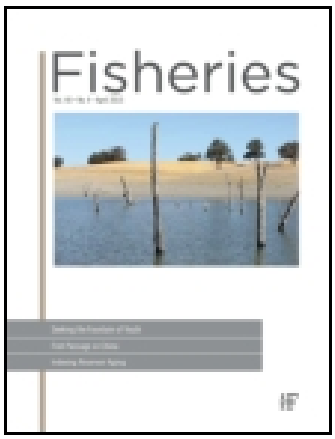

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Putting the Red Back in Redfish Lake, 20 Years of Progress Toward Saving the Pacific Northwest's Most Endangered Salmon Population

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ABSTRACT: *In November 1991, the U.S. National Marine Fisheries Service listed Snake River Sockeye Salmon (*Oncorhynchus nerka*) as endangered under the U.S. Endangered Species Act (ESA). The last known remnants of the Snake River stock return to Redfish Lake in the Sawtooth Valley in central Idaho. In the ensuing two decades since the ESA listing, many actions have been taken to conserve the population, including the initiation of a hatchery-based gene rescue program. The chief aim of this article is to describe the development and implementation of hatchery-based gene rescue activities, review present-day release strategies and associated adult returns, and describe a new effort underway to expand program production to more effectively address recolonization and local adaptation objectives. In addition, we describe achievable population triggers to allow the transition from a hatchery-based effort to a habitat-based effort that should allow natural population recovery to proceed.*

Poniendo al lomo rojo de vuelta en el Lago Redfish, veinte años de progreso en el salvamento de la población de salmón más amenazada del noroeste

RESUMEN: *En noviembre de 1991, el Servicio Nacional de Pesquerías Marinas de los Estados Unidos de Norteamérica, ingresó al salmón (*Oncorhynchus nerka*) en el Acta de Especies Amenazadas de los Estados Unidos (AEA) bajo la categoría de amenazado. Los últimos remanentes conocidos del stock del Río Snake, regresaron al Lago Redfish, Valle Sawtooth, en la porción central de Idaho. Dos décadas después de haber ingresado esta especie al acta, se han llevado a cabo varias acciones tendientes a conservar a la población, entre las que se incluye el inicio de un programa de rescate genético. El objetivo del presente trabajo es describir el desarrollo e implementación de actividades de rescate genético basado en cultivos, revisar las estrategias actuales de liberación y posterior retorno de adultos y describir la nueva iniciativa de expandir el programa de producción para abordar de forma más efectiva la recolonización y los objetivos de adaptación local. Adicionalmente, se describe cómo se usarán detonantes poblacionales que permitan una transición entre esfuerzos basados en cultivos y esfuerzos basados en hábitats con el fin de facilitar la recuperación de las poblaciones.*

INTRODUCTION

Snake River Sockeye Salmon (*Oncorhynchus nerka*) from the Columbia River Basin are one of the most depleted stocks of salmonids in the world (Nehlsen et al. 1991; Waples and Johnson 1991; Flagg et al. 2004). In November 1991, the U.S. National Marine Fisheries Service (NMFS) listed Snake River Sockeye Salmon as endangered under the U.S. Endangered Species Act (ESA; Waples and Johnson 1991; 56 FR 58619 1991). The two other population groups of anadromous salmon that occur in the upper headwaters of the Salmon River are listed as threatened under ESA (spring/summer Chinook Salmon [*O. tshawytscha*] and steelhead [*O. mykiss*]). The last known remnants of this stock return to Redfish Lake in the Sawtooth Valley in Idaho (Figure 1). Sockeye Salmon returning to Redfish Lake travel a greater distance from the Pacific Ocean (1,448 km) and to a higher elevation (1,996 m) than any other Sockeye Salmon population in the world. Additionally, Redfish Lake supports the southernmost population of the species (Burgner 1991; Waples et al. 2011). Together these characteristics presented a strong argument for the ecological uniqueness of Redfish Lake Sockeye Salmon and subsequent designation as an Evolutionarily Significant Unit (ESU; Waples 1991). Five lakes in the Sawtooth Valley historically contained Sockeye Salmon: Redfish, Pettit, Alturas, Stanley, and Yellowbelly lakes (Bjornn et al. 1968). Reestablishment of natural returns of Sockeye Salmon in at least three of these lakes is considered necessary for maintenance and protection of the ESU (NMFS 2011).

Prior to modern settlement, Sockeye Salmon runs to the Snake River basin were estimated at about 150,000 fish, of which about 25,000–30,000 may have returned to the Sawtooth Valley in Idaho (Evermann 1896; Selbie et al. 2007). Paleolimnological data suggest that the onset of decline in Snake River Sockeye Salmon was concurrent with inception and intensification of commercial fisheries in the lower Columbia River in the mid- to late 1800s (Selbie et al. 2007). Within the upper

Salmon River basin, additional population stressors for Redfish Lake Sockeye Salmon have included mining and irrigation activities, non-game fish control efforts, *and* fish passage barriers constructed at lake outlets, harvest, predation, inadequate regulatory mechanisms (Bjornn et al. 1968; Flagg et al. 2004; Hebdon et al. 2004). From 1910 to 1934, a small hydroelectric project (Sunbeam Dam) blocked most or all returns to the upper Salmon River basin (Bjornn et al. 1968). From the 1930s on, a number of major hydroelectric dams were developed on the Columbia/Snake River system. Lower Granite Dam (Figure 1), at about 700 km from the Pacific Ocean, is the most upstream dam in the migration route of Snake River Sockeye Salmon.

The Salmon River enters the Snake/Columbia River system about 100 km upstream of Lower Granite Dam (Figure 1) and runs free-flowing for its entire 684 km length from its headwaters in the Sawtooth Mountains. The Salmon River portion of the migration route to Redfish Lake is sparsely developed. This migratory reach has some agriculture and irrigation impacts but also large stretches of wilderness. Almost 90% of the habitat in the Sawtooth Valley is within the U.S. Forest Service's Sawtooth National Recreational Area. The watersheds are in relatively pristine condition. The Sawtooth Valley lakes (and Redfish Lake in particular) are recreational destinations and are highly valued for their scenic qualities and clear water.

