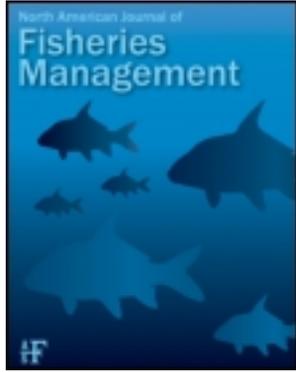


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ARTICLE

Reproductive Behavior and Success of Captive-Reared Chinook Salmon Spawning under Natural Conditions

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Abstract

In response to declining returns of Pacific salmon *Oncorhynchus* spp., captive-rearing programs have emerged as one approach to maintain natural-origin stocks while mechanisms responsible for their decline are addressed. However, it remains unclear if observed differences in reproductive behavior between captive-origin (captive) and natural-origin (natural) Chinook Salmon *O. tshawytscha* in laboratory experiments accurately predict reproductive success of captive salmon in the natural environment. Over a 4-year period, 859 natural Chinook Salmon juveniles were collected for full-term rearing in captivity. From these, we returned 247 maturing adults to their natal stream over 2 years, assessed trends in habitat use, monitored their courtship and spawning behaviors, and sampled their redds to determine if fertilized eggs were present. Habitat use followed a logical trend toward spawning areas as the season progressed. Captive fish were smaller and spawned later than did natural fish, but their size did not prevent females from constructing redds or prevent males from courting and fertilizing eggs. Captive fish were observed participating in 16 spawning events over two seasons. Captive and natural males displayed the same courtship behaviors, but natural males were more aggressive. Captive females selected redd sites similar to those of natural females and displayed digging behavior consistent with published observations. Eggs were collected from 22 of the 26 redds sampled, and survival to organogenesis was 68.3% in 2001 and 34.6% in 2002. The decline in 2002 was at least partially due to an apparent failure of females from brood year 1997 to produce viable eggs. We estimated captive fish contributed 19,000 eyed eggs to the population. If the 859 juveniles reared in captivity had been left in the stream, fewer than one adult would be expected to have returned. Growth, timing of spawning, and egg survival issues remain in captive fish, which illustrates a need to focus future research on improved culture techniques.

In response to declining returns of Pacific salmon *Oncorhynchus* spp. over much of their range during the past several decades, hatchery conservation programs have emerged as one approach to maintain local populations while the underlying mechanisms responsible for their decline are addressed (Flagg et al. 1995; Sayre 1995; Berejikian et al. 2004; Hebdon et al. 2004). These programs commonly take one of two general forms, and are generally referred to as captive broodstocking and captive rearing. These programs are typically initiated by

collecting naturally produced adults or juveniles from their natal environment and rearing them to sexual maturity in artificial culture conditions. At this point, the two techniques diverge. In a broodstock program, the adults are spawned in captivity and most of the resulting progeny are released at one or more life history stages (e.g., eyed egg, parr, or smolt) into their natal waters. A small number of progeny are typically retained in culture to continue the broodstock (see Flagg et al. 2004). Conversely, in a captive-rearing program, adults are returned to

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their natal waters and allowed to spawn with other captive-origin (captive) or natural-origin (natural) individuals (see Kuligowski et al. 2005). The subsequent brood group is again collected from the natural population, resulting in a hatchery program that is fully integrated with the natural population.

The captive-rearing concept has several theoretical and practical advantages over broodstocking. By including naturally produced juveniles in the program each year, natural selection is allowed to function as the parents compete for spawning access and mates (Berejikian et al. 2010, 2011) as well as during the period eggs or juveniles are in the stream environment. Hatchery selection is also reduced since artificial spawning is not needed (Hankin et al. 2009), although some selection undoubtedly occurs during rearing. Facility demands are also reduced in a captive-rearing program because it is not necessary to rear large numbers of juveniles to a specific life stage before release. For example, in this program we only needed to rear approximately 300 individuals per brood year to adulthood, when fish left the facilities between the ages 2 and 5.

Before captive-rearing programs can be considered more than experimental in nature, fundamental questions about the reproductive potential of these fish in the natural environment must be answered (Fleming and Gross 1992, 1993; Flagg and Mahnken 1995; Berejikian et al. 2001a, 2001b). Previous work comparing the spawning behavior of natural- and hatchery-origin Chinook Salmon *O. tshawytscha* and Coho Salmon *O. kisutch* in artificial channels (Berejikian et al. 1997, 2001a, 2001b) and in the natural environment (Chebanov and Riddell 1998) reported measurable differences between the two groups. In these studies, natural males usually dominated hatchery males when competing for mates, and when dominant, hatchery males generally displayed lower courtship frequencies prior to spawning than did natural males. Similar results have been reported for Atlantic Salmon *Salmo salar* (Fleming et al. 1996, 2000) of natural and production-hatchery-origin fish spawning together in artificial channels. However, it remains unclear how these differences may affect the ability of captive fish to reproduce in the natural environment.

Because captive Chinook Salmon have not previously been evaluated in the natural environment, it was also not known if these fish would make appropriate habitat selections prior to spawning. In addition, habitat use by maturing Chinook Salmon between the time of entry into spawning streams and the onset of spawning has not been described well in the literature. Pools, cut banks, and large woody debris (LWD) can provide protection from predators and probably help conserve depleted energy reserves for spawning, and we have observed natural-origin Chinook Salmon staging in these habitat types before spawning in other systems.

