecting the breeding success of females spawning in the artificial stream.

Breeding Success. No difference was seen in the ability of hatchery and wild females to deposit their eggs. Average egg deposition across the test groups was 92.8% in wild and 90.4 % in hatchery females (paired-t test; t = 0.80, P = 0.228). There was a significant difference in the survival of eggs spawned; mean egg-to-fry survival in wild females averaged 60.5% and was 53.2% in the hatchery origin fish (paired-t test; t = 2.99, P = 0.012). We also examined PED survival in the two types of fish (Table 3). On average, wild females transformed 52.8% of their eggs into fry while 45.3% of the eggs carried by hatchery fish produced fry. This difference bordered on significance (paired-t test; t = 1.77, P = 0.063).

Table 3. Mean percent spawned, AED and PED survival rates of hatchery and wild spring Chinook females placed into the artificial stream 2001 – 2005.

Population	Female Origin	Mean Percent Spawned	Mean AED Survival	Mean PED Survival
2001 A	Hatchery	87.8%	24.7%	20.2%
	Wild	85.9%	37.5%	32.4%
2001 B	Hatchery	91.8%	57.2%	48.6%
	Wild	96.2%	71.0%	66.4%
2002 A	Hatchery	83.4%	49.1%	38.7%
	Wild	96.9%	55.8%	52.3%
2002 B	Hatchery	89.4%	50.6%	39.9%
	Wild	95.2%	62.8%	56.5%
2003	Hatchery	95.9%	69.0%	64.5%
	Wild	89.3%	66.6%	51.3%
2004	Hatchery	98.5%	57.1%	56.4%
	Wild	93.6%	62.8%	55.5%
2005	Hatchery	78.9%	64.4%	49.3%
	Wild	89.3%	66.2%	55.5%
	Mean Hatchery	90.4%	53.2%	45.4%
	Mean Wild	92.8%	60.5%	52.8%
Mean Wild – Mean Hatchery		2.4%	7.3%	7.5%

The capacity to deposit eggs (% spawn) was positively associated with fry production in hatchery fish in three out of seven test groups. Similar positive associations were found in wild females in four of the test groups. In these test groups, 45 - 84% of the variation in fry production could be explained by the ability of a female to deposit eggs. In half the test groups, however, no correlation between egg deposition and fry production was found. This counter-intuitive result probably happened because little variation in egg deposition appeared to occur among the females. All were equally capable of spawning eggs but their deposited eggs seemed to survive at variable rates. In just three out fourteen cases AED survival in females was positively correlated with how completely they had spawned. In the remaining test groups, females that had deposited just a portion of their eggs had egg-to-fry survival rates that were equivalent to individuals that had deposited most or all of their eggs. For both types of females, AED survival accounted for 75 to 98% of the variation in PED survival. Consequently, the capacity to spawn eggs did not guarantee breeding success. Instead the quality of the incubation environment a female created appeared to strongly affect her capacity to convert eggs to fry.

Longevity. Origin had little affect on female longevity. In one test group wild females did have longer mean lifetimes, however, in the remaining six test groups no difference was seen. Kendall's Correlation analyses between female longevity and percent spawned, AED and PED survival were performed. Out of the 42 correlations performed, fourteen exhibited significant positive relationships between longevity and our measures of breeding success. Twenty-two others were non-significant but had positive slopes. If the probability of obtaining a positive slope is 0.5 the likelihood of obtaining 36 positive slopes out of 42 trails by chance is quite remote ($P < 0.001$). Consequently, in our experimental setting, longevity in females appeared to be an important factor in determining their breeding success.

Distribution Patterns. Once released into the artificial stream females could move freely throughout the sections that were allotted to their test group. Overall distribution within the artificial stream was not uniform. In five of the populations, most of the females (44% – 66%) established redd territories in the lowest section available to them. Females spawning in these sections had 4.8 - 7.5 m^2 (weighted mean of 5.8 m^2) of space for redds. Conversely fish spawning elsewhere in the artificial stream had 10 to 74 m^2 (weighted mean of 21.3 m^2) of space for redd locations. Previous studies have shown that high instantaneous densities of spawning females increases egg retention and lowers survival of deposited eggs in salmonids (Quinn et al. 2007). This trend was observed in the artificial stream and is shown in Figure 2 that combines information from both types of females collected 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 AED and PED survival (dependent variables) on density (m^2/female). Both were significant, 21% of the variation in AED ($P = 0.044$) and 48% in PED survival ($P < 0.001$) 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 looked at redd distributions in the artificial stream in three ways. First, contingency Chi Square tests were used to see if 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 ($X^2 = 2.81$, $P = 0.245$ for the 2 x 3 analysis; $X^2 = 2.60$, $P = 0.627$ for the 2 x 5 test).

