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Comparing the Reproductive Success of Yakima River Hatchery- and Wild-Origin Spring Chinook

Yakima/Klickitat Fisheries Project Monitoring and Evaluation

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Yakima/Klickitat Fisheries Project Monitoring and Evaluation

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Summary

A growing body of literature suggests that adult salmon produced by artificial culture are not as reproductively successful as wild fish when they spawn under natural conditions. Behavioral, morphological, and physiological divergences have been observed between hatchery and wild fish. These disparities are the likely proximate causes of the differences seen in the reproductive success of hatchery and wild salmonids. Two evolutionary paradigms have been proposed to explain why salmonids cultured in hatcheries are genetically and phenotypically different from wild cohorts. The first proposes that natural selection has been significantly relaxed in hatcheries. Consequently, fish that normally would have perished because of the possession of unsuitable traits are able to survive. If these traits have a genetic basis, they may become established in a hatchery population and cause its productivity to be less than expected if the fish are once again exposed to natural selection pressures. The second theorizes that environmental and social conditions in hatcheries are less variable than in the natural environment and that these conditions will remain relatively constant from one generation to the next. In this circumstance, selection for genetic traits that adapt fish to artificial culture will become prevalent in the population. Such traits may be mal-adaptive under natural conditions.

Many of the studies that have compared the reproductive success (RS) of hatchery and wild fish, however, have used non-local hatchery fish that have experienced multiple generations of hatchery culture. Few efforts have been made where both the hatchery and wild fish have originated from the same population. When such studies have been performed differences in the competency of the fish to produce offspring have not been detected or are not as great as those expressed when non-local hatchery fish have been used.

The hatchery spring Chinook produced by the Yakima Fisheries Project originated from wild fish returning to the upper Yakima River. When they return as adults, almost all of them will spawn naturally in the Yakima River. The offspring they produce are expected to augment the Yakima spring Chinook population. Whether such an increase will occur or how great it may be depends on two factors, the ability of hatchery fish to reproduce under natural conditions and the capacity of their offspring to survive to maturity. One of the objectives of the Yakima Fisheries Project is to determine whether the hatchery-origin adults produced by the project have experienced any reduction in their ability to reproduce under natural conditions. To accomplish that objective an observation stream was built in 2000 on the grounds of the Cle Elum Supplementation and Research Facility. Beginning in 2001 hatchery and wild spring Chinook from the upper Yakima River stock have been introduced into the stream and allowed to reproduce.

Microsatellite DNA is used to establish the genetic relationships between the adults placed into the stream and fry that are produced by each population. Six populations consisting of mixtures of wild and hatchery fish have been placed into the stream. Pedigree assessments have been completed on five of them. These assessments have shown that the reproductive success in males is often twice as variable as that experienced by females. In the five populations so far examined; wild males (age 4 and 5)

produced the most offspring. The success of comparable hatchery males relative to wild males ranged from 37% to 113%. Hatchery and wild males maturing as 3-yr-olds (jacks) and as 1- and 0-yr-olds (precocious males) were also used in the study populations. They were not as successful at producing offspring as the larger hatchery and wild males.

During 2001 and 2002 two populations of hatchery and wild fish were placed into the observation stream each year. Each one occupied about half of the structure. In these populations wild females exhibited a superior capacity to deposit eggs. In addition, their eggs survived to the fry stage at higher rates. This survival advantage ranged from 1.9 to 11.7%. In 2003 the entire observation stream was made available to a single population of fish in an effort to reduce intrasexual competition among the females for redd locations. In this year, hatchery females were better at depositing eggs (12.5%) and their buried eggs also achieved a higher egg-to-fry survival rate (3.4%). This suggests that at low population levels hatchery females were as competent as wild fish in burying eggs and in producing fry.

Although variation in the reproductive success of females was lower than that seen in males it could be quite variable. For example, coefficient of variation values calculated on female RS ranged from 34 to 77% in the populations we examined. Numerous factors may affect RS in females. We examined the potential impact of body size, longevity, redd defense, agonistic interactions, instantaneous density, water velocities in the redd area, how long it took to establish a redd, and proximity to neighboring fish on the ability of females to produce offspring. Two of these factors, redd defense and longevity proved to be the most important. The other factors had little or no impact on female RS.

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Introduction

The Yakima River supplementation program for spring Chinook (*Oncorhynchus tshawyscha)* is an example of a salmon recovery effort occurring in the Pacific Northwest that utilizes native broodstock. A portion ($\leq$ 50%) of the wild spring Chinook returning to the upper Yakima River are taken into the Cle Elum Supplementation Research Facility (CESRF) for breeding and subsequent rearing prior to being released into their natural habitat. The concept of using native broodstock and recycling them through artificial culture until abundance increases or becomes stabilized has been referred to as supportive breeding (Laikre and Ryman 1996). It is, however, a controversial strategy. Behavioral, morphological, and physiological differences have been observed in hatchery and wild adult salmonids (Fleming and Petersson 2001).

These differences were likely created by divergent environmental conditions or relaxed or dissimilar selection pressures extant in hatcheries. They may negatively impact hatchery fish when they reside in natural environments (Einum and Fleming 1997; McGinnity et al. 1997; Fleming et al. 2000; Dannewitz et al. 2004). A growing body of literature suggests, for example, that adult salmon produced by artificial culture are not as reproductively successful as wild fish when they spawn under natural conditions. Dannewitz et al. (2004) point out, however, that many of these studies compared the reproductive success of non-local hatchery fish with native salmonids or with fish that had experienced multiple generations in a hatchery. Few efforts have assessed the reproductive success of hatchery and wild fish that possess a common genetic history (Dannewitz et al. 2004)

The study described in this report was designed to make such a comparison. Its principal objective was to directly compare the reproductive success of hatchery- and wild-origin spring Chinook by allowing them to spawn together under quasi-natural conditions. The hatchery fish used in the study experienced a single generation of artificial culture and were derived from spring Chinook that were native to the upper Yakima River. Spawning occurred in an observation stream that was built in 2000 at the CESRF. Wild and hatchery-origin spring Chinook returning to the upper Yakima River were introduced into portions of the stream and allowed to spawn. Extensive behavioral and environmental observations were made on the fish while they resided in the stream. Moreover, microsatellite DNA was obtained from each adult fish and microsatellite DNA was also collected on representative samples of the fry produced by each set of adults. These samples were used in pedigree assessments making it possible to estimate the number of offspring each adult fish produced.

Six populations of adult fish have so far been placed into the observation stream and pedigree evaluations have been completed on five of them. In this report we describe and interpret the results obtained from these analyses. In addition, we evaluated the impact that eight factors had on the reproductive success of females spawning in the observation stream.

Methods

Observation Stream

In August 2000, an observation stream was constructed on the grounds of the CESRF. It was built so direct comparisons of the reproductive success of hatchery- and wild-origin spring Chinook could be made in a quasi-natural environment. The stream is 127 m long by 7.9 wide and has a "U" shaped footprint. It is subdivided by eight concrete cross weirs into seven sections, a curved section or elbow that is 21.0 m long by 7.9 m wide and six straight sections that measure 15.2 m long by 7.9 m wide. The stream has banks with 2:1 slopes that are armored with large river rock (10 to 30 cm in diameter) and when it is in operation its wetted width ranges from 4.3 to 5.5 m. Water depth is generally greater than 30 cm and is maintained by inserting notched dam boards in the cross weirs. The streambed is lined with geotextile to prevent water loss and is filled with 90 cm of double washed stream gravel that ranges in size from 7.1 mm to 100 mm in diameter. The stream is cleaned every summer prior to fish introduction by using a Bobcat Tractor and portable water pumps. Gravel samples taken immediately after cleaning have indicated each section has a Fredle Index value that equals or exceeds 7 (Lotspeich and Everest 1981).

Discharge water from 18 raceways located at the CESRF is pumped into the stream from late August through May by using up to four, 25 hp electric pumps. Water velocities and stream depth measurements are made throughout the stream at two times, once immediately prior to adult introduction and again during the incubation period. Depth and velocity data are analyzed using the six-tenths-depth method (Buchanan and Somers 1969) to calculate the volume of water entering the stream. Water temperature is recorded once every two hrs by placing StowAway Tidbit Temperature Loggers at the entrance and exit portions of the stream.

