The productivity and viability of Snake River Sockeye Salmon hatchery adults released into Redfish Lake, Idaho

Suggested Running Head: Re-introduction of Sockeye Salmon into Redfish Lake, ID.

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<A>Abstract

In 1991, the Snake River Sockeye Salmon Captive Broodstock Program was initiated to prevent extinction and preserve genetic diversity of this evolutionarily significant unit protected by the Endangered Species Act. At the time of listing, the Redfish Lake population was considered functionally extinct. One of the recovery strategies entails the release of adults for volitional spawning in Redfish Lake for re-building of the natural population. In this paper, we describe the productivity metrics from this strategy. We evaluated eight spawn years to address three primary questions: 1. “What egg-to-smolt, smolts per female, and smolt-to-adult (SAR) metrics result from recent adult releases? 2. How do these metrics compare to estimates for Redfish Lake historically and estimates for other sockeye populations throughout the range?” and 3. “Does the current combination of smolts per female and SARS result in population replacement?” Replacement was determined as two adult recruits per female assuming an even sex ratio. We found that the reintroduced adults, despite being derived from a multi-generational captive broodstock, were able to successfully spawn and produce offspring that migrated to the ocean and returned as adults. Smolt abundance, size, and age data suggest that the population is functioning below density dependence. However, increased smolt production did not translate into greater adult returns and this is likely due to out-of-basin factors. Productivity metrics were similar to those of the wild population in Redfish Lake during the 1950-60s. However, both current and historic productivity estimates were near the low end of the range for other sockeye populations and have not resulted in population replacement. Until freshwater and out-of-basin survival can be improved, our data suggest that adult releases will continue to be an important recovery strategy to prevent cohort collapse and to re-build naturally spawning populations.

<A> Introduction

Captive broodstock programs have been established in both Europe and North America as a safety net to conserve genetic diversity and reduce the extinction probability of highly imperiled fish species and/or populations (Carr et al. 2004; Cooper et al. 2009; Withler et al. 2011; Saltzgiver et al. 2012; Osborne et al. 2013; Withler et al. 2014). Captive broodstock programs are distinct from other hatchery programs in that fish remain in a hatchery environment throughout their entire life-cycle (Flagg and Mahnken 1995; Miller and Kapuscinski 2003; Berejikian et al. 2004; Hebdon et al. 2004) and are genetically managed to avoid inbreeding depression and unintended selection (Kozfkay et al. 2008; Sturm et al. 2009; Kalinowski et al. 2012; Conrad et al. 2013; Fisch et. al. 2012; O'Reilly and Kozfkay 2014; Fisch et al. 2015). The primary goal of a captive broodstock is to retain the extant population (and its genetic diversity) in protective culture until the causes that threaten persistence can be alleviated; but adults or juveniles are released in the wild if numbers are available beyond what is needed for the replacement broodstock. While captive broodstocks are less common relative to other types of hatchery programs, they may become more widespread with increasing environmental and climatic threats to population persistence and can be an important means of rebuilding declining or extirpated populations (Flagg and Mahnaken 1995; Waters et al. 2015).

For Snake River Sockeye Salmon *Oncorhynchus nerka*, a captive broodstock program was initiated prior to its listing as endangered under the U.S. Endangered Species Act (NMFS 1991). At the time of listing, only one remnant population remained in Redfish Lake located at the headwaters of the Salmon River drainage in the Sawtooth Valley basin, Idaho (Figure 1). This population exists at the extreme of the worldwide distribution as the most southerly, farthest inland and highest elevation spawning population and was on the brink of extinction, with one adult returning in 1989 and zero adults returning in 1990 (Waples et al. 1991). The captive broodstock program was created over an eight-year period and captured multiple age-classes, life-stages, and life-histories in the collection of the founding broodstock including all of the wild, anadromous adults that returned from 1991-1998, smolts that emigrated from Redfish Lake from 1991-1993, and residual adults collected in Redfish Lake from 1992-1995 (Kalinowski et al. 2012; Kline and Flagg 2014). The creation of the captive broodstock prevented the imminent extinction of the population.

Sockeye Salmon display life-history diversity in age structure and residency that allowed it to persist at critically low levels prior to hatchery intervention. Many different age combinations of freshwater and saltwater residency are represented within a cohort. Anadromous sockeye salmon typically spend one or two years in the lake before they undergo smoltification and migrate to the ocean and then spend an additional one to four years in the ocean before returning to freshwater to spawn (Burgner 1991). Redfish Lake is also unique in that it is one of only two lakes in the Pacific Northwest where three life histories of native *O. nerka* reside: anadromous, residual, and kokanee (Nichols et al. 2016). Residual Sockeye Salmon are a resident *O. nerka* ecotype, considered part of the listed population (Waples et al. 1997), that are capable of reproducing with the anadromous ecotype and producing both residual and anadromous offspring (Bjornn et al. 1968; Burgner 1991; Rieman et al. 1994; Godbout et al. 2011). While Bjornn suspected the presence of residuals in the 1950's and 1960's, residuals were not physically documented in Redfish Lake until 1992. Managers began to actively search for the smaller, resident adults during spawning after otolith microchemistry results indicated that many of the smolts leaving Redfish Lake in 1991 had a resident, female parent (Rieman et al. 1994, Waples et al. 1997). It has been hypothesized that residual Sockeye in Redfish Lake prevented extirpation of the population while Sunbeam Dam was in operation from 1910-1934

(Waples et al. 1997). Both the anadromous and residual ecotypes spawn on beach shoals and spawn in late October and November, whereas kokanee spawn in a tributary of the lake from August through September. The resident population of kokanee is genetically divergent from the residual and anadromous ecotypes due to these differences in spawn-timing and location and not considered part of the listed population (Cummings et al. 1997, Waples et al. 2011).

At the outset of the captive broodstock program, there was uncertainty regarding Sockeye Salmon survival in captivity and their productivity and contribution to recovery once they were released in the natural environment (Flagg et al. 2004). Given the range of possible outcomes, the release of captive-reared adults has been widely debated among fishery professionals (Fraser 2008; Araki and Schmid 2010). In some cases, hatchery adults have been unsuccessful at spawning after release (Carr et al. 2004; Griffiths et al. 2011) or have been able to successfully spawn but have had negative impacts on reproductive fitness of natural populations (Araki et al. 2007; Araki et al. 2008; Christie et al. 2014). In other cases, salmon reintroductions have produced demographic increases (Berejikian et al. 2009; Hess et al. 2012; Withler et al. 2014). The variability in outcomes can be complex and multi-faceted depending on species, available habitat, geographic location, phenotypic and behavioral traits, and approach.