Second we also examined whether female origin affected where within a section, redds were established. 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 ($X^2 = 6.73$, $P = 0.081$) suggesting that females of both types 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

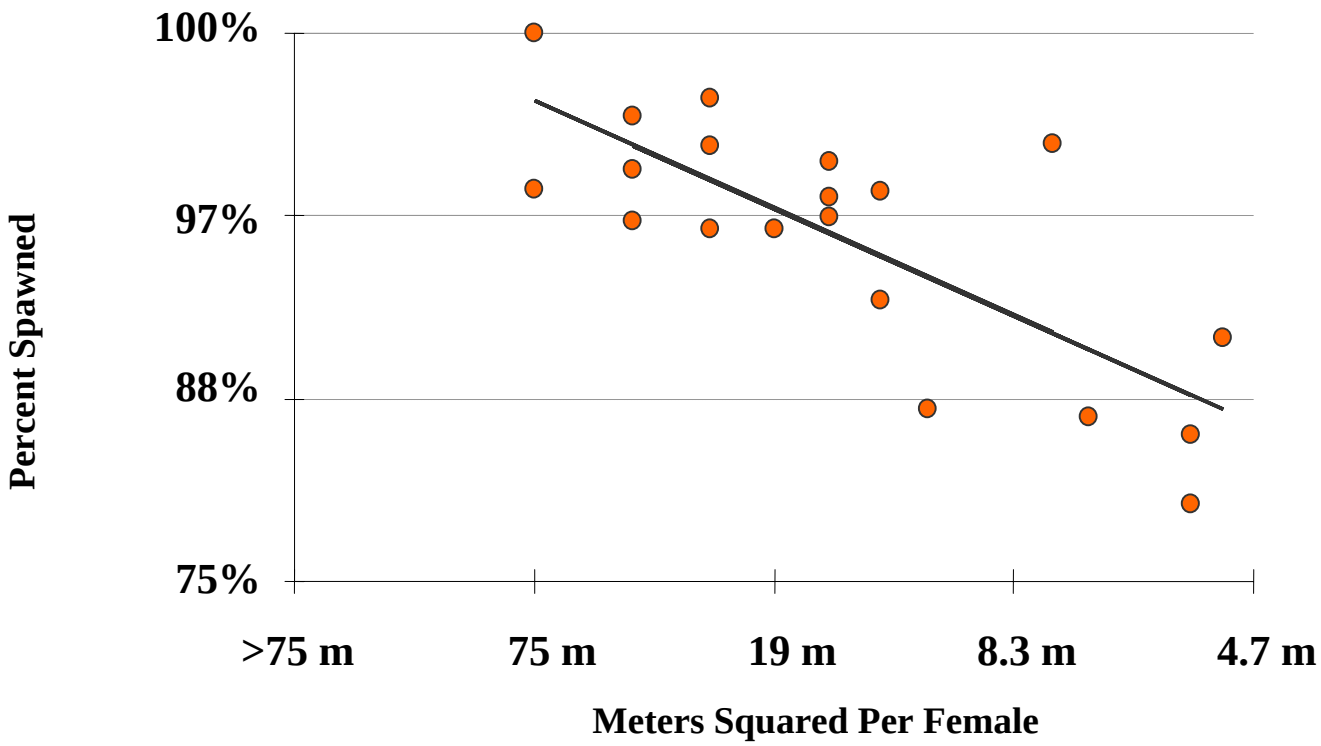


Figure 2. The effect of spawner density on mean egg retention in the spring Chinook salmon females placed in the artificial stream. Data from hatchery and wild females were combined across all seven test groups as no difference was found in their ability to deposit eggs.

was chosen significantly more often than the other three upstream subsections for redd sites ($X^2 = 55.09$, $p = < 0.001$). In fact, 58% of all the wild and 42% of all the hatchery females 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 ($X^2 = 1.61$, $P = 0.447$)

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 females 20 min before and 10

