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ARTICLE

Phenotypic Comparisons among Natural-Origin, Hatchery-Origin, and Captive-Reared Female Spring Chinook Salmon from the Tucannon River, Washington

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Abstract

We examined the effects of hatchery rearing on FL, weight, egg size, fecundity, relative fecundity, and reproductive mass of female spring Chinook Salmon *Oncorhynchus tshawytscha* from a population that had been in captivity for 0 (natural-origin), 18 (hatchery-origin), and 48 (captive-reared broodstock) months. Age-4 captive-reared broodstock females that were reared for their entire life in the hatchery environment had significantly lower mean FL, weight, fecundity, relative fecundity, and reproductive mass, but had significantly larger eggs than age-4 females from the other groups after correcting for body size. Hatchery-origin females had significantly lower fecundity than natural-origin fish. Our findings illustrate a phenomenon of lower overall reproductive potential for hatchery-reared fish in the form of reduced fecundity that decreases as time spent in the hatchery environment increases. We also observed that progeny of captive-reared broodstock parents, released as smolts and recaptured as returning age-4 adults, have a size and fecundity distribution that is similar to the hatchery-origin adults, suggesting that the decrease in fecundity was not a genetically linked trait.

Considerable controversy exists over the use of hatchery supplementation programs due to the potential for increased risks of adverse effects to the natural fish population (see reviews by Waples 1991; Brannon et al. 2004; Araki et al. 2008; Kostow 2009). One concern is that the hatchery environment exposes fish to different developmental and evolutionary forces or domestic selection that may shape their phenotype (Fleming et al. 1994). This may change the direction of selection and cause genetic divergence from the wild population (Lynch and O'Hely 2001; Ford 2002). In most organisms, progeny phenotypes tend to be influenced more by the genotype or environment of their mother than by the genotype or environment of their father (Heath et al. 1999). This large effect of maternal (relative to paternal) genotype or environment is referred to as a maternal effect, or when mediated by maternal environmental conditions, as an inherited environmental effect (Heath et al. 1999).

Studies that have examined hatchery environmental effects on salmonids have tended to focus on Coho Salmon *Oncorhynchus kisutch* and steelhead *O. mykiss* (Swain et al. 1991; Kostow 2004; Campbell et al. 2006). Knudsen et al. (2008) compared reproductive traits of wild-origin female spring Chinook Salmon *O. tshawytscha* with first-generation hatchery-origin females to determine whether their reproductive traits had diverged after a single generation of artificial propagation. Their findings suggested that a single generation of conservation hatchery propagation using wild broodstock produces hatchery fish with reproductive traits similar to wild fish, given comparable body size (Knudsen et al. 2008). However, most integrated hatchery programs use both hatchery and natural-origin broodstock, not 100% wild broodstock, so the findings from Knudsen et al. (2008) would probably not apply to the majority of hatchery programs.

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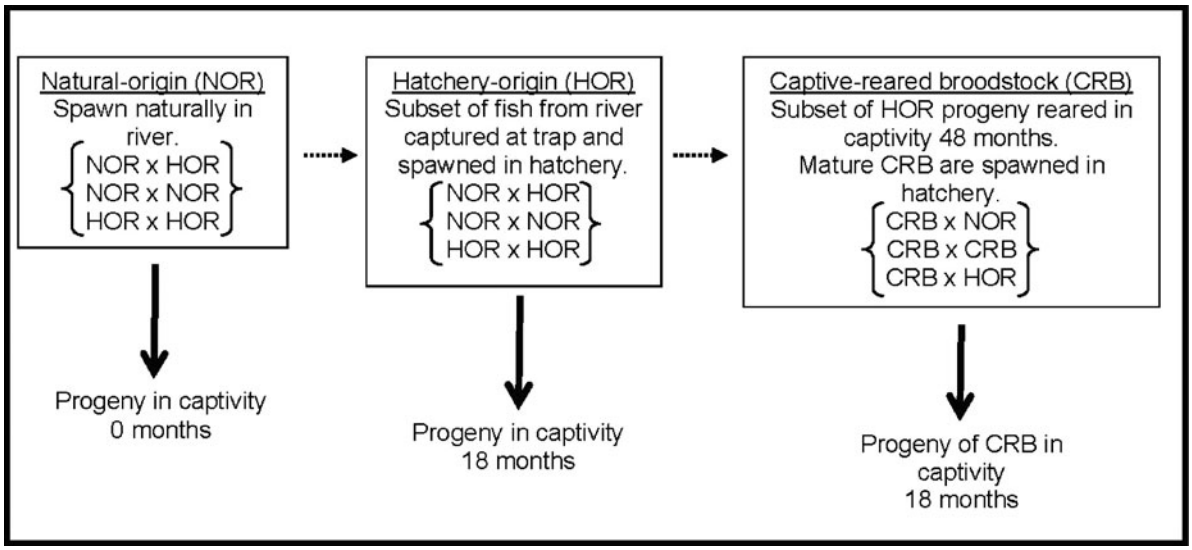

FIGURE 1. Tucannon River spring Chinook Salmon groups used for phenotypic comparisons. Possible spawning crosses are shown in brackets. Spawning crosses for fish spawned in the hatchery environment are listed in order of priority.