The focus of this study was to assess the productivity of adult Snake River Sockeye Salmon released into Redfish Lake, Idaho. An earlier evaluation in the program measured the effectiveness of adult releases and response in freshwater productivity, however, the contribution of released adults could not be independently quantified due to the inability to differentiate natural production from eyed-eggs that were placed into lake incubation boxes (Hebdon et al. 2004). We selected eight spawn years (2004–2011) in which captive-reared and anadromous adults were released to spawn volitionally. These years were chosen for analysis because eyedegg releases were not implemented in Redfish Lake during this time-frame. Captive-reared adults have been reared exclusively in the hatchery from egg to sexual maturity. Anadromous fish are the offspring of predominantly captive-reared parents that had been released to the wild as adults to volitionally spawn or hatchery-reared juveniles that were released into the wild as smolts and have successfully undergone seaward migration, and returned to their natal spawning grounds as adults. Anadromous adults were trapped and those not spawned for the captive broodstock were released into Redfish Lake for natural spawning. Anadromous adults were released with captive-reared adults as part of the recovery strategy to increase naturally-spawning Sockeye Salmon abundance and re-establish a self-sustaining population in Redfish Lake (NMFS 2015).

Our objective was to evaluate the contribution from adult releases by answering three primary questions: 1. “What freshwater productivity (smolts per female and egg-to-smolt survival) and post-juvenile productivity (smolt-to-adult [SARs]) rates result from adult releases? 2. How do these productivity metrics compare to historic data from the 1950’s and 1960’s and to other sockeye populations throughout the range?” and 3. “Does the current combination of smolts per female and SARs result in population replacement?” Replacement was determined as two adult recruits per female assuming an even sex ratio. Information presented here will provide baseline data to monitor population status changes through time as recolonization efforts continue using this recovery strategy in Redfish Lake and other natal lakes in the Sawtooth Valley basin. Evaluation of this release strategy is critical to our understanding of how hatchery fish can contribute to rebuilding natural spawning populations to meet recovery objectives.

<A> STUDY SITE

Adult Sockeye Salmon were released in Redfish Lake, located in the Sawtooth Valley basin of central Idaho (Figure 1). Redfish Lake is located 1,996 m above sea level and is 1,448 km from the Pacific Ocean. Redfish Lake is the largest historic Sockeye Salmon rearing lake within the Sawtooth Valley basin with a surface area of 615 ha. Lakes in the Sawtooth Valley basin are glacial-carved and considered ultra-oligotrophic, but high in oxygen (Budy et al. 1998). Redfish Lake has a relatively pristine watershed, with virtually no development because it lies within a National Recreation Area (NMFS 2015).

<A>METHODS

We report the number of adults released into Redfish Lake for volitional spawning and the resulting productivity metrics (egg-to-smolt, smolts per female, SAR return rates) from this release strategy. Estimates of age and abundance for the different juvenile life-stages (deposited eggs in the gravel, smolts, returning adults) were required to calculate these productivity estimates for each spawn year. Spawn year (SY) is defined as the calendar year in which adults were released to volitionally spawn and the year in which their offspring were born. Below, we describe the specific methods and calculations used to estimate potential egg deposition (PED) from the released females, the number and age composition of smolts, and the number and age composition of returning anadromous adults that resulted from natural spawning in Redfish Lake.

<B> Adult Releases.----

Captive-reared (2004 – 2007) and a mixture of captive-reared and anadromous adults (2008 – 2011) were released during September to spawn volitionally in Redfish Lake. Captive-reared fish were cultured in freshwater at the National Marine Fisheries Service Burley Creek hatchery near Port Orchard, Washington (NMFS-FW) as well as at the Idaho Department of Fish and Game (IDFG) Eagle Fish Hatchery (IDFG-FW). Captive-reared fish were also cultured from smolt to adult in seawater at the National Marine Fisheries Service Manchester Marine Culture facility (NMFS-FW/SW). Captive broodstocks were maintained at separate facilities to avoid catastrophic loss. Rearing methodologies are reported in Baker et al. (2009) for freshwater and Frost et al. (2008a,b) for freshwater and saltwater rearing. Prior to release, the maturation status and sex of captive-reared adults was determined using the ultrasound techniques described in Frost et al. (2014) and fork-length was recorded. Beginning with SY 2005, tissue samples were also taken from adults prior to release for genetic parentage analysis.

<B> Estimating potential egg deposition.----

We developed regression equations using length-fecundity relationships for each rearing group spawned in the hatchery to develop PED estimates for fish spawning in Redfish Lake in the same year. We chose to evaluate these relationships by rearing group (freshwater [IDFG-FW, NMFS-FW], saltwater [NMFS-FW/SW), anadromous), given the different rearing conditions and hatchery practices that resulted in different proportions of females released from each group annually and different sizes of the females, as well as different sets of years for each group. Data used to estimate potential egg deposition were from SY 2010-2015 for the NMFS-FW/SW females, 2004-2012 for the NMFS-FW females, 2004-2015 for the IDFG-FW females, and 2008-2015 for the anadromous females. Models were used to estimate the effects of fish size (fork length) and SY relative to fecundity to determine whether years could be pooled within each rearing group. Only length was used in the model with NMFS-FW/SW females, given the fact that the years when these fish were released were different from the years when these fish were spawned in the hatchery. Linear regression analysis with fork length as a continuous covariate, year as a factor, and their interaction was included in the modeling framework. Akaike's Information Criterion (AICc) adjusted for sample size was used to compare relative model support for the data (Burnham and Anderson 2002). The AICc values were compared, and the model with Delta AICc equal to 0.0 was determined to be best supported by the data.

After the best supported models were chosen, we assumed that all released females were successful at spawning and developed PED estimates based upon the fork length of the released females. Total annual egg deposition for Redfish Lake for SYs 2004 to 2011, with associated standard error (SE), was estimated using the following equations:

$$Total\ Egg\ Deposition = \sum_{i=1}^{n} C_{\mathrm{I}} + C_{\mathrm{Y}} + C_{\mathrm{L}} \times \mathrm{L}_{i} + C_{\mathrm{YxL}} \times \mathrm{L}_{i}$$

where n was the number of released adults within which fecundity was predicted, C_{I} was the regression coefficient for the intercept, C_{Y} was for year, C_{L} was for length, $C_{\mathrm{Y \times L}}$ was for their interaction, and L_{i} was the fork length for fish i and Y×L was their interaction.

$$\frac{Var(Total\ Egg\ Deposition)}{\mathrm{n}^2} = Var_{\mathrm{I}} + Var_{\mathrm{Y}} + \mathrm{L_{avg}}^2 \times Var_{\mathrm{L}} + \mathrm{L_{avg}}^2 \times Var_{\mathrm{YxL}} + 2\left[Cov_{\mathrm{I,Y}} \times \mathrm{L_{avg}} \times Cov_{\mathrm{I,L}} + \mathrm{L_{avg}} \times Cov_{\mathrm{I,YxL}}\right] + 2 \times \mathrm{L_{avg}} \times \left[Cov_{\mathrm{Y,L}} + Cov_{\mathrm{Y,YxL}}\right] + 2 \times \mathrm{L_{avg}}^2 \times Cov_{\mathrm{L,YxL}} + Var_{\mathrm{Model\ Error}}$$

where Var was the model-estimated variance for the subscripts defined above and for the unexplained or residual variance, Model Error. Cov was the model-estimated covariance between each value in the subscript pair, and $\mathrm{L_{avg}}$ was the average length of n adults. We used the square root of Var (Total Egg Deposition) as the Standard Error (SE) of total egg deposition. Statistical analysis was completed using the program R (R Core Team 2017).