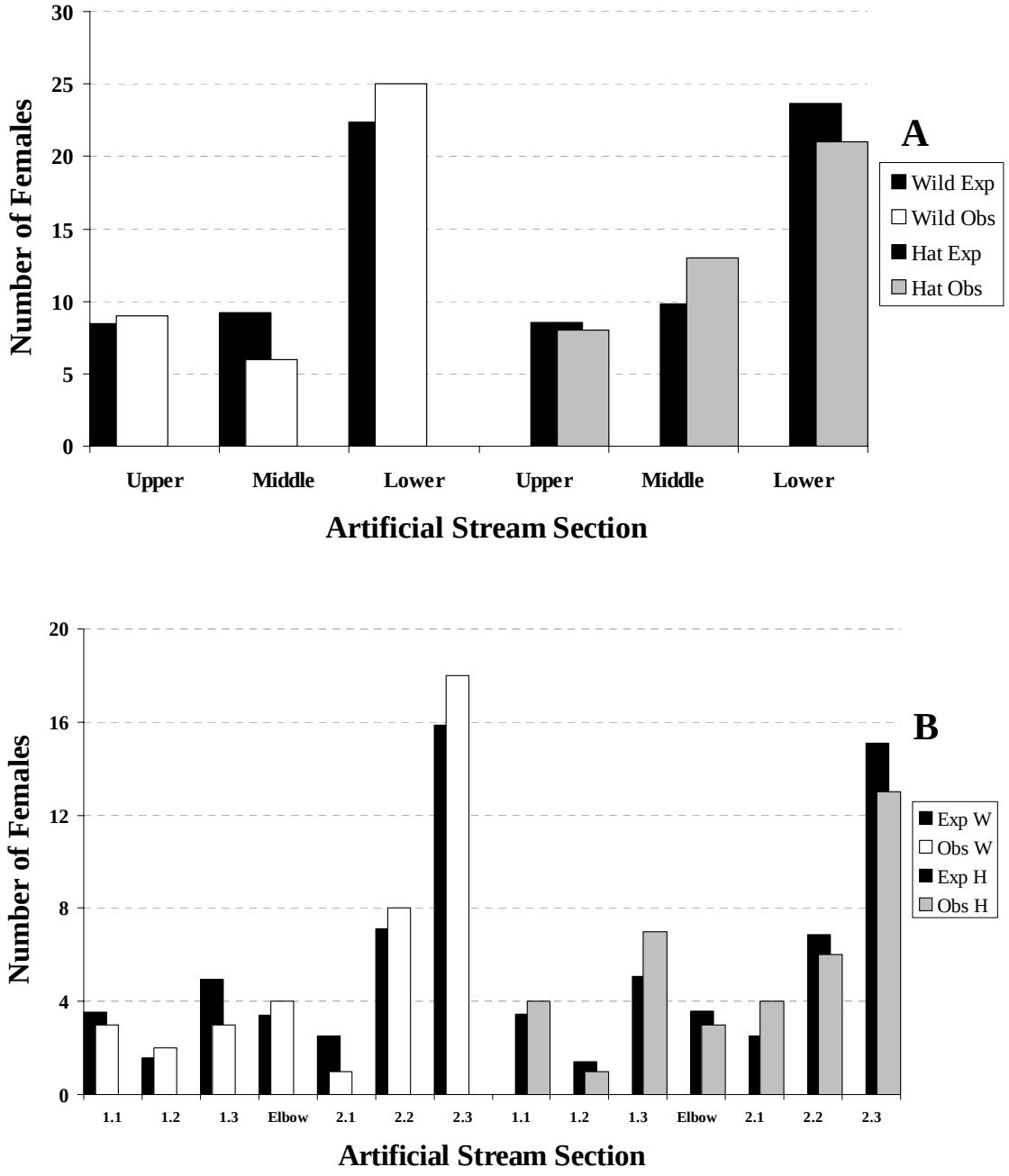


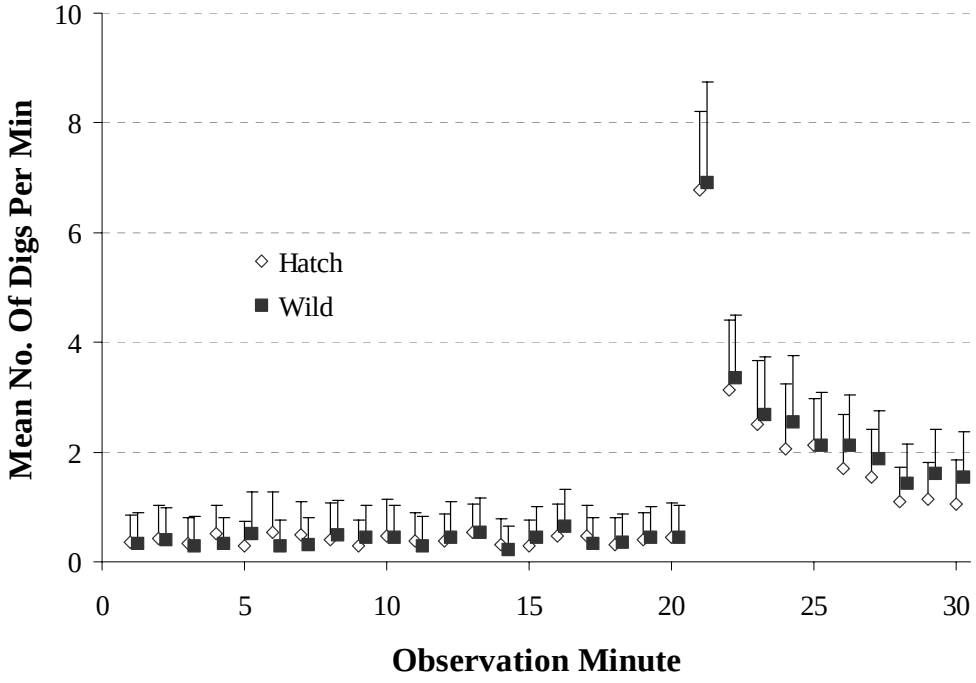
Figure 3 The expected and observed distribution patterns of wild and hatchery origin spring Chinook salmon females in the artificial stream. A: test groups allowed to spawn in three continuous sections of the stream; B: test groups allowed to use the entire stream.

min after spawning. No differences in digging frequency were seen. Both types of females, averaged one digging act every 2.5 min prior to spawning. Immediately after egg deposition, digging frequency in hatchery and wild females increased by more than an order of magnitude

eventually decreasing to pre-spawning levels 20 to 30 min later (Figure 4). The number of body flexures per dig prior to spawning was quite variable ranging from 2 to 16 but averaged between 5 and 8 in both types of females. Immediately after spawning four or less 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 minutes after spawning it had reached six 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 on 32 hatchery and 33 wild females. The