In this study, we released sexually maturing, captive Chinook Salmon into their natal stream and monitored their reproductive behavior and habitat use. Our objectives were to (1) determine how behavioral differences observed in captive Chinook Salmon in previous studies affected their ability to

reproduce in the natural environment, (2) estimate embryo survival to organogenesis (developmental stage characterized by the formation of internal organs and circulatory system) in eggs from captive females under natural conditions, and (3) describe habitat use by captive Chinook Salmon prior to spawning in a natural stream environment.

METHODS

This study took place in the West Fork Yankee Fork Salmon River (WFYF), located in central Idaho (Figure 1). Habitat conditions in the WFYF are nearly pristine, with little or no human development. Hatchery influence has also been minimal. Prior to this study, the stream had received three relatively small releases of Chinook Salmon parr in 1977 ($N = 57,000$), 1978 ($N = 51,000$), and 1994 ($N = 25,000$; Idaho Department of Fish and Game, unpublished data).

Fish contributing to this study were collected as juveniles from brood years 1996–1999. Our goal was to collect 300 juveniles from each brood year, but this goal was not met in 3 of the 4 years. Brood year 1996 juveniles ($N = 120$) were collected as parr (87%) and smolts (13%) using a rotary screw trap (E.G. Solutions, Corvallis, Oregon) located in the WFYF near the confluence with the Yankee Fork Salmon River. Those from brood years 1997 ($N = 210$) and 1998 ($N = 229$) were collected as parr by beach seining in the lower WFYF, and those from brood year 1999 were collected as eyed eggs by hydraulic extraction (McNeil 1964; Collins et al. 2000; Berejikian et al. 2011) from redds within the lower 4 km of the WFYF. However, due to the 3-year maturation window for Chinook Salmon, not all of the maturing individuals from any single brood year were available for this 2-year study.

After collection, the juveniles were reared at two hatchery facilities until approximately 1 month before spawning. Juveniles were reared in freshwater from the time of collection through smoltification at the Idaho Department of Fish and Game (IDFG) Eagle Fish Hatchery (Eagle), Eagle, Idaho. Venditti et al. (2003a) provide additional detail on fish rearing at Eagle. During the time natural-origin smolts were migrating to the Pacific Ocean, we transferred the majority of fish to the National Oceanic and Atmospheric Administration (NOAA) Fisheries, Manchester Marine Experimental Station (Manchester), Manchester, Washington, for rearing in saltwater to a point approximately 1 to 2 months prior to sexual maturity. Maynard et al. (2003) provide additional detail on fish rearing at Manchester. Approximately 20% of each cohort remained at Eagle for their entire life cycle to provide a measure of protection against possible catastrophic loss at Manchester. Near the beginning of the sexual maturation process, fish were transported to Eagle for a period of freshwater maturation before being returned to the WFYF to reproduce naturally.

Maturing individuals were identified into two maturation sorts approximately 6 weeks apart using one of two techniques. In 2001, maturing fish were identified at both facilities by visual