To facilitate fish observations, a 2.1 m tall observation wall was installed on both banks of the stream. The wall was built by attaching camouflage netting to fence posts set on 2.4 m centers. Top and bottom rails were attached to the posts to help support the netting. Openings, at eye level were cut into the netting every 2 meters along its length. Observations made on spring Chinook spawning in the Yakima River revealed that both sexes moved extensively on their spawning grounds. To accommodate this type of behavior the observation stream was subdivided into two equal parts referred to as the upper and lower portions. Each portion consisted of three of the straight sections and therefore was 45.6 m long by 7.9 m wide. A grid system made of 0.6 cm nylon cord was stretched approximately 30 cm over the surface of the water. The squares in the grid measured 1.5 m wide by 3 m long and each was provided with a unique alphanumeric designation so that fish movements and locations could be recorded. A more detailed description of the observation stream can be found in Schroder et al (2003).

Selection Of Hatchery- And Wild-Origin Spring Chinook

Wild- and Hatchery-origin Spring Chinook returning to the upper Yakima River from April through August are randomly selected at the Roza Adult Monitoring Facility and transported to the CESRF where they are held in 30.5 m long by 4.6 wide by 3 m deep concrete raceways. Beginning in early September fish are inspected once a week to assess their maturity. Mature fish destined for the observation stream were captured by dip net and anesthetized in a 1:19,000 part solution of MS222 (Bell 1964). Once docile, the fish are weighed to the nearest gram, have fork lengths taken to the nearest mm, and are tagged with numbered 3.8 cm in diameter Petersen Disks. DNA samples are taken from each fish by removing a small amount of fin material from the trailing posterior corner of the dorsal fin. These samples are placed into 100% ethanol and transported to WDFW's genetic lab for microsatellite DNA extraction and characterization. Immediately after tagging, one or two individuals were placed into an insulated 124 *L* cooler and transported to the observation stream where they were released into the uppermost part of the stream designated for their population.

The four assemblages of fish placed into the observation stream in 2001 and 2002 were allowed to spawn in either the upper or lower portions of the stream. Beginning in 2003, the entire observation stream was made available to a single population of fish. The shift from using about half of the stream per population to using the entire stream was done for two reasons. One was to provide the fish with more opportunities to move and therefore to express behaviors seen in natural spawning populations. The second was to reduce the intrasexual competition among females for space. Table 1 shows the area allotted per female in the five populations that were placed in the observation stream during 2001 – 2003.

Table 1.The amount of space allotted females in the spawning populations introduced into the observation stream from 2001 through 2003.

Year	Portion Of Observation Stream	Number Of Females	Meters Squared Per Female
2001	Upper	19	12.5
	Lower	18	13.2
2002	Upper	22	10.8
	Lower	19	12.5
2003	Entire Stream	26	21.5

Assessing Reproductive Success In The Spring Chinook Adults Placed Into The Observation Stream

The reproductive success of each adult fish placed into the observation stream was estimated by performing a pedigree analysis based on microsatellite DNA. This analysis matched the genotypes of prospective parents to those that existed on putative offspring. A sub-sample of offspring was collected by placing modified fyke nets with attached live boxes at the ends of each portion of the observation stream. The traps were installed in January, several weeks prior to fry emergence to ensure that a representative sample was obtained. The live boxes were checked daily, captured fry were counted, and a sample was taken by randomly removing ten percent of the fry caught on each day and preserving them in 100% ethanol. Table 2 shows the number of fry used in the pedigree evaluations for the 2001, 2002, and 2003 populations.

Table 2. The number of spring Chinook fry analyzed to determine the reproductive success of adults placed into the observation stream in 2001, 2002, and 2003.

Year	Portion Of Observation Stream	Number Of Fry Used In The Pedigree Evaluations
2001	Upper	989
	Lower	778
2002	Upper	1566
	Lower	1261
2003	Entire Observation Stream	2750

Standard microsatellite DNA methods were employed to determine the genotypes of the parent fish and fry. Template DNA was extracted from whole fry and adult tissues by using chelex resin and microsatellite DNA was selectively amplified by using the polymerase chain reaction. Microsatellite alleles were run on an automated sequencer and genotypes were assessed using GENEMAPPER software. CERVUS software was used to assign the sampled fry to the adults placed into the stream. For a complete account of these methods and individual results for the 2001 and 2002 populations see Young and Kassler (2005) in this report.

Post Mortem Observations

Longevity

How long a fish lived in the channel was regarded as an important indicator of fish quality. Individuals that lived for relatively long periods were assumed to be in better physical condition than those that died after a short period of time. Longevity data were collected by inspecting the channel for fresh carcasses at dawn, at dusk, and multiple times each day. Each fish placed into the same portion of the observation stream was given the same start time for its residency. The number of hours it lived was calculated by adding the hours between the common start time and when it died. In some cases we did not observe an exact time of death, for example fish may have perished sometime during the night. Consequently, longevity information was regarded as ordinal data when they were used in statistical tests

Weight, Length, and Gamete Retention

After a fish died it was weighed to the nearest gram and its fork length was measured in mm. The number of eggs a female retained was determined by opening the coelomic cavity and counting the eggs that not been spawned. Eggs that were firmly attached to the ovarian membrane were not included. Males were also dissected and their testes were carefully extracted and weighed to the nearest gram hundredth of a gram.

Estimating Potential and Actual Egg Deposition Values

The Potential Egg Deposition (PED) or fecundity of each female placed into the observation stream was estimated by using formulas that regressed body weight and egg weight on fecundity. The formulas were derived by using information collected on females used as broodstock at the Cle Elum Hatchery. Separate formulas were generated for 4- and 5-yr-old fish and new ones were produced each year to account for annual variation. Actual Egg Deposition (AED) or an estimate of the number of eggs a female deposited in the observation stream was calculated by subtracting any eggs she may have retained at death from her estimated fecundity. Occasionally, some of the females shed eggs during the tagging process. When this occurred, the eggs were counted and subtracted from her PED estimate.

Behavioral Observations

Scan and focused observations (see Schroder et al. 2003 for details) were made on the adults while females prepared nests and spawned. During these observations, the location, color patterns, reproductive status, and frequency of courtship and agonistic behaviors were continuously recorded by using audiotapes. Depending upon the number of observers available, 60 to 90 hrs of taped observations were obtained on each population. The audiotapes were transcribed by hand using symbols and English. While being transcribed a stopwatch was in operation making it possible to break the observations into one-minute time intervals. Scan observations typically lasted 4 to 10 minutes and focused on the activities of a single fish and the individuals it interacted with. On a few occasions focused observations took place and these often lasted 90 minutes or more. They were used to describe the interactions that occurred around a female while she prepared a nest, spawned, and buried her eggs. The transcribed descriptions were placed into two databases. One quantified agonistic behavior while the other indicated the frequency of courtship, nest building, and egg burial activities. In Schroder et al. (2004) we used information from these databases to explore the importance of six agonistic traits and three courting behaviors on the reproductive success of males spawning in the upper section of the stream in 2001. In this report we examine the importance of eight factors on the reproductive success of females that were placed into the lower section of the experimental stream in 2001.

The traits examined were 1) redd tenure, 2) time needed to establish a territory, 3) proximity to neighboring territorial females, 4) agonistic behavior, 5) instantaneous density, 6) longevity, 7) body size, and 8) water velocities in the redd area. Below are more precise definitions for each of these factors and a description of how each was measured.

1) *Redd Tenure*: Females were placed into two groups. One group was represented by fish that had been evicted from their territory by another female or had otherwise abandoned their redd site for an extensive period of time. The other

group consisted of females that remained over their redd sites until death or near death.

2) *Time Needed To Establish A Territory*: Two factors can affect when a female establishes a territory. In some circumstances she may not be physiologically ripe and therefore is not motivated to search for and establish a spawning location. In other instances, females can be inhibited from securing a territory by attacks she receives from other fish in her population. Females in the studied population were placed into two groups; one consisted of fish that had established territories within eight hrs after being introduced into the observation stream. Fish that did not establish territories as rapidly were placed in the other group. Most of them appeared to have found spawning locations during their first night in the observation stream.
3) *Proximity To Neighboring Territorial Females*: Maps of each female's location and territorial borders were made three times every day when females were constructing their redds. These maps were consolidated into a single summary map that showed the general outline of each female's territory after she finished spawning. Maps were made by standing on a bank and sketching the outline of the gravel area a female had disturbed by her digging activities. The final summary map was used to estimate the distance that existed between one territory and another. The distance to the nearest three neighboring territories was ascertained for each female from the summary maps. These values were summed and divided by three to provide a mean distance to her nearest neighbors. These were the fish that were expected to interact the most with the target female.
4) *Agonistic Behavior*: Three general measures of agonistic behavior were determined for each female. The first one quantified the average number of agonistic interactions a female experienced during a minute. It was calculated by summing all the positive (target female attacking another fish, male or female) and negative (target female being attacked by another fish, either a male or female) agonistic interactions a female was observed to experience by the total number of minutes she was observed. This random variable was called *Interactions Per Minute*. The second agonistic variable was referred to as *% Positive Ago*. It was calculated by dividing the total number of positive agonistic interactions a female was observed to make by the total number of agonistic (both positive and negative) she experienced during the time she was observed. The last variable was called *% Positive Territorial Ago.* In this instance, the total number of positive agonistic actions a territorial female experienced was divided by the total number of agonistic interactions she was observed to experience.
5) *Instantaneous Density*: The instantaneous spawning density experienced by a female was calculated by dividing wetted area of the 15.2 m long by 7.9 m wide subsection she spawned in by the total number of females spawning in that sub-section. This variable examines the consequences of instantaneous densities on territory size and on the ability to produce offspring.
6) *Longevity*: As described above each population was routinely surveyed for carcasses to estimate the time and date each fish died. The number of hrs between when when a fish was introduced into the observation stream and when it was

recovered as a carcass was determined by subtracting its entrance date and time from the time and date of its death.

