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COMMUNICATION

Efficacy of a Short-Term Captive Broodstock Program Compared with Hatchery-Origin Spring Chinook Salmon Derived from the Same Population

Michael P. Gallinat,* Joseph D. Bumgarner, and Lance A. Ross
Washington Department of Fish and Wildlife, 600 Capitol Way North, Olympia, Washington 98501, USA

Abstract

We examined the efficacy of a one-generation (five brood years: 1997–2001) captive broodstock program for spring Chinook Salmon *Oncorhynchus tshawytscha* by comparing survival rates of captive broodstock progeny (CBP; F_2) with that of hatchery-origin fish (HOR) from a conservation hatchery supplementation program in which both groups were derived from the Tucannon River (Washington State) population for the 2000–2006 brood years. Survival rates compared were egg to fry, fry to smolt, egg to smolt, total (ages 3–5) and adult (ages 4+) smolt-to-adult-return (SAR) survival, and total (ages 3–5) and adult (ages 4+) progeny-to-parent (P:P) ratio. Total escapement and adult P:P ratios were also examined to determine if observed demographic benefits to the population continued after the captive broodstock program ended. The CBP group had lower within-hatchery survival than the HOR group, with significant differences in survival at the egg-to-fry and egg-to-smolt stages due to poor egg viability. Mean untransformed total and adult SARs for the CBP were half those of the HOR group; however, SARs did not differ significantly. The CBP also had significantly lower total and adult P:P ratios than the HOR group and were below replacement for six of the seven brood years. While the captive broodstock provided additional fish for release that would not have been available otherwise, overall the CBP performed poorly and below expectations compared with the HOR group, both within the hatchery and after release. The captive broodstock program provided a short-term demographic boost, most notable in the 2008–2010 return years, but the benefit did not carry over after the program ended.

Along the west coast of North America, conservation-oriented hatchery programs are used in the attempt to increase population numbers of threatened and endangered Pacific salmon *Oncorhynchus* spp. and steelhead *O. mykiss* (Brannon et al. 2004; Waples et al. 2007). The goal of these hatchery programs is to enhance natural production while minimizing the genetic and ecological impacts to wild populations (Fisch et al. 2015).

Conservation-oriented hatchery supplementation programs (hereafter "supplementation programs") typically spawn broodstock collected from the natural environment that can be comprised of both natural and hatchery-origin fish. After a specified period of hatchery rearing, juveniles are released into the natural environment. These types of programs are designed to produce fish that, once reintroduced back into the wild, become naturally spawning fish (Trushenski et al. 2010). In contrast, captive broodstock programs are being used in gene rescue programs, where fish are kept in captivity throughout their life (from egg to spawning adults) to offset mortality that occurs in the natural environment and rapidly increase the number of available gametes. Captive broodstock programs are becoming important components of conservation efforts to prevent the extinction of endangered and threatened species (Fraser 2008; Williams and Hoffman 2009).

Both supplementation and captive broodstock programs utilize the protection of the hatchery environment to increase survival and potentially provide a demographic boost to population numbers until factors contributing to the population decline can be addressed (Frankham 2008). However, the use of anadromous Pacific salmon in both supplementation and captive broodstock programs is regarded as experimental in nature and has had mixed results as a conservation measure in the recovery and restoration of listed populations (Rinne et al. 1986; Flagg and Mahnken 1995; Fraser 2008).

A reduction in performance (e.g., relative reproductive success, survival, spawning behavior) is often reported for

*Corresponding author: michael.gallinat@dfw.wa.gov
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hatchery-origin fish relative to their natural-origin counterparts (Lynch and O'Hely 2001; Ford 2002) and is thought to have both genomic (Hindar et al. 1991; Waples 1991; Araki et al. 2007, 2009) and nongenomic origins (Krueger and May 1991; Kostow 2009). A concern for both supplementation and captive broodstock programs is that fish in the hatchery undergo relaxed natural and sexual selection pressures relative to individuals in the wild and selection for traits that carry high fitness in captivity, but low fitness in the wild, can occur (Waples 1991; Ford 2002; Araki et al. 2007; Frankham 2008). Similarly, differing environmental or nutritional signals provided to developing hatchery- and natural-origin fish can result in differences that have nongenomic origins. For example, Gallinat and Chang (2013) found significantly lower reproductive potential in captive brood and supplementation-reared females compared with natural-origin females of the same stock, with fecundity decreasing as time spent in the hatchery environment increased. Stark et al. (2018) also found significantly lower egg viability and egg-to-fry survival from captive-reared salmonids compared with natural-origin salmonids spawning in the East Fork Salmon River. Many of the biological changes that can occur as the result of captivity are unknown (Horreo et al. 2017), but reducing the number of generations in captivity is expected to reduce the extent or degree of domestication selection (Frankham 2008; Horreo et al. 2017).

In the mid-1970s, the Lower Snake River Compensation Program was enacted under the Water Resources Development Act of 1976 (Section 102) to provide mitigation from the expected losses of Pacific salmon and steelhead caused by the four lower Snake River dams (USACE 1975). As a result, 10 hatcheries and 12 hatchery satellite facilities were constructed and/or modified to mitigate for losses throughout the Snake River basin (Herrig 1990). In the state of Washington, Lyons Ferry Hatchery was constructed and Tucannon Fish Hatchery was modified to rear Pacific salmon and steelhead for the Lower Snake River Compensation Program. For Tucannon River spring Chinook Salmon *Oncorhynchus tshawytscha*, an annual release of 132,000 smolts was expected to return 1,152 adults on average (USACE 1975).

The Tucannon River spring Chinook Salmon hatchery program began in 1985 by collecting wild-origin adults for broodstock, and by 1989, both wild and hatchery-origin fish were collected for broodstock. Total adult returns (wild and hatchery) from 1985 to 1991 were estimated between 300 and 600 fish (Bugert et al. 1992). While the overall returns were stable, returns of hatchery adults were fewer than originally anticipated using the original survival assumptions (age 4 and older [age 4+] smolt-to-adult-return [SAR] survival rate of 0.87%). Monitoring during this period also determined that the natural population produced adults at levels below replacement (~0.8 returns/spawner), while the supplementation program progeny-to-parent (P:P) ratio was about 1.9 and appeared to be providing an overall benefit even though it was operating below original survival assumptions. Prior to enacting any sport or tribal spring Chinook Salmon fisheries in the Tucannon River, the National Marine Fisheries Service listed Snake River spring/summer Chinook Salmon as "threatened" under the Federal Endangered Species Act due to depressed and/or declining returns to the Snake River basin (NMFS 1992). Due to the Endangered Species Act listing and because the hatchery program was originally initiated with wild-origin fish, the Tucannon River spring Chinook Salmon hatchery program was transitioned from a harvest mitigation program to an integrated conservation supplementation program to assist in the preservation and rebuilding of the natural population, designed with mating and weir or trap management protocols that allow for gene flow between the hatchery-origin and natural-origin components in the hatchery and on the spawning grounds.