Since 1991, a group of agencies including the Idaho Department of Fish and Game (IDFG), NMFS, the Shoshone-Bannock Tribes, and the Bonneville Power Administration (BPA) have been collaboratively engaged in Snake River Sockeye Salmon recovery efforts. Actions have been coordinated through the multi-agency Stanley Basin Sockeye Technical Oversight Committee, the primary technical body associated with the recovery effort. Program goals were developed with input from management and federal action agencies. The near-term goal was to avoid extinction and to maintain remaining genetic diversity and population heterozygosity. The long-term goal is to rebuild populations to facilitate delisting and to increase abundance to levels sufficient to support sport and tribal harvest needs (Flagg et al. 2004; Hebdon et al. 2004; IDFG 2010). Numerous actions have been conducted and over 30 peer-reviewed articles have been published on various components of restoration ef-

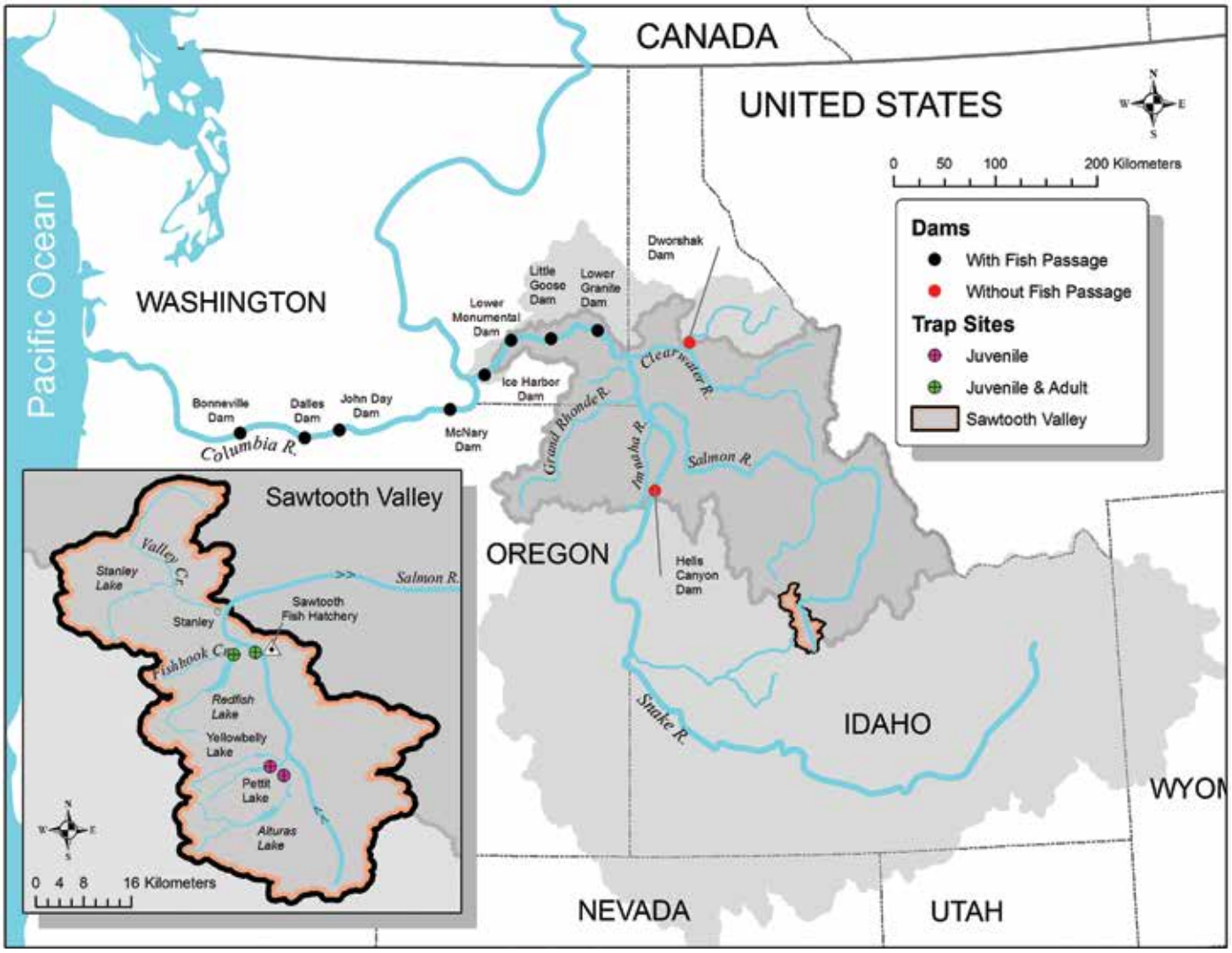

Figure 1. Map of the Columbia River basin, locations of mainstem and lower Snake River hydropower dams and Snake River Sockeye Salmon recovery habitat in the upper Salmon River basin, Idaho.

forts, including determination of lake carrying capacity and zooplankton dynamics; fish growth, survival, and migration dynamics; genetics; alterations of barriers and improvements in fish passage; and husbandry methodologies (Box 1).

Throughout this 20-year effort, the core of the Redfish Lake Sockeye Salmon program has been a hatchery-based captive broodstock program developed to preserve population genetics. In this article, we describe the results of this gene rescue effort that are helping stabilize population genetics and demographics and expand the abundance of wild fish. We also provide the methods we are using to develop achievable population triggers to allow the transition from a hatchery-based effort to a habitat-based effort that should allow natural population recovery to proceed. It is our hope that this summary will serve as a useful case history and blueprint for other fisheries professionals in need of an approach to combat an impending aquatic extinction event.

RESULTS AND DISCUSSION

Captive Broodstock Phase

Based on probable extinction scenarios and the pending ESA listing, in May 1991 a decision was made by IDFG, NMFS, and the Shoshone-Bannock Tribes to collect out-migrating smolts and to retain any anadromous adults that returned to Redfish Lake in the Sawtooth Valley in Idaho to begin a captive broodstock program (Flagg et al. 1995; Hebdon et al. 2004). This was controversial because in the early 1990s, the application of captive broodstock technology to Pacific salmon was considered highly experimental and success was uncertain (Flagg et al. 1995; Schiewe et al. 1997). Nonetheless, the only other alternative at the time appeared to be extinction (Flagg et al. 2004).

Broodstock Development

The present-day Redfish Lake Sockeye Salmon captive broodstocks were established from 16 anadromous adults, 26 residual Sockeye Salmon, and 886 out-migrating smolts collected during the early-mid 1990s from Redfish Lake and surrounding habitats (Table 1). Residual Sockeye Salmon are genetically similar to anadromous Sockeye Salmon but complete their life cycle in fresh water (see Burgner [1991] for a review). To avoid the risk of catastrophic loss of broodstocks, separate captive broodstocks were established in the beginning (see also Pollard and Flagg 2004). Annually, equal brood lots of eggs (about 500 each) from both captive-reared and ocean-return adults are developed at the IDFG Eagle Fish Hatchery near Boise, Idaho. One group is incubated and reared by IDFG and the other group is raised at NMFS facilities in Washington State (Manchester Research Station, Port Orchard, WA; Burley Creek Hatchery, Kitsap County, WA; see Baker et al. [2012]

BOX 1. Published articles by researchers involved with the Redfish Lake Sockeye Salmon recovery program.