two-sample Kolmogorov-Smirnov test that compared how rapidly eggs were buried failed to disclose an overall difference in how long it took hatchery and wild females to cover newly spawned eggs ($P = 0.414$). However more wild females covered their eggs within the first minute after spawning (70% vs. 56%) than hatchery fish. In addition, two of the hatchery fish left their eggs exposed for more than 35 min while the longest period of exposure in a wild female was 13 minutes (Figure 5).

Redd Abandonment. Out of 149 females placed in the artificial stream 139 established redds and 32 of those were abandoned for more than one day. 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 hrs or sooner after leaving their redd. Evictions were rare; only two were observed and a.



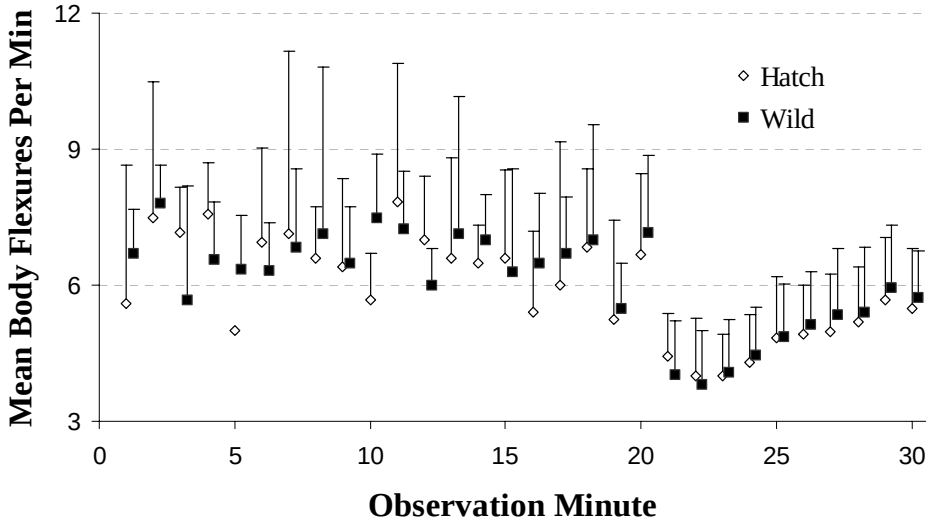


Figure 4. The digging frequency and average number of body flexures used per digging episode in hatchery and wild females 20 min before and 10 min after spawning. Error bars represent one standard deviation from the mean. Spawning occurred at minute 20.