In 1994, total Tucannon River spring Chinook Salmon returns were estimated at 140 fish and declined to 54 fish in 1995 (Bumgarner et al. 1996). These consecutive years of low returns prompted the Washington Department of Fish and Wildlife (WDFW) to initiate a captive broodstock program with 1994 brood year (BY) juveniles on hand at Lyons Ferry Hatchery. This effort was suspended following predictions that returns in 1996 and 1997 would be similar to pre-1994 levels. The improved returns projected for 1996 and 1997 did not materialize, and floods in the Tucannon River basin during both years eliminated most of the natural production. Moreover, an 80% loss of the 1997 BY hatchery egg take occurred because of a malfunction of a water chiller at the hatchery. Due to continued low returns, losses to both natural and hatchery production, and the fact that the natural population remained below the replacement level, the captive broodstock program was reinitiated with BY 1997 fish on hand at Lyons Ferry Hatchery. However, due to the risks involved (e.g., genetic divergence, domestication, potential catastrophic loss in the hatchery), it was agreed that the captive broodstock program would only be implemented for one generation (i.e., five BYs total: 1997–2001; Gallinat et al. 2009). The production goal for the captive broodstock program was 150,000 smolts annually. At this level of smolt production, 300 adult fish/year would return if an anticipated SAR survival rate of 0.2% were achieved. In aggregate, the returning adults from the captive brood and supplementation programs could then be expected to return 600–700 fish annually between 2005 and 2010, similar to total pre-1994 returns.

Performance characteristics (fecundity, growth or size, spawn timing, survival, etc.) of hatchery fish derived from different types of programs (e.g., conservation

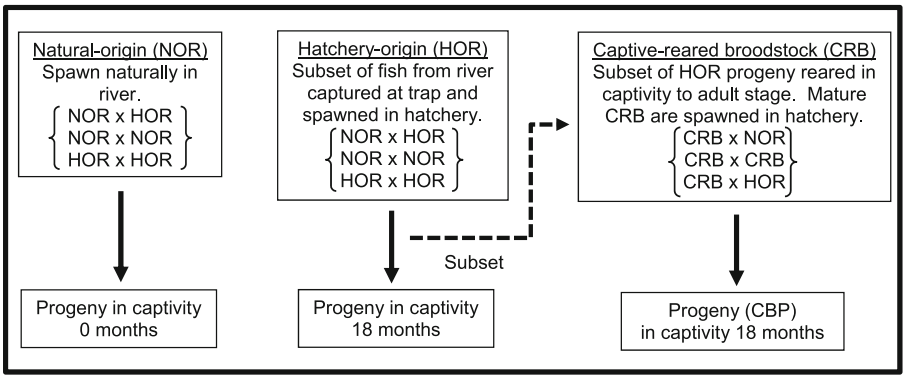

FIGURE 1. Tucannon River spring Chinook Salmon groups used for survival comparisons. Possible spawning crosses are shown in brackets. The spawning crosses for fish spawned in the hatchery are listed in order of priority.

supplementation versus captive broodstock) are important in evaluating the efficacy of different practices in meeting their overall objectives. Success of captive broodstock programs has largely been measured by the number of eggs, fry, and adults produced in captivity, rather than the performance of the fish after release (ISRP 2004). Studies also conducted on populations that have a common genetic background provide a chance to understand the mechanisms behind changes caused by the hatchery environment (Gallinat and Chang 2013). Fecundity, egg size, spawning timing, and length at age of the captive broodstock for this population have been published elsewhere (Gallinat et al. 2009; Gallinat and Chang 2013). Progeny from the captive broodstock program reared in parallel with the supplementation program at the Lyons Ferry Hatchery complex offered the opportunity to compare the in-hatchery and postrelease performance of these two strategies. Our comparisons (egg-to-fry, fry-to-smolt, and egg-to-smolt survival) offer insight into hatchery performance and performance following release (total [ages 3–5] and adult [age 4+] SAR survival and P:P ratio and total escapement back to the Tucannon River) and allow for characterization of the contributions of these two strategies to the demographic benefit to the population.

METHODS

Group definitions.— We defined the study groups as follows: (1) hatchery-origin (HOR) fish used for the supplementation program were the product of artificial reproduction of both natural-origin (NOR) and HOR fish but were released into the natural environment after 18 months of hatchery rearing as yearling smolts (Figure 1), and (2) captive broodstock progeny (CBP) are the progeny (F_2) from captive broodstock females (F_1) that were crossed with NOR, HOR, or other captive broodstock males (F_1) and the CBP were released after 18 months of hatchery rearing as yearling smolts (Figure 1).

Study area.— The Tucannon River is a third-order stream in southeastern Washington State and flows into the Snake River between Little Goose and Lower Monumental dams approximately 622 km from the mouth of the Columbia River (Figure 2). Stream elevation rises from 150 m at the mouth of the Tucannon River to 1,640 m at the headwater (Bugert et al. 1991). The total watershed area is about 1,295 km^2 (Gallinat et al. 2009). Mature NOR and HOR spring Chinook Salmon adults migrate to the Tucannon River basin from April to June and spawn from late August through September. Spawning and juvenile rearing of NOR fish in the Tucannon River typically occurs upstream of river kilometer (rkm) 35 (measuring from its confluence with the Snake River) (Gallinat et al. 2008). The majority of NOR smolts emigrating out of the system are about 18 months old, have a mean fork length of 105–113 mm, and rear in the ocean for 1–3 years until mature (Gallinat and Chang 2013).

Hatchery facilities.— Three different WDFW facilities (Lyons Ferry Hatchery, Tucannon Fish Hatchery, and Curl Lake Acclimation Pond) contributed to the production of HOR and CBP fish. The Lyons Ferry Hatchery is located on the Snake River (at rkm 90, measuring from it confluence with the Columbia River) at its confluence with the Palouse River (Figure 2) and was used for broodstock holding and spawning, incubation, and early life stage rearing until production marking and tagging. The Tucannon Fish Hatchery is located at rkm 59 on the Tucannon River (measuring from it confluence with the Snake River) and has an adult trap for broodstock collection (Figure 2). The Tucannon Fish Hatchery was used for intermediate overwinter juvenile rearing of both CBP and HOR fish prior to final acclimation at Curl Lake Acclimation Pond in the upper basin (Figure 2). Curl Lake Acclimation Pond is a 0.85-hectare natural-bottom lake (mean depth = 2.7 m;

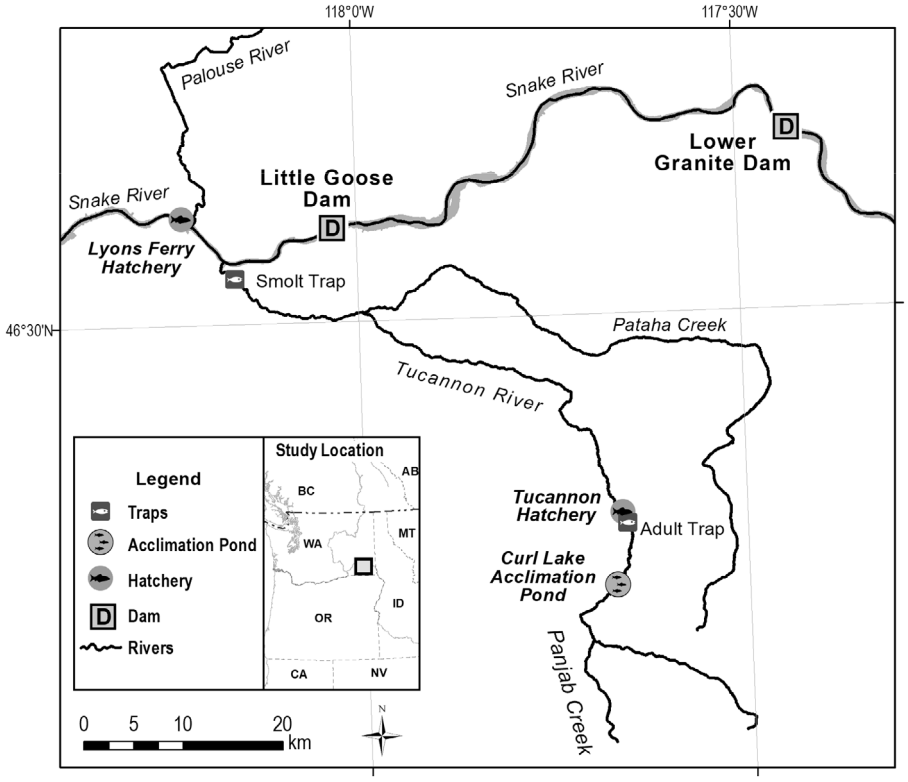

FIGURE 2. Location of the Tucannon River basin, a tributary of the Snake River, and locations of Lyons Ferry Hatchery, Tucannon Hatchery, and Curl Lake Acclimation Pond.

