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ARTICLE

Achieving Productivity to Recover and Restore Columbia River Stream-Type Chinook Salmon Relies on Increasing Smolt-To-Adult Survival

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Abstract
We analyzed and compared productivity and survival rates of populations of stream-type Chinook Salmon *Oncorhynchus tshawytscha* from the upper and middle ranges of their distribution in the Columbia River basin. These two groups of populations undergo vastly different exposures during migration through the Federal Columbia River Power System (FCRPS). Declines of the Snake River populations, listed as threatened under the U.S. Endangered Species Act, have been associated with the development and operation of the FCRPS. In contrast, John Day River stream-type Chinook Salmon populations, which were less affected by the FCRPS, have declined to a lesser extent and are not listed. Smolt-to-adult survival rates (SARs) accounted for a majority of the variation in life cycle survival rates of Snake River Chinook Salmon. Productivity declined to 13% and 44% of historical productivity levels for Snake River and John Day River populations, respectively. A synthesis of previous studies contrasting anthropogenic impacts between the two regions supports the conclusion that FCRPS impacts explain the large difference in population productivity. Our results suggest that SARs of 4% would result in an expected productivity of up to 70% of historical levels (a SAR level consistent with regional restoration objectives). The SARs have been shown to be highly influenced by conditions within the FCRPS (e.g., water velocity and passage through dam powerhouses). Marine conditions also influence SARs; however, meaningful management actions are only available to affect conditions within the FCRPS. Given the importance of SARs to overall life cycle productivity, recovery and restoration strategies need to prioritize actions that have potential to substantially increase SARs by addressing the significant impacts of main-stem dams. This study highlights the importance of considering river management options in the face of increasingly variable and warming ocean conditions.

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Overall life cycle survival and recruitment of Pacific salmon *Oncorhynchus* spp. are regulated by conditions in both freshwater and marine environments (Bradford 1995; Bisbal and McConnaha 1998; Peterman et al. 1998; Lawson et al. 2004; Michel 2019). The relative importance of freshwater and marine factors is seldom quantified because a long time series of life-stage-specific demographic data is required and often unavailable. Understanding the relative influence of these factors is critical to manage and craft actions that can restore depressed Pacific salmon populations (NPCC 2014).

Major anthropogenic changes have affected life cycle survival and recruitment of Columbia River basin stream-type Chinook Salmon *Oncorhynchus tshawytscha*. Large hydroelectric dams have been built in the Snake and Columbia River migration corridor (Figure 1) in the latter half of the 20th century (Raymond 1988; ISG 1999; Budy et al. 2002). Declines in Snake River life cycle survival, productivity, and smolt-to-adult survival rates (SARs) coincident with completion and operation of the Federal Columbia River Power System (FCRPS) have been well documented in the literature (Raymond 1988; Petrosky et al. 2001; Wilson 2003; Schaller et al. 2014). The number of dams encountered by smolts emigrating from the Snake River increased from two in the early 1950s to eight by 1975. One effect of reservoir impoundment has been a 10-fold reduction in water velocity. Managers have sought to mitigate the impacts of these projects by modifying the physical structures of dams, among other remedial actions. Freshwater habitat had also been altered in many Snake and mid-Columbia tributaries since European settlement, although several spawning and rearing areas of the Snake River basin remain in a relatively pristine condition (Thurow et al. 1997; Thurow 2000; Budy and Schaller 2007; NOAA 2017). Harvest of Columbia River basin Pacific salmon stocks has been reduced or eliminated as many have been listed under the Endangered Species Act (ESA). Consequently, a large hatchery system, under the Lower Snake River Compensation Plan, has been built to mitigate for lost harvest and to supplement wild populations. Individual populations may be managed with any combination of these four basic approaches: hydrosystem actions, habitat remediation, harvest limits, or hatchery inputs. How effective each management approach has been to improve life cycle survival and recruitment has been debated vigorously.

Mitigation programs (e.g., Fish and Wildlife Program under Northwest Power Act; NPCC 2014) and ESA management actions (e.g., National Oceanic and Atmospheric Administration Biological Opinions and Recovery Plans; NMFS 2000; NOAA 2014, 2017) have provided incremental improvements in FCRPS passage and survival, but much of the focus remains on restoring tributary habitat. However, tributary habitat restoration projects require adequate numbers of spawning adult fish to realize benefits. A program has been implemented over the last 25 years that increases the proportion of water discharge that is spilled over the FCRPS dams to reduce the numbers of smolts that pass through the powerhouses (bypass and turbine routes). That action has been associated with higher levels of SARs for both Snake River stream-type and ocean-type Chinook Salmon (Buchanan et al. 2011; Haeseker et al. 2012; Schaller et al. 2014; CSSOC 2017). Despite these incremental efforts, both SARs and full life cycle survival rates have remained very low. A focus on key limiting factors is crucial for success of all restoration activities (Budy and Schaller 2007; NPCC 2014).