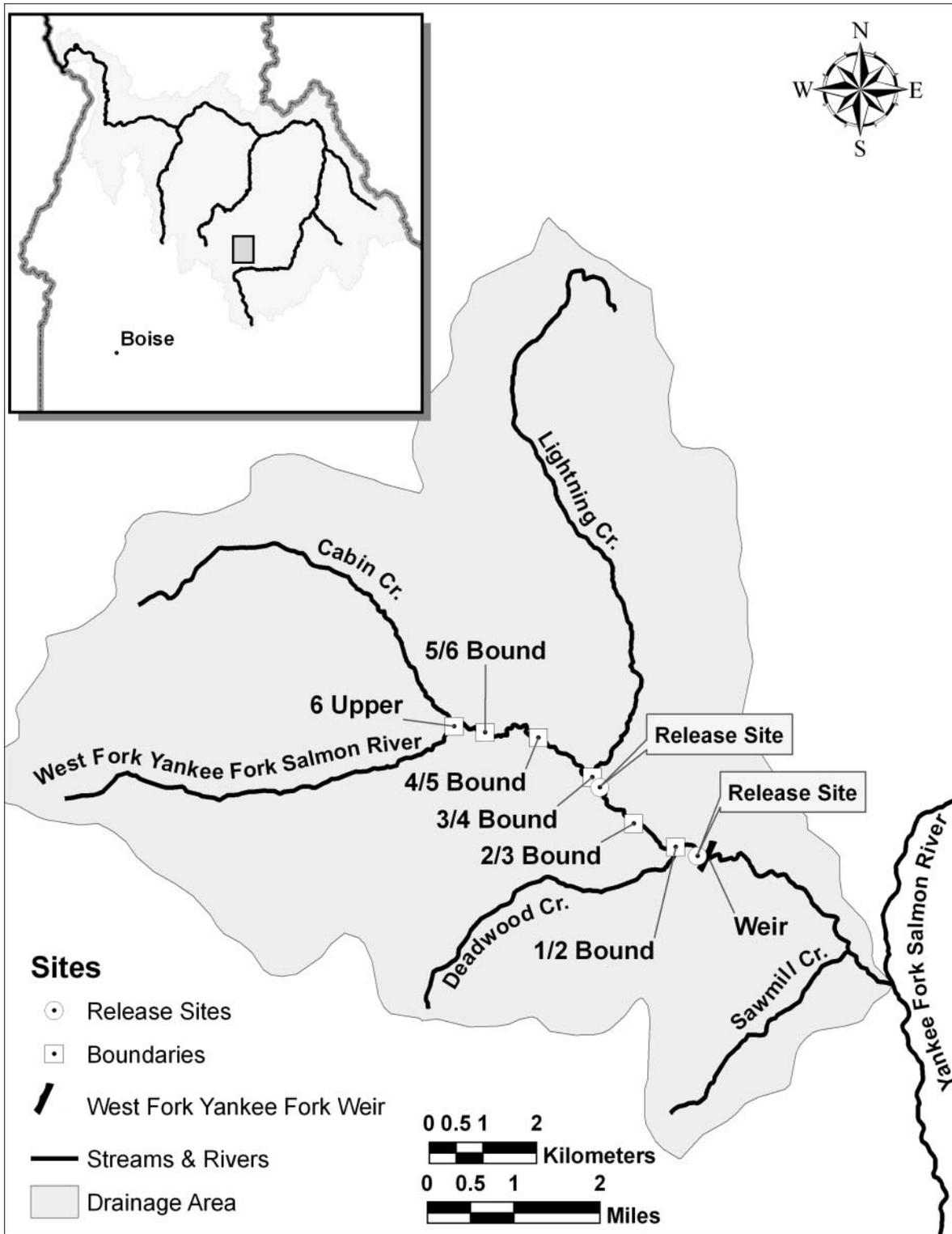


FIGURE 1. Location of the West Fork Yankee Fork Salmon River (WFYF) and major tributaries. Captive-reared Chinook Salmon were released at two locations in the WFYF in August 2001 and 2002, and allowed to distribute volitionally. The study section was divided into six reaches of approximately equal length (1.6 km) to facilitate systematic sampling upstream from a fish weir. The boundary between reaches is represented by Bound.

inspection and tactile manipulation of the gonads through the body wall. Maturing fish from Manchester were transferred to Eagle immediately after both maturation sorts. In 2002, maturing fish at Manchester were identified using portable ultrasound equipment (Aloka SSD-500V with an Aloka Electronic Linear Probe UST-556L-7.5) and transferred to Eagle. A second maturation sort was conducted at Manchester using visual inspection and tactile manipulation, and maturing fish were transported to Eagle in a second shipment. The degree of maturation of fish held at Eagle was determined by visual and tactile inspection. Fish not determined to be maturing remained in culture at both locations until their fifth year. Those not maturing at age 5 were culled.

We fitted all maturing adults with color-coded and numbered disk tags (2.54 cm diameter) before release for volitional spawning. Color codes identified fish to brood year and the color code and number combination allowed observers to identify individual fish. Prior to tagging, fish were anesthetized in a solution of MS-222 (tricaine methanesulfonate, buffered to neutrality with sodium bicarbonate), weighed to the nearest 1 g, measured to the nearest 1 mm FL, and scanned for a PIT tag, which identified its brood year. We attached disk tags to the fish by passing a stainless steel pin through a hole in the center of the tag and then through the dorsal musculature of the fish just ventral to the midline of the dorsal fin. A corresponding tag (with the same number and color code) was then slipped onto the pin on the opposite side of the fish. The pin was trimmed to length, and the second tag was secured in place by forming a loop at the end of the pin with needle-nose pliers.

The study section on the WFYF was approximately 9.7 km in length and contained high quality Chinook Salmon spawning habitat. To prevent emigration of captive fish we constructed a blocking weir at the downstream end of the section. The components of the weir were flown to the site via helicopter and assembled on site. Trap boxes built into the weir allowed technicians to pass natural fish that entered the traps in either direction or return captive fish that attempted to move downstream back into the study section. Shortly after the weir was assembled, captive fish were flown to one of two release areas (in two 60-L coolers), which contained abundant holding habitat and consisted of three to five closely spaced pools. The first release site was near the downstream end of the study section and the second was near the middle (Figure 1). We transported no more than six captive adults at a time, and total flight time (from loading to release) was approximately 10–15 min depending on release site. We did not construct a migration barrier at the upstream limit of the study reach because habitat conditions (abundant bedrock, large cobble, and stream size) above the confluence of the WFYF and Cabin Creek made spawning above this point unlikely.

Data collection began approximately 24 h after fish were released. The study section was divided into six reaches, each approximately 1.6 km in length, to permit systematic observations of Chinook Salmon activities upstream from the weir. Observers were assigned one to four stream reaches to survey

each day, which allowed the entire study section to be monitored every 1–2 d. Observers walked slowly upstream watching for Chinook Salmon and, when observed, recorded habitat association as well as fish behaviors. We did not quantify the relative availability of the different habitat types, but assumed this remained constant with the stable flows during the time period from late August through October each year, so trends in use reflect real shifts throughout the spawning season.

When an individual Chinook Salmon was located, the fish was observed for 5 min and we recorded its general behavior and associated habitat type (Table 1). This technique provided a standardized measurement of trends in fish behavior and habitat use over time. If multiple fish were observed simultaneously, behavior and habitat information were recorded separately for each individual.

We determined from previous work that the postrelease behavior of captive Chinook Salmon could be divided into three general time periods of roughly equal duration centered on peak spawning activity. We classified these as early, peak, and late spawning periods. The timing of peak spawning varied between years, so general behaviors exhibited by Chinook Salmon during the standardized 5-min observation periods were examined to determine when spawning-related activities represented the highest proportion of observations. This became the peak spawning period, and the early and late periods were then assigned. We then plotted observed behaviors and habitat associations during these three periods to examine how behaviors and habitat associations changed throughout the study.