volume = 22,203 m^3) adjacent to the Tucannon River and located about 6 km upstream of Tucannon Fish Hatchery.

Supplementation program broodstock.— The supplementation program broodstock goal was to collect up to 100 adults at the Tucannon Fish Hatchery adult trap from throughout the run, comprised of both NOR and HOR returns (target 1:1 ratio). Tucannon River HOR fish used for broodstock were verified by coded wire tag (CWT) extraction at the time of spawning. Ages of NOR and HOR females used for spawning ranged from 4 to 5 years old, and ages of NOR and HOR males used for spawning ranged from 3 to 5 years old. Jack (age-3) male spawning contribution averaged 4.5% over the course of the study (range = 2.1–6.8%). During spawning for the supplementation program, a 2 × 2 factorial fertilization strategy was incorporated to increase effective population size and maintain genetic diversity (Busack and Knudsen 2007). At fertilization, eggs from two ripe females and semen from two males were selected based on their origin and availability with priority for HOR × NOR crosses (Figure 1). The eggs from each female were split into approximately two equal halves, with one male added to one half of each female's eggs and the other male to the other half. After about 30 s, the halves were recombined into single egg lots per female. The eggs produced from the spawning of the supplementation broodstock for the 2000–2006 BYs are the HOR group used for comparison to the CBP group.

Origination of the captive broodstock.— The captive broodstock population was selected from fry produced from the supplementation program from the 1997 to 2001 BYs (WDFW et al. 1999). Because the captive broodstock males matured at an earlier age than females, additional fry were collected from the 2002 BY to have enough captive males available at the end of the captive broodstock program to cross with captive females. We chose to collect fry from the supplementation program to lessen the effects of removing more fish from the natural population and because of potential disease concerns from bringing fish in from the river. Bacterial kidney disease screening using enzyme-linked immunosorbent assay of kidney tissue from all females was performed (Munson et al. 2010), and progeny from the lowest optical density categories were used for the captive broodstock as bacterial kidney disease has been a large source of mortality in other captive broodstock programs (Flagg and Mahnken 1995). Priority of fry selection for the captive broodstock (in the following order) was given to NOR × NOR, NOR × HOR, and HOR × HOR matings from the supplementation program.

The proportion of NOR fish used for establishing the captive broodstock averaged 39% over the program's history (range = 5.9–53.9%).

The fertilization strategy employed led to progeny that were half-siblings from pairs of females. All matings that were sired by the same males were considered one family unit to avoid within-family matings in the future. As a result, while only 15 family units were chosen for the captive broodstock program, actual contributions of male and female parents (population size) to the captive brood program on a yearly basis was higher. The effective population sizes of captive broodstock for the 1997–2002 BYs were 53, 58, 42, 56, 58, and 59, respectively, and generally exceeded the goal of 50 fish suggested by Allendorf and Ryman (1987) and Verspoor (1988) to limit the loss (<1%) of genetic variability in most salmonid species.

Eighty fry from each of the 15 family units were selected (1,200 total fish) from each BY. Rearing vessels at Lyons Ferry Hatchery included 15 1.2-m-diameter (0.5-m-deep) circular tanks for rearing juvenile captive broodstock and eight 6.1-m-diameter (1.1-m-deep) circular tanks for rearing the captive broodstock adults. Both the 1.2- and 6.1-m circular rearing tanks were covered with camouflage netting to provide shade, lessen stress, and prevent jumping out of tanks. The 1.2-m circular fiberglass tanks held family units individually before they were large enough to mark. Fish were tagged after 1 year, and family units were reduced to 30 fish/family (450 fish/BY) by random selection at this time. Family units for the captive brood program were double-tagged (in both adipose fin and snout) with uniquely coded CWTs and with a unique alphanumeric visual implant tag inserted behind the eye. These steps provided the necessary marks to verify that members of the same family unit were not mated together.

After CWT and visual implant tagging, all fish from an individual BY were transferred to a single 6.1-m circular fiberglass tank for rearing to maturity. Hatchery staff visually estimated size and growth to prescribe feeding rates to minimize stressors to sampling and handling that might jeopardize fish health. Size-at-age goals were set as follows: age 1 = 20–25 g, age 2 = 150–200 g, age 3 = 900 g, and age 4 = 4,000 g.

During late June to early July, captive broodstock that were age 2 or older were examined for signs of sexual maturation. Maturation was determined by a darkening in body coloration as other morphological characteristics indicating sexual maturation were not readily apparent. Mature female captive broodstock were injected with erythromycin (Erythro-200; Abbott Laboratories, Abbott Park, Illinois) at 20 mg per kilogram of body weight at sorting to prevent bacterial kidney disease. Mature captive broodstock were transported to holding raceways (3.1 m × 1.8 m × 24.4 m) at Lyons Ferry Hatchery in common with, but separated by screens from, the supplementation broodstock (NOR and HOR) collected from the Tucannon River. Broodstock from both programs were treated with a formalin flush (167 ppm) every other day to control fungus (*Saprolegnia* sp.).

During spawning, captive broodstock and HOR and NOR adults were anesthetized with an unbuffered solution (45–50 mg/L) of tricane methanesulfonate (Western Chemical, Ferndale, Washinton) and examined weekly for ripeness (late August to early October). Although peak spawn timing was about 2 weeks later for the captive broodstock than for fish collected from the river (Gallinat et al. 2009), we were still able to spawn some captive broodstock females with NOR and HOR males each year. Final contribution of males crossed with captive broodstock females was 72% captive broodstock males, 19% NOR males, and 9% HOR males. Spawning adults from the captive broodstock were younger than those from the supplementation program, with females beginning to mature at age 3 and males starting to mature at age 2. Spawning adults less than age 4 (minijacks, jacks, jills) comprised 34.1% of the spawning adults on average from the captive broodstock program (range = 0.0–66.7%). For both the supplementation and captive broodstock programs, ripe females were killed and the eggs excised and collected into numbered plastic buckets and placed in coolers on an insulated layer of ice. Milt from males was collected into numbered plastic bags, oxygenated, and stored on an insulated layer of ice until used for fertilization. Fertilization of the captive broodstock followed the same 2 × 2 factorial matrix described earlier for the supplementation broodstock. Fertilized eggs were recombined, one female per bucket, and disinfected in an iodophor bath at a rate of 100 ppm for 1 h. The eggs produced from the spawning of the captive broodstock for the 2000 to 2006 BYs make up the CBP group used for comparison to the HOR group.