Our study examined the environmental effects of hatchery rearing on FL, weight, egg size, fecundity, relative fecundity, and reproductive mass on female spring Chinook Salmon that had been in captivity for 0, 18, and 48 months. This allowed for the examination of specific phenotypic traits that may be expressed and selected for in the hatchery environment. Specifically, studies conducted on populations that have a common genetic background provide a chance to understand the mechanisms behind changes caused by the hatchery environment. The three reproductive groups in the Tucannon River of Washington State are described as follows: (1) natural-origin fish that were the product of natural reproduction of natural- and hatchery-origin fish spawning in the Tucannon River and were in captivity for 0 months; (2) hatchery-origin fish used for supplementation stocking that were the product of artificial reproduction in a hatchery, but were released after 18 months as yearling smolts and trapped as returning adults and whose parents represented approximately a 50:50 mixture of hatchery- and natural-origin adults trapped in the Tucannon River; and (3) captive-reared broodstock that represented a subsample of the hatchery-origin group that were not released but, instead, reared to sexual maturity in captivity (48 months). We focused on the single-generation effects of the hatchery environment on the phenotypic expression of size and reproductive (e.g., egg size and fecundity) traits rather than the multigenerational effects of artificial propagation. We also compared the phenotypic traits between a sample of age-4 females identified as captive-reared broodstock progeny and a sample of age-4 hatchery-origin females that returned in 2008. Both groups were released at similar sizes after 18 months of hatchery rearing and differed only in parentage. This comparison was to determine whether both groups had similar phenotypic traits or if there was evidence of phenotypic divergence. The groups used for phenotypic comparisons are described in Figure 1.

METHODS

Study population.—The Tucannon River is a third-order stream in southeastern Washington that flows into the Snake River between Little Goose and Lower Monumental dams approximately 622 river kilometers (rkm) from the mouth of the Columbia River (Figure 2). Spring Chinook Salmon adults migrate to the Tucannon River basin in the spring and spawn during the early fall. The adults generally spawn and the juveniles rear upstream from rkm 35 in the river. Natural-origin smolts leaving the system are about 18 months old, have a mean FL of 105–113 mm, and rear in the ocean for 1–3 years until mature.

The Tucannon River spring Chinook Salmon population steadily declined after the construction and operation of the federal Columbia and Snake river hydropower system (USACE 1975; Nehlsen et al. 1991). The decline has been attributed to mortalities of adults and juveniles during migration through four hydropower dams on the Columbia River and two hydropower dams on the Snake River (USACE 1975), and habitat loss or degradation in the Tucannon River along with other environmental factors such as variable ocean conditions, drought, and floods (Columbia Conservation District 2004). The population is currently listed as "threatened" under the U.S. Endangered Species Act as part of the Snake River Spring/Summer Chinook Salmon evolutionary significant unit (March 25, 1999; FR 64(57):14517–14528).

In 1985, the Washington Department of Fish and Wildlife (WDFW) began a spring Chinook Salmon hatchery supplementation program in the Tucannon River by trapping wild endemic