Endangered Species Act recovery and broadscale rebuilding (stable populations supporting harvest) goals have been formulated over the last several years (e.g., NOAA 2017; CBPTF 2019; IDFG 2019). The Interior Columbia Technical Recovery Team developed viability criteria to achieve ESA recovery (low or very low risk of population extinction; ICTRT 2007). The Northwest Power and Conservation Council's (NPCC) Fish and Wildlife Program identified main-stem survival objectives (SARs in the range of 2–6% and averaging 4%) for listed Pacific salmon populations (NPCC 2014) to achieve sufficient survival rates to recover ESA-listed populations and progress towards broadscale rebuilding goals.

The purpose of this paper is to examine the historical SARs, productivity values, and annual life cycle survival rates of Columbia River basin stream-type Chinook Salmon and to use this information to guide our present understanding of how survival rates in the smolt-to-adult life stage can influence the overall productivity of these populations. We accomplish this by updating a long time series of spawner–recruit data reported in Schaller et al. (2014) and comparing those data with SARs to determine how much variation in life cycle survival rates is explained by SAR values. The smolt-to-adult life stage in this paper includes mortality during seaward migration and in the marine environment. We also synthesize the work of previous peer-reviewed studies to identify potential management actions for improving SARs.

Our study advances Schaller et al.'s (2014) investigation of spatial and temporal lines of evidence to assess the decline of Snake River stream-type Chinook Salmon populations in response to development and operation of the FCRPS. We compare and contrast populations in Idaho and Oregon over time to relate the effects of past management approaches on life cycle survival and recruitment. We analyze and compare productivity and survival rates of stream-type Chinook Salmon populations from two regions of the Columbia River basin that undergo vastly different exposures during migration through the FCRPS. That analysis provides insight into broadscale SAR rebuilding objectives and their consistency with achieving ESA viability for abundance and productivity goals. Declines in abundance

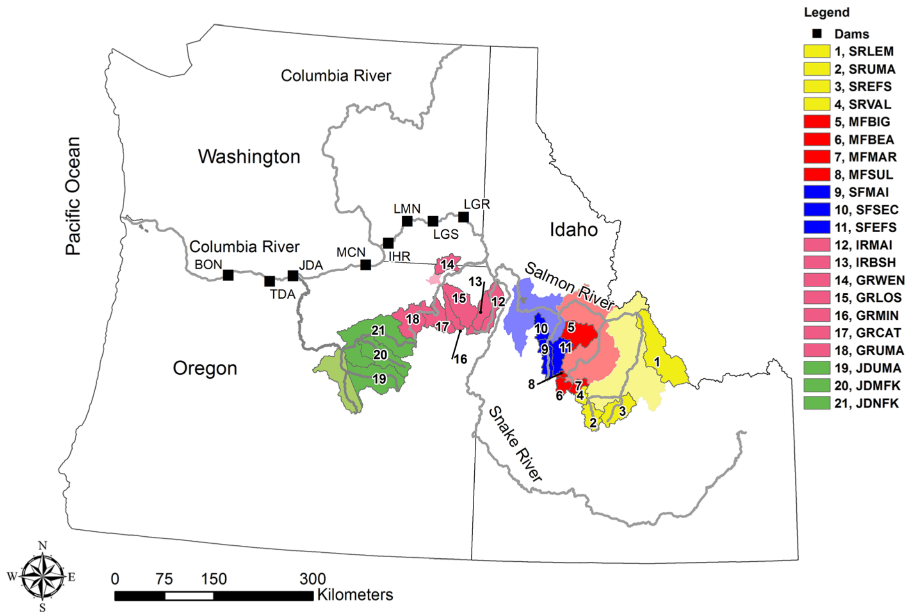

FIGURE 1. Map of the Columbia and Snake rivers, showing the spawning and rearing areas currently occupied by John Day River and listed Snake River stream-type Chinook Salmon (colored shaded areas). The study populations are within five major population groups: John Day River (green), Grande Ronde–Imnaha (pink), South Fork Salmon (blue), Middle Fork Salmon (red), and Upper Salmon River (yellow). Population abbreviations used in the legend are defined in Table 1. The dates of dam completion for eight hydropower dams on the lower Snake River and Columbia River are as follows: Lower Granite Dam (LGR) in 1975, Little Goose Dam (LGS) in 1970, Lower Monumental Dam (LMN) in 1969, Ice Harbor Dam (IHR) in 1961, McNary Dam (MCN) in 1953, John Day Dam (JDA) in 1968, The Dalles Dam (TDA) in 1957, and Bonneville Dam (BON) in 1938. Smolt collection and transportation facilities are at LGR, LGS, LMN, and MCN.

and productivity of Snake River stream-type Chinook Salmon over the latter half of the 20th century are associated with development and operation of the FCRPS (Schaller et al. 2014); these populations have been listed as threatened under the ESA since 1992. In contrast, productivity of mid-Columbia stream-type Chinook Salmon declined to a lesser extent over this period and those populations remain unlisted. Populations from the two regions experience a diverse variety of anthropogenic impacts to tributary spawning and rearing habitats and from hatchery programs and harvest management. Finally, the results of these analyses and our synthesis of the literature help to provide focus for management and restoration activities that have the potential to increase SARs to achieve ESA viability criteria and progress towards broadscale population goals. This comprehensive approach could be applied broadly to other river systems by doing the following: (1) prioritizing the restoration actions for a population based on biological considerations and (2) informing the allocation of limited financial resources effectively to recover and rebuild the populations.