7) *Body Size*: Body size equals the weight of each female at the time she was introduced into the observation stream
8) *Water Velocities In The Redd Area*: Water velocity measurements were taken in each section of the observation stream immediately after spawning had occurred. In 2001, 775 water velocity measurements were obtained from the lower portion of the observation stream by using a Swoffer Digital flowmeter. In each subsection, nine cross sectional transects were established. The first transect was 1.52 m below the upstream cross weir. Transects were then established every 1.52 m thereafter. Point measurements along each transect were taken every 30 cm. The summary maps that showed the border outlines of each female's redd territory were superimposed on the maps showing the water velocity values obtained at each sampling point. Velocity readings that fell within the boundaries of a territory were averaged to produce a reified value of how fast water was moving over a redd territory.

Statistical Approaches Used

Analysis of Pedigree Results

The pedigree assignments made on fry sampled from the 2001, 2002, and 2003 populations were sorted to determine the number of individuals in the samples that had originated from hatchery and wild parents. For example, up to six different types of males were present in some of the populations. The sorting process made it possible to determine the total number of fry each of these groups contributed to the fry sample. Because the number of progeny each adult contributed to the sampled fry population was ascertained it was also possible to determine the mean number of progeny each type of adult contributed to the sampled population. Ranges, standard deviations, and coefficient of variation values for each type of hatchery and wild fish were also calculated.

Chi square analyses were used to test whether hatchery and wild fish differed in their capacity to produce offspring. In the tests that evaluated differences among males the underlying assumption was that each male, regardless of origin or life-history type had an equal opportunity to produce offspring. Suppose that a total of twenty males had spawned in a population and that 1000 fry had been examined. Under the assumption of equal contribution rates, each male would be expected to contribute fifty progeny to the sampled fry population. Assume further, that ten of the males were hatchery-origin fish; in this case the total expected number of fry these males would contribute equals 500 or 50 fry per individual x 10 the number of hatchery origin individuals. The Chi square tests were performed to test the null hypothesis that hatchery- and wild-origin males with various life history strategies (4 & 5 yr-olds, jacks, and precocious males) contributed at expected rates to the analyzed fry samples originating from their population. When differences occurred, additional chi-square analyses were performed when necessary to determine the relative contribution rates of each type of male in the population (Zar 1999).

Chi square tests were also used to evaluate the contribution rates of females. Unlike males, only two types of females were present in each population, those that were wild or hatchery in origin. The reproductive success of a female depends upon her ability to deposit eggs and on the survival of her deposited eggs. Consequently, two sets of chi-square analyses were performed, one examined whether hatchery and wild females had comparable abilities to deposit eggs while the second tested whether the survival of the eggs they deposited survived at similar rates. To perform these analyses the PED and AED values associated with each female were used.

A hypothetical example will help illustrate how PED and AED values were used. Assume that ten hatchery and ten wild females spawned in a portion of the observation stream and that the total fecundity (PED) of all the females equaled 70,000 eggs. Suppose also that a total of 10,000 eggs had been retained by the fish. This means that on average each female deposited 85.7% of her eggs (10,000/70,000 = .857). The PED value of each female placed into population is multiplied by .857 and then all of these values are summed within a female class to provide the expected number of eggs deposited by this type of female. Chi square tests compare this expected sum to an observed value. The observed values were determined by subtracting the number of eggs a female retained at death from her estimated PED. This number equals the AED or "actual" number of eggs deposited by a female. All the AED values for females in the same class (hatchery or wild) were summed to give a total AED value for each type of female. Observed and expected values were compared using chi-square methods. Since only two types of females were present the resulting chi-square values were modified by using Yates correction factor (Zar 1999).

Tests comparing the survival rates of deposited eggs to fry were performed in a similar manner. The underlying assumption was that female type or origin would not affect the survival of buried eggs. Suppose that hatchery and wild females had both deposited 30,000 eggs into a portion of the observation stream. Consequently, half of the 60,000 deposited eggs came from wild females and half from hatchery females. Assume that 1000 fry from this population had undergone a pedigree evaluation. Our null hypothesis would predict that 50% or 500 of the sampled fry would originate from wild females and 50% would come from hatchery females. In the analyses, these expected numbers of fry were compared to the numbers determined by the pedigree evaluation.

Our efforts to evaluate the capacity of hatchery- and wild-origin adults to produce fry in 2001 and 2002 were performed under similar circumstances. Adult densities, gravel composition, water flow, temperature regimes, and other environmental conditions, for example, appeared to be comparable. In each of these populations the same null hypotheses were being tested. We used heterogeneity chi-square analyses (Zar 1999) to determine whether all of the samples could have originated from a single population. When that occurred an overall chi-square analysis on data pooled from each of the homogenous populations was performed.

Evaluating The Importance Of Female Traits And Environmental Factors On RS

Redd Tenure. One-way ANOVAs were used to compare the RS of females that had been evicted or who abandoned their redds for prolonged periods of time with those who had remained on their territories until death or near death. One test evaluated the capacity of the females in each class (Evicted vs. Territorial) to convert their eggs (PED) to fry. The other looked at the production of fry from eggs deposited by each fish. In the first analysis the random variable equaled the number of fry each female had contributed to the fry sample that had undergone the pedigree evaluation. Before these numbers could be used, however, they had to be adjusted and transformed. In its original state the pedigree analysis showed the number of fry originating from each female. We also knew what the PED value was for every fish. Females with relatively high fecundities are expected, on average, to contribute more fry to a random sample than those with lower fecundities. To adjust for differences in fecundity, an average PED value for all the females in the population was determined. Then we calculated the number of fry each female would be expected to contribute to a fry sample if she had this average fecundity value. This was done by the using the following formula:

$$\text{Expected Number of Fry} = \frac{(\text{No. Of Fry Observed In The Pedigree Analysis}) \times (\text{Mean Fecundity})}{(\text{Actual Fecundity})}$$

The expected or adjusted values were considered to be counts and therefore the square root transformation was used to normalize them so that an ANOVA could be performed.

The random variable in the second ANOVA was also the number of fry each female contributed to the pedigree sample. These values were adjusted by calculating an average AED value and using it in a formula comparable to one shown above. Consequently, the adjusted numbers represented the number of fry each female was expected to contribute to the pedigree sample if all of them had deposited the same number of eggs into their redds. This allowed us to compare the survival rates of the eggs deposited by "evicted" and "territorial females". As in the first analysis, the adjusted values were modified by the square root transformation.

Time Needed To Establish A Territory. One-way ANOVAs were used to compare the RS of females that had established territories soon after introduction into the observation stream versus those that took more than 8 hrs to establish a territory. One of these tests examined the capacity of each type of female to convert all of her eggs (PED) into fry while the other examined whether the survival of deposited eggs in a redd (AED) was affected by how long it took a female to establish a territory. The random variable in the first analysis was the number of fry each female contributed to the pedigree sample after it had been adjusted by assuming each female had the same PED value. Similarly, the random variable in the second ANOVA was the number of fry each female contributed to the pedigree sample after it had been adjusted by assuming each female had identical AED values. These counts were modified by the square root transformation prior to conducting the ANOVAs.

Proximity To Neighboring Territorial Females. Kendall's coefficient of rank correlation (Sokal and Rholf 1995) was used to evaluate the relationship between the proximity of neighboring females and the production of fry. Two tests were performed. One evaluated whether there was a relationship between PED and neighbor proximity on fry production while the other examined how proximity to neighboring territorial females might impact buried (AED) egg-to-fry survival. As in the previous two analyses, the number of fry each female contributed to the pedigree fry sample was adjusted by either standardizing fecundity or AED values. Adjusted fry numbers were then calculated as described above. BIOMstat (Rohlf and Slice 1999) software was used to perform the analyses.