SUBJECT	REFERENCE
Habitat/limnology evaluations	Budy et al. 1995; Luecke et al. 1996; Gross et al. 1998; Pilati and Wurtsbaugh 2003; Sawatzky et al. 2006; Selbie et al. 2007
Lake fertilization evaluations	Budy et al. 1998; Gross et al. 1997; Wurtsbaugh et al. 2001; Griswold et al. 2003
Predator/prey and life history evaluations	Beauchamp et al. 1997; Steinhart and Wurtsbaugh 1999; Massee et al. 2007; Kendall et al. 2010
Juvenile fish growth and survival evaluations	Steinhart and Wurtsbaugh 2003; Powell et al. 2010
Juvenile and adult migration studies	Hebdon et al. 2004; Keefer et al. 2008; Griswold, Koler, and Taki 2011
Genetics	Winans et al. 1996; Kozfkay et al. 2008; Waples et al. 2011; Kalinowski et al. 2012; O'Reilly and Kozfkay 2014
Gene rescue hatchery methodologies	Flagg et al. 1995, 2004; Schiewe et al. 1997; Flagg and Mahnken 2000; Berejikian et al. 2004; Pollard and Flagg 2004; Heindel et al. 2005; Swanson et al. 2008; Maynard et al. 2012

Table 1. Wild adult and juvenile Sockeye Salmon collected to develop the Redfish Lake captive broodstock program.

Collection year	Anadromous adults	Residual adults[a]	Out-migrating smolts
1991	4 (3 male, 1 female)		759
1992	1 male	5 (4 male, 1 female)	79
1993	8 (6 male, 2 female)	18 (16 male, 2 female)	48
1994	1 female		
1995		3 male	
1996	1 female		
1997			
1998	1 male		
TOTAL	16 (11 male, 5 female)	26 (23 male, 3 female)	886

[a]Residual Sockeye Salmon are genetically similar to anadromous Sockeye Salmon but complete their life-cycle in freshwater (see Burgner [1991] for a review).

and Maynard et al. [2012] for facility and operational descriptions).

Two adult traps are installed annually to capture returning Sockeye Salmon. One trap is located on Redfish Lake Creek approximately 1.4 km downstream from the outlet of Redfish Lake and the second on the mainstem Salmon River at the IDFG Sawtooth Fish Hatchery (Figure 1). Trapped adults may be held at the IDFG Eagle Fish Hatchery (for spawning) or released to Redfish Lake to spawn naturally (see Figure 2 for a diagram that characterizes general program operations). The decision to "hold or release" specific adults is based on "real-time" genetic analyses conducted by IDFG (Kozfkay et al. 2008; O'Reilly and Kozfkay 2014). Such analyses take into account individual and family representation as well as relatedness of returning adults. Through 2005, pedigree information (e.g., known origin/lineage of individual members of the population) was used to develop annual spawning designs (Kozfkay et al. 2008; O'Reilly and Kozfkay 2014). From 2006 to present, a suite of 7–16 microsatellite loci have been used. This approach provides information on multiple population attributes, including (1) relative founder contribution, (2) the genetic importance of individuals, (3) genetic diversity and heterozygosity within and among individuals, and (4) relative relatedness among individuals (Kozfkay et al. 2008; O'Reilly and Kozfkay 2014). Annually, maximum avoidance of inbreeding matrices are developed to identify band sharing proportions (e.g., mean kinship information) among all possible mate combinations to minimize inbreeding (Ballou and Lacy 1995). Based on genetic distance, modified factorial mating schemes are developed to guide mate selection (Kozfkay et al. 2008). Eggs and fish destined for various reintroduction strategies are isolated to maximize the ability to track returning Sockeye Salmon back to release strategy and family (Heindel et al. 2005; Baker et al. 2012; Maynard and Flagg 2012). Performance metrics are monitored to document maturation and spawning processes for captive broodstocks, including rate of maturation, age of maturation, fecundity, gamete quality, and egg survival to the eyed stage of development.

Broodstock Outcomes

The fish culture program for Redfish Lake Sockeye Salmon has produced over 10,000 adult descendants from the 16 wild adults that returned to the Sawtooth Valley during the 1990s (Baker et al. 2012; Maynard and Flagg 2012; Maynard et al. 2012). The genetic focus of the program and adherence to principles of conservation aquaculture has enabled us to retain approximately 95% of the original founding genetic variability that remained in the population (Kalinowski et al. 2012). Although easily overlooked, a major program accomplishment was simply the development of fish culture protocols for rearing Sockeye Salmon full term to maturation. Earlier rearing attempts for various species of Pacific salmon and steelhead had suggested that captive broodstocks would have poor performance, with low egg survival, low egg-to-adult survival rates, and reduced size of captive-reared adults compared to wild fish (Flagg and Mahnken 1995; Schiewe et al. 1997). Overall, the Redfish Lake Sockeye Salmon captive broodstock effort has experienced much better production success than the earlier programs (Table 2). Egg survival to the eyed stage of development has improved to levels that usually exceed 80% and fry-to-maturation survival is now routinely around 80%. Size of fish in culture can now be manipulated to exceed that of wild fish. Average egg size of captive-reared females exceeds that of ocean-return females (11.4 compared to 17.0 eggs/g), although average fecundity of captive-reared females is still lower than that of ocean-return females (1,846 compared to 2,560 eggs/female).

The population amplification potential identified by Flagg et al. (1995) for captive broodstocks has been realized for the Redfish Lake Sockeye Salmon captive broodstock program. If the 16 returning adults (11 males and 5 females; Table 1) that were taken into captivity had been released to the Redfish Lake to spawn naturally, it is likely that the population would have gone extinct. According to data collected between 1955 and 1964, natural egg-to-smolt survival for Redfish Lake Sockeye Salmon was generally less than 6.0% and smolt-to-adult survival (from the Sawtooth Valley, through ocean residence, and upstream return; geometric mean) was 0.44% (Bjornn et al. 1968; Flagg et al. 1995; Hebdon et al. 2004). If the five female adults incorporated in the captive broodstock had each naturally spawned an average of about 2,500 eggs (Table 2), approximately 750 ocean-going smolts would have been produced. This, in turn, would have generated approximately three adult returns to the Sawtooth Valley equating to a survival rate of approximately 0.03% (i.e., 750 smolts * 0.0044). These fish would have been spread over a 4- to 10-year return window, or less than a fraction of an adult per year. Based on these figures, without intervention, extinction would have been all but certain. For groups of Redfish Lake Sockeye Salmon in captive