<B> Smolt trapping and estimating smolt production, smolts per female, and egg-to-smolt survival.-----

A fish trap located near the outlet of Redfish Lake was operated in each study year during the entire juvenile migration season from the first week of April through mid-June (Figure 1).

All captured Sockeye smolts were enumerated, anesthetized in buffered tricaine methanesulfonate (MS-222), measured to fork length (nearest 1.0 mm), and weighed (nearest 0.1 g). The first 30-50 natural smolts captured per day were PIT tagged (Prentice et al. 1990) and released approximately 250 m upstream of the trap one-half hour after sunset. Trap efficiency was estimated daily by the proportion of PIT tagged fish recaptured in the trap. Annually, the trapping operations were grouped into one to four intervals based on stream discharge and consistent trapping probabilities to account for heterogeneous trapping efficiency across the season (Steinhorst et al. 2004). The total number of natural-origin juvenile smolts was derived using a modified Bailey adjusted Lincoln-Peterson estimator with 95% bootstrap confidence intervals (software GSRUN 7.0; Steinhorst et al. 2004).

During trapping, scales were removed from a subsample of 5 natural-origin fish from each 5-mm length group. Scales were separated and laid between microscope slides and aged using the methods of Jearld (1983). Length-at-age values derived from length frequencies were determined using the Rmix computer program. Rmix was developed by Du (2002) as an add-on program to the R computing environment (R Core Team 2017) that utilized the original MIX program developed by MacDonald and Green (1988). Rmix uses a maximum likelihood estimation method to estimate the parameters of a mixture distribution with overlapping components, such as the overlapping length distributions associated with smolt estimates of different ages. Rmix proportions were multiplied by the total estimate of natural migrants to determine the number of age-1 and age-2 smolts represented during each juvenile migration year. Standard errors for the abundance of each age class and length of each age class were also produced by Rmix.

Total smolt production $(\hat{N})$ for each SY was calculated as:

$$\hat{N} = \hat{S}_{y1}\hat{p}_{y1} + \hat{S}_{y2}\hat{p}_{y2}$$

where S_{y1} and S_{y2} are smolt numbers in years y1 and y2, and p_{y1} and p_{y2} are the proportions of the SY in those years. Mean smolt production was also calculated for the evaluation period. Given that smolt numbers and SY proportions were estimated independently, then the estimated variance of the smolt total was:

$$\hat{V}(\hat{N}) \approx {\hat{S}_{y1}}^2\hat{V}(\hat{p}_{y1}) + {\hat{p}_{y1}}^2\hat{V}(\hat{S}_{y1}) + \hat{V}(\hat{S}_{y1})\hat{V}(\hat{p}_{y1})$$

$$+{\hat{S}_{y2}}^2\hat{V}(\hat{p}_{y2}) + {\hat{p}_{y2}}^2\hat{V}(\hat{S}_{y2}) + \hat{V}(\hat{S}_{y2})\hat{V}(\hat{p}_{y2})$$

The number of smolts per female was estimated by dividing the number of females released by the number of smolts produced from the corresponding SY. Egg-to-smolt survival was calculated by dividing total smolt production by the potential egg deposition estimate for each SY. Regression analyses were conducted to determine the relationship between the number of released females and reproductive output as measured by the log-transformed number of smolts and total number of deposited eggs. These results were compared to historic freshwater productivity in Redfish Lake (Bjornn et al. 1968).

<B> Adult Trapping, Estimating smolt-to-adult return rates (SARs), Population Replacement----

Anadromous adults were trapped annually across the entire adult migration period from mid-July through mid-October at either the Redfish Lake Creek weir or at a weir located on the upper Salmon River at the IDFG Sawtooth Fish Hatchery (Figure 1). Returning, natural-origin anadromous adults (e.g. offspring of adult releases into Redfish Lake) were identified as having an intact adipose fin. Data collected for natural-origin anadromous fish included fork length (nearest 0.5 cm), sex, scales, and fin clips for genetic analysis.

In 2008 and 2009, adipose-intact adults returning to the Redfish Lake Creek trap were assumed to be the progeny of natural production from Redfish Lake and scales were used to assign ages because genetic samples were not taken from adults released in 2004. Four to five scales from each fish were collected from the left side above the lateral line and slightly posterior to the dorsal fin (as identified in Devries and Frie 1996). Program personnel viewed and aged scales using methods identified in Schrader et al. (2011).

Parentage analyses (PBT) was used to assign adult offspring back to their respective SY starting in 2010 since genetic samples were collected from adults released in 2005-forward. Whole DNA was extracted using a Nexttec DNA isolation kit according to the manufacturer instructions. Samples were genotyped with a panel of 13 to 16 microsatellite loci, and a minimum of 9 loci per individual were needed for inclusion in the analyses (see the authors for genotyping protocols). The software *Cervus* v. 3.0 (Kalinowski et al. 2007) was used to perform the parentage analyses using parents with known sex. Up to one mismatch was allowed, and only two parentage assignments were accepted. Once the parents were identified, the age and origin of each returning fish could be determined.

Age could not be assessed for every returning adult with the above methods. In some cases, scales were not collected or the scale was unreadable. Missing tissue samples, mutations, genotyping errors and/or incomplete genotypes can lead to the inability to assign parentage to every fish. Age/length keys (Isermann and Knight 2005) using known ages of fish as determined by scales/genetics and corresponding fish lengths were used to annually assign ages to adults that could not be aged by either of the above methods. The software FishR Vignette (Program R) was used to assign ages using the semi-random method (Ogle 2013, 2016).

SARs (from Redfish Lake to Redfish Lake) were estimated by adding the age-3, age-4, and age-5 anadromous returns from each SY and dividing by the estimated total smolt production for that SY ($\widehat{N}$). We estimated the variance of the SARs as:

$$\hat{V}(\widehat{SAR}) \approx \frac{\widehat{SAR}(1-\widehat{SAR})}{\hat{N}} + \frac{\sum_i \hat{V}(\hat{h}_i)}{\hat{N}^2} + \frac{\widehat{SAR}^2}{\hat{N}^2}\hat{V}(\hat{N})$$

and the 95% confidence interval as:

$$\left(\widehat{SAR} - 1.96\sqrt{\hat{V}(\widehat{SAR})}, \widehat{SAR} + 1.96\sqrt{\hat{V}(\widehat{SAR})}\right)$$

where $\hat{h}_i$ was the estimated adult count from ages I = 3-5 and $\hat{V}(\hat{h}_i)$ was the estimated variance, and $\hat{V}(\hat{N})$ from above was the estimated variance around total smolt production $\hat{N}$. SARs were compared to historic estimates produced by Bjornn et al. (1968). The number of returning adults was also regressed against the number of released females for each SY.