METHODS

We evaluated life cycle survival rates and SAR patterns for stream-type Chinook Salmon populations from the Snake and John Day rivers and synthesized findings from peer review literature in the context of environmental and management changes that have occurred over the past 70 years. Stream-type Chinook Salmon from both regions have similar life history characteristics (Schaller et al. 2007), producing yearling smolts that migrate seaward in April and May and return as adults in spring and early summer after spending 2 or 3 years at sea; a small fraction of males return after a single year (i.e., jacks). Ocean fishery exploitation of both evolutionarily significant units (ESUs) is negligible (Schaller et al. 2000; PFMC 2011). The number of federal dams encountered by emigrating juvenile Pacific salmon increased during the period of data collection from two to eight for Snake River populations and from two to three for John Day River populations. Most of the additional dam construction occurred in the late 1960s and early 1970s. The geomorphology and habitat quality of the populations' freshwater spawning and rearing habitat are diverse within the Snake River basin and some, like the Grande Ronde and Imnaha rivers, have very similar attributes to those in the John Day River basin. The John Day and Middle Fork Salmon rivers have no hatcheries, but the Middle Fork Salmon River has more high quality habitat. Historically, all populations supported main-stem Columbia River harvest rates exceeding 50%, as well as substantial tributary harvest.

Recently, main-stem harvest rates have been constrained greatly under the U.S. versus Oregon Fisheries Management agreement. No directed nontribal harvest on wild fish occurs in the Snake River basin, while the John Day River populations experience limited terminal harvest under certain conditions (U.S. v. Oregon 2018).

Subject populations.— Study populations include 18 populations from four major population groups (MPGs) of the Snake River spring–summer Chinook Salmon ESU and three populations from the John Day MPG of the mid-Columbia spring Chinook Salmon ESU (Figure 1). Freshwater spawning and rearing habitat quality varies among the populations. Budy and Schaller (2007) calculated habitat quality scores and defined habitat quality ratings for Snake River stream-type Chinook Salmon populations using NMFS (2004) habitat impairment ratings (Table 1). Habitat quality for study populations in the Middle Fork Salmon MPG were consistently rated high quality. The majority of the Middle Fork Salmon River and tributaries lies within the Frank Church River of No Return Wilderness Area or within adjacent federal lands, and the habitat is relatively pristine, diverse, and connected (Thurow 2000; NOAA 2017). Habitat quality was rated as medium in the South Fork Salmon MPG populations. The habitat is largely under federal jurisdiction and portions are high-quality habitat. However, several areas have been degraded by road construction, timber harvest, and domestic livestock grazing (NOAA 2017). Populations in the Upper Salmon and Grande Ronde–Imnaha MPGs have a mix of habitat quality ratings ranging from low to high. Federal lands, including wilderness, dominate the upper elevations of the Upper Salmon MPG, with lower elevations and valley bottoms often in private ownership; habitat quality impacts include irrigation withdrawals, grazing, timber harvest, and mining (NOAA 2017). While the Grande Ronde–Imnaha MPG has experienced habitat degradation, some of the habitat today is in good condition; the Minam and Wenaha River populations inhabit wilderness and the Imnaha River also has high-quality habitat. The upper main-stem Grande Ronde River, Catherine Creek, and Wallowa–Lostine River populations experience altered hydrology, reduced habitat quality, and complexity (NOAA 2017). Impacts to habitat quality for the John Day River populations include altered hydrology, irrigation withdrawals, grazing, timber, and mining. Using the Budy and Schaller (2007) approach and NMFS (2004) habitat impairment ratings, we estimated that habitat quality was rated as low for the three John Day River populations. The John Day and Grande Ronde–Imnaha MPGs share the dominant geology and biome of the Blue Mountain ecoregion (Table 1).

The potential influence of hatchery fish varies widely across the study populations (Table 1). No hatchery Chinook Salmon are released within the Middle Fork Salmon and John Day MPGs. Hatchery programs for Chinook Salmon in the other three MPGs include the main-stem South Fork Salmon River, main-stem Upper Salmon River, and Grand Ronde–Imnaha River populations, except the Minam and Wenaha rivers, to mitigate for FCRPS impacts to salmonid productivity and harvest opportunity losses (Table 2). Supplementation programs have been implemented within some Snake River populations with the goal of maintaining or increasing natural abundance, while maintaining the long-term productivity (Venditti et al. 2018). Examples include Johnson Creek in Idaho and the Lostine–Wallowa River, upper Grande Ronde River, Catherine Creek, and main-stem Imnaha River populations in Oregon (Feldhaus et al. 2017).

We updated the spawner and recruit data compiled and analyzed by Schaller et al. (2014) with six more brood years (Figure 2). We summarized natural spawner abundance of Snake River populations relative to the minimum abundance threshold viability criterion (ICTRT 2007) for a recent period (1998–2010) that coincides with FCRPS management actions undertaken in National Oceanic and Atmospheric Administration Biological Opinions (NMFS 2000, 2004; NOAA 2014). Monitoring and evaluation emphasizing placement of passive integrated transponder (PIT) tags in emigrating juveniles to track passage and survival through the FCRPS increased during this period. Comparable SAR metrics based on PIT tags exist for both Snake River and John Day River populations in the recent period (McCann et al. 2017).