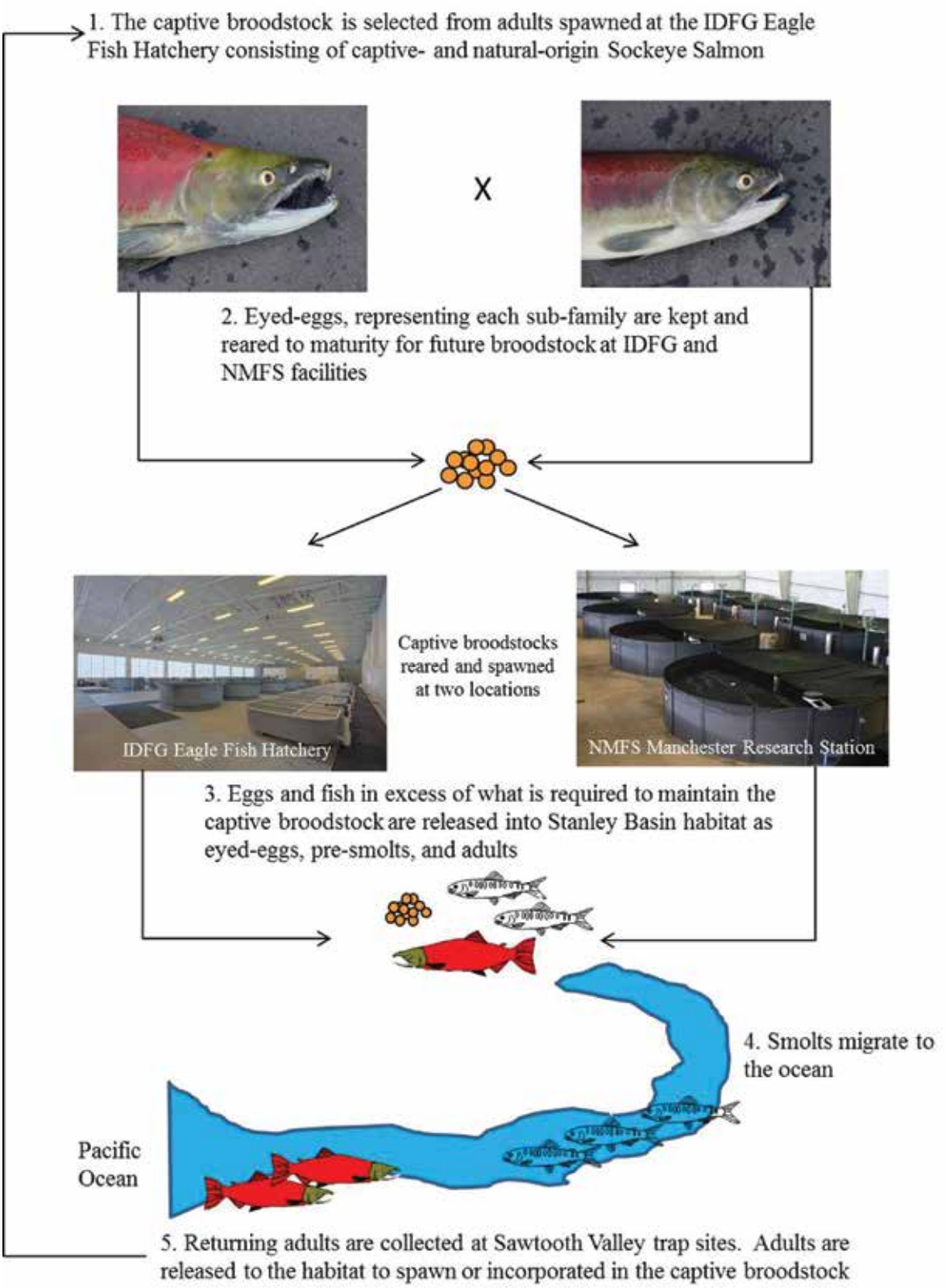

Figure 2. Schematic depicting the general operations of the Redfish Lake Sockeye Salmon captive broodstock program.

Table 2. In-hatchery spawner information and associated egg and fry-to-maturation survival for Eagle Fish Hatchery captive broodstock and anadromous Redfish Lake Sockeye Salmon.

Spawn year	Female spawner weight (g)		Fecundity (n)		Egg size (eggs/g)		Eyed egg survival (%)		Fry-to-maturation survival (%)
	H[a]	W[b]	H	W	H	W	H	W	H
1991	NA[c]	1,100	NA[c]	2,177	NA[c]	NA[c]	NA[c]	90.86	NA[c]
1992	NA[c]	NA[c]	NA[c]	NA[c]	NA[c]	NA[c]	NA[c]	NA[c]	NA[c]
1993	1,801	1,160	2,182	3,160	12.25	15.63	46.58	58.53	70.82
1994	1,681	1,183	2,134	2,896	7.92	20.53	50.98	95.99	71.35
1995	2,630	NA[c]	1,576	NA[c]	21.61	NA[c]	68.06	NA[c]	NA[c]
1996	2,165	866	2,171	2,067	8.74	20.56	63.43	84.95	56.35
1997	2,093	NA[c]	2,206	NA[c]	10.03	NA[c]	60.22	NA[c]	88.39
1998	941	NA[c]	1,199	NA[c]	11.15	NA[c]	48.12	NA[c]	79.84
1999	1,990	635	1,981	1,619	9.686	21.56	38.52	93.26	83.78
2000	2,987	1,389	2,647	2,751	8.87	15.22	55.19	62.60	91.48
2001	1,517	1,223	2,148	2,687	10.74	13.46	41.13	60.52	80.16
2002	1,050	NA[c]	1,343	NA[c]	10.52	NA[c]	54.40	NA[c]	78.50
2003	1,246	1,282	1,627	2,578	10.65	19.32	88.77	98.00	89.63
2004	1,158	1,191	1,674	2,322	10.13	18.12	70.77	90.00	87.22
2005	1,094	1,404	1,707	2,450	11.90	18.29	69.55	82.00	86.61
2006	1,431	1,343	1,844	2,248	11.03	17.58	77.86	62.71	93.58
2007	1,077	1,424	1,618	2,828	12.26	17.1	74.29	80.18	80.04
2008	1,189	1,475	1,808	2,668	12.07	14.84	91.14	91.61	63.97
2009	1,137	1,486	1,616	2,749	12.34	14.86	90.10	88.16	70.17
2010	1,106	1,452	1,596	2,799	11.89	12.88	80.60	87.86	NA[d]
2011	1,557	1,484	1,994	2,749	12.21	14.86	76.47	82.84	NA[d]
2012	1,331	1,360	1,854	2,766	13.08	17.19	85.71	90.86	NA[d]
Mean	1,559	1,262	1,846	2,560	11.45	17.00	66.59	81.88	80.69
Geomean	1,476	1,237	1,816	2,531	11.21	16.81	64.49	80.76	79.96
sd	564	232	341	373	2.76	2.62	16.66	13.31	10.73

[a]Hatchery (H) captive broodstock adult data.
[b]Wild (W) anadromous adult data.
[c]Complete records not available.
[d]Life cycle incomplete.

broodstock culture, egg survival to the eyed stage and fry-to-adult survival have each averaged about 80% in recent years (Table 2), equating to an overall egg-to-adult survival rate of approximately 65%. For this endangered population, the survival advantage afforded by the captive broodstock program over natural production has been greater than 2,000% (i.e., 0.65/0.0003).