The CBP and HOR groups.— The eggs from both programs were incubated in either vertical stacked tray incubators or isolation buckets and treated every other day with formalin at 1,667 ppm (37% formaldehyde) for 15 min for fungus control. Fry from both groups were placed into separate outside raceways (3.1 m × 30.5 m × 1.1 m) at Lyons Ferry Hatchery in December and fed the same commercial feed (Bio-Oregon, Longview, Washington). At Lyons Ferry Hatchery, the entire facility (incubation, raceways, circular tanks, and adult holding ponds) is supplied with pathogen-free, constant-temperature well water (11°C) throughout the year.

The CBP and HOR fish were tagged with unique CWTs to identify groups at Lyons Ferry Hatchery in mid-September, 1 year following spawning. The HOR fish were also tagged with a visual implant elastomer (VIE) tag (Northwest Marine Technology, Shaw Island, Washington) behind the right eye. The VIE tag allowed for external identification of the HOR group after they were

combined for final acclimation in Curl Lake Acclimation Pond. More importantly, this was done to exclude CBP adults from being collected for broodstock in the future to prevent further potential hatchery domestication and potential crosses with siblings. Following marking and tagging at Lyons Ferry Hatchery, juveniles were transferred to Tucannon Fish Hatchery to rear in either 12.2-m-diameter circular ponds (0.6 m deep) or 4.6-m × 1.5-m × 35.1-m and 3.1-m × 0.9-m × 24.4-m raceways. At Tucannon Fish Hatchery, river water is used as the main source for rearing, which allows for a more natural winter temperature profile. However, well and spring water is mixed with river water to keep temperatures above 4.4°C. A subsample of fish from each group was tagged with passive integrated transponder (PIT) tags in January. In mid-February, both HOR and CBP juveniles were transferred to Curl Lake Acclimation Pond for a minimum of 4 weeks of acclimation before release. During acclimation, fish were fed by a truck-mounted feed blower. Observed mortalities were collected, counted, and assigned to their respective group based on presence or absence of the VIE tag by hatchery personnel. Predation (primarily avian) is known to occur during acclimation, but it is assumed that predation is not biased towards one group over the other. Water temperatures in Curl Lake Acclimation Pond during acclimation ranged between 4.4 and 12.8°C. Individual lengths and weights were recorded from a minimum of 250 fish from each group before the volitional release began. The fish could volitionally emigrate from the lake from mid-March to late April, after which any remaining fish were forced out by draining the lake in entirety. The size-at-release goal for both programs was 30 g/fish for the 2000–2004 BYs and 50 g/fish for the 2005–2006 BYs.

Most BYs of the HOR and CBP groups were healthy throughout their rearing at Lyons Ferry Hatchery and Tucannon Fish Hatchery and upon release. The only exception was the 2001 BY in which bacterial kidney disease was diagnosed in both the HOR and CBP groups. The fish were treated with erythromycin-medicated feed and mortality declined following treatment.

Data analysis.—We recorded the number of males and females that were used during spawning at the hatchery to determine the number of spawners. To calculate fecundity for the captive broodstock and HOR individual females, eggs were physically shocked at the eyed egg stage, with the dead eggs counted and removed. Water was drained from the remaining live eggs, and a random sample of 100 eggs was collected and weighed from each female. The total number of live eggs for each female was estimated by dividing the total live egg weight by the egg size (g/egg). The live egg estimate was then decreased by 4% to compensate for water adherence to the eggs (WDFW Snake River Lab, unpublished data). The total number of live eggs estimated and dead eggs counted were combined to estimate total fecundity (eggs/female). The number of CBP and HOR fry that were ponded in December to raceways at Lyons Ferry Hatchery was calculated by using standard gravimetric hatchery inventory techniques (Piper et al. 1982).

For survival comparisons, we used the number of smolts released from Curl Lake Acclimation Pond. Using the data described above, we calculated egg-to-fry (number of fry divided by fecundity × 100), fry-to-smolt (number of smolts released divided by the number of fry × 100), and egg-to-smolt (number of smolts released divided by fecundity × 100) survival rates.

Adult returns to the Tucannon River were derived from a combination of redd counts, adult trapping, spawning ground carcass recoveries, sex ratios, and prespawn mortality estimates (Gallinat et al. 2008). Data collected from carcasses included scale samples and noting the presence of VIE tags or fin clips, and all snouts were removed from carcasses for CWT extraction and origin determination. Acetate impressions were made from scale samples and aged by experienced personnel at the WDFW Scale Age Lab (Olympia, Washington). No returning fish less than age 3 or greater than age 5 were recovered from the Tucannon River. Estimates of SAR survival were derived by dividing the number of total (ages 3–5) and adult (ages 4+) returns by the number of smolts released, calculated as a percent, and used to compare performance between the HOR and CBP groups. We calculated BY-specific total (ages 3–5) and adult (ages 4+) P:P ratios as an indicator of population growth rate (adult returns divided by the number of spawners).

All survival estimates were arcsine square root transformed since percentages form a binomial, rather than a normal, distribution (Zar 1996). After transformation, Statgraphics Plus 5.0 software (Manugistics, Rockville, Maryland) was used for all statistical analyses. Due to high variance among years, a nonparametric Mann–Whitney (Wilcoxon) rank-sum test was used to compare medians. The null hypothesis was that both medians were equal versus the alternate hypothesis that the medians were not equal. All statistical tests were performed at the 95% confidence level.

RESULTS

The number of eggs, fry, and smolts and their size at release from Curl Lake Acclimation Pond for the CBP and HOR groups by BY is shown in Table 1. The increase in size at release for the 2005 and 2006 BYs reflects a management change in the attempt to increase survival and returns. Survival estimates from the CBP and HOR fish used for in-hatchery and postrelease comparative analyses are provided in Table 2 and show that the number of returning adults from the 2005 and 2006 BYs increased greatly for both groups.

TABLE 1. Data summary by life stage (eggs, fry, smolts) and the mean weight (g) and mean length (FL; mm) with coefficient of variation (CV) of the smolts released from the Tucannon River spring Chinook Salmon captive broodstock progeny (CBP) and hatchery supplementation (HOR) programs for the 2000–2006 brood years.

Brood year	Total fecundity	Number of fry	Smolts released	Mean smolt weight (g)	Mean smolt length (mm)	Smolt length CV
			CBP			
2000	14,577	4,323	3,055	51	163.5	10.8
2001	281,303	195,264	140,396	33	135.3	17.2
2002	176,544	50,462	44,784	34	135.0	15.1
2003	309,416	164,800	130,064	34	135.0	17.3
2004	310,819	140,874	132,312	30	132.9	13.3
2005	261,845	93,971	90,056	61	166.3	14.3
2006	162,736	79,432	78,176	57	158.5	18.8
			HOR			
2000	128,980	123,313	102,099	29	133.1	13.2
2001	184,127	174,934	146,922	35	139.4	16.3
2002	169,364	151,531	123,586	39	141.7	15.6
2003	140,658	126,400	71,154	36	138.8	16.2
2004	140,459	128,877	67,542	34	139.5	10.1
2005	161,345	151,466	149,466	57	162.0	13.5
2006	62,934	57,192	52,735	54	157.9	17.0

For within-hatchery juvenile life stage survivals (egg to fry, fry to smolt, egg to smolt), we found differences between some of the comparisons. Mean untransformed egg-to-fry survival was 44% (SE = 5.5) for CBP and 92% (SE = 0.9) for the HOR group (Table 2). After transformation, the average rank for CBP egg-to-fry survival was 4.0 and the average rank for HOR egg-to-fry survival was 11.0. The *W*-statistic was 49.0, and the HOR egg-to-fry survival medians were significantly greater than those of the CBP group, with a *P*-value of 0.002 (Figure 3).