Agonistic Behavior. Linear regressions were used to evaluate the potential influence of agonistic interactions on female RS. Two of these analyses looked at how adjusted fry counts (dependent variable or Y) were influenced by the average number of agonistic interactions a female experienced per minute (independent variable or X). Two others examined whether adjusted fry counts (Y) were affected by the percentage of time she was an aggressor [attacks on other fish/ (attacks on other fish + attacks on female from other fish)] The last two regressions looked at this same relationship except restricted it to when a female was territorial. The arc sin and square root transformations were used to normalize the percentage and fry count data prior to performing the regression analyses. Finally, a paired t-test was performed to determine whether the tendency to attack other fish in females was affected by whether she possessed a territory or not.

Instantaneous Density. One way ANOVAs were used to assess the potential affect of three different instantaneous spawning densities on the ability of females to convert their eggs to fry, and on the eggs they buried to produce fry. As in the ANOVAs described above adjusted fry counts were used as the random variables in these analyses.

Longevity. Kendall's coefficient of rank correlation was used to evaluate the relationships between how long a female lived in the observation stream (longevity) with her ability to convert eggs into fry and her ability to convert buried eggs into fry.

Body Size. Regression analyses were performed to examine the relationship between body size and the occurrence of fry in the pedigree sample. In this instance, both adjusted and non-adjusted fry numbers were used.

Water Velocity In The Redd Area. The mean water velocity values obtained over each female's redd were used as independent variables in two regression analyses. One examined the affect that water velocity had on the ability of females to convert their eggs to fry and the other looked at the consequence of water velocity over a redd on the survival of buried eggs to fry. Adjusted fry counts were the dependent variables in these tests.

Results

Pedigree Assessments

Tables 3a and b show the number of hatchery and wild fish placed into each section of the observations stream and how successful they were at producing offspring in the fry samples that were used in the pedigree analyses. Both have seven columns, the first indicates the year and portion of the observation stream that was used, the next two list the types and numbers of fish placed into the channel. When only one representative of a fish type (e.g. wild jack) was placed into a population it was not shown because range, standard deviation, and coefficient of variation statistics could not be calculated. The mean number of offspring values in column four represent the total number of sampled

Table 3a. The mean number of offspring produced in the pedigree samples by various types of males introduced into the observation stream in 2001, 2002, and 2003.

MALES						
Population	Type Of Male	Number	Mean # Of Offspring Per Male In Fry Sample	Number Of Offspring Per Male Range	Stdev	CV
Upper 01	Wild	12	49.08	0 - 246	83.05	169.20%
	Hatchery	9	41.44	0 - 133	45.06	108.73%
Lower 01	Wild	10	34.70	0 - 88	36.80	106.05%
	Hatchery	7	39.14	0 - 157	55.97	143.00%
	Precocious W	5	0.20	0 - 1	0.45	223.61%
	Precocious H	7	18.14	2 - 36	13.70	75.54%
Upper 02	Wild	11	94.00	1 - 249	84.19	89.57%
	Hatchery	11	34.27	0 - 110	34.20	99.79%
	Precocious W	5	7.20	0 - 36	16.10	223.61%
	Precocious H	7	8.00	0 - 33	12.01	150.17%
Lower 02	Wild	9	66.44	8 - 212	68.49	103.07%
	Hatchery	7	64.57	12 - 147	46.80	72.48%
	Precocious H	8	21.75	0 - 63	21.12	97.12%
Entire 03	Wild	14	104.64	0 - 321	94.62	90.42%
	Hatchery	11	84.00	0 - 225	91.60	109.05%
	Hatchery Jack	5	13.00	0 - 32	17.35	133.46%
	Precocious W	13	10.54	0 - 57	16.25	154.16%
	Precocious H	7	9.57	0 - 18	6.97	72.85%

fry originating from each type of adult divided by the number of adults in that class. For instance, in the Upper 01 population twelve wild males fathered 589 of the fry used in the pedigree analysis. The average number of fry for each of these individuals was thus 49.08 (589/12).

Comparisons between the mean number of fry produced by each type of male cannot be made across populations because as Table 2 illustrates the number of fry used in the pedigree assessments varied from one population to the next. Conversely, examining statistics such as the coefficient of variation across populations does provide a way of assessing how variable the capacity to produce offspring was for each type of male. Table 3b depicts the same information for females.

Table 3b. The mean number of offspring produced in the pedigree samples by the hatchery- and wild-origin females introduced into the observation stream in 2001, 2002, and 2003.

FEMALES						
Population	Type Of Male	Number	Mean # Of Offspring Per Female In Fry Sample	Number Of Offspring Per Female Range	Stdev	CV
Upper 01	Wild	9	64.33	0 - 134	45.45	70.64%
	Hatchery	10	31.41	0 - 79	31.41	76.60%
Lower 01	Wild	10	49.10	5 - 112	36.45	74.23%
	Hatchery	8	35.88	7 - 54	15.98	44.53%
Upper 02	Wild	11	79.82	32 -128	27.49	34.44%
	Hatchery	11	62.55	18 - 108	32.53	52.02%
Lower 02	Wild	8	79.00	44 - 111	27.16	34.38%
	Hatchery	11	57.18	31 - 116	24.01	41.99%
Entire 03	Wild	13	87.31	1 - 159	60.23	68.99%
	Hatchery	13	124.23	70 - 206	45.87	36.93%

Table 4 shows the results of the chi-square tests used to compare the reproductive success of the various types of males placed into the observation stream. This table has eight columns. The first one indicates the year the adult fish were placed into the observation stream, and the second one shows what part of the stream the fish used. The third column indicates the type of males placed into the stream. Up to six different types may have been placed into each population. Wild Prec. are wild precocious males that had matured either in the first year of life or so called "zero-aged" individuals or those that matured during their second year referred to as 1-year-olds. Zero-aged wild precocious males ranged in size from 77 to about 100 mm in fork length whereas 1 yr-old wild precocious males varied from 113 mm to 158 mm in length. They were collected from the Yakima River and brought into the Cle Elum Hatchery and held for several weeks before being placed into the channel. Hatch Prec. are hatchery precocious males. All of these males were 1-yr-olds and their fork lengths ranged from 172 mm to 227 mm. Hatchery and wild jacks are males that matured at age 3 while hatchery and wild males were individuals that had matured at ages 4 and 5.

The fourth column "No. Of Males In Class" indicates the number of males of each type that went into a population. The next column "% Of Type In The Population" is the number of males in a class divided by the total number of males in its population. For example, there were two wild jacks in the Upper 2001 Population since 24 males were in the population they represented 8.3% (2/24 = 0.0833) of the male population. The next column "% Of Fry Fathered" indicates the percentage of fry that originated from each type of male that were present in the fish used in the pedigree evaluations. If all the males were equal in their capacity to produce fry the two percentages (percent of type in population and percent of fry fathered) would be equal to one another. As Table 4 shows this is not the case, large discrepancies between these two percentages often occurred.

The last two columns represent an attempt to explain the origin of these differences. The column entitled "Success Relative To Wild Males" expresses the relative RS of each male type to the wild males that were present in a population. Relative success values were determined by dividing the mean number of fry produced by a type of male by the mean number of fry produced by the wild males. Values less than 100% generally indicated that the male type was less successful at producing fry than wild males. Conversely values in excess of 100% suggested that the males in that class were more successful than the wild males they competed against. The last column in Table 4 shows the results of multiple chi-square tests that were performed on the pedigree data. Typically, different types of males in each class did not produce similar numbers of progeny. Zar (1999) suggests that chi-squares can be repeatedly performed to gain additional insights by removing the group with the highest individual chi-square value, and then re-running the analysis without this group. The results of these tests are summarized in the far right hand column of the table. For example, in 2003 the following relationships were found,

WM > HM & WJ > HJ, Hprec, & Wprec

The number of males in each class must be considered when these results are being interpreted. In the above example, only one wild jack was present so it is difficult to know whether this individual was a typical representative. In other cases, however, like the hatchery jack class, seven males were present which helps ameliorate or dampen the effects of natural variation in RS. In males such variation can be quite high as Table 3a

Table 4. The reproductive success of spring Chinook males spawning in the Cle Elum observation stream.