Initial Fish Reintroduction Phase

Although the initial focus of the captive broodstock program was gene rescue, excess eggs and fish were produced each year. Experimental reintroduction strategies were developed to take advantage of that production. These included release of captive-reared prespawning adults, eyed eggs, presmolts, and smolts, along with adults from these releases that returned from the ocean (Hebdon et al. 2004). Estimates of nursery lake carrying capacity and temporal limnological information have also been used to guide the development of annual reintroduction plans (Teuscher and Taki 1996; Griswold, Taki, and Letzing 2011; see also Box 1). Habitat evaluation and improvements actions include assessments of primary and secondary productivity, zooplankton species diversity and biomass assessment, O. nerka density and biomass assessment, and whole-lake fertilization (Griswold,Taki, and Letzing 2011; Box 1).

Through 2011, our efforts have produced over 3.8 million eggs and fish for reintroduction to Sawtooth Valley lakes and tributary streams. Of these, 1.6 million were released as presmolts, 1.1 million as smolts, 1.1 million as eyed eggs in egg boxes, and 8,000 as prespawning adults (Baker et al. 2012). With few exceptions, presmolt releases have occurred annually in the three primary Sockeye Salmon nursery lakes in the Sawtooth Valley (Alturas, Pettit, and Redfish lakes). Eyed egg releases have occurred primarily in Alturas and Pettit lakes, prespawning adult releases in Redfish Lake, and smolt releases in the outlet of Redfish Lake (i.e., Redfish Lake Creek) and in the main Salmon River near the IDFG Sawtooth Fish Hatchery (Figure 1).

Reintroduction Outcomes

The ability to evaluate reintroduction strategies by life stage at release and location of release (e.g., receiving water) has remained a top program priority since inception. We evaluated rigorously the relative success of different reintroduction strategies to help interpret which approaches are most successful (Hebdon et al. 2004; IDFG 2010; Griswold, Koler, and Taki 2011; see also Box 1).

Since 1998, adult returns and maturing adults reared full-term in captivity have been released annually to spawn naturally in Redfish Lake. The first fish from the captive breeding program released as juveniles returned to the Sawtooth Valley as adults in 1999 (Table 3). Numerous adults have been observed building redds and spawning (Table 3). Adult releases have been associated with increases in the out-migration of naturally hatched (in-lake) smolts from Redfish Lake (Hebdon et al. 2004). The largest adult returns to date occurred between 2008 and 2011, with over 3,900 fish returning during that period (Table 3). Most adult returns during the 2008–2011 time period were produced from a combination of 2004–2006 brood year juvenile releases. Through a combination of external, internal, and genetic marks, we were able to assign the majority of adult returns to a known combination of prespawning adult, presmolt, and smolt release options (Kozfkay et al. 2008; Baker et al. 2012). To compare relative benefits of each release strategy, we calculated each strategy's smolt-to-adult return rate for this as the ratio of adult returns divided by the corresponding out-migration estimate (Skalski 1998; Lady et al. 2001; Steinhorst et al. 2004; Tuomikoski et al. 2012). Calculated values represent "basin-to-basin" survival (i.e., Sawtooth Valley to Sawtooth Valley). Analyses were conducted by brood year, which allowed age-3, age-4, and age-5 adult returns to be aggregated and assessed relative to the estimated number of out-migrating smolts produced in a common spawn year.

For brood years 2004–2006, average smolt-to-adult return rates for Sockeye Salmon produced from juveniles released as smolts were over threefold greater than average rates for adults produced from Redfish Lake presmolt releases (i.e., 0.60% vs. 0.17%; Figure 3). Average smolt-to-adult return rates for Sockeye Salmon produced from natural spawning events in Redfish Lake were over threefold higher than results from smolt releases (i.e., 1.84% vs. 0.60%) and over 10-fold higher than rates for adults produced from presmolt releases (Figure 3). For these three brood years, over 83% of returning adults originated from smolt releases, whereas the presmolt release option accounted for only about 3% of all returning adults (Table 4). Importantly, the relatively small number of smolts produced from in-lake spawning events accounted for over 13% of the adult returns during this period (Table 4). Observed smolt-to-adult return rates for natural-origin fish have exceeded the minimum 2% rate we estimate is required for population self-sustainability (Figure 3; Flagg et al. 2004).

The results indicate that properly scaled smolt releases could be sufficient to produce enough adults (e.g., 5,000) from the ocean to recolonize Redfish Lake and that the juveniles produced from subsequent spawning events could have the increased fitness needed to substantially increase smolt-to-adult return rates to a point matching or exceeding self-sustainability. Our results also indicate that apparent "extinction vortex"–type scenarios (Soule 1986) could be reversable for this population. These results led managers to begin developing estimates of production levels necessary to eventually achieve population stablization and recovery.

Table 3. Anadromous Sockeye Salmon returns to the Sawtooth Valley, ID; numbers of anadromous and captive-reared adults released to spawn in Redfish Lake and numbers of subsequent redds (nest areas excavated by females) observed

Return year	Anadromous returns	Released to spawn in Redfish Lake[a]		Observed redds
		Anadromous	Captive-reared	
1999	7	3 (0)	18 (10)	8
2000	257	120 (41)	36 (NA)[b]	20 to 30
2001	26	14 (7)	65 (37)	12 to 15
2002	22	12 (7)	177 (62)	10
2003	3	0	309 (152)	42
2004	27	0	244 (135)	104
2005	6	0	176 (50)	78
2006	3	0	465 (247)	172
2007	4	0	498 (254)	195
2008	650	571 (207)[c]	396 (172)	338
2009	833	651 (169)	680 (331)	201
2010	1,355	1,209 (489)	367 (199)	155
2011	1,117	990 (414)	558 (277)	385
2012	257	173 (79)	622 (268)	306

[a]Total anadromous and captive-reared adults released to spawn in Redfish Lake (number of females in parentheses).
[b]Thirty-six captive-reared Sockeye Salmon released (sex unknown).
[c]An additional 51 anadromous Sockeye Salmon migrated upstream of the adult trap without handling (sex unknown).