We updated the series of data that relates abundance of parents to their progeny using the methods and definitions of spawners and recruits described in Schaller et al. (2014). Numbers of spawners and spawning ground recruits for Snake River populations were estimated through brood year 2009 or 2010 by state and tribal fisheries agencies for the National Oceanic and Atmospheric Administration Fisheries ESA 5-year review process (NFSC 2015). The Big Sheep Creek (Imnaha River tributary) population was functionally extirpated in the recent period, and spawner and recruit data were updated only through brood year 2004. We expanded estimates of spawning ground recruits to preharvest recruits to the Columbia River mouth (Figure 2; Table 2). We updated the John Day River spawner and recruit data from spawner redd counts and Columbia River harvest estimates maintained by U.S. v. Oregon Technical Advisory Committee (unpublished data). The age composition and hatchery fractions from Bare et al. (2016) are used to estimate the abundance of adult recruits to the Columbia River mouth.

Survival rate index.— We applied a survival rate index (SRI) to characterize annual changes in life cycle survival rates (Schaller et al. 1999) and compared index values with population recruitment during a baseline period, before most of the current dams were built, to survival rates

TABLE 1. Study populations of Chinook Salmon by major population group, with selected habitat and hatchery characteristics.

Major population group	Population[a]	Abbreviation[a]	Adult life history type[a]	Ecoregion[b]	Weighted habitat quality score[c]	Habitat rating[d]	First year of hatchery return[e]
Upper Salmon River (USR)	Lemhi River	SRLEM	Spring	MR	7.80	Low	NA
	Upper Salmon River main stem	SRUMA	Spring	IB	5.55	Medium	1985
	East Fork Salmon River	SREFS	Spring–summer	MR–IB	3.50	High	1984
	Valley Creek	SRVAL	Spring	IB	5.20	Medium	NA
Middle Fork Salmon River (MFS)	Big Creek	MFBIG	Spring–summer	IB	2.00	High	NA
	Bear Valley Creek	MFBEA	Spring	IB	1.50	High	NA
	Marsh Creek	MFMAR	Spring	IB	2.00	High	NA
	Sulphur Creek	MFSUL	Spring	IB	3.00	High	NA
South Fork Salmon River (SFS)	South Fork Salmon River main stem	SFMAI	Summer	IB	4.70	Medium	1982
	East Fork South Fork Salmon River	SFEFS	Summer	IB	4.40	Medium	2002
	Secesh River	SFSEC	Summer	IB	4.25	Medium	NA
Grande Ronde–Imnaha rivers (GRIM)	Imnaha River main stem	IRMAI	Spring–summer	BM	2.95	High	1986
	Big Sheep Creek	IRBSH	Spring	BM	4.60	Medium	1993
	Wenaha River	GRWEN	Spring	BM	3.35	High	NA
	Lostine River	GRLOS	Spring	BM	8.95	Low	2004
	Minam River	GRMIN	Spring	BM	3.75	High	NA
	Catherine Creek	GRCAT	Spring	BM	13.00	Low	1987
	Upper Grande Ronde River main stem	GRUMA	Spring	BM	9.05	Low	1987
John Day River (JDA)	John Day River upper main stem	JDUMA	Spring	BM–CP	13.05	Low	NA
	Middle Fork John Day River	JDMFK	Spring	BM–CP	11.70	Low	NA
	North Fork John Day River	JDNFK	Spring	BM–CP	10.90	Low	NA

[a]Source: ICTRT (2007).

[b]U.S. Environmental Protection Agency ecoregion captures the dominant geology and biome; CP = Columbia Plateau, BM = Blue Mountains, IB = Idaho Batholith, and MR = Middle Rockies.

[c]Source: NMFS (2004) and Budy and Schaller (2007); a higher score indicates a greater probability of degradation.

[d]Habitat quality for Snake River ESU from Budy and Schaller (2007); habitat quality for John Day populations applied the methods of Budy and Schaller (2007) in this study.

[e]First year in which adult (>age-4) Chinook Salmon returned from hatchery program(s) operating within a population; NA = not applicable.

during the smolt-to-adult life stage. The SRIs are deviations from predicted recruits and spawners, accounting for density-dependent effects for the period preceding the completion of the FCRPS (Schaller et al. 1999, 2014; Schaller and Petrosky 2007). We classified the spawner and recruit data for each population into two periods (before 1970 and after 1974) defined by FCRPS development and operations affecting the threatened Snake River

TABLE 2. Summary statistics for the recent period (brood years 1998–2010) for Snake River and John Day River stream-type Chinook Salmon populations. Major population groups (MPGs) and population abbreviations are defined in Table 1; other abbreviations are as follows: MAT = minimum abundance threshold, NOS = natural origin spawners, and NA = not applicable.