Population replacement was defined as a minimum of two natural-origin adult recruits per released female and assumed an evenly split sex ratio. For this estimation, no density dependent effects or harvest was assumed. Replacement rates were calculated using the following equation:

*Smolts per Female * SARs ≥ 2*

<A> RESULTS

<Adult releases>.---------

The number of released adults by rearing type is presented in Table 1. From 2004-2006, only adults from NMFS were available to release into Redfish Lake. Starting in 2007, releases also included adults from IDFG and in 2008, anadromous adults returned from this release strategy and other hatchery release strategies (Hebdon et al. 2004; Kline and Flagg 2014) and were released into Redfish Lake. The total number of adults released ranged from 176 in 2005 to 1,621 in 2010 (Table 1). Within these releases, the number of total females ranged from 50 in 2005 to 688 in 2010 (Table 1). While attempts were made to equalize sex-ratios between males and females upon release, this was not always possible.

<B> *Potential egg deposition.------*

Based upon AIC criteria, the model that included the year and length interaction was the best fit for IDFG-FW and NMFS-FW females (Table 2). For anadromous fish, the year and length additive model was determined to be the best fit (Table 2). For the NMFS FW/SW fish, the length-only model was used. This resulted in separate linear regression equations for each rearing group and SY.

Estimated potential egg deposition within Redfish Lake ranged from 91,748 eggs in 2005 (SE 10,800) when 50 females were released to a maximum of 1,697,192 eggs in 2010 when 688 females were released (SE 196,445; Table 3). Across study years, annual mean egg deposition was 788,879. Anadromous females were longer and more fecund than captive-reared females, averaging 2,679 eggs compared to 1,641 eggs per female in 2008-2011.

<B> *Smolt production, egg-to-smolt survival, smolts per female.*

The total number of smolts resulting from natural production ranged from 4,822 (SE 654) in SY 2007 to 27,765 (SE 1,638) in SY 2010 (Table 3, Figure 2). There was a significant, positive relationship between the number of females released in Redfish Lake and smolt production (r^2 =0.73, P=0.004, Figure 3). Mean annual smolt production in Redfish Lake was estimated to be 11,593. Across all years, the majority (63% - 98%) of smolts migrated from Redfish Lake at age-1 (Table 4). Average length of age-1 fish ranged 96-117 mm, while that of age-2 fish ranged 125-146 mm (Table 4). There was a significant positive relationship between the number of deposited eggs and the log-transformed number of smolts (r^2 = 0.86, P <0.001, Figure 2).

Egg-to-smolt survival ranged from 1.0% (SY 2009) to 6.6% (SY 2005; Table 3). Mean egg-to-smolt survival for the study period was estimated to be 2.1%. The number of smolts per female averaged 41.3 and ranged from 19.0-121.8 (Table 3). SY 2005 had the fewest number of females released, but produced the highest number of smolts per female (Figure 3).

<B> *Smolt-to-adult return rates (SAR) and replacement rates.-----*

From 2008 to 2016, 1,183 natural-origin adults returned to Redfish Lake and 916 were offspring from SYs 2004–2011. In 2007, only three natural-origin adults returned and none of these were age-3 adults from SY 2004. Of the 1,183 returning adults, age-length keys were used to age 8% of the fish. The majority of natural-origin adults returned at age-4 (75%) and 22% returned at age-5. Natural-origin adults recruiting from each SY ranged from 28 (SY 2011) to 374 (SY 2010; Table 3).

SARs across study years averaged 1.12% and ranged from 0.2% in 2011 to 3.2% in 2006 (Figure 4). The SAR for natural-origin adults from SY 2006 had the highest SAR values for any other SY, with 2005 having the second highest estimate (Figure 4). We observed no significant relationship between the number of females released and number of adult recruits returning from a given SY ($r^2 = 0.14$, $P = 0.35$).

The relationship between the number of smolts per female and SAR is logarithmic (Figure 5). At the current mean estimate of 41 smolts per female, a corresponding SARs > 4.9% would be needed to reach population replacement. Conversely, with an estimated SAR of 3.0% (SY 2006), 66 smolts per female would be required to reach replacement. At the average observed SAR of 1.12%, 179 smolts per female are needed to reach replacement. While we have observed SARs (3.19%) and smolts per female (120) that would have exceeded population replacement if in accordance during these study years, high freshwater productivity and smolt to adult survival rates have not occurred during the same SY.

<A> Discussion

This study reported productivity metrics for adult releases into Redfish Lake for the first time since the late 1960's (Bjornn et al. 1968). Our results indicate that hatchery adults released for re-introduction efforts has successfully begun to build a natural spawning population of Sockeye Salmon in Redfish Lake. We present the productivity metrics from this release strategy in order to evaluate the status of the Redfish Lake population relative to what existed in the latter half of the nineteenth century and to provide a reference point for the next several decades. This information is not only useful for tracking progress towards the establishment of a self-sustaining natural spawning population but identifies key life-history events where survival may be limiting replacement.

Our contemporary estimates of freshwater productivity indicate that the current conditions in Redfish Lake do not appear to be limiting juvenile production. observed a strong, positive response in smolt production with increasing numbers of released females and deposited eggs. Estimates of smolt size and age at migration also suggest that juvenile Sockeye Salmon are acquiring adequate dietary resources in Redfish Lake. Bjornn et al. (1968) observed a positive relationship between the age that Sockeye juveniles migrated from Redfish Lake and their growth during the first summer in the lake. When the mean length of a year class approached 100 mm, over 90% of smolts migrated as yearlings (Bjornn et al. 1968). During this evaluation, smolts were of similar size-at-age as those reported in the 1960's (Bjornn et al. 1968). We did not observe decreasing average smolt size or an increase in the proportion of age-2 smolts as the total number of females or smolts increased, which might be expected if density dependence was occurring (Kyle et al. 1988). We believe that smolt abundance has the capability of increasing even further with the release of more females into Redfish Lake; particularly anadromous females that are larger in size and capable of depositing more eggs.

Increased smolt abundances, however, did not translate into more returning natural-origin adults as a result of highly variable and low SARs.

extreme temperatures in the migratory corridor led to significant losses of adult Snake River Sockeye in migration year 2015 (NMFS 2016). These losses would have impacted the SARs for SY 2010 and SY 2011. Other studies have shown that ocean productivity, as measured by the Pacific Decadal Oscillation (PDO), plays a major role in salmon and steelhead survival and can drive adult return rates for many populations (Mantua et al. 1997; Peterman and Dorner 2011; Petrosky and Schaller 2010; Anderson et al. 2014; Williams et al. 2014). Snake River SARs were found to be highly correlated with SARs from the nearest extant populations of Sockeye Salmon in the Columbia River and there was a significant relationship between PDO and adult returns, indicating that a common variable within the marine portion of their life-cycle was affecting post-juvenile productivity (NOAA 2009). (2015) suggested that much of the life-cycle mortality experienced by Snake River Sockeye Salmon occurred in the marine environment and was due to low ocean productivity and shifts in preferred zooplankton food species. Nevertheless, it is critically important to maximize the numbers of juvenile migrants as a safeguard against variable marine and migratory conditions to ensure that some natural-origin adults return.