BOX 2. Scenarios for sliding scale logistics for managing hatchery vs. wild escapements in high vs. low wild fish abundance years for Redfish Lake Sockeye Salmon (modified from HSRG 2009).

Variable sliding scales are useful for managing salmon abundance so that in low abundance years more hatchery-origin fish of the appropriate population component are allowed to reach the spawning grounds to reduce demographic risk to the respective populations. As an example:

- Each year, depending on NOR[a] run size, pNOB[b] and pHOS[c] are allowed to "float" or slide. Managers should establish an acceptable level of removal of NORs for use in the hatchery brood. This will be a fixed percentage of the total NOR return (say 40%) and will not change, regardless of NOR return.
- In years of high NOR abundance, this 40% could make up 100% of the needed hatchery brood (pNOB = 100%). In that case, no HORs[d] would be used in the hatchery brood. Hatchery fish can be allowed to reach the spawning ground (pHOS) if needed to achieve an appropriate number of fish spawning naturally (for demographic benefit and maximum use of available habitat). This, however, would not be required during years of very high NOR returns because both objectives (pNOB and natural spawning) may be met with NORs.
- In years of low NOR abundance, the same 40% of the NOR return would be removed for use in the hatchery brood (pNOB). However, in these years, that 40% may make up only a small part of the needed brood (i.e. pNOB 10%). In these years, enough HORs should be used to achieve needed hatchery brood and additional HORs should be allowed to spawn naturally (pHOS) to achieve the minimum acceptable level of naturally spawning.
- The goal of this sliding scale is to achieve an "average" PNI[e] over time of the desired level (0.67 or 0.5) depending on the population designation even though it may not be achieved in any one year. PNIs of >0.5 are required for the natural environment to influence evolutionary processes.
- A good way to determine the level of NORs that should be removed each year (see above) is to review the return of NORs over a long time frame and iterate what level (30%, 40%, 50%) is needed, on average, to achieve the desired PNI.

[a] NOR is the numerical natural-origin return in the watershed.

[b] pNOB is the proportion of natural-origin spawners taken into the broodstock.

[c] pHOS is the proportion of hatchery-origin spawners in the natural habitat.

[d] HOR is the numerical hatchery-origin return in the watershed.

[e] PNI = pNOB/(pNOB + pHOS) and is the proportional mean fitness of the integrated population relative to the natural population.

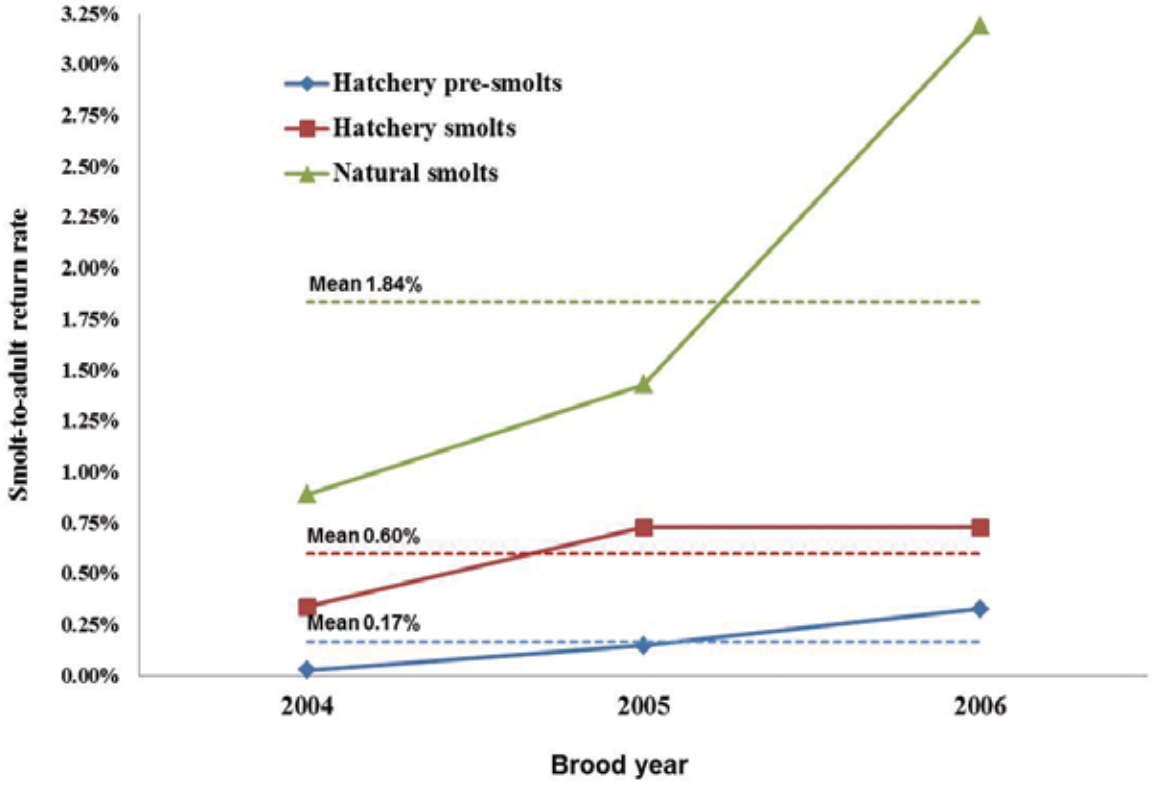

Figure 3. Smolt-to-adult survival rates for Redfish Lake natural-origin smolts, hatchery-origin smolts released as pre-smolts in Redfish Lake , and hatchery-origin smolts released in Redfish Lake Creek and the Salmon River at the Sawtooth Fish Hatchery. Dashed lines represent mean smolt-to-adult rates. Rates represent Sawtooth Valley to Sawtooth Valley survival.

Table 4. Contribution of juvenile Sockeye Salmon out-migrants from brood years 2004–2006 to adult returns back to Sawtooth Valley trap sites. Out-migrant groups include Redfish Lake natural-origin smolts, hatchery-origin smolts released as presmolts in Redfish Lake, and hatchery-origin smolts released in Redfish Lake Creek and the Salmon River at the Sawtooth Fish Hatchery.

Origin of juvenile out-migrants	Number of adult returns by juvenile origin[a]	Percentage of total return
Hatchery-origin presmolts released in Redfish Lake	83	3.2
Hatchery-origin smolts released in the Salmon River and Redfish Lake Creek	2,133	83.6
Natural-origin smolts produced in Redfish Lake	339	13.3
Total	2,555	

[a] Adult Sockeye Salmon linked to out-migrant origin using diagnostic marks and tags.