Region and MPG	Population	Brood years	Fraction of hatchery spawners after 1997	MAT	NOS after 1997	NOS as % MAT	NOS as % before 1970	Recruits after 1997	Recruits as % before 1970
Snake River									
USR	SRLEM	1957–2010	0.00	1,000	164	16	10	270	4
	SRUMA	1957–2010	0.36	1,000	473	47	35	812	12
	SREFS	1957–2010	0.01	1,000	365	37	20	690	12
	SRVAL	1957–2010	0.00	500	119	24	17	243	12
MFS	MFBEA	1957–2010	0.00	750	518	69	32	937	15
	MFMAR	1957–2010	0.00	500	272	54	27	582	12
	MFSUL	1957–2010	0.00	500	74	15	22	148	11
	MFBIG	1957–2010	0.00	1,000	237	24	38	371	17
SFS	SFMAI	1957–2009	0.38	1,000	824	82	34	1,672	30
	SFEFS	1957–2009	0.37	1,000	355	36	42	743	30
	SFSEC	1957–2009	0.04	750	658	88	99	1,247	83
GRIM	IRMAI	1949–2010	0.61	1,000	528	53	24	1,036	15
	IRBSH	1964–2004	0.79	500	20	4	3	42	2
	GRWEN	1949–2010	0.04	750	431	57	29	711	11
	GRLOS	1949–2009	0.41	1,000	373	37	44	1,046	22
	GRMIN	1954–2010	0.02	750	467	62	46	877	25
	GRCAT	1953–2010	0.44	1,000	135	14	12	392	8
	GRUMA	1956–2009	0.37	1,000	46	5	11	211	10
John Day River									
JDA	JDUMA	1959–2010	0.03	NA	926	NA	495	1,826	269
	JDMFK	1960–2010	0.03	NA	716	NA	439	1,241	180
	JDNFK	1959–2010	0.03	NA	1,751	NA	102	2,621	43

populations following the methods and definitions of Schaller et al. (1999). The two periods provide a contrast of main-stem river conditions before and after completion of the final two Snake River dams. During the post-1974 period, smolts were collected and transported around dams in barges and trucks, turbines were screened, and other management actions were implemented to improve passage at the dams (Raymond 1979; Budy et al. 2002). Population status during the historical base period was generally considered by managers as healthy and harvestable (CBPTF 2019; IDFG 2019), while the post-1974 period was characterized by major population declines, ESA listings, and multiple FCRPS mitigation actions. Populations experienced wide variations in sea surface temperatures in both periods, as indicated by the Pacific Decadal Oscillation (PDO) index (Mantua et al. 1997). While PDO index values averaged lower in the historical base period than in the post-1974 period, Chinook Salmon in both periods experienced warm and cool marine conditions and the annual PDO index values overlapped considerably between periods (http://research.jisao.washington.edu/pdo/PDO.latest.txt).

We used the updated spawner and recruit data to estimate productivity, defined in Schaller et al. (1999), as the natural logarithm of the ratio of recruits to spawners [ln (R/S)] in the absence of density-dependent mortality. The spawner and recruit data were fit to the Ricker recruitment function (Ricker 1975). Critical to the application of this approach is the expectation of a temporal change in density-independent mortality, such as that imposed by development and operation of hydroelectric dams or an oceanic regime shift, will be reflected primarily in the intercept (Ricker a) rather than in the slope (β) of the regressions. Evidence of nonstationarity is well established in the fisheries literature (Walters 1987; Zhang et al. 2018; Litzow et al. 2019). We examined nonstationarity in the recruitment functions (Hilborn and Walters 1992; Ruggerone 2003; Zhang et al. 2018; Litzow et al. 2019) by updating the analysis of covariance presented in Schaller et al. (1999, 2014) and Schaller and Petrosky (2007) to

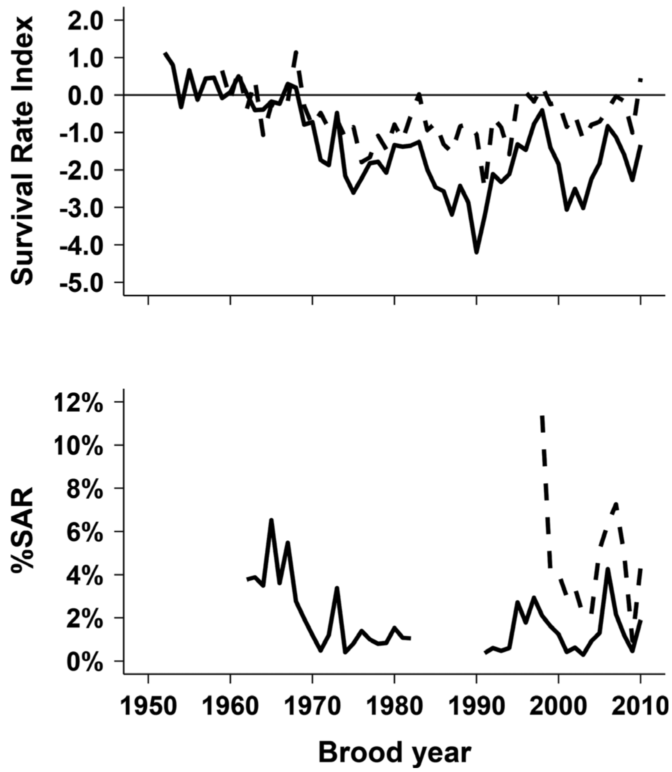

FIGURE 2. Survival rate index patterns (top panel) and smolt-to-adult survival rate (SAR; bottom panel) for Snake River (solid line) and John Day River (dashed line) stream-type Chinook Salmon.

quantify differences in the intercepts (Schaller et al. 2014; equation 2) that would represent the period effect on productivity. Updated model fits were estimated in the R programing environment (R Core Team 2018).