When we observed courtship behaviors during the standardized observation period, additional observation protocols were initiated. If a new redd was present, we flagged it and recorded the disk tag code of the female. During this second set of observations, we made detailed records of fish behavior (Table 1) in 10-min intervals to predict the time until spawning and to determine how the frequency of courtship behaviors changed during the time leading up to and immediately after spawning. If, based on these frequencies, the observer judged spawning would occur within 1–2 h they remained with that spawning group (typically one female along with one or more competing males) and continued to record all courtship behaviors in 10-min blocks until 30 min after spawning.

From these records, we compared the frequency of courtship behaviors (behavior events/10-min interval) by natural and captive males. Male courtship behaviors of interest included quivers, crossovers, and aggression. In a quiver, the male darts toward the female at a 30–45° angle and just before contact performs a high frequency, low amplitude undulation of the body (Tautz and Groot 1975). A crossover involves the movement of the male from one side of the female to the other with the male's head passing over the female's caudal peduncle (Hartman 1969; Tautz and Groot 1975). Aggression was an attempt by one male to chase another male away from the vicinity of the redd. Courtship and aggression frequencies were computed for both male types during each 10-min observation period. Average values for each

TABLE 1. Habitat and behavior variables recorded during observations of captive-reared Chinook Salmon released into the West Fork Yankee Fork Salmon River for volitional spawning, August–October, 2001–2002.

Variable	Definition
Habitat types	
Vegetation	Aquatic macrophytes or overhanging terrestrial vegetation
Cut bank	Stream extends under the terrestrial surface
Pool	Area of low gradient, increased water depth, and low velocity
Large woody debris (LWD)	Woody material > 1 m in length and > 10 cm in diameter
Riffle–run	Shallow, swiftly flowing, stream section
Pool tail-out	Gradient break at the downstream extent of a pool
General behaviors (both sexes)	
Staging	Remaining in one position, not associated with a redd
Milling	Movement not resulting in longitudinal displacement
Moving (A)	Movement in an upstream direction
Moving (B)	Movement in a downstream direction
Aggression	Aggression between Chinook Salmon of undetermined sex
Holding	Maintaining position on or near a redd
Courting	Active male and receptive female
Spawn	Observed release of eggs and milt
Male courtship	
Quiver	Dart toward female ending with body vibrations
Crossover	Movement to opposite side, head passing over peduncle
Aggression (A)	Male on male aggression
Aggression (B)	Male on female aggression
Aggression (C)	Male on other species aggression
Following	Female present, no redd present
Satellite	Holding away or downstream from a courting pair
Female courtship	
Aggression (A)	Female on female aggression
Aggression (B)	Female on male aggression
Aggression (C)	Female on other species aggression
Test dig	2–6 body flexures, not concentrated
Nest dig	5–8 body flexures in a concentrated area
Cover dig	8–12 body flexures along redd perimeter
Nesting	Redd grooming, trenching, or defense

observation period, relative to the time of spawning (designated as time zero), were computed for natural and captive males and plotted to determine how similar (or dissimilar) overall behavior patterns and frequencies were between the two groups. Bounds

on the errors were computed for each observation period (pre- and postspawning) to construct approximate 90% confidence intervals (CIs) around the point estimates using the formula $CI = X \pm 1.6(\text{SD}/\sqrt{n})$, where X is the mean number of behaviors observed during that 10-min interval pre- or postspawning, SD is the standard deviation for the behavior in that interval, and n is the number of spawning events with males of that origin (Neter et al. 1988). Bounds for all observation periods overlapped for both years, so behavioral data from both years were pooled.

We also performed a similar analysis to assess the digging behavior (see Tautz and Groot 1975) of captive females spawning with natural and captive males. We assumed all digs before egg deposition were nest digs and those after deposition were cover digs. Dig frequencies (number of digs/10 min) and CIs were computed for each 10-min observation period as described above. Average values and approximate 90% CIs for each observation period relative to spawning were computed and plotted for captive females being courted by natural and captive males. The mean estimates of dig frequency were also compared with values from the published literature.

After spawning, we hydraulically sampled eggs from a portion of redds produced by captive females to verify egg deposition, estimate embryo survival to organogenesis, and estimate potential contribution of eyed eggs to the population. We used thermographs located within the study section to estimate the number of Celsius temperature units (CTU; sum of mean daily temperatures in °C) developing embryos received. We collected eggs after they had received a minimum of 200 CTU to ensure the embryo had reached organogenesis (Velsen 1980; Piper et al. 1989) and generally before the embryos reached the eyed stage. Opaque eggs or those having fungal growth were considered dead. Clear eggs were classified as viable and fixed in Stockard's solution (Velsen 1980), which causes embryos in early organogenesis to become visible. Eggs in this category were further determined to be fertilized or unfertilized depending on the presence or absence of an embryo in the fixed egg. The number of eggs in each category was enumerated and the percentage in each computed. Finally, we estimated the potential number of eyed eggs (E_N) produced by captive females as:

$$E_N = N_R \times V \times 0.5F$$

where N_R is the number of redds spawned by captive females, V is the mean proportion of fertilized eggs in the redds, and F is the mean fecundity of captive females (Venditti et al. 2003a, 2003b). Fecundity estimates were adjusted for observed egg retention by captive Chinook Salmon in a spawning channel (Berejikian et al. 2001b).

In 2002, we recorded the number of live and dead eggs in redds spawned by natural females, while collecting the next program cohort. We provide these data as a baseline to compare egg survival from captive females. Redds selected for this purpose were located in similar habitat in the WFYF below the study section. We timed our sampling with the

TABLE 2. Number and average FL (mm) of captive-reared Chinook Salmon by brood year (BY) released into the West Fork Yankee Fork Salmon River in August 2001–2002.