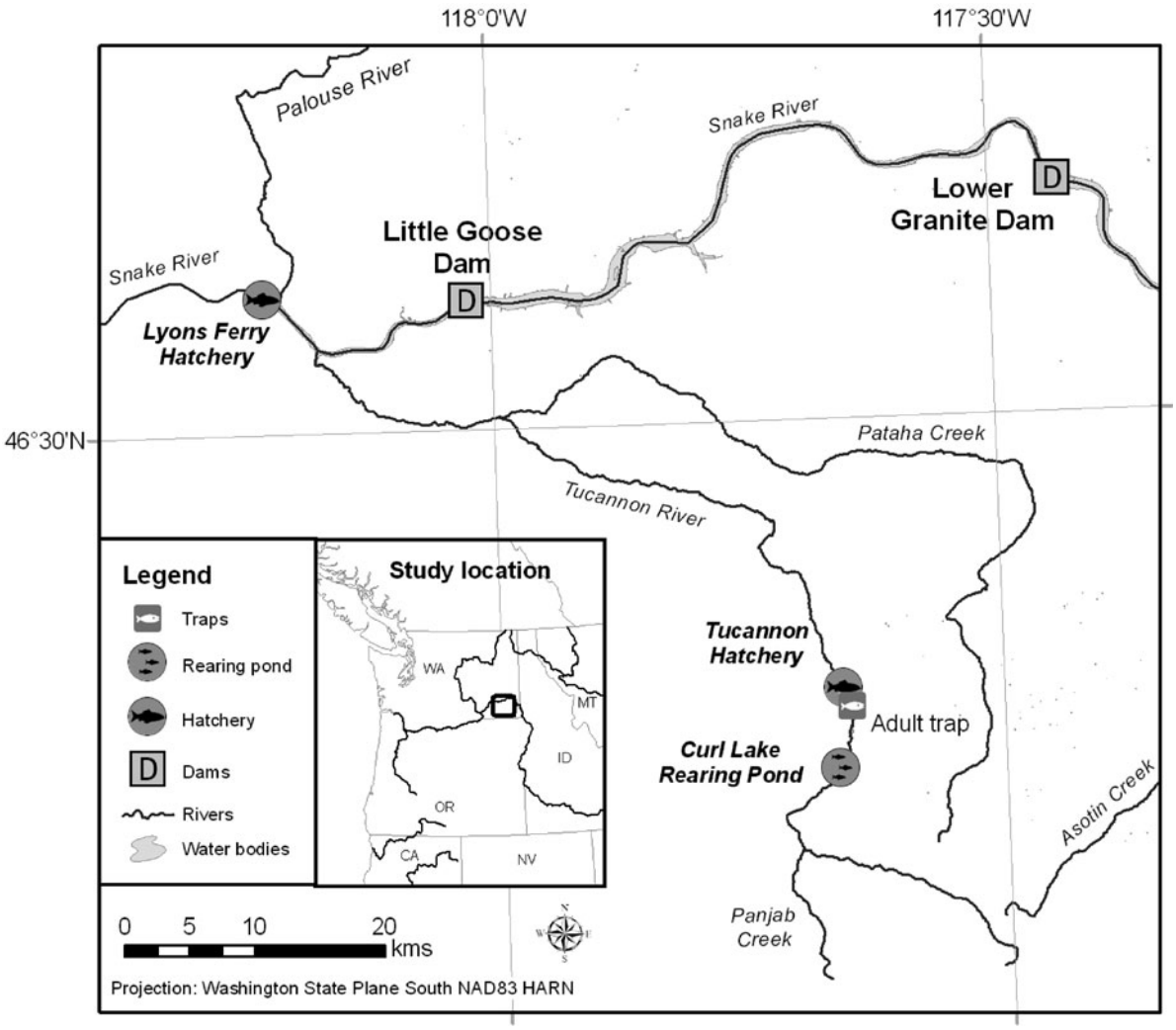

FIGURE 2. Location of the Tucannon River, adult salmon trap, and Lyons Ferry Hatchery Complex facilities within the Snake River Basin, Washington.

adults for broodstock. The first hatchery smolts were released in 1987. Since 1989, the hatchery broodstock has consisted of both natural- and hatchery-origin fish (Table 1).

The hatchery program is a fully integrated conservation program, designed to allow gene flow between the hatchery and natural components both in the hatchery and on the spawning grounds. Recent genetic analysis looking at 14 microsatellite loci (13 coast-wide Genetic Analysis of Pacific Salmon [GAPS] loci plus *Ssa-197*) found that the genetic diversity of spring Chinook Salmon in the Tucannon River has not significantly changed as a result of the hatchery supplementation or captive brood programs (Kassler and Dean 2010).

In 1994, the total adult escapement declined severely to fewer than 150 fish, and in 1995 was estimated at 54 fish (Table 1). The WDFW and tribal comanagers determined the risk of extinction was high enough to warrant aggressive intervention beyond the existing hatchery supplementation program in the form of a captive broodstock program. Captive broodstock programs differ from conventional hatchery supplementation programs in that fish are held in the hatchery environment throughout their life to ensure a readily available gamete source.

With the two hatchery programs operating concurrently we were able to examine the effects of different levels of hatchery rearing on the same stock. "Natural" is used throughout this paper to describe fish that are progeny of parents spawned and reared in a natural environment, regardless of the origin of the parents (Figure 1).

Hatchery operations.—Tucannon Fish Hatchery is located at rkm 59 on the Tucannon River and uses an adult trap to collect broodstock from throughout the run. Broodstock are transported to the Lyons Ferry Hatchery, located on the Snake River at its confluence with the Palouse River in southeastern Washington (Figure 2). Lyons Ferry Hatchery is used for broodstock holding and spawning, egg incubation, and early life rearing. Wells supply constant temperature (11°C) water to the hatchery. After juveniles are coded-wire-tagged at Lyons Ferry Hatchery,

TABLE 1. River escapement of natural-origin, hatchery-origin, and captive-reared broodstock (CRB) progeny of Tucannon River spring Chinook Salmon and broodstock collected from the adult trap and spawned for the 1985–2008 run years. The last column shows numbers of fish spawned in the captive-reared broodstock program. Numbers represent a combination of sexes and brood years.