Smolt-to-adult survival rates.— Estimates of SARs for the Snake River and John Day River populations were obtained from McCann et al. (2017, 2018). Snake River SARs from brood years 1962–2010 (smolt migration years 1964–2012) represented smolts arriving at the uppermost Snake River dam (Lower Granite since 1975) and adults and jacks returning to the Columbia River mouth (Petrosky and Schaller 2010). These values represent preharvest SARs because (as noted above) ocean exploitation of these populations is negligible. The smolt-to-adult life stage includes mortality during seaward migration and in the marine environment. Snake River SARs were based on PIT tag estimates from 1994 forward and run reconstruction methods in prior years; no SARs were available for 1985–1993 due to insufficient marking during those years (Petrosky et al. 2001). We use this combination of historical run reconstruction SARs and the recent PIT-based SARs as the primary data set. Historical run reconstruction SAR estimates for Snake River populations encompass survival variations that can be compared to historical changes in management practices and variation in the freshwater and marine environment. For the recent period, we use the PIT tag SAR estimates that are the basis of contemporary and future monitoring programs in the Columbia River basin using PIT tags to estimate SARs and survival rates at multiple life stages for discrete demographic units. John Day River SARs based on PIT tag estimates for brood years 1998–2010 represent smolts arriving at John Day Dam and adults and jacks returning to the Columbia River (McCann et al. 2017, 2018). Run reconstruction estimates of SAR prior to the onset of PIT tagging are unavailable for the John Day River.

Survival rate index versus smolt-to-adult survival rate.— We examined the influence of freshwater migratory and ocean survival rates (i.e., SARs) on scaled life cycle survival rates (i.e., SRIs) by evaluating how much of the variation in SRIs could be explained by SAR values. Snake River overall average SRI was regressed against ln (SAR) for brood years 1962–2010 (equation 1) and plotted by decade of smolt migration to examine temporal patterns.

$$\mathrm{SRI}_j = \alpha + \beta \cdot \ln(\mathrm{SAR}_j) + \varepsilon_j \quad (1)$$

where α is the intercept, β is the regression slope, j is the brood year, and ε_j is the normally distributed residual.

We also examined the relationship of average SRI and ln(SAR) for each MPG to assess spatial patterns within the Snake River ESU. Average SRIs for the John Day River populations were regressed against ln(SAR) for brood years 1998–2010. We assessed the relationship between SRI against ln(SAR) for a combined John Day River and Snake River data set. Finally, we examined the predicted SRI at different levels of SAR to evaluate the efficacy and general applicability of the NPCC 2–6% SAR objectives to recover and rebuild those populations.

Run reconstruction sensitivity analysis.— The PIT-tag-based SARs for the Snake River populations have averaged about 70% of those based on run reconstruction (McCann et al. 2018). Therefore, we conducted a sensitivity analysis to examine the robustness of conclusions from our primary data set. For this purpose we used the Snake River SARs estimated both with run reconstruction methods and PIT tag marking and subsequent detections (Camacho et al. 2018; McCann et al. 2018). We expanded the run-reconstruction-based SARs (calculated for adult returns to Lower Granite Dam) to the Columbia River mouth using the annual ratios of run-reconstruction-based SAR to PIT-tag-based SAR (McCann et al. 2018) and regressed the aggregate Snake River SRI against run-reconstruction-based ln(SAR) for brood years 1962–2010 to bound the expected response between SAR and SRI. We then examined the predicted SRI at different levels of run-reconstruction-based SAR compared to predictions from the PIT-tag-based method. This sensitivity analysis was only possible for the Snake River aggregate for these brood years.

RESULTS

Population Summary Statistics

Average spawner abundance of the Snake River populations during the recent period was about one-third that of the baseline, prior to full FCRPS development (Table 2), despite decreases in Columbia River fishery exploitation, modifications to passage at the dams, and a mass juvenile fish transportation program. Recruitment of Snake River populations declined fivefold to 19% of the base period. The abundance of Snake River natural-origin spawners during brood years 1998–2010 averaged 40% of the minimum abundance threshold, well less than ESA abundance delisting criterion. Hatchery-origin spawners comprised a variable proportion of total spawners in Snake River populations, ranging from 0% to 79%.

John Day River spawner abundance increased in recent years (1998–2010) relative to the base period (Table 2), due in part to reductions in Columbia River fishery exploitation following FCRPS development and juvenile passage improvements at John Day Dam. Recruitment increased relative to the base period for two populations and declined for the third population. Hatchery strays comprised an estimated 3% of total spawners in the John Day River populations during 1998–2010.