Mean untransformed fry-to-smolt survival was 86% (SE = 4.4) for CBP and 78% (SE = 6.6) for the HOR group (Table 2). The average ranks for the CBP and HOR groups were 8.1 and 6.9, respectively, with a *W*-statistic of 20.0, which was not significantly different ($P = 0.609$; Figure 4).

Egg-to-smolt comparisons also found differences between the CBP and HOR groups. The mean untransformed egg-to-smolt survival for the CBP group was 38% (SE = 4.2) and for the HOR group it was 72% (SE = 6.4) (Table 2). After transformation, the average rank was 4.1 for CBP and 10.9 for the HOR group. The *W*-statistic was 48.0, with a significant *P*-value of 0.003 (Figure 5).

For adult life stage survivals (SAR, P:P), we observed differences between some of the comparisons. Mean untransformed total SAR was 0.15% (SE = 0.09) for CBP and 0.30% (SE = 0.13) for the HOR fish (Table 2). However, no significant differences (*W*-statistic = 33.0, $P = 0.304$) in the median total SARs were found (Figure 6). The mean untransformed adult SAR was 0.10% (SE = 0.06) for CBP and 0.21% (SE = 0.07) for the HOR group (Table 2). No significant difference (*W*-statistic = 38.0, $P = 0.096$) in the median adult SARs were evident after transformation (Figure 6).

The mean untransformed total P:P ratio for the CBP group was 0.73 (SE = 0.47), and it was 3.79 (SE = 1.65) for the HOR group (Table 2). The HOR group had significantly (*W*-statistic = 40.5, $P = 0.047$) higher median total P:P ratios after transformation (Figure 7). The adult P:P ratios of the CBP were below replacement for six of the seven BYs, while the HOR group was above replacement for six of the seven BYs (Table 2). The mean untransformed adult P:P survival for the CBP group was 0.53 (SE = 0.36), and it was 2.56 (SE = 0.94) for the HOR group (Table 2). The HOR group had significantly (*W*-statistic = 44.0, $P = 0.015$) higher medians for adult P:P ratios than the CBP group (Figure 7).

As previously stated, the Tucannon River experienced low returns (1994–1997; mean = 165 total fish) prior to the start of the captive broodstock program (Figure 8). As fish from the captive broodstock program were beginning to mature, returns to the Tucannon River increased in 2001 and 2002. However, runs declined again from 2003 to 2007, even with the addition of CBP fish returning as adults during the latter part of that time period (Figure 8). The population then experienced a large demographic boost from NOR, HOR, and CBP returns from 2008 to 2010 (mean = 1,858 total fish) but has experienced a precipitous decline in recent years (2016–2021; mean = 385 total fish; Figure 8).

TABLE 2. Untransformed life stage survival data for juveniles (egg to fry, fry to smolt, egg to smolt) and total (ages 3–5) and adult (ages 4+) age-groups (smolt to adult return [SAR] and progeny to parent [P:P]) from the Tucannon River spring Chinook Salmon captive broodstock progeny (CBP) and hatchery supplementation (HOR) programs for the 2000–2006 brood years.

Brood year and mean	Egg-to-fry survival (%)	Fry-to-smolt survival (%)	Egg-to-smolt survival (%)	Total SAR % (ages 3–5)	Adult SAR % (ages 4+)	Total P:P (ages 3–5)	Adult P:P (ages 4+)
			CBP				
2000	29.7	70.7	21.0	0.00	0.00	0.00	0.00
2001	69.4	71.9	49.9	0.01	0.01	0.06	0.05
2002	28.6	88.7	25.4	0.00	0.00	0.01	0.01
2003	53.3	78.9	42.0	0.02	0.01	0.06	0.05
2004	45.3	93.9	42.6	0.06	0.06	0.23	0.23
2005	35.9	95.8	34.4	0.40	0.22	1.44	0.80
2006	48.8	98.4	48.0	0.54	0.42	3.31	2.58
Mean	44.4	85.5	37.6	0.15	0.10	0.73	0.53
			HOR				
2000	95.6	82.8	79.2	0.15	0.13	2.15	1.79
2001	95.0	84.0	79.8	0.09	0.07	1.22	1.04
2002	89.5	81.6	73.0	0.10	0.09	1.30	1.24
2003	89.9	56.3	50.6	0.10	0.10	0.95	0.92
2004	91.8	52.4	48.1	0.18	0.15	1.36	1.16
2005	93.9	98.7	92.6	0.46	0.27	7.26	4.20
2006	90.9	92.2	83.8	1.03	0.63	12.30	7.59
Mean	92.4	78.3	72.4	0.30	0.21	3.79	2.56

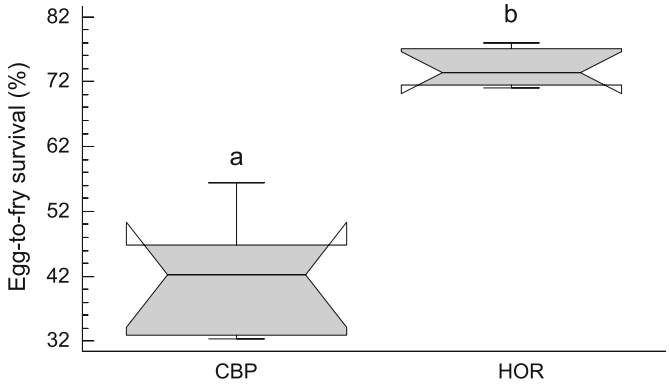

FIGURE 3. Notched box-and-whisker plot of arcsine square-root-transformed egg-to-fry survival (%) for Tucannon River spring Chinook Salmon captive broodstock progeny (CBP) and hatchery supplementation (HOR) fish from the 2000 to 2006 brood years. The line inside the box represents the median, and the box extends from the lower quartile to the upper quartile, covering the center half of each sample. The whiskers extend from the box to the minimum and maximum values of each sample. The notch displays the confidence interval around the median. Plots with different letters above them are statistically different with $P < 0.05$.

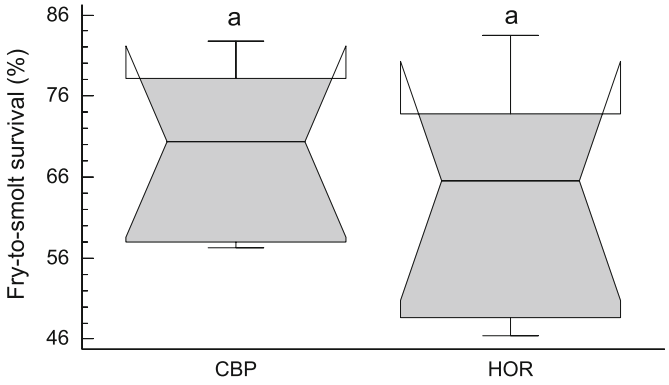

FIGURE 4. Notched box-and-whisker plot of the arcsine square-root-transformed fry-to-smolt survival (%) for Tucannon River spring Chinook Salmon captive broodstock progeny (CBP) and hatchery supplementation (HOR) fish from the 2000 to 2006 brood years. The line inside the box represents the median, and the box extends from the lower quartile to the upper quartile, covering the center half of each sample. The whiskers extend from the box to the minimum and maximum values of each sample. The notch displays the confidence interval around the median. Plots with the same letter above them are not statistically different with $P > 0.05$.