Release year	BY	FL (mm)		<i>N</i>
		Average (SD)	Range	
2001	1996	422.3 (76.3)	350–502	4
	1997	542.0 (66.2)	328–630	42
	1998	538.4 (79.0)	335–655	43
	All	536.5 (76.1)	328–655	89
2002	1997	532.9 (48.6)	453–620	25
	1998	557.8 (54.2)	443–665	54
	1999	361.7 (20.1)	297–400	77
	All	462.3 (102.9)	297–665	158 ^a

^aTwo fish released in 2002 had lost their PIT tags, making it impossible to determine the brood year to which they belonged.

temperature data described above, except we sampled these redds at approximately 300 CTU to ensure the embryos had reached the eyed stage of development.

RESULTS

Maturing, captive Chinook Salmon released into the WFYF to spawn voluntarily were substantially smaller than natural adults returning to the WFYF and other nearby locations. Fish released on August 17, 2001 ($N = 89$) were from brood years 1996–1998 and averaged 536.5 mm FL (Table 2). Captive Chinook Salmon released on August 8, 2002 ($N = 158$) averaged 462.3 mm FL and consisted of fish from brood years 1997–1999 (Table 2). Natural-origin carcasses collected from throughout the WFYF during 2001–2002 ($N = 16$) averaged 784 mm FL (SD = 111; range, 680–1,040 mm; IDFG, unpublished data), and natural-origin adults returning to the nearby Sawtooth Fish Hatchery ($N = 1,539$) during the same years averaged 808 mm FL (SD = 115; range, 430–1,090 mm; see Snider et al. 2003, 2004).

General behaviors observed in captive Chinook Salmon during standardized observation periods were similar during both years of the study and followed a consistent pattern as sexual maturation progressed. Captive fish distributed themselves throughout the study section with relatively few fish (0 in 2001 and approximately 10% in 2002) entering the downstream trap box. (One natural male entered the upstream trap box in 2002 and was passed into the study section). We made a total of 1,467, 2,050, and 665 observations of behavior in the early, middle, and late spawning periods, respectively. The dominant behavior during the early spawning periods was staging (Figure 2). During the peak spawning period, staging and courting became the dominant behaviors as fish competed for mates and prepared and defended redds. Courting and holding on or below redds became the dominant activities during the late spawning period (Figure 2).

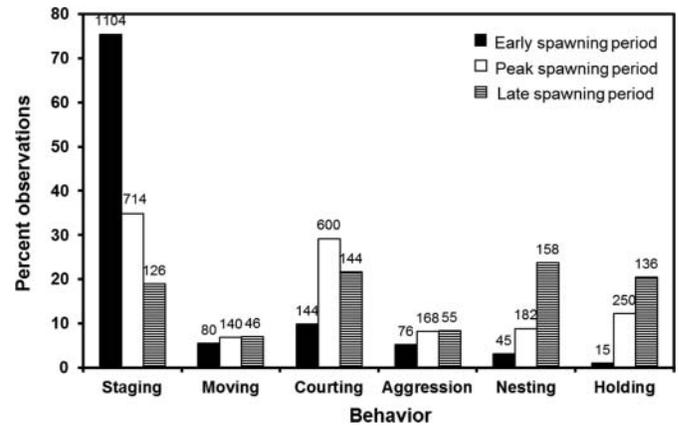


FIGURE 2. Behaviors of captive-reared Chinook Salmon released to spawn voluntarily in the West Fork Yankee Fork Salmon River in the summers of 2001 and 2002. In 2001 the early period extended from August 19 to August 30, the peak period was August 31–September 11, and the late period extended from September 12 to September 23. In 2002, the early period extended from August 9 to August 23, the peak period was August 24–September 8, and the late period extended from September 9 to September 23. Values above the bars represent the number of observations.

Habitat use observed in captive Chinook Salmon also reflected the increasing trend toward spawning-related activities. We made a total of 1,478, 1,760, and 665 observations of habitat associations during the early, middle, and late spawning periods, respectively. During the early spawning period, pools, LWD, and cut banks were all heavily used habitat types (Figure 3). Riffles and runs were also frequently used at this time, but this may be because fish are more visible in these habitats than they are in pools or when they are associated with LWD. Pool tail-outs and riffles and runs became the most-used habitat types during the peak spawning period (Figure 3). These two habitat types (tail-outs and riffle–run) became even more heavily used during the late spawning period. Captive Chinook Salmon were rarely

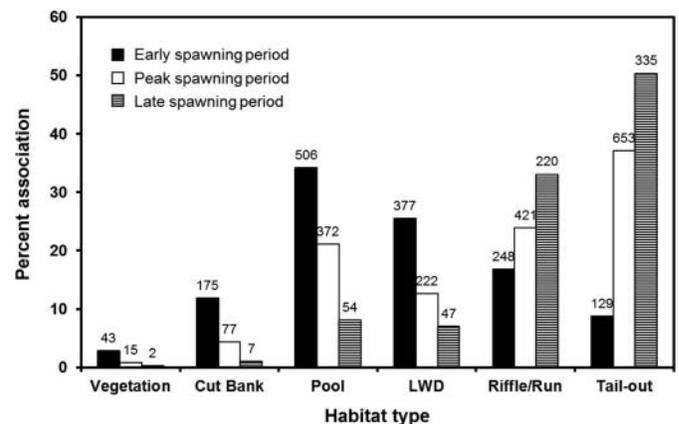


FIGURE 3. Habitat use of captive-reared Chinook Salmon released to spawn voluntarily in the West Fork Yankee Fork Salmon River in the summers of 2001 and 2002. Early, peak, and late periods are the same as described in Figure 2. LWD = large woody debris. Values above the bars represent the number of observations.

observed associated with aquatic vegetation, although this habitat type was rare in the WFYF.