The adults that have been used to re-establish natural production have been exposed to multiple generations within captivity but do not appear to exhibit reduced productivity when compared to historic estimates from wild adults (Bjornn et al 1968). We found that contemporary egg-to-smolt survival estimates fell within the range of those historically reported for Redfish Lake (Range 0.58% -143%; Bjornn et al. 1968). Contemporary estimates of post-juvenile productivity, as measured through SARs, even exceeded the historic range for SY2006 (Range 0.14% - 1.83%; Bjornn et al. 1968). It difficult to compare current estimates with those observed during the 1960s due to downriver harvest rates potentially as high as 60% (Bjornn et al. 1968) and fewer Snake River dams at that time.

Both the historic and current productivity estimates for Sockeye Salmon in Redfish Lake were near the lower end of the range of other Sockeye Salmon populations. Bradford (1995) reported that average egg-to-smolt survival ranged from 3.2% to 6.2% for seven populations of Sockeye Salmon. Chapman et al. (1995) reported that egg-to-smolt survival for Lake Wenatchee Sockeye ranged from 1.7 to 12.3% and egg-to-smolt survival for Okanogan sockeye ranged from 2.4 to 38%. Hyatt et al. (2005) reported wild sockeye salmon egg-to-smolt survival for Tatsamenie and Tahltan lakes in British Columbia as 5.8 and 3.6 percent, respectively. SAR's were also lower when compared to northern populations in British Columbia and Alaska (Range 1.34% to 3.4%, Bradford 1995; Chilko Lake BC, 2-5%; DFO 2017) and upper Columbia River populations (Range 0.67% - 9.43%, NOAA 2009; Range 0.2% to 23.5% Williams et al. 2014). Productivity levels were more similar to levels observed in other critically low populations such as the Cultus Lake (avg 76 smolts per spawner; smolt-to-adult survival for 2003-2005 = 1%; Bradford et al. 2010; Ackerman et al 2014) and Sakinaw Lake populations (egg-to-smolt survival ranged 0.1% - 6%, SAR ranged 0% to 0.8%;Withler et al. 2014; COSEWIC 2016).

These comparisons suggest that the Redfish Lake population, when examined in the 1950s and 1960s, may have already experienced declines in productivity. There are intrinsic differences in food availability, predation, and limnological characteristics in each rearing lake (Finkle and Harding 2015) and differences related to migratory conditions and distance to the ocean, impoundments, ocean rearing location, age structure, and harvest. The Redfish Lake population had already experienced a population bottleneck prior to Bjornn's evaluation during the 24 years when Sunbeam Dam was in place. It was hypothesized that the prior loss of the anadromous return to Redfish Lake reduced nutrient loading and contributed to low production (Wurtsbaugh et al. 1997). It is also possible that the Redfish Lake population always had lower productivity relative to other Sockeye populations due to its location at the periphery of the range in North America in a high-elevation, oligotrophic lake.

Smolt production from residual females in Redfish Lake likely introduced some degree of bias in both the current and historic rates of freshwater productivity. Bjornn et al. (1968) originally hypothesized that residual production could be an influence when egg-to-smolt survival rates were as high as 21% and 143%, which is biologically impossible for the latter estimate. The estimate for SY 2005 (6.6%) appears to be an outlier among current estimates and indicates that residual production may have been a factor. Although the residual population is difficult to enumerate, night-time snorkel surveys continue to document the presence of these fish during spawning. Residuals are much smaller in size (i.e., similar to resident kokanee) and their egg size and fecundity is low compared to captive-reared or anadromous females (Burgner 1991). The overall smolt production from residual spawning events is uncertain. However, we suspect that the contribution may be greater when there is less competition or uneven sex ratios; as the years with presumably greater residual contribution were the years when less than 50 anadromous or captive-reared females were released to spawn.

The SARs can also be biased if there are errors in aging or if there was adult straying between trapping locations. Ageing errors generally decrease strong cohorts and inflate weak cohorts that either precede or follow the strong cohort (Campana et al. 2001). These errors can have more of an impact on the SAR values for the weaker cohorts and inflate mean SAR values (Copeland et al. 2007). Parentage analysis provides an accurate estimate of age structure and origin and removes this bias (Seamons et al. 2009). However, scale aging was used for two of the return years, which may have led to some small degree of bias in the productivity metrics for SY 2004 and SY 2005. For these same years, we also assumed that any natural-origin fish trapped at Redfish Lake Creek was the offspring of adult releases into Redfish Lake and not the product of another lake or release strategy (e.g. egg boxes in other lakes). Genetic parentage assignments from the eight most recent years of anadromous returns indicated an average stray rate of 1.0% between trapping locations. If this rate was consistent during the years we evaluated, it likely had little effect on SARs and would not significantly change the interpretation of our results.

In order for the Redfish Lake population to grow and become self-sustaining, survival will need to increase at multiple life-stages. This is the case in spite of productivity metrics that fell within historical ranges. The current survival rates are low compared to other Sockeye Salmon populations and without an increase in freshwater survival, SARs would need to exceed 4.9% for population replacement. Redfish Lake resides in a national recreational area and there has been little human development although boating activities and natural events could increase siltation and reduce groundwater upwelling or substrate permeability during incubation (B. Griswold, Biolines Consulting, personal communication). Natural production potential in Redfish Lake may have also been subsumed by the resident, kokanee population and reductions of the kokanee population might facilitate the re-establishment of Sockeye Salmon (Gross et al. 1998). Freshwater and post-juvenile productivity are inter-related as increased freshwater growth rates can lead to increased SARs (Koenings and Burkett 1987; Henderson and Cass 1991;

Koenings et al. 1993). Conversely, increased numbers of anadromous adult spawners can increase freshwater productivity (Gross et al. 1998; Cederholm et al. 1999). For Cultus Lake, the number of smolts per spawner decreased by 50% when the number of adult spawners was below 7,000 adults (Cultus Sockeye Recovery Team 2005). Gross et al. (1998) indicated that increasing SARs and the numbers of anadromous, spawning adults in Redfish Lake would provide greater benefit than lake fertilization. Until survival can be improved, releasing captive-reared adults into the lake to volitionally spawn will prevent cohort collapse during years of unfavorable ocean productivity, when fewer anadromous adults return (Kline and Flagg 2014). Additionally, both captive-reared and anadromous adult releases will continue to help build a natural spawning population within Redfish Lake during periods of favorable marine growth and survival (Kline and Flagg 2014).