	River escapement by origin				Broodstock spawned by origin			
Run year	Natural	Hatchery	CRB progeny	Total run	Natural	Hatchery	CRB progeny	CRB program
1985	591	0	0	591	8	0	0	0
1986	636	0	0	636	91	0	0	0
1987	582	0	0	582	83	0	0	0
1988	410	19	0	429	90	0	0	0
1989	336	109	0	445	55	67	0	0
1990	494	260	0	754	30	32	0	0
1991	260	268	0	528	40	31	0	0
1992	418	335	0	753	37	45	0	0
1993	317	272	0	589	45	42	0	0
1994	98	42	0	140	35	34	0	0
1994	21	33	0	54	9	30	0	0
1996	165	85	0	250	33	42	0	0
1997	160	191	0	351	38	51	0	0
1998	85	59	0	144	45	41	0	0
1999	3	242	0	245	3	118	0	0
2000	82	257	0	339	8	65	0	20
2001	718	294	0	1,012	52	52	0	249
2002	350	655	0	1,005	42	51	0	204
2003	248	196	0	444	41	34	0	345
2004	400	170	3	573	48	40	0	347
2005	289	117	14	420	47	46	2	200
2006	140	109	4	253	36	52	0	86
2007	198	127	19	344	51	28	3	0
2008	534	417	240	1,191	40	35	39	0

they are transferred to Tucannon Fish Hatchery to rear through the winter on a mixture of well, spring, and river water before being transferred to the Curl Lake Rearing Pond (Figure 2) to acclimate. Fish are acclimated in river water for 6 to 8 weeks in the spring before being volitionally released. Hatchery fish were reared according to the comanagers Salmonid Disease Control Policy and Integrated Hatchery Operation Team fish health policy (Peck 1993; Watson 1996).

The hatchery supplementation broodstock goal was for up to 100 adults trapped from the river composed of both natural- and hatchery-origin returns (1:1 ratio). Natural- and hatchery-origin fish are used in the broodstock for two reasons: to achieve the hatchery production goal without excessively reducing the abundance of natural spawning fish, and to decrease the possibility of inadvertently creating separate populations of the Tucannon River spring Chinook Salmon population through a steady infusion of naturally produced, endemic adults. Returning hatchery fish used in the hatchery supplementation broodstock were verified to have come from the Tucannon River population by reading each fish's coded wire tag after it was spawned.

The captive broodstock was started by collecting 80 sac fry from 15 family groups (1,200 fish total) from the hatchery supplementation program for five brood years between 1997 and 2001. Each of the family groups was subsequently reduced to 30 fish per family (450 fish per brood year) after the first year of rearing. Captive broodstock were tagged by family group with an alphanumeric visible implant tag placed behind the eye of each fish and a coded wire tag in its snout. Tags were used to verify family groups during subsequent spawning in order to prevent full- or half-sibling matings. After tagging, the captive brood families were combined by brood year for rearing. Complete details on the collection and rearing procedures for the captive brood and hatchery supplementation programs are provided in Gallinat et al. (2009).

The captive broodstock were reared outdoors at Lyons Ferry Hatchery under natural photoperiod conditions. During late June and early July, captive-reared broodstock age-2 or older were examined for signs of sexual maturation. Sexually mature captive-reared broodstock were transported to broodstock holding raceways in common with, but separated by screens, from broodstock (hatchery- and natural-origin) collected from the Tucannon River.

During spawning, the total number of eggs from two females were divided into two groups and fertilized by two males

following a 2 × 2 factorial spawning matrix approach. Due to the relatively small size of the population, this mating strategy was used to increase the effective population size and to maintain genetic diversity (Busack and Knudsen 2007). The priority on each spawn day was for natural-origin fish to be crossed with hatchery-origin and captive-reared broodstock.

Data collected from spawned fish included age at maturity from scale samples (natural-origin) or coded wire tag information (hatchery-origin and captive-reared broodstock), FL, and weight (combined gonad and somatic tissue). Acetate impressions were made from collected scale samples and aged at the WDFW Scale Lab by experienced personnel. Ages were determined as the number of years from fertilization (brood year) to spawn year.

Heath et al. (1999) found a highly significant effect of maternal (but not paternal) size on larval Chinook Salmon body size at 45 d postfertilization. After 45 d postfertilization, the effect of maternal body size (relative to paternal size) began to decrease (Heath et al. 1999). At the eyed egg stage (26–28 d postfertilization) in our study, eggs were shocked, water was drained from the egg mass, and dead eggs were counted and removed. Based on Heath et al. (1999) we assumed that differences in egg size at 26–28 d postfertilization are attributed to maternal effects. A random sample of live eggs collected with a 100-count egg counter (www.marisource.com) was weighed and the mean weight per egg was used to define egg size. The total number of live eggs was estimated using the total weight of live eggs divided by egg size. This estimate was decreased by 4% to compensate for water adherence to the eggs (WDFW Snake River Lab, unpublished data). The total numbers of live and dead eggs were combined to estimate fecundity. Partially spawned fish were excluded from our data set.

Relative fecundity was calculated by dividing fecundity by body weight (kg) (Knudsen et al. 2008). Relative fecundity was used to correct for the effect of body size on the number of eggs produced by each female.