Survival Rate Index

Average productivity and survival rates declined more for Snake River than for John Day River populations following FCRPS completion. Average productivity declined from the pre-1970 baseline by 2.04 for Snake River populations and by 0.82 for John Day River populations for brood years 1975–2010 (Table 3; Figure 2, top panel). In other words, the expected ratio of recruits to spawners (R/S) declined to 13% ($e^{-2.04}$) and 44% ($e^{-0.82}$) of the historical productivity level for Snake River and John Day River populations, respectively. Although the magnitude of decline differed between Snake River and John Day River populations, the SRIs were highly correlated ($r = 0.68$) over the entire time series. Within the Snake River populations, the average decline in productivity was similar for populations in high- and low-quality habitat (–2.23 and –2.36, respectively; Table 3).

Snake River populations with > 10% hatchery fractions on the spawning grounds experienced declines in productivity similar to those with lower hatchery fractions (–1.99 and –2.17, respectively; Table 3).

Smolt-To-Adult Survival Rates

Snake River preharvest SARs decreased from about 4% in the 1960s to about 1% in the post-1974 period (Figure 2, bottom panel). Snake River SARs in the post-1974 period have varied widely, ranging from as low as 0.3% (2003 brood year) to as high as 4.3% (2006 brood year). In recent brood years (1998–2010), the geometric mean of Snake River SARs was 1.1%. The SARs were less than 2% in 10 of 13 years and less than 1% in 5 years. In contrast, recent John Day River SARs ranged from 0.9% to 11.4%, averaging 3.9% and exceeding 2% in 12 of 13 years (Figure 2). Although differing in magnitude, the ln(SAR) values of Snake River and John Day River populations were highly correlated ($r = 0.77$) in recent years.

Survival Rate Index versus Smolt-To-Adult Survival Rates

Migratory and ocean survival explained much of the variation in recruitment of Chinook Salmon in all of the study populations. A large portion of the variation (80%) in Snake River SRIs was explained by ln(SAR) for brood years 1962–2010 (Table 4). The SARs in the 1960s (1964–1969 smolt migrations) ranged from 3.5% to 6.5%, while parental spawner levels resulted in preharvest recruitments within the expected range (by definition) for the base period. Both SARs and SRIs declined in the 1970s and remained depressed in subsequent decades (Figure 3). The relationship between SRI and SAR appears very consistent across the decades. The prediction line indicates that a preharvest SAR of 2% is associated with 35% of base-period productivity; preharvest SARs of 4% and 6% are associated with 70% and 106% of base-period productivity, respectively (Table 5).

The pattern of SRIs and SARs is quite similar across the geographic range of the four Snake River MPGs (Table 4; Figure 4). The slope of the regression for the South Fork Salmon River MPG is less than for the other MPGs, however. Historical levels of productivity are associated with SARs approaching 5–6% for all ESA-listed Snake River MPGs upstream of Lower Granite Dam (Table 5).

The pattern of John Day River SARs and SRIs is generally similar to that in the Snake River (Table 4; Figure 4), although the John Day River sample size (13) was limited. The John Day River prediction line indicates that a preharvest SAR of 2% is associated with 45% of base-period productivity; preharvest SARs of 4% and 6% are associated with 67% and 85% of base-period productivity, respectively (Table 5). A regression of combined Snake River and John Day River SAR data explained a high degree of variation in SRIs (82%) and indicates that a preharvest SAR of 2% is associated with 34% of base-period

TABLE 3. Analysis of covariance results for Ricker recruitment functions that used period (treatment) and spawners (covariate) for stream-type Chinook Salmon MPGs and populations from the Snake River and John Day River regions, brood years 1950s–2010. The MPG and population abbreviations are defined in Table 1.

Region and MPG	Population	Brood years	Intercept before 1970	Intercept after 1974	Intercept difference	Intercept *P*-value	Slope	Slope *P*-value	R^2	Slope homogeneity *P*-value
					Snake River					
USR	SRLEM	1957–2010	2.62	0.62	2.01	<0.01	–0.0008	<0.01	0.24	<0.01
	SRUMA	1957–2010	2.95	1.17	1.78	<0.01	–0.0010	<0.01	0.48	0.71
	SREFS	1957–2010	2.99	0.84	2.15	<0.01	–0.0010	<0.01	0.26	0.10
	SRVAL	1957–2010	3.05	0.86	2.19	<0.01	–0.0027	<0.01	0.35	<0.01
MFS	MFBEA	1957–2010	3.91	1.11	2.80	<0.01	–0.0016	<0.01	0.34	0.11
	MFMAR	1957–2010	3.87	0.93	2.94	<0.01	–0.0023	<0.01	0.39	0.06
	MFSUL	1957–2010	3.69	0.96	2.73	<0.01	–0.0066	<0.01	0.39	0.05
	MFBIG	1957–2010	2.99	1.15	1.84	<0.01	–0.0029	<0.01	0.30	<0.01
SFS	SFMAI	1957–2009	1.75	0.64	1.11	<0.01	–0.0004	<0.01	0.28	<0.01
	SFEFS	1957–2009	2.45	1.03	1.42	<0.01	–0.0016	<0.01	0.38	0.25
	SFSEC	1957–2009	1.60	1.17	0.43	0.09	–0.0012	<0.01	0.26	0.02
GRIM	IRMAI	1949–2010	2.39	0.66	1.73	<0.01	–0.0006	<0.01	0.57	<0.01
	IRBSH	1964–2004	1.65	–0.81	2.46	0.09	–0.0009	0.32	0.23	0.92
	GRWEN	1949–2010	2.51	0.46	2.05	<0.01	–0.0008	0.01	0.38	0.16
	GRLOS	1949–2009	3.21	1.07	2.14	<0.01	–0.0018	<0.01	0.54	0.54
	GRMIN	1954–2010	2.41	0.80	1.60	<0.01	–0.0010	<0.01	0.45	0.08
	GRCAT	1953–2010	2.74	0.23	2.50	<0.01	–0.0009	<0.01	0.40	0.36
	GRUMA	1956–2009	3.40	0.59	2.81	<0.01	–0.0036	<0.01	0.53	0.21
					John Day River					
JDA	JDUMA	1959–2010	1.86	1.08	0.78	<0.01	–0.0008	<0.01	0.36	<0.01
	JDMFK	1960–2010	1.89	1.43	0.47	0.17	–0.0017	<0.01	0.44	0.02
	JDNFK	1959–2010	2.66	1.45	1.22	<0.01	–0.0007	<0.01	0.61	0.41