Population							
Year	Stream Sections	Male Type	No. Of Males In Class	% Of Type In The Population	% Of Fry Fathered	Success Relative To Wild Males	Chi-Square Results
		Wild Jack	2	8.3	0.5	5.1%	
		Hatch Jack	1	4.2	2.4	48.9%	
		Hatch Male	9	37.5	37.6	84.4%	
2001	Upper 1-1 – 1-3	Wild Male	12	50.0	59.4	100.0%	WM > HM > HJ > WJ
		Wild Prec.	5	15.6	0.1	0.6%	
		Hatch Jack	2	6.3	1.3	14.41%	
		Hatch Prec.	7	21.9	16.3	52.28%	
		Wild Jack	1	3.1	2.4	54.76%	
		Hatch Male	7	21.9	35.2	112.80%	
2001	Lower 2-1 –2-3	Wild Male	10	31.3	44.6	100.0%	HM & WM > Hprec & WJ > HJ > Wprec
		Wild Prec.	5	13.9	2.3	7.7%	
		Hatch Jack	1	2.8	0.5	8.5%	
		Hatch Prec.	7	19.4	3.6	8.5%	
		Wild Jack	1	2.8	3.3	52.32%	
		Hatch Male	11	30.6	24.1	36.46%	
2002	Upper 1-1 – 1-3	Wild Male	11	30.6	66.2	100.0%	WM > WJ > HM > Hprec, HJ, & Wprec
		Wild Prec.	2	7.1	1.0	9.0%	
		Hatch Jack	1	3.6	0.4	7.5%	
		Hatch Prec.	8	28.6	13.8	32.7%	
		Wild Jack	1	3.6	1.8	34.6%	
		Hatch Male	7	25.0	35.8	97.2%	
2002	Lower 2-1 –2-3	Wild Male	9	32.1	47.3	100.0%	WM & HM > Hprec & WJ > HJ & Wprec
		Wild Prec.	13	25.5	5.0	10.1%	
		Hatch Jack	7	13.7	2.4	9.2%	
		Hatch Prec.	5	9.8	2.4	12.42%	
		Wild Jack	1	2.0	3.1	82.2%	
		Hatch Male	11	21.6	33.7	80.3%	
2003	Entire Observation Stream	Wild Male	14	27.5	53.4	100.0%	WM > HM & WJ > HJ, Hprec, & Wprec

illustrates, CV values for RS can exceed 180% in this sex.

The reproductive success of each female is constrained by three factors, the number of eggs she carries into a spawning ground (her fecundity), her ability to deposit these eggs (construct nests and successfully spawn), and the survival of her deposited eggs to the fry stage and to all the life stages that follow. Our analysis of female RS was restricted to looking at how successful hatchery- and wild-origin females were in depositing their eggs, and upon the survival of their buried eggs to the fry stage.

The capacity of hatchery- and wild-origin females to deposit eggs is compared in Table 5. This table has ten columns. The first four are similar to those used in Table 4, they indicate the year the spawning population was created (column 1), the area of the observation stream where the fish spawned (column 2), female type (either wild or hatchery), and the number of fish representing each type or class of female. The next column "Expected # Of Eggs Deposited" equals the sum of the fecundity estimates for each type of female multiplied by the average percentage of eggs that all the females in the population successfully deposited. In the upper part of the Observation Stream in 2001 for example, the combined number of eggs possessed by wild and hatchery origin females was estimated to be 79,112. The 19 females in this population were found to have retained 22,693 eggs or on average each female deposited 71.3% of her eggs. This overall average deposition rate was multiplied by the total number of eggs each type of female brought into the stream to provide an "Expected # Of Eggs Deposited" value. In this instance, the total fecundity of all the wild fish placed into the upper part of the stream equaled 37,408 eggs; the total they were expected to deposit equaled 37,408 x .713 or 26, 678. A similar "expected value" for the hatchery fish was determined the same way—fecundity of each hatchery fish was summed and this total was multiplied by the average egg deposition rate for the females placed into that section. The next column equals the number of eggs that were actually deposited. The eggs retained in each female by type were summed and subtracted from the estimated number of eggs that type of female was expected to possess at the time they were introduced into the observation stream. The nine wild females placed into the upper part of the channel in 2001 retained 10,959 eggs. Since their expected total fecundity was 37,408 the number of eggs they deposited equaled 37,408 – 10,959 or 26,449. The same approach was used in each of the five populations shown on the table.

The next column, "Percent Deposited" indicates the percentage of eggs each type of female was able to successfully deposit in the observation stream. This value was determined by dividing the observed eggs deposited by the total fecundity of all the females of the same type. Or in the case of the wild females placed in the upper section of the stream in 2001 it equaled 26,449/37,408 or 70.7%. The next column, "Deposition Relative To Wild Females" compares the deposition rates of both types of females by subtracting the percent deposited value of wild females from the percent deposited value achieved by the hatchery females. Using the upper 2001 population once again as an example, this value equaled 71.9 (deposition rate of hatchery females) – 70.7 (egg

Table 5. The effects of fish origin on the capacity of female spring Chinook to spawn and deposit eggs in the observation stream located at Cle Elum.

Population		Female Type	No. Of Females In Class	Expected # of Eggs Deposited	Observed # of Eggs Deposited	Percent Deposited	Deposition Relative To Wild Females	Chi Square Value	Result
Year	Stream Sections								
2001	Upper 1-1 – 1-3	Wild	9	26,678	26,449	70.7%	+1.2%	3.7	Fail to Reject H_O
		Hatch	10	29,741	29,970	71.9%			
2001	Lower 2-1 –2-3	Wild	10	33,215	33,883	91.1%	-3.9%	29.3	Reject H_O Wild > Hatch
		Hatch	8	27,962	27,294	87.2%			
2002	Upper 1-1 – 1-3	Wild	10	41,146	45,722	93.9%	-18.4%	991.9	Reject H_O Wild > Hatch
		Hatch	8	43,318	38,743	75.5%			
2002	Lower 2-1 –2-3	Wild	8	28,276	30,588	91.1%	-11.9	327.7	Reject H_O Wild > Hatch
		Hatch	11	38,546	36,234	79.2%			
2003	Entire Channel	Wild	13	48,838	45,222	81.0%	+12.5%	517.4	Reject H_O Hatch > Wild
		Hatch	13	52,361	55,977	93.5%			

deposition rate of wild females) or +1.2% suggesting that hatchery females were slightly better or equal to wild individuals at depositing their eggs. The last two columns show the results of the Chi-Square tests used to evaluate whether wild or hatchery females were better at depositing their eggs.

In the first four populations (upper and lower populations in 2001 and 02) each female was provided with 12.8 square meters of potential spawning area. Under these conditions, wild females were either comparable (one time) or better (3 times) at depositing their eggs than hatchery females. In 2003, the entire spawning channel, including the elbow was made available to the females. In this year 26 females were released and the instantaneous density was 21.3 m^2 per female. In this case, hatchery females were better at depositing their eggs than their wild counter parts.

Table 6 compares the egg-to-fry survival rates of hatchery- and wild-origin females spawning in the observation stream. This table has eleven columns, the first four are similar to those found in tables 4 and 5 as they indicate the year, observation stream sections or area where the fish spawned, female type, and number of hatchery and wild females in each of the populations. The next two columns show the expected and observed number of fry each type of female produced. The total number of fry used in each pedigree assessment can be determined by summing either the expected or observed values shown for each population. For example, in the upper 2001 population, the pedigree evaluation disclosed that 579 fry had originated from wild females and 410 were derived from hatchery females. When summed these values equal 989, the total number of fry used in the pedigree evaluation for that population. Table 5 indicated that 56,419 eggs had been deposited in the upper 2001 population and that wild females accounted for 26,449 or 46.9% of the eggs while 29,970 or 53.1% originated from hatchery females. Under an assumption of equal survival we would expect 989 x 0.469 or 463.6 of the sampled fry to have originated from wild females and 989 x 0.531 or 525.4 to be produced by hatchery females. Comparable expected and observed numbers of fry in the other populations are depicted in columns 5 and 6. Similarly, the expected percentage of fry originating from each type of female can be found in column seven that is labeled "Expected Percentage In Sample." The values in the eighth column "Observed Percentage In Sample" equal the number of fry from each female type found in the fry sample that was used in the pedigree assessment divided by the total number of fry in the sample. For wild females in the upper 2001 population that would equal 579/989 or 58.5%.

The next column "Fry Production Relative To Wild Females" expresses the difference between the expected occurrence of hatchery origin fry and what was actually observed. In the upper 2001 population, the null hypothesis of equal egg-to-fry survival predicted that 53.1% of all the fry sampled would originate from hatchery-origin females. The pedigree analysis showed that 41.5% of them actually did come from hatchery females. The percentages shown in column nine "Fry Production Relative To Wild Females" equal the expected percent minus the observed percent. Or in this example it equals 53.1% - 41.5% or ~11.7%. Consequently, eleven percent fewer fry from hatchery females were seen in the upper 2001 population than expected. Chi-square tests were performed to see

Table 6. Comparing the deposited egg-to-fry survival rates of wild- and hatchery-origin spring Chinook placed into the Cle Elum Observation stream in 2001, 02, and 03.