Female salmon may allocate similar amounts of reproductive effort but partition it differently (e.g., small eggs and high fecundity may be equal in energy expenditure to large eggs and low fecundity). To account for differences in fecundity caused by egg size, reproductive mass was calculated by multiplying fecundity by egg size to provide total reproductive contribution in grams.

Any phenotypic differences observed among the two groups of hatchery fish may also be expressed in their progeny as a heritable trait, or may simply be a result of the length of time that fish are exposed to the hatchery environment. The progeny from both the hatchery-origin and captive-reared broodstock programs were reared in similar environments and at similar rearing densities, and were the same size at release (Gallinat et al. 2009). All juveniles released from both programs were tagged by group with coded wire tags, but were not fin-clipped to prevent their inclusion in the sport fishery. Based on 1985–2004 brood year coded wire tag recoveries, the sport, commercial, and treaty ceremonial harvest combined accounted for less than 6% of the adult fish recovered (Gallinat and Ross 2009). Therefore, any observed phenotypic differences between the groups in this study should not have been caused by selective fishing mortality. In 2008, age-4 female progeny from the hatchery-origin and captive-reared broodstock programs (2004 brood year) were collected and examined in a similar manner as previously described.

Statistical analysis.—Six phenotypic traits—FL, weight, egg size, fecundity, relative fecundity, and reproductive mass—were compared among the three groups of varying levels of hatchery rearing using the dominating portion of returning females (age 4) where sufficient data were available for all groups. Hatchery-origin and natural-origin groups had at least five observations per group for each year from 2001 to 2008 while captive-reared broodstock data were available from 2001 to 2006. The three-group comparisons are based on data collected during 2001–2006. We expected environmental factors, such as ocean conditions and weather, could potentially affect the phenotypic traits and that the magnitude of the effect was likely to vary from year to year. For each group we initially performed multiple comparisons with *P*-values adjusted by permutation resampling to test for differences of means among years for each variable. The results showed no clear patterns or significant trends for all variables by group. We proceeded to compare each trait among groups using a linear mixed model containing a single fixed group effect and a random year effect. The mixed model approach takes into account the clustering nature of the data. Samples collected for a given year are likely to experience a similar level of environmental influence. The model equation is expressed as $Y_{ijk} = \mu + \alpha_i + b_{ij} + e_{ijk}$, where μ, α_i represent unknown fixed intercept and group effects respectively, and b_{ij} and e_{ijk} are random variables representing the year effect and error, respectively.

Theoretically, morphometric variables such as fecundity and body size measurements are closely related due to allometric growth. It is also expected that both body size and fecundity traits were affected by hatchery rearing (Thorpe 2004; Campbell et al. 2006). We further developed two linear mixed models in which egg size and fecundity were the response variables. In each of these mixed models, the fixed effects included not only the group effect, but also relevant phenotypic traits as covariates, and the year effect remained random. These models explored the relationship between fecundity traits and body size, and revealed additional hatchery-rearing effects on the fecundity traits that cannot be explained through the affected body size. Fork length, weight, and fecundity were log transformed to improve linearity assumptions. The model-building process initially included all covariates for fixed effects and then removed those, except for group effect, that were not significant by type III *F*-tests. Interaction terms between group and each remaining covariate were tested one at a time by the order of the magnitude of the type III *F* statistics. Those significant by type III *F*-test were added to determine the final models. Model fitting was

done using SAS version 9.1.3, procedure MIXED with REML as the estimating method (SAS 2004).

High correlations were expected and observed ($r > 0.88$) among fecundity, weight, and FL. To avoid collinearity problems in model building, the normalization technique by Lleonart et al. (2000) was applied to the above variables.

We applied the technique by keeping weight unchanged and having FL and fecundity normalized according to a standard value of weight. A standard value of weight of 2,915 g was chosen by comparing 95% CIs of mean weight for each group and selecting the midpoint of the intersection portion of those CIs. The normalized FL and fecundity have the influence of weight removed and retain the unique individual shape deviation.

In 2008, a sample of age-4 females was identified as progeny of the captive-reared broodstock. We compared the six phenotypic traits of that group with a sample of age-4 hatchery-origin females that returned in 2008. We performed two-sample *t*-tests for differences in means with *P*-values adjusted by permutation resampling for multiplicity of tests.