Since the inception of the monitoring program in 1985, WDFW has estimated the adult P:P ratio of NOR and HOR fish annually. To illustrate the importance of the HOR fish to the preservation of the Tucannon River spring Chinook population, the NOR fish have only been above replacement for 10 (31%) of 32 years, while the HOR fish have been above replacement for 24 (75%) of 32 years. The survival performance of the CBP fish was expected to be similar to the HOR fish but in the end was only above replacement in 1 (14%) of the 7 years (Figure 9), while the HOR and NOR fish were above replacement in 6 (86%) and 4 (57%) of the same 7 years, respectively.

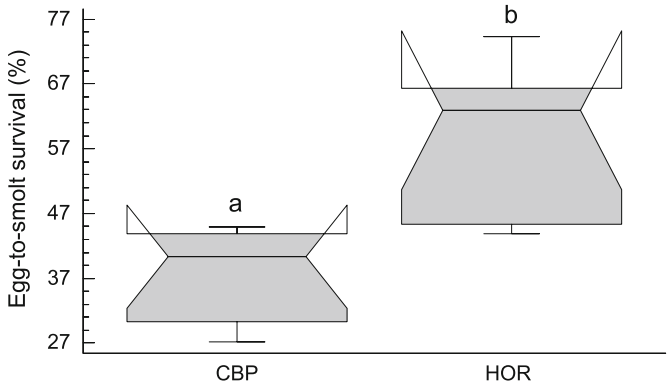

FIGURE 5. Notched box-and-whisker plot of the arcsine square-root-transformed egg-to-smolt survival (%) for Tucannon River spring Chinook Salmon captive broodstock progeny (CBP) and hatchery supplementation (HOR) fish from the 2000 to 2006 brood years. The line inside the box represents the median, and the box extends from the lower quartile to the upper quartile, covering the center half of each sample. The whiskers extend from the box to the minimum and maximum values of each sample. The notch displays the confidence interval around the median. Plots with different letters above them are statistically different with $P < 0.05$.

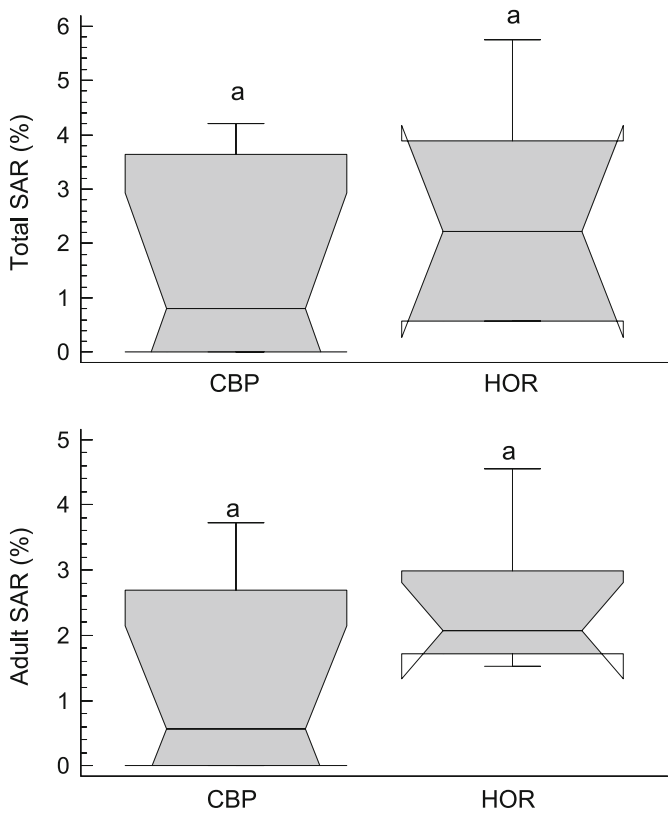

FIGURE 6. Notched box-and-whisker plots of the arcsine square-root-transformed total (ages 3–5; top panel) and adult (ages 4+; bottom panel) smolt-to-adult-return (SAR) survival (%) for Tucannon River spring Chinook Salmon captive broodstock progeny (CBP) and hatchery supplementation (HOR) fish from the 2000 to 2006 brood years. The line inside the box represents the median, and the box extends from the lower quartile to the upper quartile, covering the center half of each sample. The whiskers extend from the box to the minimum and maximum values of each sample. The notch displays the confidence interval around the median. Plots with the same letter above them are not statistically different with $P > 0.05$.

DISCUSSION

While the captive broodstock program was successful in producing additional smolts for release, the CBP performed poorly compared with the HOR group from release to adult returns and did not meet the adult return goal of 300 adults/year until the size-at-release goal was increased to 50 g/fish during the last two BYs of the program. The poor performance was surprising given that both groups were reared under identical conditions for 18 months before release, and juveniles appeared identical in physical characteristics. The major differences between the two groups were as follows: (1) the parents (all the females, majority of the males) that produced the CBP were raised entirely in captivity, (2) the captive broodstock spawners were younger and smaller in size compared with the supplementation program fish, (3) spawn timing of the captive brood adults was later, although they did overlap with HOR and NOR spawn timing (Gallinat et al. 2009), and (4) egg survival of captive broodstock females was significantly lower than that of NOR and HOR females (Gallinat and Chang 2013). Similar to our experience, other captive programs of Pacific salmon have been plagued with high mortality rates, spawn timing outside that of fish collected from their natal river (both HOR and NOR), precocious maturation of males, low egg viability, and captive adults that are smaller than wild fish (Flagg and Mahnken 1995; Schiewe et al. 1997).

Egg survival has historically been low for captive broodstock programs, typically ranging from 30% to 60% compared with >80% for wild females (Flagg and Mahnken 1995). Venditti et al. (2013) suggested that poor egg survival was due to maternal factors and that male gamete quality did not appear to be a factor. Gallinat (2006) found that sperm motility was not a significant factor in the higher egg mortality of the Tucannon River Spring Chinook Salmon captive broodstock program. We also excluded males as a factor in our study since we spawned HOR and NOR males with HOR, NOR, and captive broodstock females and only the captive broodstock females had consistently lower egg survival. Initial overall fertilization rate of Redfish Lake Sockeye Salmon *Oncorhynchus nerka* captive broodstock was only 30% using milt from anadromous males, suggesting that poor egg quality was to blame (Johnson and Pravecek 1995).