Population: Year	Population: Stream Sections	Female Type	No. Of Females In Class	Expected # of Fry In Sample	Observed # of Fry In Sample	Expected Percentage In Sample	Observed Percentage In Sample	Fry Production Relative To Wild Females	Chi Square Value	Result
2001	Upper 1-1 – 1-3	Wild	9	463.6	579	46.9%	58.5%	-11.7%	53.6	Reject H_O Wild > Hatch
		Hatch	10	525.4	410	53.1%	41.5%			
2001	Lower 2-1 –2-3	Wild	10	419.5	491	53.8%	63.1%	-7.7%	18.5	Reject H_O Wild > Hatch
		Hatch	8	360.5	287	46.2%	36.9%			
2002	Upper 1-1 – 1-3	Wild	10	847.7	878	54.1%	56.1%	-1.9%	2.3	Fail To Reject H_O
		Hatch	8	718.3	688	45.9%	43.9%			
2002	Lower 2-1 –2-3	Wild	8	577.2	632	45.8%	50.1%	-4.3%	9.4	Reject H_O Wild > Hatch
		Hatch	11	683.8	629	54.2%	49.9%			
2003	Entire Channel	Wild	13	1228.9	1135	44.7%	41.3%	+3.4%	12.8	Reject H_O Hatch > Wild
		Hatch	13	1521.1	1615	55.3%	58.7%			

if any of the observed differences from expectation were significant. The Chi-square values from those tests are shown in the next column and immediately to the right of that is a column that interprets the results of these tests. In three of the populations, wild females achieved higher egg-to-fry survival rates than hatchery fish. In one case no difference was found and in the 2003 population hatchery females had significantly higher egg-to-fry survival rates.

To completely understand what has transpired both Tables 5 and 6 should be examined. In the upper 2001 population, for instance, hatchery and wild females were equally capable of depositing eggs yet wild females achieved a significantly higher egg-to-fry survival rate. Conversely in the upper 2002 population, wild females were more successful at burying their eggs yet the eggs deposited by both types of females produced fry at equivalent rates. The interpretation of this type of information may be made easier if it is possible to pool the chi square tests used to examine how fish origin affected their capacity to bury eggs, and produce offspring. Nine heterogeneity chi-square tests (Zar 1999) were performed to see if the results of the pedigree assessments could be pooled. These tests are presented in Tables 7a, b, and c. Table 7a shows that it was not possible to pool the chi square tests that compared the ability of different types of males to produce offspring. Each of the five populations that were created contained disparate combinations of males that apparently led to differing social interactions. When tests were run to see if the populations created during the same year could be pooled the same result occurred. Similarly, it was not possible to pool the chi square tests that were performed to examine differences in the ability of hatchery and wild females to deposit their eggs (Table 7b). However, when the chi square tests that evaluated differences in the survival of eggs deposited by wild and hatchery females were examined it was found that those populations created in the same incubation year could be pooled. This suggests that the social conditions the fish found themselves in were unique in each population but the environmental conditions during the incubation period were similar during each year.

The results of the pooled chi-square performed on the 2001 populations indicated that if the eggs deposited by hatchery- and wild-origin fish had survived at similar rates, 50.6% of the fry analyzed in the pedigree sample would have originated from wild females. The results of the pedigree evaluation, however, indicated that wild females had produced 60.5% of the fry. Therefore the sample possessed 9.9% more fry originating from wild females than expected. In the pooled 2002 samples, the expected proportion of fry originating from wild females was 50.4%. The observed proportion was 53.4%. As in 2001, more fry from wild females were observed (~3%) than expected. Conversely, in 2003, when females were allowed to spawn throughout the entire channel, hatchery-origin females contributed 3.4% more fry to the pedigree sample than expected (*see* Table 6). This may indicate that under conditions where the females had greater opportunities to move and establish territories hatchery fish were better or equivalent to wild females in their ability to produce offspring.

Table 7a. Results of the heterogeneity chi-square tests used to determine if pedigree results collected in 2001, 2002, and 2003 on wild- and hatchery spring Chinook males introduced into the observation stream could be pooled.

Testing whether all the male populations 01, 02, and 03 could be pooled									
	Wild			Hatchery			Total	Uncorrected	
Population	Obs	n in class	Expected	Obs	n in class	Expected	n	Chi Square	DF
01 Upper	589	12	549.7	373	9	412.3	962	6.6	1
01 Lower	347	10	365.3	274	7	255.7	621	2.2	1
02 Upper	1034	11	705.5	377	11	705.5	1411	305.9	1
02 Lower	598	9	590.6	452	7	459.4	1050	0.2	1
Entire 03	1465	14	1337.8	924	11	1051.2	2389	27.5	1
Total Of Chi Squares								342.4	5
Pooled Chi Square	4033		3549.0	2400		2884.0		147.2	1
Heterogeneity Chi Square								195.1	4
Conclusion	Reject the homogeneity null hypothesis, the male populations cannot be pooled								

Testing whether the male 01 populations could be pooled									
	Wild			Hatchery			Total	Uncorrected	
Population	Obs	n in class	Expected	Obs	n in class	Expected	n	Chi Square	DF
01 Upper	589	12	549.7	373	9	412.3	962	6.6	1
01 Lower	347	10	365.3	274	7	255.7	621	2.2	1
Total Of Chi Squares								8.8	2
Pooled Chi Square	936		915.0	647		668.0		1.1	
Heterogeneity Chi Square								7.6	1
Conclusion	Reject the homogeneity null hypothesis, the 2001 populations cannot be pooled								

Table 7a. Results of the heterogeneity chi-square tests used to determine if pedigree results collected in 2001, 2002, and 2003 on wild- and hatchery spring Chinook males introduced into the observation stream could be pooled continued.

Testing whether the male 02 populations could be pooled									
	Wild			Hatchery			Total	Uncorrected	
Population	Obs	n in class	Expected	Obs	n in class	Expected	n	Chi Square	DF
02 Upper	1034	11	705.5	377	11	705.5	1411	305.9	1
02 Lower	598	9	590.6	452	7	459.4	1050	0.2	1
Total Of Chi Squares								306.1	2
Pooled Chi Square	1632		1296.1	829		1164.9		183.9	1
Heterogeneity Chi Square								122.2	1
Conclusion	Reject the homogeneity null hypothesis, the 2002 populations cannot be pooled								

Table 7b. Results of the heterogeneity chi square tests used to determine if the chi square tests used to investigate the capacity of hatchery- and wild-origin spring Chinook females to deposit their eggs into the observation stream in 2001, 2002, and 2003 could be pooled.

Testing whether the ability to bury eggs in wild and hatchery females could be pooled across 2001 and 02							
	Wild		Hatchery		Total	Uncorrected	
Population	Obs	Expected	Obs	Expected	n	Chi Square	DF
01 Upper	26449	26677.7	29970	29741.4	56419	3.7	1
01 Lower	33883	33215.1	27294	27962.0	61177	29.4	1
02 Upper	45722	41146.3	38742	43317.2	84464	992.1	1
02 Lower	30588	28275.6	36234	38546.4	66822	327.8	1
Total Of Chi Squares						1353.0	4
Pooled Chi Square	136642	129314.7	132240	139567.0	268882.0	799.8	1
Heterogeneity Chi Square						553.2	3
Conclusion	Reject the homogeneity null hypothesis, the 01 and 02 egg deposition data cannot be pooled						

Table 7b. Results of the heterogeneity chi square tests used to determine if the chi square tests used to investigate the capacity of hatchery- and wild-origin spring Chinook females to deposit their eggs into the observation stream in 2001, 2002, and 2003 could be pooled continued.

Testing whether the ability to bury eggs in wild and hatchery females could be pooled within 2001							
	Wild		Hatchery		Total	Uncorrected	
Population	Obs	Expected	Obs	Expected	n	Chi Square	DF
01 Upper	26449	26677.7	29970	29741.4	56419	3.7	1
01 Lower	33883	33215.1	27294	27962.0	61177	29.4	1
Total Of Chi Squares						33.1	2
Pooled Chi Square	60332	59892.8	57264	57703.4	117596	6.6	1
Heterogeneity Chi Square						26.5	1
Conclusion	Reject the homogeneity null hypothesis, the two 2001 populations cannot be pooled						

Testing whether the ability to bury eggs in wild and hatchery females could be pooled within 2002							
	Wild		Hatchery		Total	Uncorrected	
Population	Obs	Expected	Obs	Expected	n	Chi Square	DF
02 Upper	45722	41146.3	38742	43317.2	84464	992.1	1
02 Lower	30588	28275.6	36234	38546.4	66822	327.8	1
Total Of Chi Squares						1319.9	2
Pooled Chi Square	76310	69421.9	74976	81863.6	151286	1262.9	1
Heterogeneity Chi Square						57.0	1
Conclusion	Reject the homogeneity null hypothesis, the two 2002 populations cannot be pooled						

Table 7c. Results of the heterogeneity chi square tests used to determine if the chi square tests used to investigate the egg-to-fry survival rates achieved by hatchery- and wild-origin spring Chinook females in the observation stream in 2001, 2002, and 2003 could be pooled.