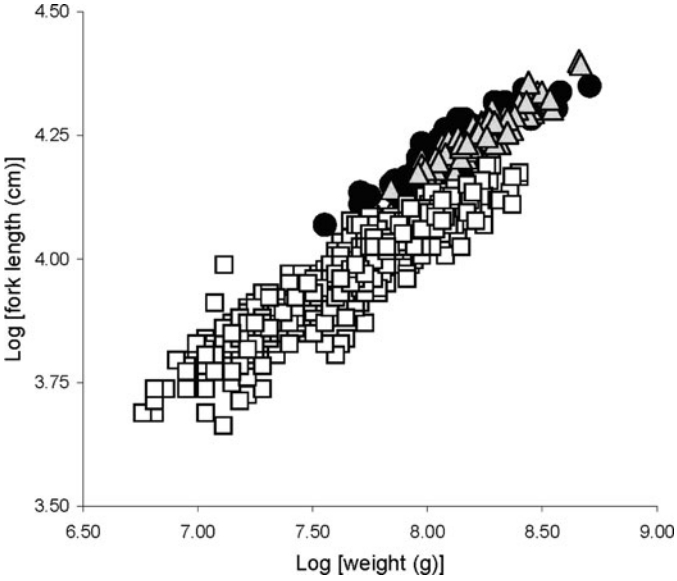

FIGURE 3. Relationship between log (weight) and log (FL) for age-4 Tucannon River hatchery-origin (black circles), natural-origin (gray triangles), and captive-reared broodstock (white squares) spring Chinook Salmon females.

RESULTS

Phenotypic Trait Comparison

The sample sizes, means, and SEs of the data collected for the selected phenotypic traits are presented in Table 2. The differences of FL and weight among the three groups are illustrated in Figure 3. The linear mixed models containing group as the only fixed effect yielded significant results for all six traits. Overall group effect for FL, weight, fecundity, and reproductive mass was highly significant ($P = 0.000$). The group effect was also significant for egg size and relative fecundity ($P = 0.011$ and 0.002, respectively). Comparisons of means between each pair of groups are summarized in Table 3. Mean values of all six traits of the captive-reared broodstock group were significantly different from means of the hatchery-origin and natural-origin groups. The captive-reared broodstock group had smaller means for all traits except egg size. Differences between the hatchery-origin and natural-origin groups were mostly not significant except for fecundity. Natural-origin females had higher fecundity, on average, than did hatchery-origin females.

Fecundity and Egg Size Related to Other Size Measures

Results of the two final models including other phenotypic traits as covariates are summarized in Table 4. Egg size was positively associated with weight and negatively associated with normalized FL and normalized fecundity. The group effect was still significant with the inclusion of the covariates. Given the same size, shape, and fecundity values, the captive-reared broodstock group had larger eggs than did the hatchery-origin and natural-origin groups. The difference between the hatchery-origin and natural-origin groups was not significant and none of the interaction terms were significant. Fecundity was positively associated with weight and negatively associated with egg size ($P = 0.000$). Given the same weight and egg size, there was no significant difference in fecundity among groups. Since normalized FL was

TABLE 2. Sample size (*n*), mean, and SE for the selected phenotypic traits for age-4 captive-reared broodstock (CRB), hatchery-origin (HOR), and natural-origin (NOR) female Tucannon River spring Chinook Salmon. Collection years are shown for each group.

	CRB 2001–2006			HOR 2001–2008			NOR 2001–2008		
Phenotypic trait	*n*	Mean	SE	*n*	Mean	SE	*n*	Mean	SE
FL (cm)	708	52.8	0.19	135	69.0	0.32	141	70.6	0.32
Weight (kg)	708	2.17	0.02	135	3.53	0.06	141	3.90	0.05
Fecundity (eggs/female)	708	1,664	20.05	135	2,982	56.20	141	3,419	56.08
Egg size (g)	708	0.256	0.002	135	0.231	0.003	141	0.230	0.002
Relative fecundity (eggs/kg)	708	779.3	6.24	135	846.1	10.21	141	879.6	9.70
Reproductive mass (g)	708	425.9	5.78	135	687.3	14.46	141	787.4	13.86

TABLE 3. Results from mixed models containing a group effect and a random year effect for age-4 female captive-reared broodstock (CRB), hatchery-origin (HOR), and natural-origin (NOR) Tucannon River spring Chinook Salmon (2001–2006 data). Type III tests of fixed effects are significant for all models (an asterisk denotes contrast of group means is significant at the 0.05 level).

	Comparisons between group means: F statistics (P-value)		
Phenotypic trait	CRB versus HOR	CRB versus NOR	HOR versus NOR
FL (cm)	209.85 (0.000)*	258.51 (0.000)*	1.43 (0.247)
Weight (kg)	49.64 (0.000)*	77.34 (0.000)*	2.28 (0.150)
Fecundity (eggs/female)	60.53 (0.000)*	115.04 (0.000)*	6.84 (0.018)*
Egg size (g)	6.05 (0.025)*	9.73 (0.006)*	0.30 (0.588)
Relative fecundity (eggs/kg)	4.69 (0.043)*	17.01 (0.001)*	2.77 (0.106)
Reproductive mass (g)	33.84 (0.000)*	62.27 (<0.000)*	3.36 (0.085)

removed from the model, the data suggested that fecundity was more closely related to weight than length.