Kozfkay et al. (2017) saw improvement in Salmon River, Idaho, Chinook Salmon captive broodstock egg viability with saltwater rearing and the use of chilled water and noted that it could provide improvements

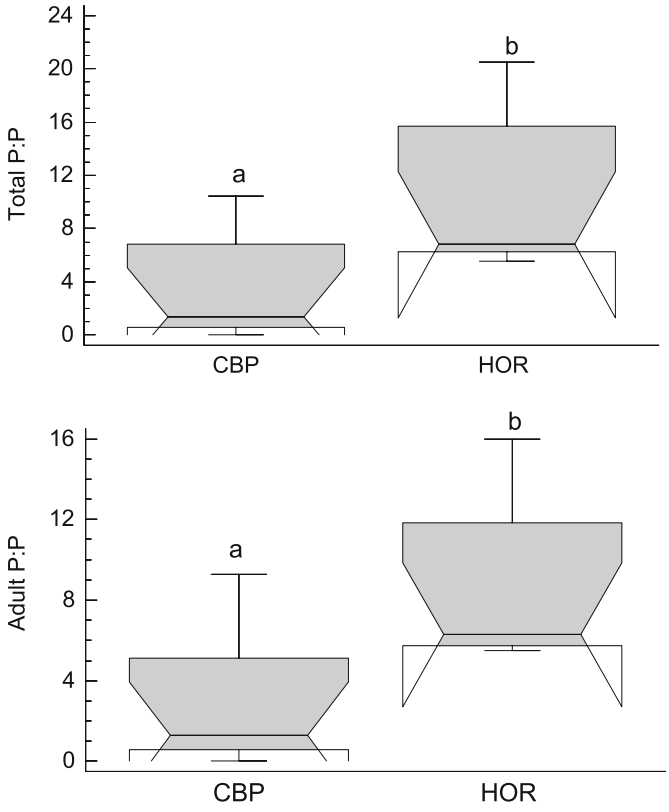

FIGURE 7. Notched box-and-whisker plots of the arcsine square-root-transformed total (ages 3–5; top panel) and adult (ages 4+; bottom panel) progeny-to-parent (P:P) ratio for Tucannon River spring Chinook Salmon captive broodstock progeny (CBP) and hatchery supplementation (HOR) fish from the 2000 to 2006 brood years. The line inside the box represents the median, and the box extends from the lower quartile to the upper quartile, covering the center half of each sample. The whiskers extend from the box to the minimum and maximum values of each sample. The notch displays the confidence interval around the median. Plots with different letters above them are statistically different at $P < 0.05$.

relative to maturation size, fecundity, and reproductive success. In contrast, egg and fry loss were much higher for Dungeness River Chinook Salmon captive broodstock reared in saltwater pens versus those reared in freshwater (Freymond et al. 2001). They hypothesized that the warm water conditions of the net pens in summer when the ova were maturing or the timing of moving the maturing fish to the hatchery just prior to spawning was to blame for the poor-quality eggs (Freymond et al. 2001). The Redfish Lake captive broodstock program attempted several strategies to improve initial Sockeye Salmon survival and egg viability problems early in the program, including modification of the standard brood diet, incubating eggs at different temperatures, and controlling mating crosses to expand the genetic base of the few remaining fish (Johnson and Pravecek 1996). The modifications to the brood diet included replacing 50% of the standard protein of fish meal with Antarctic krill, increasing selenium (water at the hatchery was deficient in selenium), and increasing levels of vitamins E and C (Johnson and Pravecek 1996). The White River spring Chinook Salmon captive broodstock program used hormone injections to increase egg viability due to the incomplete maturation of ova in that program (Hillman et al. 2021). Further experimental research with unlisted Chinook Salmon captive broodstock populations would be beneficial in identifying nutritional, hormonal, or other factors associated with poor egg quality and low early life stage survival.

The main argument against using captive broodstock or supplementation programs is that rearing in the hatchery leads to domestication selection (Hindar et al. 1991; Reisenbichler and Rubin 1999). However, other researchers argue that these genetic risks are overstated and that long-term effects have little to no empirical basis (Brannon

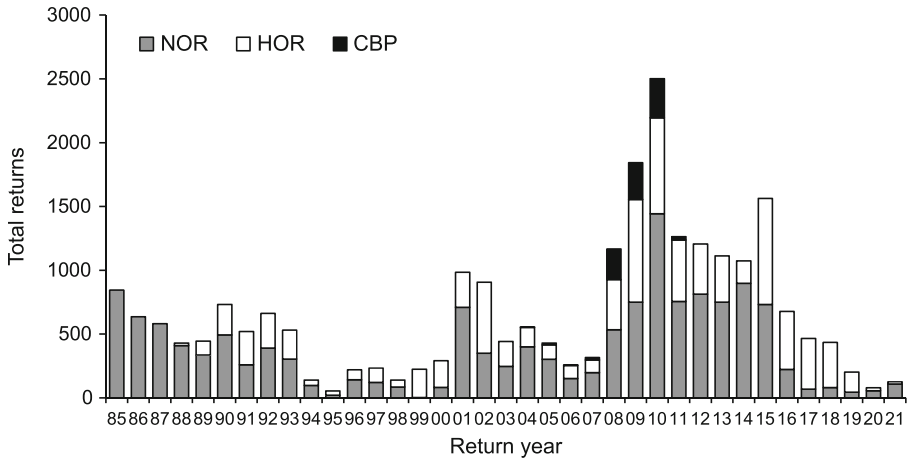

FIGURE 8. Total spring Chinook Salmon escapement back to the Tucannon River for captive broodstock progeny (CBP), hatchery supplementation (HOR) fish, and natural-origin (NOR) fish for the 1985–2021 return years.

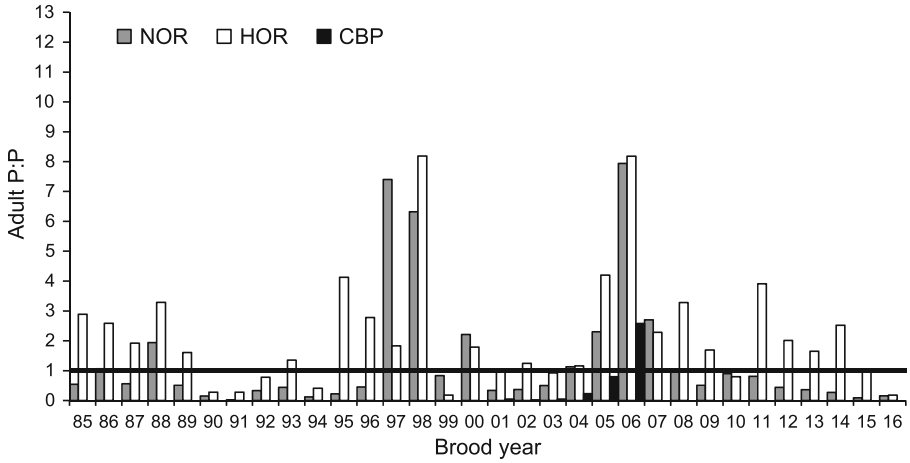

FIGURE 9. Adult (ages 4+) progeny-to-parent (P:P) ratio of Tucannon River spring Chinook captive broodstock progeny (CBP), hatchery supplementation (HOR) fish, and natural-origin (NOR) fish for the 1985–2016 brood years. The black line represents the replacement level.

et al. 2004; Fraser 2008). A study on steelhead populations supplemented with hatchery-produced fish from native genotypes detected no changes to estimates of effective population size, genetic variation, or temporal genetic structure within any population nor altered genetic structure (Gow et al. 2011). Genetic analysis of Tucannon River spring Chinook Salmon found that genetic diversity had not significantly changed from the presupplemented population as a result of the hatchery supplementation or captive brood programs (Kassler and Dean 2010). Similarly, genetic diversity from three captive broodstock and conventional supplementation programs in the Grande Ronde River basin in Oregon (Catherine Creek, Lostine River, and upper Grande Ronde River) did not change from the preprogram period (Eddy et al. 2018). Nonetheless, it should be noted that genetic change in the Tucannon population could have occurred at loci that were not examined, or conversely, it is possible that the lack of any change could be due to poor reproductive success of the hatchery fish. Another possible explanation is that epigenetic modification (Luyer et al. 2017) induced by hatchery rearing (in the absence of genetic differentiation) caused the differences in postrelease performance between the CBP and HOR fish in our study.