Planning for the Future

In an effort to advance the program's long-term goal of rebuilding and recovering the stock, project managers developed a tiered or phased approach that includes increasing the number of adult Redfish Lake Sockeye Salmon returns, incorporating more natural-origin returns in hatchery spawning designs and on spawning grounds, and moving toward the development of an integrated conservation program that takes advantage of local adaptation (IDFG 2010).

In their draft recovery planning process, NMFS identified biological goals of 1,000 naturally spawning Sockeye Salmon in Redfish Lake and 1,500 (combined) in two other Sawtooth Valley lakes (NMFS 2011). To estimate the number of smolts needed to return adequate adults to recolonize Redfish Lake, we modeled the population using the Columbia River Basin Hatchery Scientific Review Group's (HSRG) all-H analyzer (HSRG 2009; Michael et al. 2009; Paquet et al. 2011). We conservatively estimated full initial adult seeding for Redfish Lake at 2,000 spawning pairs and a subsequent natural smolt production potential of over 150,000 juveniles (IDFG 2010; see also limnology and population dynamic research papers listed in Box 1). We then used the smolt-to-adult return ratios from our evaluation of 2004–2006 brood returns to determine how returns from natural spawning events would fluctuate over time. Our calculations indicated that releasing 1 million hatchery-reared smolts could, under ideal circumstances, initially produce approximately 5,000 returning adult fish, which over time could result in the return of over 1,600 naturally produced adults. Juveniles produced from ocean-return adults would theoretically develop (through local adaptation) increased fitness necessary to increase smolt-to-adult return rates to levels that match or exceed self-sustainability (i.e., the 2% level shown for our test releases in the Reintroduction Outcomes section).

We used model results to adjust the proportion of natural-origin spawners taken into the broodstock (pNOB) and the proportion of hatchery-origin (pHOS) to natural-origin (pNOS) adult Sockeye Salmon released to the habitat for natural spawning. See Paquet et al. (2011) for a full review of pNOB, pHOS, pNOS, and other population metrics such as proportionate natural influence (PNI). Emphasis was placed on increasing the use of ocean-return adults and ensuring adequate numbers in the habitat for natural spawning. We used sliding scale logistics (Box 2) to develop rulemaking for managing abundance. In low abundance years, a higher ratio of pHOS of the appropriate population component would be allowed to reach the spawning grounds to reduce demographic risks. In high abundance years, pHOS would be greatly reduced and focus would be on allowing natural (wild) fish to dominate spawning.

We then structured two "next phases" of the project to (1) establish parameters for expanding the project and producing enough fish to recolonize the historic habitat and (2) provide for development of local adaption and the rebuilding of natural population structure. We also developed aggressive targets for phasing out both the captive broodstock and, ultimately, all hatchery intervention components of the program (Table 5).

We considered the capacity of Sawtooth Valley nursery lakes to support expansion efforts as well as freshwater competition among sympatric forms of *O. nerka* as potentially limiting factors in developing smolt production targets for the program. The strategy to release 1 million smolts during the recolonization phase of the program is consistent with estimates of lake carrying capacity developed by Stockner (2000, as cited by B. Griswold, Biolines Environmental Consulting, personal communication; NMFS 2014). Stockner estimated that Redfish Lake is capable of producing approximately 474,000 smolts per year as well as supporting an optimal escapement of 19,000 adult spawners. Under a program of whole-lake fertilization, these values increase to 1.1 million smolts and 46,700 adult spawners

Redfish Lake also supports a nonandromous Kokanee population founded from out-of-basin sources beginning in the 1920s and continuing through the 1980s (Bowler 1990). Kokanee and Sockeye Salmon compete for limited food resources. Several researchers have postulated that certain heritable traits associated with anadromy manifest themselves as outcomes that should prove advantageous when *O. nerka* conspecifics compete for food resources in freshwater (for a review, see Wood and Foote 1990; Taylor and Foote 1991; Wood 1995; Wood et al. 1999). Though encouraging, the resiliency of the food web to support program expansion is untested. Accordingly, Redfish Lake trophic dynamics will continue to be monitored by program cooperators and whole-lake fertilization will remain an option to be implemented as needed.

Recolonization Phase—Expanding the Program

The recolonization phase will focus on producing and releasing increased numbers of smolts, returning more adults from the ocean to Idaho collection sites, incorporating more ocean-return adults in hatchery spawning designs, and releasing more ocean-return adults to spawn naturally. Program managers have already begun implementing this phase of the program. Eggs for the expanded smolt program will be produced at IDFG and NMFS facilities. Spawning plans will be structured to include a minimum of 10% natural-origin adults in the broodstock (pNOB 10%). In the initial stages of the recolonization phase, an average of just under 5,000 ocean-return Sockeye Salmon (i.e., 637 and 4,347 natural- and hatchery-origin adults, respectively) are projected to return to the Sawtooth Valley annually (Table 5). Specific biological triggers are in place to guide the transition to the final (local adaptation) phase of the program including the ramp-down and ultimate discontinuation of captive broodstock efforts at NMFS and IDFG facilities (Table 5).

Releasing ocean-return adults in Pettit and Alturas Lakes could occur when adult escapement to Redfish Lake exceeds 5,000 fish (IDFG 2010). Allowing adult escapement to reach this level before allocating returning adults to other lakes will provide managers the opportunity to observe Redfish Lake fish habitat use and productivity over an appropriate range of adult spawning densities. Adult Sockeye Salmon that mature in the hatchery (i.e., captive broodstock) will continue to be released to Redfish, Pettit, and potentially Alturas lakes during the recolonization phase of the program. Adult Sockeye Salmon captured at the Sawtooth Hatchery weir and identified as Pettit or Alturas Lake origin will be transferred to their respective lake or origin and released to spawn (Table 5).

Local Adaptation Phase—Rebuilding Natural Populations

This phase of the program emphasizes the importance of local adaptation and the potential of natural-origin fish to in-

Table 5. Population outcomes, objectives and triggers for recolonization and local adaption recovery phases of the Redfish Lake Sockeye Salmon captive broodstock program.