Comparison of Progeny from Captive-Reared and Hatchery Programs

The ranges of both fecundity and length of age-4 captive-reared broodstock progeny females were more similar to age-4 hatchery-origin females than to the captive-reared broodstock females that they were derived from (Figure 4). Results of the two-sample t-tests with adjustment for multiple testing showed no significant difference in mean values of all six traits between the two groups. Descriptive statistics of the data are given in Table 5.

DISCUSSION

Decreased body size has been associated with decreased fecundity, smaller eggs, lower reproductive success, and lower survival of progeny (Kostow 2009). However, despite the smaller size on average, the age-4 captive-reared Chinook Salmon broodstock females had significantly larger eggs even after accounting for size, shape, and fecundity. Fleming and Gross (1992) reported that they also found hatchery-reared Coho Salmon had larger eggs than did wild females. In contrast, research by Heath et al. (2003) found that hatchery rearing relaxes natural selection favoring large eggs, allowing fecundity selection to drive rapid evolution of small eggs. They stated that these small eggs could lead to reduced survival and limit the success of hatchery programs. However, Heath et al. (2003) may have incorrectly attributed an ocean environmental effect and female variation on egg size to a genetic change as a result of hatchery enhancement (Beacham 2003; Fleming et al. 2003). The broodstock they studied was also developed to satisfy a "niche" market, and matures at a much smaller size and has unusually small eggs (Beacham and Murray 1993; Beacham 2003).

Egg size can have important fitness consequences, so there is a selective advantage for producing large eggs even within the hatchery environment (Heath et al. 1999). Kinnison et al. (2001) also found that egg size is strongly correlated with initial offspring fry size in salmonids and offspring size is, in turn, correlated with survival in salmon. Large egg size was insufficient to compensate for other deficiencies and did not appear to increase survival in our study since mortality to eye-up was 49% for captive-reared broodstock eggs compared with hatchery eye-up mortalities of 4% and 3% for hatchery-origin and natural-origin fish, respectively. The high egg mortality from the captive-reared broodstock group may be related to environmental, physiological, dietary, or other unknown factors. Patterson et al. (2004) found that captive Sockeye Salmon *O. nerka* also

TABLE 4. Summary of final models for egg size and fecundity for age-4 female captive-reared broodstock (CRB), hatchery-origin (HOR), and natural-origin (NOR) Tucannon River spring Chinook Salmon (2001–2006 data). The directions of fixed effects are summarized using plus "+" and minus "−" symbols, which refer to the signs of the slopes in the regression (adj: denotes variables are normalized to the standard weight).

		Type III F-test		
Response	Fixed effects	Direction	F statistic (P-value)	Significant contrast
Egg size (g)	Group	CRB > HOR > NOR	12.35 (0.000)	CRB > HOR, CRB > NOR
	Weight	+	108.75 (0.000)	
	FL, adj	−	7.40 (0.007)	
	Fecundity, adj	−	659.89 (0.000)	
Log (fecundity)	Group	No difference	1.74 (0.190)	
	Log (weight)	+	2292.76 (0.000)	
	Log (egg size)	−	565.89 (0.000)	

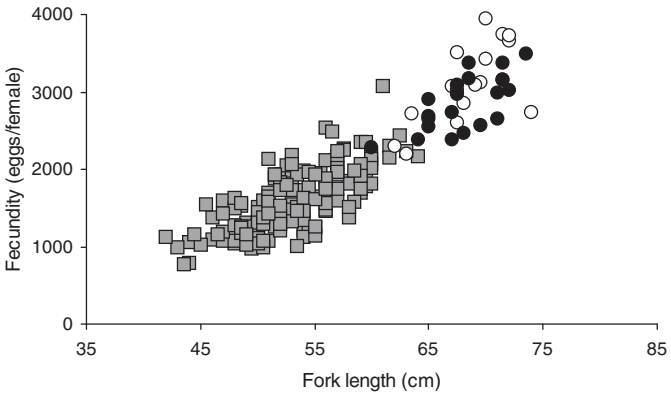

FIGURE 4. Comparison of FL and fecundity of age-4 captive-reared broodstock progeny females (black circles) and age-4 hatchery-origin (white circles) Tucannon River spring Chinook Salmon females that returned to the Tucannon River in 2008. Captive-reared broodstock females (gray squares) from the 2004 brood year that were the parents of the age-4 captive-reared broodstock progeny are included for comparison.

had significantly lower mean egg survival than did natural-origin fish and attributed it to confinement stress.

Tucannon River spring Chinook Salmon migrate 622 km from the mouth of the Columbia River to the mouth of the Tucannon River (Marvin and Nighbor 2009). This long migration may explain the difference in egg size between the migrating fish (natural-origin and hatchery-origin) and the nonmigrating, captive-reared broodstock group. A reduction in ovary investment due to migration costs has been noted in several salmon species (Kinnison et al. 2001; Campbell et al. 2006). The energy costs of migration are expected to be reflected by a variation in egg size, since eggs continue to gain mass until just prior to spawning and egg number is determined well in advance of final maturation (Kinnison et al. 2001). Beacham and Murray (1993) and Healey (2001) suggested that a limited amount of energy is expended on egg production in more northern stocks and stocks with long freshwater migrations. Thus, because of a readily available food supply and protected hatchery environment, the captive-reared broodstock may be able to allocate more energy into producing larger eggs than the migrating natural-origin and hatchery-origin fish.