Population growth rates and survival may increase as more anadromous adults return to the program and are released to spawn in Redfish Lake. Not only can anadromous spawners provide marine-derived nutrient loading that can boost survival and growth of juvenile sockeye salmon, but they may also be more successful spawners. We assumed that all females spawned successfully, deposited eggs into spawning gravel of equivalent quality, and had equivalent rates of egg viability and survival. Sockeye salmon display high variance in reproductive success (Mehranvar et al.2004) and there could be differences in reproductive success by rearing type, especially between captive-reared and anadromous fish. The anadromous adults are larger and have more body coloration and these traits may be advantageous during spawning (Fleming and Gross 1994; Steen and Quinn 1999; Foote et al. 2004; Garcia de Leaniz et al. 2007). Berejekian and Ford (2004) suggested that the duration of rearing in captivity can have an impact on domestication selection and reproductive success. Other studies have indicated differential reproductive success between hatchery and natural conspecifics (Fleming and Gross 1993; Fleming and Petersson 2001; Williamson et al. 2010; Anderson et al. 2012; Ford et al. 2012; Kozfkay et al. 2017) and have related this difference to age at maturation, fish size and competition, spawn-timing, redd construction and location, or egg viability (Williamson et al. 2010; Anderson et al. 2012; Ford et al. 2012, Stark et al. 2018). Juvenile fitness-related traits such as size and emergence timing have also been linked to maternal phenotype (Braun et al. 2013).

Adaptive evolution might be necessary before population increases are observed (Anderson et al. 2014). Much of the available literature suggests that domestication selection can occur during hatchery rearing (Araki et al. 2007; Araki et al. 2008; Christie et al. 2012), but Fraser (2008) hypothesized that captive-reared fish could re-adapt to the wild within a timeframe similar to that during which domestication selection occurred in the hatchery. Evans et al. (2014) provided empirical support that increased survival of offspring can occur after one generation of exposing parents to the natural environment and suggested that traits were being selected that were adapted to natural conditions. For Snake River Sockeye Salmon, there is an opportunity for adaptive evolution to occur as the population becomes more wild-exposed and adult releases shift from predominantly captive-reared adults to hatchery, anadromous adults that are reared in the hatchery until the smolt-stage, to natural-origin anadromous adults that are born in Redfish Lake (IDFG 2010; NMFS 2015). Therefore, it is possible that domestication selection can be reversed by limiting the time in captivity and with increased wild-exposure.

As natural Sockeye Salmon populations continue to be rebuilt, continued monitoring of these productivity metrics will be important for understanding the production potential of Redfish Lake and other natal lakes. This information not only provides a baseline to track the status of the population through time but acts as a baseline to assess the outcomes for future restoration and recovery actions. Additional research is needed regarding the factors that affect survival in freshwater and marine environments. Evaluations of the reproductive performance of fish released into Redfish Lake and the other natal lakes will also be important for assessing the relative contributions by rearing type and life-time fitness. Our results suggest that the captive broodstock program can be used to re-establish Snake River Sockeye Salmon throughout their natal range and supports the supposition that survival and fitness may increase as the population becomes more wild-exposed through anadromy. Ultimately the performance of the population will depend on a combination of environmental, genetic, and ecological factors.

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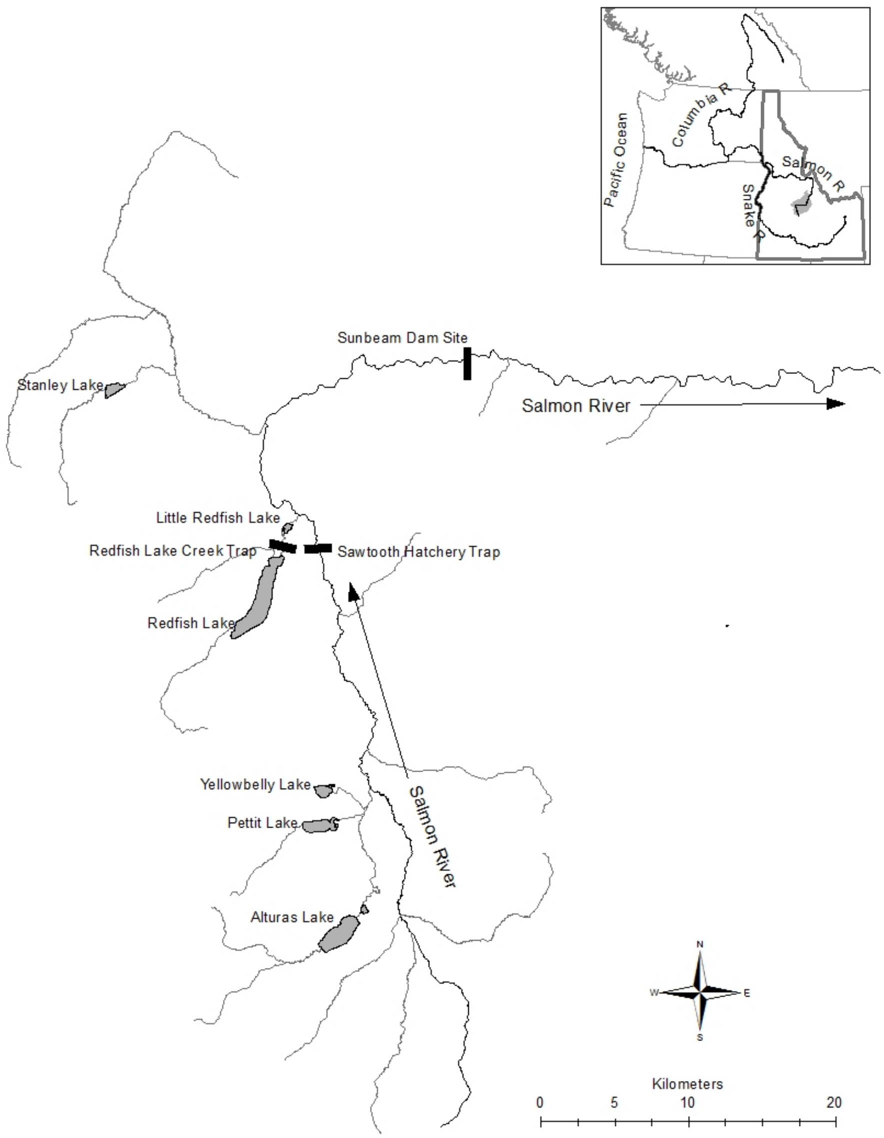
Figure 1. Map of the upper Salmon River watershed and location of Redfish Lake in the Sawtooth Valley basin in central Idaho. The trapping locations on Redfish Lake Creek and at the Sawtooth Hatchery are presented along with the former location of Sunbeam Dam.

Figure 2. Estimated Sockeye Salmon potential egg deposition (PED) historically (Bjornn et al. 1968) and for current spawn years 2004-2011 and the number of smolts estimated as leaving Redfish Lake.

Figure 3. Number of emigrating Sockeye Salmon smolts (right axis) resulting from captive and anadromous adult releases (left axis) into Redfish Lake for volitional spawning.

Figure 4. Historic Sockeye Salmon smolt-to-adult survival as estimated by Bjornn et al. 1968 and current smolt-to-adult survival (SY 2004-2011) with 95% CI. *Year refers to the emigration year for Bjornn et al. (1968) and the spawn year for which the fish were born for current data.

Figure 5. Diagram depicting the combinations of Sockeye Salmon freshwater productivity and SARs which can result in population replacement. The current range of estimates observed during SY 2004-2011 are presented for each year. The dark curved line represents population replacement.