Testing if AED egg-to-fry survival data from the 2001 and 2002 populations could be pooled							
	Wild		Hatchery		Total	Uncorrected	
Population	Obs	Expected	Obs	Expected	n	Chi Square	DF
01 Upper	579	463.6	410	525.4	989	54.0	1
01 Lower	491	430.9	287	347.1	778	18.8	1
02 Upper	878	847.7	688	718.3	1566	2.4	1
02 Lower	632	577.2	629	683.8	1261	9.6	1
Total Of Chi Squares						84.8	4
Pooled Chi Square	2580	2319.5	2014	2274.5	4594	59.1	3
Heterogeneity Chi Square						25.7	
Conclusion	Reject the homogeneity null hypothesis, AED egg-to-fry survival information from the 01 and 02 populations cannot be pooled						

Testing if AED egg-to-fry survival from the 2001 populations could be pooled							
	Wild		Hatchery		Total	Uncorrected	
Population	Obs	Expected	Obs	Expected	n	Chi Square	DF
01 Upper	579	463.6	410	525.4	989	54.0	1
01 Lower	491	430.9	287	347.1	778	18.8	1
Total Of Chi Squares						72.8	2 1
Pooled Chi Square	1070	894.5	697	872.5	1767	69.7	1
Heterogeneity Chi Square						3.1	1
Conclusion	Do not reject the homogeneity null hypothesis. If survival from deposited eggs had been equal in hatchery and wild females then 50.6% of all the fry used in the pedigree assessments would have originated from wild females. The pooled pedigree data from the 2001 populations shows that 60.5% of the fry came from wild females, indicating that eggs deposited by wild females survived at higher rates than those deposited by hatchery-origin females.						

Table 7c. Results of the heterogeneity chi square tests used to determine if the chi square tests used to investigate the egg-to-fry survival rates achieved by hatchery- and wild-origin spring Chinook females in the observation stream in 2001, 2002, and 2003 could be pooled continued.

Testing if AED egg-to-fry survival from the 2002 populations could be pooled							
	Wild		Hatchery		Total	Uncorrected	
Population	Obs	Expected	Obs	Expected	n	Chi Square	DF
02 Upper	878	847.7	688	718.3	1566	2.4	1
02 Lower	632	577.2	629	683.8	1261	9.6	1
Total Of Chi Squares						11.9	
Pooled Chi Square	1510	1424.9	1317	1402.0	2827	10.2	2
Heterogeneity Chi Square						1.7	1
Conclusion	Do not reject the homogeneity null hypothesis. If survival from deposited eggs had been equal in hatchery and wild females then 50.4% of all the fry used in the pedigree assessments would have originated from wild females. The pooled pedigree data from the 2002 populations shows that 53.4% of the fry came from wild females, indicating that eggs deposited by wild females survived at a slightly higher rate than those deposited by hatchery-origin females.						

The Affects Of Female Traits And Environmental Factors On Female RS

Two of the eight traits examined affected the reproductive success of females. If a fish was evicted from her redd or abandoned it for any reason her ability to convert eggs into fry, and the survival of her buried eggs to the fry stage was adversely impacted. Additionally, how long a female lived after she was introduced into the observation stream was positively linked to her ability to convert her eggs into fry. Moreover, eggs deposited by relatively long-lived females had higher survival rates. This may have occurred because such females were able spend more time on redd shaping and were also able to defend their redds for longer periods. Only one agonistic variable, the number of agonistic interactions a female experienced per minute affected their reproductive success. In this instance, an inverse relationship between survival of buried eggs and the occurrence of agonistic interactions per minute occurred. Consequently females that were not engaged in continuous aggression with nearby fish achieved higher progeny survival rates than those that were interacting regularly with neighboring individuals. Additionally, the linear regression analysis that examined the relationship between female body wt and fry production was significant when non-adjusted fry numbers were used. However, when fry numbers were adjusted, female weight was not related to the ability to convert eggs into fry, or on the survival of deposited eggs to the fry stage.

The other factors examined; time needed to establish a territory, proximity to neighboring territorial females, instantaneous density, and water velocity in the redd area had no appreciable effect on the RS of females. Table 8 summarizes the traits examined, the statistical tests used, the null hypotheses tested and the results of each test.

Table 8. Results of the tests used to evaluate the effects of various traits and environmental conditions on the reproductive success of females placed into the lower section of the observation stream in 2001.

Trait	Test	Null Hypotheses Tested	Results
Redd Tenure	One-Way ANOVA	1) Females that are evicted or abandon their territories are able to produce fry at the same rate as individuals that continuously defend their redds 2) Eggs deposited by females that abandon their redds or were evicted from their territories survived to the fry stage at the same rate as those deposited by females that continuously guarded their redds	1) Reject H_o females that remained on their nests produced more fry 2) Reject H_o eggs deposited in nests continuously guarded by a females produce more fry
Time Needed To Establish A territory	One-Way ANOVA	1) How long it takes a female to establish a territory does not affect her ability to convert eggs into fry 2) How long it takes a female to establish a territory does not affect the survival of the eggs she deposits	1) Fail to reject H_o 2) Fail to reject H_o
Proximity To Neighboring Females	Kendall's coefficient of rank correlation	1) The proximity of territorial females does not affect the ability of females to convert their eggs into fry 2) The proximity of territorial females does not affect the survival of deposited eggs	1) Fail to reject H_o 2) Fail to reject H_o
Agonistic Behavior	Linear Regression	1) The number of agonistic interactions experienced by females does not influence their ability to convert eggs to fry 2) The number of agonistic interactions experienced by females does not affect the survival of buried eggs	1) Fail to reject H_o 2) Reject H_o at alpha 0.10. An inverse relationship between the occurrence of agonistic interactions and buried egg survival exists
	Paired-t-Test	3) The percentage of time a female attacks other fish while she is territorial has no affect on her ability to convert eggs to fry 4) The percentage of time a female attacks other fish while she is territorial does not affect the survival of her deposited eggs 5) How aggressive a female is toward other fish is not influenced by her territorial status	3) Fail to reject H_o 4) Fail to reject H_o 5) Reject H_o When a female establishes a territory she becomes more aggressive

Table 8. Results of the tests used to evaluate the effects of various traits and environmental conditions on the reproductive success of females placed into the lower section of the observation stream in 2001 continued. . .

Trait	Test	Null Hypotheses Tested	Results
Instantaneous Density	One-Way ANOVA	1) The instantaneous density of territorial females in an area a female is spawning in does not affect her ability to convert eggs to fry 2) The instantaneous density of territorial females in an area a female is spawning in does not affect the survival of her deposited eggs	1) Fail to reject H_o 2) Fail to reject H_o
Longevity	Kendall's coefficient of rank correlation	1) There is no relationship between how long a female lives in the observation stream and her capacity to convert eggs to fry 2) There is no relationship between female longevity and the survival of the eggs she deposits to the fry stage	1) Reject the H_o A positive relationship exists between female longevity and the ability to convert eggs to fry 2) Reject the H_o at alpha 0.10 A positive relationship was found between female longevity and the survival of her deposited eggs to the fry stage
Body Size	Linear Regression	1) Female body size does not affect the number of fry she contributed to the fry sample used in the pedigree sample 2) Female body size does not affect the ability of a female to convert her eggs into fry 3) Female body size does not influence how well buried eggs survive to the fry stage	1) Reject H_o A positive relationship exists between female body size the occurrence of fry in the pedigree sample 2) Fail to reject H_o 3) Fail to reject H_o
Water Velocity In The Redd Area	Linear Regression	1) A linear relationship between water velocity in the redd area and the ability of a female to convert eggs to fry does not exist 2) A linear relationship between water velocity in the redd area and survival of eggs deposited in the redd does not exist	1) Fail to reject H_o 2) Fail to reject H_o

Discussion

Pedigree Results

The major objective of this study was to determine if exposure to hatchery conditions for a single generation would affect the ability of spring Chinook to spawn under natural conditions. We found that the production of offspring in spring Chinook is very variable. In the populations that were studied some individuals produced thousands of fry while others were totally unsuccessful. In general, reproductive success was more variable in males than in females (Tables 3a and 3b). The pedigree assessments also showed that hatchery-origin fish were often not as competent as their wild counterparts. Wild four- and five-year old males, for example, were more successful at producing fry than comparable hatchery males in three of the five populations examined. In the other two populations, however, hatchery and wild males produced comparable numbers of progeny.