We found that hatchery rearing of Tucannon River spring Chinook Salmon resulted in a phenomenon of lower overall reproductive potential in the form of reduced fecundity that decreased further as time spent in the hatchery environment increased. Because the fish in our study had genetically similar backgrounds, but were reared under different growth–environmental conditions, the differences observed were most probably environmentally induced. Hard et al. (2000) noted that morphometric development in hatchery fish is highly plastic and probably stems from differences between the hatchery and wild environment. The question remains whether the reduced fecundity attributed to hatchery rearing is inherited in Tucannon River spring Chinook Salmon. Our limited data, after adjusting for multiple testing, has provided some evidence that suggests fecundity was not significantly different between the captive-reared broodstock progeny and hatchery-origin fish. The captive-reared broodstock progeny that were reared in a similar manner to the hatchery-origin fish were more similar in phenotypic attributes to their hatchery cohorts than their captive broodstock parents. We hypothesize that the offspring of the hatchery-origin females that spawn in the natural environment would also follow the phenotypic pattern of the natural-origin fish, although the program currently does not have the means to test this as we are unsure which natural-origin fish were produced by hatchery-origin fish.

Phenotypic differences by themselves do not provide sufficient evidence to conclude that genotypic divergence has occurred (Knudsen et al. 2006). However, as Kostow (2004) stated, even if the phenotypic differences of the hatchery fish are not inherited they probably influence the relative fitness of the hatchery fish when they are in the natural environment and this could lead to eventual genetic divergence between the groups. Regardless of whether the observed differences were caused by genetics, environmental differences, or a mixture of the two, current hatchery practice does not produce hatchery-origin fish that are reproductively equivalent to the natural-origin fish (i.e., lower fecundity).

Araki et al. (2009) provided evidence that the genetic effects of a hatchery supplementation program were not easily erased by a full generation of fish in the wild, suggesting that

TABLE 5. Descriptive statistics for selected phenotypic traits for age-4 captive-reared broodstock progeny (CRB progeny) and hatchery-origin (HOR) female Tucannon River spring Chinook Salmon (2008 data, n = sample size). The P-values are two-sample t-test adjusted for multiple testing.

	CRB progeny ($n = 20$)		HOR ($n = 19$)		
Phenotypic trait	Mean	SE	Mean	SE	P-value
FL (cm)	67.9	0.74	68.9	0.78	0.722
Weight (kg)	3.32	0.10	3.53	0.12	0.509
Fecundity (eggs/female)	2,847	81.1	3,215	131.1	0.076
Egg size (g)	0.217	0.007	0.215	0.006	0.999
Relative fecundity (eggs/kg)	861.8	17.21	910.7	19.17	0.206
Reproductive mass (g)	621.5	32.45	693.4	35.81	0.401

recovery will probably not be immediate after a supplementation program is terminated. However, Lynch and O'Hely (2001) stated that, in principle, a natural population could recover from an excess segregation load after being isolated from a supplementation program because beneficial wild-type alleles are still present and can be returned to high frequency by natural selection. More research is needed in this area to better understand the influence hatchery supplementation has on wild populations and whether the natural environment will shift the phenotype, and eventually genotype, back to the natural population norm. However, hatchery supplementation programs are not necessarily recovery programs on their own. Without addressing the underlying mechanism that put the population in the position where intervention was necessary, there is little chance the population will be able to maintain any demographic boost provided by the hatchery program if the program is stopped.

No discussion on the risks of hatchery supplementation would be complete without also taking into account the risks of doing nothing (e.g., extinction, reduced effective population size, potential for inbreeding). We believe the risk of losing the Tucannon River spring Chinook Salmon population to extinction without the hatchery supplementation program is greater than the genetic or demographic risks posed by the hatchery program (Gallinat et al. 2008). Lande and Shannon (1996) concluded from their work that genetic variability is often less critical in the short term than other determinants of population persistence (e.g., habitat destruction, predators, competitors), but in the long term, it can play a decisive role in allowing a population to persist and adapt to a changing environment. Hatchery supplementation programs will need to balance possible adverse genetic risks while attempting to maintain population persistence. In hatchery supplementation programs, such as that for the Tucannon River spring Chinook Salmon, abundance is not only demographically important, it is also legally important in order to fulfill the requirements of the U.S. Endangered Species Act that will support delisting of the population. The Tucannon River spring Chinook Salmon captive broodstock program had a specific endpoint from the beginning as it was designed to last for only one generation (five brood years) to limit genetic risks associated with captive broodstock programs. Once the conventional hatchery supplementation program also ends, the natural environment will eventually determine which phenotypes and genotypes are best suited to persist if the population is to survive.

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