Pacific Ocean
Columbia R.
Salmon R.
Snake R.
Sunbeam Dam Site
Stanley Lake
Salmon River
Little Redfish Lake
Redfish Lake Creek Trap
Sawtooth Hatchery Trap
Redfish Lake
Yellowbelly Lake
Pettit Lake
Salmon River
Alturas Lake
N
W
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S
Kilometers
0
5
10
20

Figure 1

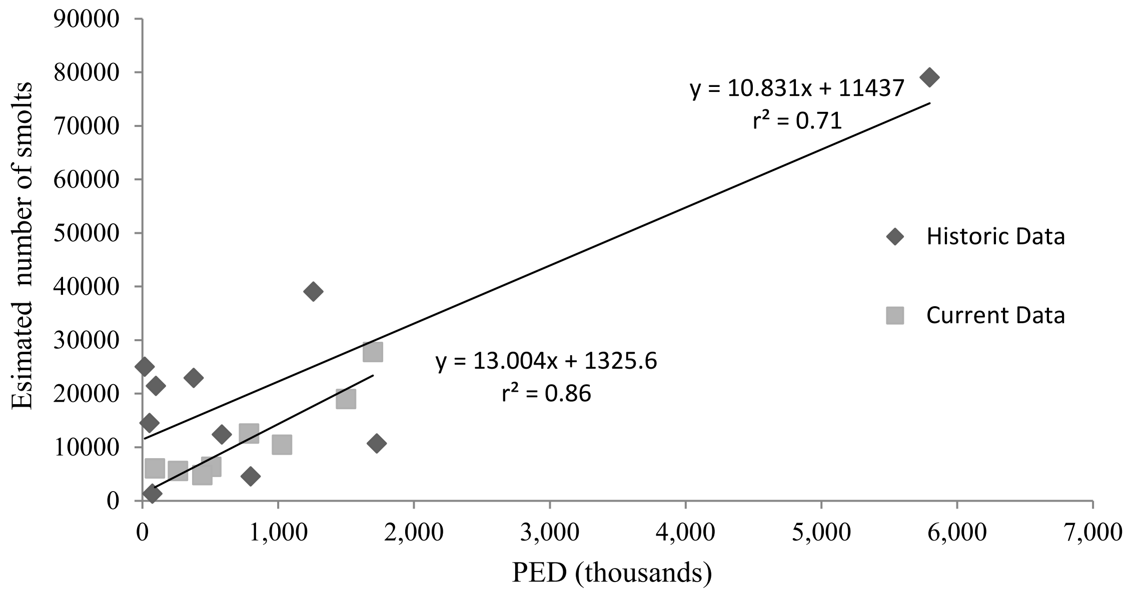

Figure 2

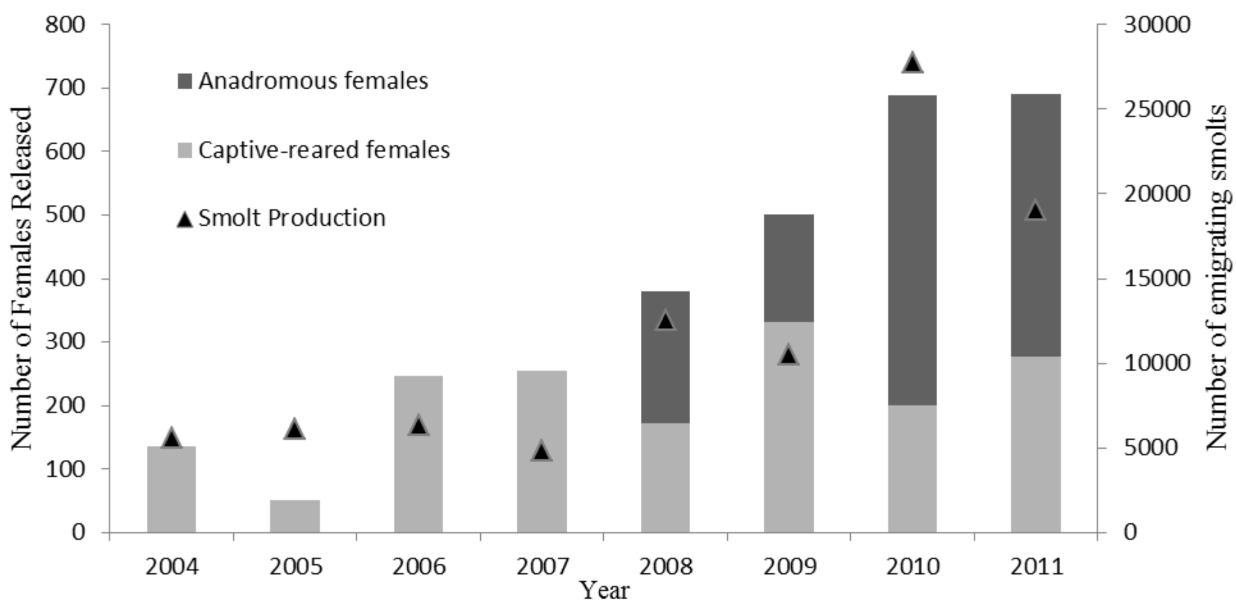

Figure 3

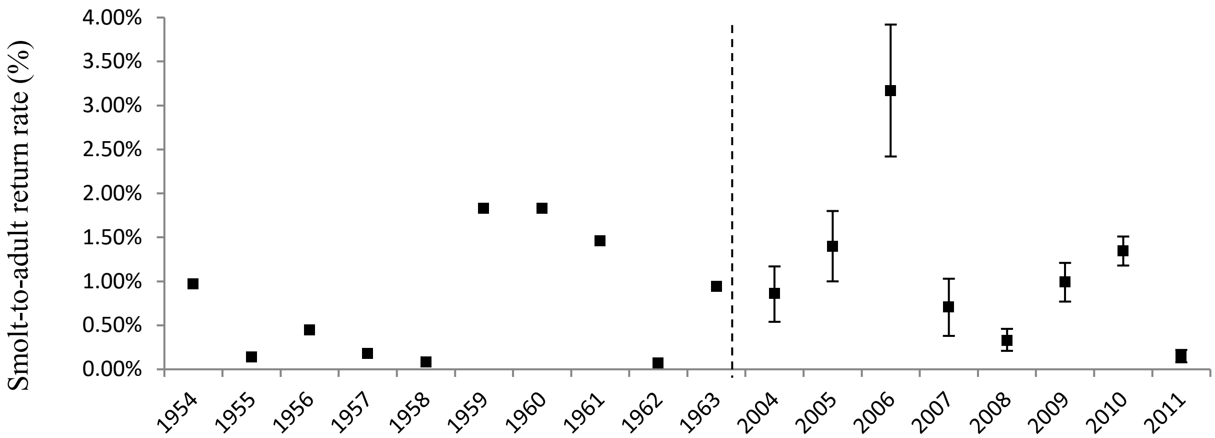

Figure 4

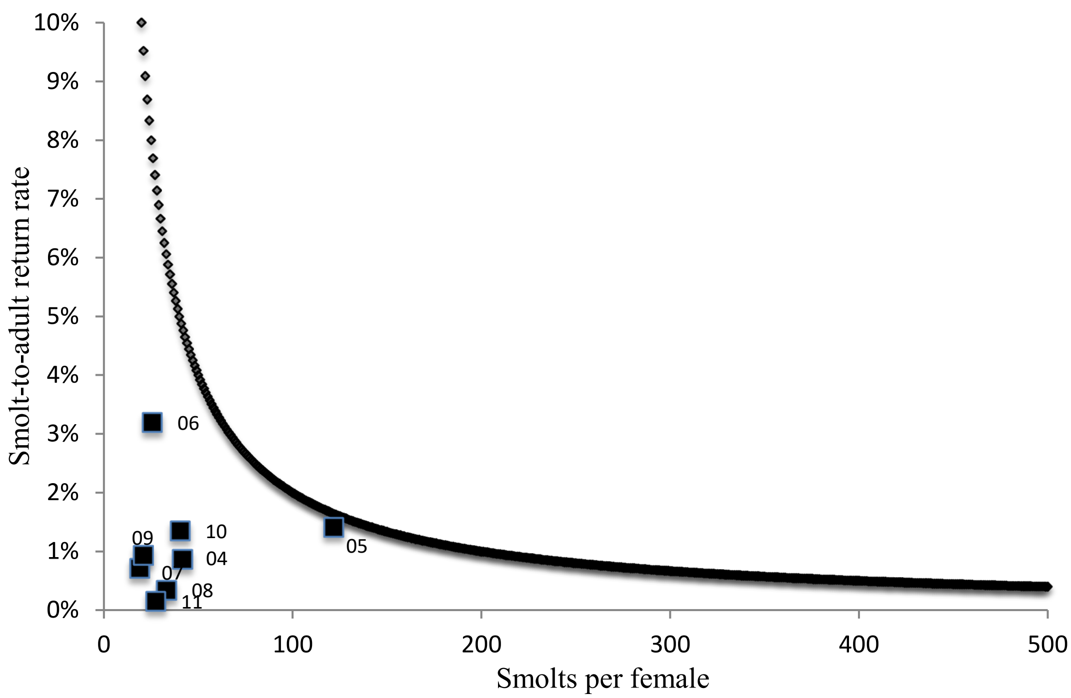

Figure 5

Table 1. Total number of Sockeye Salmon captive and anadromous adults by sex (females, males, and unknown) and rearing group (NMFS-FW/SW, NMFS-FW, IDFG-FW, Anadromous) released into Redfish Lake for volitional spawning from 2004 to 2011.

Spawn Year	Type	Females	Males	Unknown	Total
2004	NMFS-FW/SW	116	108	1	225
	NMFS-FW	19	0		19
2005	NMFS-FW/SW	20	60	3	83
	NMFS-FW	30	63		93
2006	NMFS-FW/SW	121	109		230
	NMFS-FW	126	109		235
2007	NMFS-FW/SW	96	144	1	241
	NMFS-FW	61	65		126
	IDFG-FW	97	34		131
2008	NMFS-FW/SW	61	74		135
	NMFS-FW	49	67		116
	IDFG-FW	62	82		144
	Anadromous	207	310	51*	568
2009	NMFS-FW/SW	9	89		98
	NMFS-FW	147	44		191
	IDFG-FW	175	216		391
	Anadromous	169	481		650
2010	NMFS-FW/SW	115	70	2	187
	NMFS-FW	10	0	1	11
	IDFG-FW	75	97		172
	Anadromous	488	719	1	1208
2011	NMFS-FW/SW	121	109		230
	NMFS-FW	0	0		0
	IDFG-FW	156	172		328
	Anadromous	414	574		988

*Estimated number of adults that passed through the Redfish Lake Creek adult trap and spawned in Redfish Lake.

Table 2. Results of linear regression modeling of fecundity on year and length and their interaction. AICc is Akaike's Information Criterion corrected for sample size. Delta AICc is the difference from the minimum AICc.

Rearing Strategy	Model	AICc	Delta AICc	r^2
NMFS-FW/SW	Length	N/A	N/A	0.68
NMFS-FW	Year + Length + (Year x Length)	12570.2	0.00	0.64
	Year + Length	12575.6	5.37	
	Year	13066.1	495.83	
	Length	12769.6	199.35	