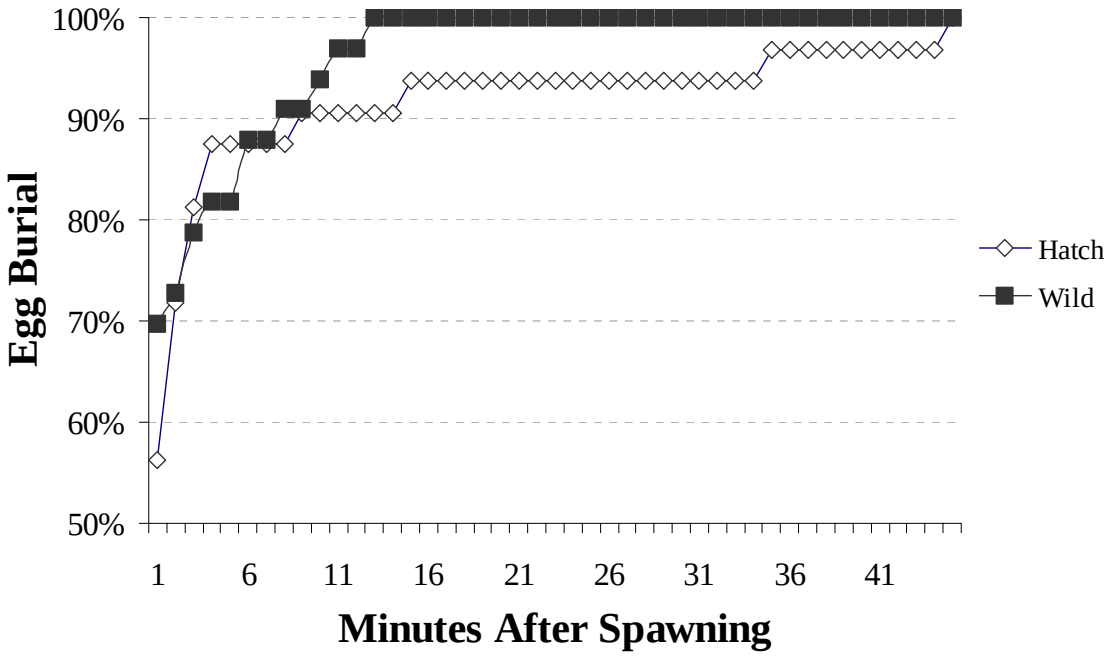


Figure 5. Cumulative frequency distributions that compare the length of time hatchery and wild female spring Chinook salmon used to cover their eggs after a spawning event in the artificial stream

different type of female was involved in each instance. Twelve hatchery (17%) and five wild females (6.6%) abandoned redds and lived for more than one day afterward. The 2 x-2 contingency Chi Square test used to see if this type of abandonment was independent of female origin was marginally non-significant ($X^2 = 3.56$, $P = 0.059$). Additionally, approximately 10 percent 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 x 2 contingency $X^2 = 0.164$ $P = 0.320$).

Discussion

We are aware of only one other study that compared the breeding success of first generation hatchery females with wild counterparts originating from the same population. Jonsson and Fleming (1993) and Fleming et al. (1997) compared the breeding success of size-matched Atlantic salmon (*Salmo salar*) females spawning in artificial arenas. They 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 superimposition. No differences were found. Yet they discovered that 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 theirs. In our study both hatchery and wild females deposited their 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 7.3% greater egg-to-fry survival rates.

We speculate that subtle inequalities in three of the female traits measured in our study may have been responsible for the difference seen in AED survival. One of these is redd

abandonment. Newly fertilized salmon eggs are sensitive to mechanical shock until blastopore closure (Jensen and Alderdice 1983), which will occur about 12 d after fertilization, depending upon water temperatures. Consequently, 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 end of sections in the observation stream (Chi Square $P = 0.081$). 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 down 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, it enhanced their egg-to-fry survival rates relative to hatchery females.