We documented 16 separate spawning events during the 2 years of study (eight each in 2001 and 2002) in which captive Chinook Salmon participated. In 2001, three of the observed spawning events involved captive females and natural males, and both fish were captive in the remaining five. In 2002, one mating involved a captive female and a natural male, and both sexes were of captive origin in the remaining seven matings. Subdominant or precocial males, or both, of natural origin were typically present, but their participation was not assessed. We observed no natural females spawning in the study reach in either year, although a small number of natural-origin redds ($N \leq 3$ each year) were present prior to releasing captive fish.

Captive males displayed the same courtship behaviors as natural males, and their courtship frequencies did not differ from natural males during the time leading up to spawning. The frequency of quivers ($N = 473$ observed) and crossovers ($N = 568$ observed) by natural males generally increased as spawning approached with a pronounced spike in quivers immediately before spawning (Figure 4A, B). Courtship frequencies by captive males remained constant or declined slightly during the period leading up to spawning ($N = 1,465$ quivers and $N = 987$ crossovers observed), but these fish exhibited the spike in quivers immediately before spawning (Figure 4A, B). Despite the different trajectories of the point estimates, all 90% CIs overlapped except at 60 min before spawning when captive males quivered at a higher rate than natural males (Figure 4A).

The largest difference between the two types of males was that captive males were significantly less aggressive than natural males before spawning. Natural males typically displayed between 10 and 15 aggressive acts within each 10-min observation period ($N = 520$ observed), while captive males only averaged around five aggressive acts ($N = 462$ observed). The 90% CIs did not overlap during any time period prior to spawning (Figure 4C).

Captive females dug and covered redds at similar rates between years and their behavior was not affected by male origin. We observed captive females making a total of 962 combined nest and cover digs during the 2 years of study. Captive females made approximately two to four nest digs during each 10-min observation period up until time of egg deposition (Figure 5). After spawning, females proceeded to cover dig almost continuously for about 10 min and maintained elevated digging frequencies for at least 30 min (Figure 5).

We collected eggs from a portion of the redds in which captive females spawned each year to estimate egg survival to organogenesis. No redd superimposition occurred in either year, so females spawning on top of previously constructed redds was not a factor in egg survival. On October 15–16, 2001, we attempted to hydraulically collect eggs from 8 of 18 redds constructed by captive females and found eggs in five of the eight redds sampled. The percentage of viable eggs in these redds ranged from 0 to 89% and averaged 54.7%. All clear eggs were fertilized.

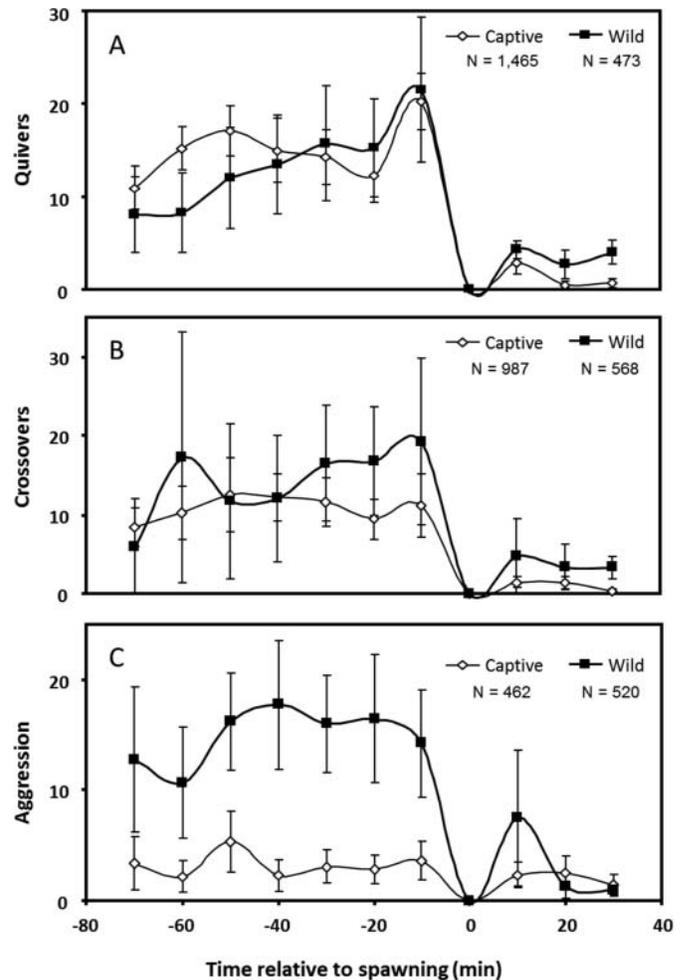


FIGURE 4. Frequency (behavior events/10-min interval) of courtship and aggression (mean \pm approximate 90%CI) observed in male captive-reared and natural-origin Chinook Salmon during observed spawning events ($N = 16$) in the West Fork Yankee Fork Salmon River in 2001 and 2002. Time zero is spawning and negative and positive numbers are minutes before and after spawning, respectively. Values in the legend represent the number of observations for that male type.