IDFG-FW	Year + Length + (Year x Length)	23623.7	0.00	0.58
	Year + Length	23643	19.22	
	Year	24492.4	868.70	
	Length	23721	97.23	
Anadromous	Year + Length + (Year x Length)	7786.11	9.78	
	Year + Length	7776.32	0.00	0.46
	Year	8038.23	261.91	
	Length	7830.40	54.08	

Table 3. Natural productivity metrics resulting from releasing Sockeye Salmon adults to volitionally spawn within Redfish Lake, ID. Number of released females, potential egg deposition (PED) and smolt migration estimates are shown for each spawn year with standard error. Egg-to-smolt survival, smolts per female, and adult recruits are also presented as well as the arithmetic mean for each metric measured during the evaluation

Spawn Year	Female spawners	Estimated PED (SE)	Smolt migration (SE)	Egg-to-smolt survival (%)	Smolts per female	Adult Recruits
2004	135	262,101 (39,237)	5,609 (621)	2.14	41.54	48
2005	50	91,748 (10,800)	6,088 (489)	6.64	121.76	85
2006	247	506,640 (53,300)	6,338 (597)	1.25	25.69	201
2007	254	441,645 (45,852)	4,822 (654)	1.09	18.98	34
2008	379	785,577 (108,497)	12,588 (884)	1.60	33.13	42
2009	500	1,027,407 (93,732)	10,502 (475)	1.02	21.04	104
2010	688	1,697,192 (196,445)	27,765 (1,638)	1.64	40.35	374
2011	691	1,498,722 (171,411)	19,033 (795)	1.27	27.54	28
Mean		789,253	11,593	2.09	41.25	114

Table 4. Sockeye Salmon natural-origin smolt production from Redfish Lake. The total estimated abundance, proportion of age-1 and age-2 smolts, and smolt length (mm) with standard error is presented for each spawn year.

Spawn Year	Estimated smolts	Age-1 Percentage	Average length Age-1 (mm) (SE)	Age-2 Percentage	Average length Age-2 (mm) (SE)
2004	5,609	91%	96 (1.84)	9%	146 (2.27)
2005	6,088	78%	110 (2.10)	22%	125 (1.53)
2006	6,338	77%	98 (1.65)	23%	131 (2.04)
2007	4,822	65%	110 (2.19)	35%	131 (2.20)
2008	12,558	98%	106 (1.43)	2%	141 (2.77)
2009	10,502	63%	109 (1.83)	37%	140 (1.95)
2010	27,765	99%	102 (1.71)	1%	145 (2.15)
2011	19,033	96%	117 (1.71)	4%	140 (1.31)