Brannon et al. (2004) believe that some of what has been referred to as "domestication" is not associated with genotype but rather acquired phenotypic changes that may disappear when in the wild or in subsequent generations of natural production. For example, Gallinat and Chang (2013) found that Tucannon River spring Chinook Salmon CBP, released as smolts and recaptured as returning age-4 adults, had size and fecundity distributions that were similar to Tucannon River HOR adults of the same size and age. They suggested that the original differences observed in fecundity, size, and low egg viability of the captive broodstock adult females compared with HOR females were environmentally induced rather than genetic. Likewise, in this paper, we did not observe significant differences in total and adult SARs between the two groups even though the proportion of minijacks and jacks used in spawning was much higher in the captive broodstock (F_1) than for the supplementation parents of the HOR group (34.1% versus 4.5%, respectively). This was likely due to having the same target size for smolts at release and shows that the CBP overcame possible genetic shift to younger age at maturation from their parents.

Our findings would suggest that at least some of the observed differences between the HOR and CBP groups can be explained by poor early gamete survival (egg to fry, egg to smolt) of the CBP rather than being caused by domestication effects. Many salmon hatcheries still lack the knowledge to rear captive broodstock that produce gametes that are equal to both supplementation programs and naturally produced fish. It has been indicated in earlier studies that decreased body size and egg quality could lead to lower survivorship of progeny (Beacham and Murray 1987). Despite their smaller size on average, age-4 Tucannon River spring Chinook Salmon captive broodstock females had significantly larger eggs than NOR and HOR age-4 females derived from the same population, even after accounting for fish length and fecundity (Gallinat and Chang 2013). Egg size has been shown to be strongly correlated with initial offspring fry size in salmonids, and offspring size is in turn correlated with survival in salmonids (Kinnison et al. 2001). However, large egg size of the Tucannon River spring Chinook Salmon captive broodstock was insufficient to compensate for other deficiencies and did not increase survival in our study population since mortality to eye-up was 49% for captive broodstock eggs compared with HOR and NOR eye-up

mortalities of 4% and 3%, respectively (Gallinat and Chang 2013).

While differences in SARs between the two groups were not statistically significant, the CBP group had consistently lower SARs. Similar to our results, Feldhaus et al. (2020) reported SARs (ages 3–5) that, on average, were higher for HOR fish than for CBP from their Catherine Creek, upper Grande Ronde River, and Lostine River spring Chinook Salmon captive broodstock programs in the Grande Ronde River basin. The fish in our study survived at a higher rate after increasing size at release, which would suggest that at least some environmental factors postrelease were limiting adult returns and survival. Likewise, Johnson et al. (2020) found that larger (average 46 g) Sockeye Salmon smolts had higher SARs than smaller (average 16 g) smolts (0.54% versus 0.23%, respectively). Full-term smolt production also produced the highest recruitment among other tested release strategies (e.g., eyed eggs and presmolts) for Redfish Lake Sockeye Salmon and has become the focus of recovery efforts involving juvenile releases (Johnson et al. 2020). They stated that the demographic benefit realized by rearing to smolt size outweighs the potential increase in domestication selection that might occur with longer time spent in captivity by the juveniles (Johnson et al. 2020).

Other captive broodstock programs have also failed to meet expectations. The Dungeness River Chinook Salmon captive broodstock program was not successful in rebuilding runs, which may have been due to the small size of fish at release (HSRG 2002). The White River captive broodstock program failed due to poor smolt quality and high postrelease mortality, which produced almost no adults, and the program was ended with the 2013 BY (Hillman et al. 2021).

Many salmonid populations in their native ranges are experiencing unprecedented population declines and/or low levels of natural recruitment (Fraser 2008). However, the long-term solutions to environmental degradation are often more difficult than the decision to establish a captive broodstock program (Snyder et al. 1996). While the use of captive populations may help focus public interest on the plight of an imperiled species, it may also provide false hope that a species is safe and allow the destruction of the habitat to continue (Snyder et al. 1996). The natural and human factors that caused the Tucannon River spring Chinook Salmon population to be listed in the first place (construction and operation of the Federal Columbia and Snake River hydropower system, habitat degradation within the Tucannon River basin, global climate change, and variable ocean conditions) have not been alleviated since the captive broodstock program was ended. While some improvements have been made to the operation of the hydrosystem to improve downstream migration success (CSS 2019) and habitat restoration efforts in the Tucannon River have been on-going over the last decade (Foltz and Buelow 2020), other limiting factors (e.g., global climate change, Pacific Decadal Oscillation) continue to drive the status of the Tucannon River spring Chinook Salmon population (Lawson 1993; Wells et al. 2006; Crozier et al. 2021).

To this day, the use of anadromous Pacific salmon in both supplementation and captive broodstock programs is unproven as a conservation measure in the recovery and restoration of listed populations. Venditti et al. (2018) examined supplemented and nonsupplemented populations of Chinook Salmon populations prior to, during, and after ending supplementation in two major drainages in Idaho. They found that supplementation increased abundance at some life stages; however, the effects did not persist after supplementation ended and had no influence on productivity (Venditti et al. 2018). We also did not see any persistence in abundance and productivity in the years after the captive broodstock program ended. Nevertheless, these types of hatchery programs are the only reason some imperiled populations have continued to persist instead of going extinct (Kline and Flagg 2014). In the Tucannon River, NOR fish for most years have been below replacement levels. As such, the Tucannon River spring Chinook Salmon HOR program has generally maintained overall abundance and may have prevented more serious population bottlenecks had the program not been in place (Gallinat et al. 2008).

Humans have yet to generate a captive bred or reared fish that, on average, will perform equally to wild fish once they are released into the wild (Fraser 2008). Our results were no different. Due to their very nature, the majority of captive broodstock programs have no specific endpoint and continue to operate while the factors that caused the population declines are being addressed. Because of their unintended consequences on phenotype, population structure, and behavior and ultimately on the viability of the population, it has been recommended that captive breeding should be used as a last resort to avoid extinction and not used as a long-term solution (Snyder et al. 1996; McClure et al. 2008).

In hindsight, the decision to start a captive broodstock program for the Tucannon River spring Chinook Salmon may have been premature. Snyder et al. (1996) stated that demonstrating that a species population is declining or has fallen below what may be a minimum viable size does not constitute enough analysis to justify captive breeding as a recovery measure. The time period of our study coincided with relatively good ocean conditions and high NOR survival rates, and because of those, the population was able to rebound from the persistent low returns in the mid to late 1990s.

Not all captive broodstock programs have seen poor results. The Redfish Lake Sockeye Salmon captive

broodstock program has achieved greater success than other salmonid captive broodstock programs and has, by all accounts, saved the stock from extinction (Kline and Flagg 2014). However, even for the Redfish Lake Sockeye Salmon program, which began in 1991, substantial increases in SAR rates must occur if complete recovery of that population is to occur (Hebdon et al. 2004). Our experience will hopefully serve as a cautionary lesson to others considering beginning a captive broodstock program. Captive broodstock programs by themselves are not a panacea and will not be enough to reestablish listed salmonids unless the factors that contributed to their decline are resolved or alleviated (Flagg et al. 1995; Fraser 2008).

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