One redd contained only dead eggs but appeared to have been constructed in high quality habitat and was well developed. Sampling revealed that this redd was constructed on a thin (approximately 7 cm) layer of gravel–cobble armoring over a large, decayed log. Omitting this redd from the analysis increased the average egg viability to 68.3%. Based on these data (68.3% viability) and an estimated fecundity of 1,221 eggs/female (Venditti et al. 2003a, 2003b), potential production by captive females in 2001 was estimated at approximately 7,500 eyed eggs. On October 8–9, 2002, we sampled 18 of the 33 redds constructed by captive females. We found eggs in 17 of the 18 redds sampled, and nine contained viable eggs. None of the redds sampled ($N = 5$) that were known to have been used for spawning by brood year 1997 females contained live eggs. The percentage of live eggs in redds sampled in 2002 ranged from 0 to 100%, and

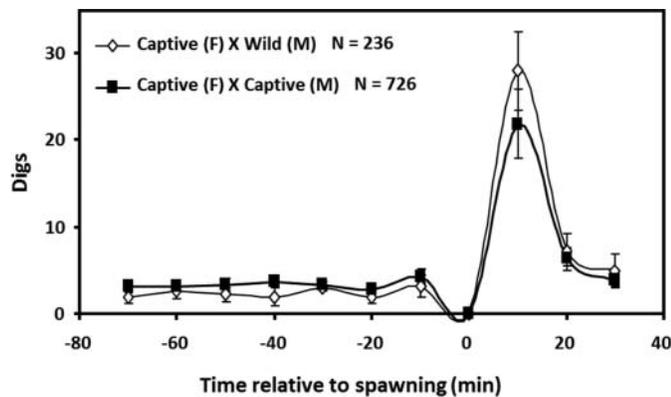


FIGURE 5. Frequency (digs/10-min interval) of digging (mean \pm approximate 90%CI) by captive-reared female (F) Chinook Salmon during observed spawning events ($N = 16$) with captive-reared ($N = 12$) and natural-origin ($N = 4$) males (M) in the West Fork Yankee Fork Salmon River in 2001 and 2002. Time zero is spawning and negative and positive numbers are minutes before and after spawning, respectively. Values in the legend represent the number of digs observed.

averaged 34.6% overall and 65.3% for those redds that contained live eggs. Based on these data (34.6% viable) and an estimated fecundity of 2,011 eggs/female, production by captive females in 2002 was estimated to be approximately 11,500 eyed eggs.

DISCUSSION

Captive fish were substantially smaller and spawned several weeks later than natural Chinook Salmon returning to the WFYF and other nearby populations. For example, natural adults passing the Sawtooth Hatchery weir (approximately 40 km upstream from the mouth of the WFYF on the Salmon River) ranged from 430 to 1,090 mm FL in 1991 (Snider et al. 2003) and from 450 to 1,090 mm in 1992 (Snider et al. 2004). However, small size did not prevent captive females from constructing redds in what appeared to be appropriate locations (e.g., pool tail-outs with clean gravel) or prevent captive males from courting, spawning, and successfully fertilizing eggs. Also, captive females spawned later than their natural counterparts, such that natural males were only available to spawn with the earliest-spawning captive females in both years, which may result in lower survival in their progeny if later spawn timing results in later emergence and smaller size going into their first winter. These two conditions appear to be common in Chinook Salmon captive rearing programs (Joyce et al. 1993; Schiewe et al. 1997; Berejikian et al. 2003).

We obtained brood stocks annually from the naturally spawning population in the WFYF, so changes in size and spawn timing in these fish were probably due to the culture environment. Steelhead *O. mykiss* and Sockeye Salmon *O. nerka* reared in captivity frequently attain body sizes that equal or exceed that of their natural cohorts (Pollard and Flagg 2004), and gonadotropin-releasing hormone implants have been used to advance spawning in captive Chinook Salmon (Berejikian

et al. 2003; Swanson et al. 2008). These remain areas where further research is needed to improve culture practices for Chinook Salmon.

The behavior and habitat use of captive Chinook Salmon after release in this study changed over time in a manner that reflected their changing requirements as the spawning season progressed. Initially, study fish were generally observed holding position or moving, often in association with pools and LWD, which is consistent with behavior documented in prespawning Atlantic Salmon (Bardonnet and Baglinière 2000). Selecting habitats with generally low water velocity and complex structures may be of benefit by helping conserve energy reserves for spawning activities (Torgersen et al. 1999) or by providing refuge from predators. As the season progressed, spawning-related behaviors became dominant and fish moved onto pool tail-outs, although pools and LWD remained important as resting and staging areas. This is consistent with the observations documented in Atlantic Salmon by Bardonnet and Baglinière (2000) and natural Chinook Salmon (D. A. Venditti, personal observation).

Several lessons can be learned from our detailed spawning observations and from the behavior patterns that emerged. In males, the pattern of courtship and frequency of aggression differed between captive fish and those of natural origin, but captive males displayed the full suite of expected behaviors. Given the competitive advantage larger size provides male salmon (Fleming and Gross 1993; Berejikian et al. 1997), our results are neither surprising nor unexpected. In an evaluation of the ability of captive Chinook Salmon to spawn and fertilize eggs in a natural stream environment, it is not necessary (or perhaps even desirable if the technique is implemented for augmentation or recovery) for captive males to outcompete males of natural origin. Captive males courted appropriately and sufficiently to induce oviposition in females and they fertilized eggs under natural conditions. The frequency of prespawn digging by captive females was similar to the average of one dig every 2.5 min (4 digs/10 min) reported for natural Chinook Salmon (Schroder et al. 2008), who also reported elevated cover digging for approximately 30 min postspawning. This indicates that captive females retained the innate drive to pair, construct redds, spawn, and provide final redd grooming. It is unlikely our tagging methods affected the performance of captive Chinook Salmon, as other studies have used disk tags to evaluate adult salmonids and have not noted any effects of the tags on either survival or behavior (Quinn and Foote 1994; Foote et al. 1997; Cowen et al. 2007; Doctor et al. 2010).