Other male life histories, such as the jack and precocious male strategies were consistently less successful than the large wild males (Table 4). In all but one case they were also less successful than four- and five-year-old hatchery males. In that instance the wild jack class was more successful than hatchery males, however, only one wild jack was in this population and therefore this difference should not be given too much weight. In the other four populations, hatchery males consistently fathered more fry than jacks and precocious males (Table 4). In three of the populations the largest precocious males were as successful as jacks in producing progeny. Our field observations on these fish indicated that jacks and precocious males adopt entirely different reproductive strategies. Jacks will attempt to court females if larger males are not present and continually interact with neighboring fish; often adopting a satellite position downstream from a courting pair. From this location, they often dart into the nest when the pair is present or spawning appears to be eminent. Precocious males on the other hand, typically station themselves directly in the center of a developing nest and remain there for prolonged periods of time. Or in some instances they will closely follow the larger anadromous fish that enter the nest site. Initially both the territorial female and courting male may attempt to drive them out, sometimes attacking them at frequencies greater than ten times per minute. Eventually, however, the larger fish become habituated to their presence and their attack frequency diminishes.

Clear dominance hierarchies develop in precocious males and their agonistic interactions are independent of those occurring between the larger fish associated with a redd. Consequently, it wasn't too surprising to see that wild precocious males had very variable reproductive success and in general were the least successful males placed into the observation stream. This occurred because they were often the smallest males in a population and were dominated by the larger and often older hatchery precocious males. When spawning occurs precocious males are typically in the heart of a nest, a location that allows them to express milt in very close proximity to the female as she releases her eggs. The pedigree analyses documented that this tactic can be very successful.

Moreover, like their larger counter parts, both hatchery and wild precocious males produced offspring from multiple females.

Unlike males, the reproductive success of females is controlled by how many eggs she carries, her capacity to deposit eggs and the ability to provide eggs with an appropriate incubation environment. In the 2001 and 2002 populations, females were introduced into 45.6 m long by 7.9 m wide portions of the observation stream. In this environment wild females were more successful at depositing their eggs in three cases and as successful as hatchery fish in the remaining population (Table 5). In all four of these populations, eggs buried by wild females survived at higher rates than those deposited by hatchery fish (Table 6). It proved possible to pool the egg-to-fry survival information collected from these four populations, making it easier to understand overall differences in egg-to-fry survival. In the 2001 populations, 60.5% of all the fry in the pedigree sample originated from wild females. If the eggs from wild and hatchery females had survived at equivalent rates 50.6% of the fry would have come from wild females. Consequently, 9.9% more fry originated from wild females than expected. Similarly, in the 2002 populations, 3.0% more fry from wild females were in the pedigree sample than expected (Table 7c). The area allotted per female in these sections varied from 10.8 m^2 to 13.2 m^2 per female. However, these density values tend to exaggerate the area in the observation stream that females find useable. About a third of the observation stream has water velocities that range from 0 to 0.15 m per sec. These zones of quite water provide the fish with places to hold but are not generally used as redd locations. Therefore it is likely that competition for space occurred among the females introduced into these sections.

Beginning in 2003, we opened up the entire observation stream to a single population of fish to reduce intrasexual competition for redd locations. In 2004 we repeated this strategy and the same thing should occur in 2005. As Tables 5 and 6 illustrate, under these conditions, hatchery-origin females spawning in the observation stream were more successful at depositing eggs and achieved higher egg to fry survival rates than wild females. When hatcheries are used as conservation tools, spawning densities will likely be low. The information we have gathered so far indicates that first generation hatchery females performed well under these circumstances. The relative success of males did not change in this section. Wild males, as in the other populations, were the most successful at producing offspring. This is not a surprising result. Male reproductive success often depends on how well an individual is able to compete against his sexual rivals. Providing females with more space didn't reduce intrasexual competition among the males for females. In extremely sparse populations, however, it is likely that male success will not be so dependent upon how he competes with rivals but rather on his ability to find females.

In summary, the pedigree results point out that wild males are generally more successful than hatchery males in producing offspring. In addition, wild females were often better at depositing their eggs and in having those eggs survive to the fry stage. However, when intrasexual competition for space was relaxed hatchery females were just as successful or more so than wild counterparts. Results from the 2004 and 2005 populations will shed more light on the importance of reduced competition for space on the reproductive success of hatchery origin females.

The Affects Of Female Traits And Environmental Factors On Female RS

We examined the influence of eight factors on the reproductive success of females in an attempt to understand what social and environmental conditions might directly impact their capacity to produce offspring. One of the most important was redd tenure and defense. If a female was evicted or abandoned her redd, her reproductive fitness decreased. In addition, how long a female lived proved to be very important. Females that entered the observation stream with adequate energy reserves to live for at least 50 or more hrs were able to spawn and protect their buried eggs.

Factors we anticipated would be important, proximity to neighboring females, agonistic behavior, and instantaneous density, did not appear to affect the RS of the females placed into the observation stream. These factors are directly related to the social circumstances a territorial female must face. We had predicted that females spawning in close proximity to other fish would experience more aggression, suffer immediate redd superimposition and have decreased territory sizes. Our analyses did show that females exposed to relatively high levels of agonistic behavior had reduced egg-to-fry survival rates. This may have occurred because the fish were attacked while attempting to bury their eggs or were otherwise inhibited from performing digging activities by neighboring fish. Females in particular will attack adjacent fish while they are digging since digging individuals cannot readily retaliate. Moreover, their digging activities may represent a potential threat to the eggs the attacking fish has already deposited. Consequently, digging episodes may serve as innate attack triggers in females.

The maps we made of the boundaries of redds clearly showed that overall territory size decreased as the number of females spawning in a section of the observation stream increased. The average territory size, for example of females spawning in a 15.2 m by 7.9 m section of the stream containing ten territorial females was slightly less than 2 m^2. It averaged about 3.5 m^2 when six females spawned in a similar section and was over 5 m^2 in a section containing just two females. Yet, eggs deposited in relatively small redds survived at rates that were equivalent to those deposited in larger ones.

Body size is another factor that would appear to be linked to female RS. Positive relationships exist between female weight and length and fecundity. Seemingly too, larger females would appear to have advantages in establishing and defending their territories because they should be able dominate smaller opponents. The regression analyses we performed on female size versus fry production indicated that body weight did affect the number of fry a female contributed to the pedigree sample. The largest females in the population contributed the most fry. However, when fry numbers were adjusted, these analyses showed that was no relationship between body size and the capacity to convert eggs to fry or for buried eggs to achieve higher survival rates. The first result reflected differences in female fecundity while the last two looked at the effects of size after fecundity and deposited egg numbers had been standardized. When that was done, it became clear that females of all sizes were comparable in their ability to convert their eggs to fry. This may not necessarily be the case in a natural spawning area. Flows and gravel composition in the observation stream are controlled. These parameters are variable in natural spawning locations and larger fish may reap some benefits because of where they are able to spawn and on how deep they are able to deposit their eggs.

Establishing and defending a territory is not directly related to size. Females searching for territories may receive attacks from more than one female so contests between territorial and non-territorial females may involve multiple fish. Moreover, territorial females are highly motivated to defend their locations because their potential fitness depends on their capacity to defend their buried eggs from being destroyed by the digging activities of other females. Non-territorial females have not made such an investment, and it probably will cost them less energy to search for an unoccupied area for egg burial than it would to evict a territorial female from her location. Our behavioral observations also revealed that females are more likely to instigate attacks after they become territorial than when they are searching for a spawning location. Consequently, non-territorial females tend to be pushed from one location to another by established individuals until they find an area that is unoccupied and suitable for egg deposition.

The water velocity measurements we obtained from the observation stream indicated that females were selective about where they established territories. Redds were constructed in areas where flows ranged between 0.15 to .46 m/sec. When a scatter plot showing egg-to-fry survival and mean water velocity over redds was made, a curvilinear relationship between these two variables appeared to occur. Redds established in areas having overall flows ranging from .24 to .38 m/sec achieved the highest survival rates. Eggs buried in redds located in lower or higher flow areas were not as successful. Areas of the observation stream having “optimal” flows were often the first to be colonized by females.

Recall that these analyses were done on a single population. Similar data have been collected on all the populations we have introduced into the observation stream. Comparable analyses will be performed and they should help us refine how social and environmental factors in the observation stream affect the RS of female spring Chinook. Many of these factors undoubtedly interact or are tightly linked to each other. Analyses examining these relationships are ongoing and they will provide additional insights on how female RS is impacted by the social and environmental conditions each fish faces during her spawning period.

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