Recolonization phase (smolt production target is one million)

Anticipated average outcomes and objectives:
• 637 natural-origin, anadromous adult returns to Redfish Lake
  • 522 released to spawn in Redfish Lake
  • 115 incorporated in captive broodstock
• 4,347 hatchery-origin, anadromous adult returns to Redfish Lake
  • 3,312 released to spawn in Redfish Lake
  • 1,035 incorporated in captive broodstock
• Option to release captive broodstock-origin, anadromous adults in Redfish Lake
• Option to release captive broodstock-origin, anadromous adults in Pettit Lake
• Option to release hatchery-origin, anadromous adults in Pettit Lake
• Option to release natural-origin, anadromous adults in Pettit Lake
• Redfish program pNOB[a] = 10%
• Redfish program pHOS[b] = not restricted
• Redfish program PNI[c] = not restricted
 	
Trigger 1: Begin to phase out NOAA safety net program when 5-year geometric mean return of anadromous adults > 1,000.
Trigger 2: Terminate Eagle Hatchery captive broodstock program when 5-year geometric mean return of anadromous adults > 2,150.
Trigger 3: Initiate local adaptation phase when 5-year geometric mean return of natural-origin adults > 750.

Local adaptation phase (smolt production target is 600,000)

Anticipated average outcomes and objectives:
• 1,647 natural-origin, anadromous adult returns to Redfish Lake
  • 1,397 released to spawn in Redfish Lake
  • 250 incorporated in broodstock
• 5,072 hatchery-origin, anadromous adult returns to Redfish Lake
  • 600 released to spawn in Redfish Lake
  • 442 incorporated in broodstock
• Option to release hatchery-origin anadromous adults in Pettit Lake
• Option to release natural-origin, anadromous adults in Pettit Lake
• Redfish program pNOB = 36%
• Redfish program pHOS = objective: ≤ 30%
• Redfish program PNI = objective: ≥ 50%
 	
Trigger 4: Begin to phase out Springfield Hatchery supplementation program when 5-year geometric mean of natural-origin, anadromous Sockeye Salmon returns meets NMFS's viability standards and associated delisting criteria.

ESA down-listing or delisting of Snake River Sockeye Salmon
Propose ESA down-listing when • The 5-year geometric mean of natural-origin adult returns to Redfish lake and one additional recovery lake meets NMFS's ESA recovery standards (down-listing) **Propose ESA delisting when:** • The 5-year geometric mean of natural-origin adult returns to three recovery lakes meets NMFS' recovery standards

[a]pNOB is the proportion of natural-origin spawners taken into the broodstock.
[b]pHOS is the proportion of hatchery-origin spawners in the natural habitat.
[c]PNI = pNOB/(pNOB + pHOS) or proportionate natural influence is an estimate of the strength of selection in the natural environment relative to that of the hatchery environment.

crease program success toward achieving delisting criteria. The local adaptation phase of the program will be initiated after the three performance triggers for the recolonization phase have been satisfied (Table 5). As the number of ocean-return adults spawning naturally in Redfish Lake increases, the number of natural-origin adults returning to all Sawtooth Valley collection sites will increase. Sliding scale management will be used to determine the number of natural-origin adults spawned in the hatchery and released to the habitat for spawning (Table 5). Natural-origin adults should be sufficiently abundant to comprise at least 35% of the total number of fish spawned in the hatchery (i.e., pNOB ≥ 35%). The number of hatchery-origin adults released to spawn in the habitat (pHOS) will be managed to not exceed 30%. The resulting proportionate natural influence (PNI) will exceed 0.50, allowing the environment to drive the fitness of the composite population (HSRG 2009; Paquet et al. 2011). Once the local adaptation phase is fully initiated, both captive broodstock programs will have been terminated. IDFG hatcheries will be managed as traditional trap and spawn operations, releasing all juvenile production as first-generation smolts.

Ultimately, the desired end result will be ESA down-listing or delisting once local adaption and fitness increases have stabilized the population (Table 5). We recognize that the ability of the Redfish Lake Sockeye Salmon population to sustain levels of abundance and productivity consistent with NMFS delisting criteria is uncertain. Though it remains our hope that demographic and fitness gains associated with program implementation will be long-lasting, uncertainties related to ocean productivity and climate conditions may result in population downturns that demand attention. If a decision is made to reinitiate short-term protective culture, the tools and protocols we have developed in the present-day gene rescue program will help the next generation of managers, researchers, and fish culturists implement future actions.

CONCLUSIONS

Overall, the Redfish Lake Sockeye Salmon captive broodstock effort has experienced much better success than the earlier captive broodstock gene rescue programs described by Flagg and Mahnken (1995, 2000) and Schiewe et al. (1997). Since the first program-produced adults started returning from the ocean in 1999, over 4,500 adults have been collected at sites in the Sawtooth Valley, over 275 times the number that returned from wild spawners during the entire decade of the 1990s.

Smolt-to-adult return rates of naturally produced Sockeye Salmon have exceeded rates of adults produced from hatchery-reared smolts by greater than threefold. This is a critical program observation because it demonstrates the potential for the population to become self-sustaining and effectively address draft NMFS recovery objectives.

Increases in fitness for animals subjected to natural vs. artificial selection processes have been much theorized by conservationists. A large number of studies have suggested that long-term hatchery rearing of fish will reduce productivity and fitness through alterations in genetic, behavioral, and physiological patterns (Flagg et al. 2000; Fraser 2008; Naish et al. 2008). Many authors have suggested that reversal of hatchery-based reductions in fitness would take at best many generations to resolve (Lynch and O'Healy 2001; Ford 2002). Similar to findings developed by Galbreath et al. (2014) for Coho Salmon (*O. kisutch*), our data suggest that fitness recovery could be much more immediate. The survival advantages and apparent rapid increased fitness demonstrated by Sockeye Salmon hatched in Redfish Lake have allowed the development of realistic population triggers for the program's expansion effort. This type of natural rebuilding scenario is the hoped for result when conservationists intervene to rescue depleted populations.

The careful stepwise efforts carried out by the Redfish Lake Sockeye Salmon program in first containing the immediate extinction threat and then addressing multiple levels of gene rescue, habitat improvements, and carrying capacity issues can be seen as a model for future endeavors. As we noted in the Introduction, over 30 peer-reviewed scientific papers and countless reports have helped set the science-based stage for program advancement. Additionally, at the onset, we convened the Stanley Basin Sockeye Technical Oversight Committee, a working group of state, tribal, federal, and nongovernmental organization partners. This cohesive structure has been foundational in guiding science for the program and is requisite for projects of this kind. It seems highly likely that without the steps undertaken by the Redfish Lake Sockeye Salmon captive broodstock program, this ESA-listed endangered stock would currently be extinct. It also seems a virtual certainty that the steps described above have put the population on the road to recovery. To our knowledge, we are the first to report on the use of population integration standards developed by the HSRG (Paquet et al. 2011) to balance both hatchery and developing natural components of critically at-risk populations. It is our recommendation that these types of planning processes become standard operating procedures for all population interventions of this type.

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