Our egg collections revealed challenges that program managers will need to address to maximize the utility of the captive-rearing technique for Chinook Salmon. A number of redds sampled contained low numbers of eggs or eggs that were not viable. Based on our observations of progressing redd development (e.g., upstream expansion as new egg pockets were added), it is likely that some of the redds where no eggs were collected actually contained eggs that we simply did not locate with our

hydraulic equipment (Berejikian et al. 2011). The fact that a number of redds contained a large number of dead eggs, compared with their natural counterparts, suggests some breakdown occurred in the physical or physiological processes required for successful spawning in the wild. Identifying and correcting the causative factor responsible for the low egg survival should remain a priority for future research. However, despite the low survival observed, captive Chinook Salmon were responsible for constructing successful redds and producing approximately 19,000 eyed eggs in the WFYF over the 2 years of the study.

We cannot be certain how many of the eggs collected were fertilized by captive males, but evidence suggests at least a portion were. Female Chinook Salmon deposit eggs in several nest pockets within a redd and can have multiple partners, so the origin of the male was not known for the eggs we collected, even in redds where captive males were observed spawning. However, captive males were observed participating in three-quarters of the spawning events we observed (12 of 16), and we believe this accurately reflects their overall contribution to spawning during this study and should be reflected in our egg collections. Additionally, experimental activities at Eagle using WFYF captive males from the brood years released demonstrated their milt was of high quality and viable. Average milt motility was found to be about 98.4% for these fish (Venditti et al. 2002), and in factorial crosses (where individual males were artificially spawned with sublots of eggs from multiple females) egg survival varied widely and was dependent primarily on maternal influence (Venditti et al. 2003b). Therefore, it seems reasonable to assume that male gamete quality was not a limiting factor.

To collect additional juveniles for this program, we removed a total of 272 eggs from six redds from natural females in 2001, and 321 eggs from five redds used for spawning by natural-origin females in 2002. Dead eggs were not enumerated in 2001, but their frequency was similar to results obtained the following year (D. A. Venditti, personal observation). In 2002, 308 of the 321 eggs were live indicating natural egg survival to the eyed stage was approximately 96% in the WFYF (IDFG, unpublished data). The high survival of eggs in redds of natural females in the WFYF suggests the lower survival in redds spawned in by captive females, in the same years, was an effect of origin and not due to habitat conditions.

Numerous studies have shown that salmonids in a hatchery program can quickly respond to artificial selection, thereby reducing their fitness when released back into the natural environment (see reviews in Berejikian and Ford 2004; Araki et al. 2008). The general interpretation of these results has been that fitness lost is fitness that can never be regained. However, natural selection can also be strong, and captive-reared individuals sourced from the local population should be capable of responding. In a reanalysis of Hood River steelhead data from Araki et al. (2007a, 2007b, 2009), Kitada et al. (2011) suggests the effect of captive rearing could be eliminated in the first generation after reintroducing hatchery fish. For highly imperiled populations, paying a fitness penalty from short-term hatchery intervention

may be more desirable than a high risk of local extirpation (Fraser 2008; Neff et al. 2011). A key unanswered question regarding hatchery conservation programs thus remains untested: How quickly can fish from a conservation hatchery program move back toward their natural fitness optimum?

We have demonstrated that captive Chinook Salmon reared to near maturity in a hatchery are capable of successfully spawning in the natural environment and can contribute to natural production in depressed populations. Females constructed redds and deposited eggs. Natural males actively competed for and spawned with captive females, and in their absence captive males demonstrated the full suite of reproductive behaviors and appeared to successfully fertilize eggs. Growth and spawn timing differ between captive and natural fish, and egg survival to organogenesis is lower in captive than in natural fish. However, captive rearing has the potential to ensure a continuum of year-to-year reproductive success, in the habitat, for populations of spring–summer run Chinook salmon at risk. For example, the 859 juveniles brought into the program (brood year 1996–1999 collections above) produced 247 adults that contributed about 19,000 eyed eggs to the population during the 2 years of study. Actual eyed-egg production from captive fish was probably even higher, since a portion of fish from each brood year matured outside of the study period. If left in the stream, based on estimated life-stage-specific survival estimates for Salmon River tributaries (25.2% egg–parr and 19.4% parr–smolt, Kiefer and Lockhart 1997), average survival of smolts from the WFYF to Lower Granite Dam (43.8%, Venditti et al. 2007), and the average Sawtooth Hatchery smolt-to-adult survival for brood years 1996–1999 (0.8%, IDFG, unpublished data), fewer than one adult would be expected to have returned from those 859 individuals. Even if one assumes an optimistic return of one adult (and that adult is female), only about 4,500 eggs could have been produced. Future research should focus on developing culture methods that enable managers to develop full-term, hatchery-reared Chinook Salmon adults that more closely approximate the natural template with respect to size at release and timing of spawning.

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