The third female trait that might have influenced AED survival was the length of time it took to cover newly spawned eggs. Few eggs were exposed in nests for longer than 1 min. In most cases (56% for hatchery and 70% for wild), eggs were immediately buried by the first covering digs performed by a female. Nevertheless, 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. Under natural conditions, such eggs would have been available to a host of predators and 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 artificial stream. Chinook salmon females, however, 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 lower-most 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 fall. Consequently, the use of multiple spawning locations in Upper Yakima spring Chinook 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 quasi-natural spawning arena for our work 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 is particularly important, as we wanted to avoid situations where later maturing females could re-excavate 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 also gave us the opportunity to track and record individual behavior and relate it to measures of breeding success.

The question posed by use of an artificial spawning arena is the same that can be posed whenever a test arena is used for any behavioral work: 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 swamp out effects observed under controlled conditions. The cumulative effect of many confounding factors will simply overwhelm the ability to perceive differences like those 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 don't 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 possible domestication effects on Upper Yakima River Chinook salmon 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 a 10% increase in the occurrence of 3-yr-old 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. Significant differences in body shape were also found between adult hatchery and wild fish that averaged 1.85% in females and 1.75% in males Busack et al. (In Press). 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. (In Press) simultaneously exposed juveniles originating from first generation hatchery and wild parents to fish predators and found that wild origin fry 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. In Press). 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), Knudsen et al. (In Press), and Busack et al. (In Press) feel that the differences they observed were mainly caused by environmental factors as opposed to genetic change. The same is likely true for the small difference in female breeding success we discovered. Conversely, the differences reported by Fritts et al. (In Press) and Pearsons et al. (In Press) are likely 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 the hatchery environment has caused subtle morphological, physiological, and behavioral alterations in first generation hatchery fish. In Table 4 we hypothetically examine what their cumulative impacts might be. Under the assumptions of the table, first generation hatchery females are 71% as effective as wild counterparts in the production of adult offspring. The salient point of the table is not the relative productivity of the two types of females, which is speculative. Rather it is the fact that small differences at each life stage can cause significant effects on the production of offspring. For example, under the scenario in the table, a conservation hatchery would need to produce about two females for every wild female used as broodstock to maintain the abundance of the recipient population. In most cases hatcheries will produce more adults than are used as

brood stock and therefore can serve as agents of conservation for depressed populations. Nonetheless, a challenge facing those who are involved with salmon conservation is to determine how fast genetically determined fitness drops due to repeated exposure to hatchery conditions. Currently we are comparing second-generation hatchery spring Chinook with natural origin recruits from the upper Yakima River to track and document genetic change caused by our supplementation program. This work is being done to ascertain the magnitude of domestication effects and their biological consequences on a salmon population experiencing hatchery conditions for the first time. Results can be used when the relative merits of alternative salmon recovery strategies are being considered.

Table 4. Hypothetical cumulative effects of inadvertent domestication on Upper Yakima River spring Chinook salmon based on observed differences between wild-origin and first generation hatchery fish.

Life History Stage	Wild	Hatchery	Assumptions	Source
Adult Female Fecundity	4200[1]	3927	Absolute fecundity is reduced by 6.5% in hatchery females	Knudsen et al. (In Press)
Number of Eggs Spawned	3898	3550	Average egg deposition in wild fish equals 92.8% and 90.4% in hatchery females	This study
Number of Fry Produced	2358	1889	Survival of deposited eggs equaled 60.5% in wild and 53.2% in hatchery females	This study
Number of Fry Produced	2358	1734	Assumes an 8.2% decrease in productivity of hatchery origin fry caused by a 2.2% increase in vulnerability to predators and a 6% decrease in obtaining resources[2]	Fritts et al. (In Press) Pearsons et al. (In Press)
Smolt Production	236	173	Assumes a 90% mortality rate from fry to smolt	Healey (1991)
Adult Production	2.4	1.7	Assumes a 1% smolt-to-adult survival rate	Bosch (2006)

[1] Approximate mean fecundity for Upper Yakima wild 4-yr-old females

[2] Fritts et al. (In Press) found that fry from hatchery parents were 2.2% more vulnerable to predation than fry from wild origin parents. Pearsons et al. (In Press) showed that wild fry were 6% more adept at acquiring needed resources as feeding stations and cover than hatchery fry.

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