productivity; preharvest SARs of 4% and 6% are associated with 66% and 98% of base-period productivity, respectively (Table 5; Figure 5).

Run Reconstruction Sensitivity Analysis

Our results are robust to the alternative SAR method. A large portion of the variation (66%) in Snake River SRIs was explained by ln(SAR) for brood years 1962–2010 using run-reconstruction-based SARs (Figure 6). The SRI versus SAR relationship based solely on run reconstruction SARs produced a similar but somewhat lower expectation of life cycle productivity at regional management objectives compared with the primary method. The prediction line indicates that a preharvest SAR of 2% is associated with 25% of base-period productivity; preharvest SARs of 4% and 6% are associated with 49% and 74% of base-period productivity, respectively (Figure 6). Our sensitivity analysis shows that both methods yield SARs that fall well short of levels needed to recover and rebuild Snake River Chinook Salmon populations.

DISCUSSION

Our study results indicate that achieving productivity objectives for Columbia River stream-type Chinook Salmon populations will require improvements to survival in the smolt-to-adult life stage. Our conclusions are robust to the change in measurement of SARs from run reconstruction to PIT tags. The SARs are a function of smolt migration conditions and the marine environment (Petrosky and Schaller 2010; Haeseker et al. 2012; Schaller et al. 2014; Michel 2019). Survival from smolt to adult stage accounted for a majority (about 80%) of the variation in complete life cycle survival rates of Snake River Chinook Salmon. The pattern of the relationship between SRI and SAR in the John Day River was similar to that in the Snake River. A single model fit to SARs of combined Snake River and John Day River data explained a large majority (82%) of the variation in SRIs. The high degree of life cycle survival variation explained by SARs shows that reliance on off-site mitigation (tributary habitat improvement) for FCRPS impacts is unlikely to achieve regional goals.

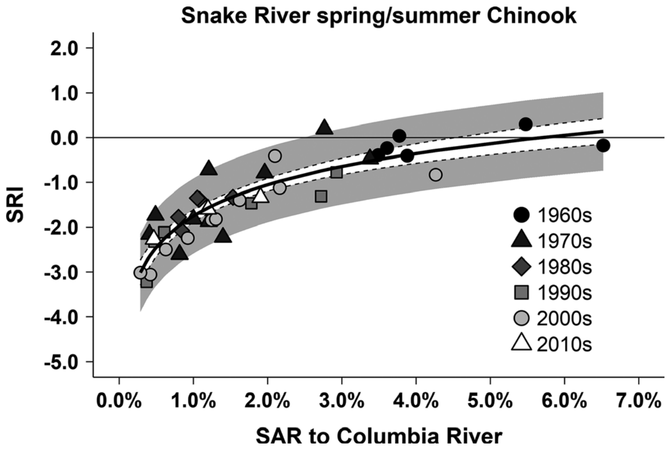

FIGURE 3. Survival rate index (SRI) and SAR patterns of Snake River stream-type Chinook Salmon by decade of smolt migration, 1964–2012. The solid line represents model estimates based on the combined (run reconstruction and PIT tag) SAR data set. The shaded (gray) region represents 95% prediction intervals, and the dashed lines represent 95% confidence intervals.

We found that historical levels of life cycle productivity for Snake River and mid-Columbia River stream-type Chinook Salmon are associated with SARs approaching 6%. The NPCC (2014) identified SAR objectives for listed salmonid populations in the range of 2% to 6%, with an average of 4%. Our results suggest that SARs of 4% would result in a productivity near 70% of the historical baseline levels. Our observations of the relationship between SARs and life cycle survival rates are consistent with those from earlier analyses (Marmorek et al. 1998; Peters and Marmorek 2001). Snake River SARs have declined substantially from about 4% in the latter portion of the base period to an average of about 1% in recent years. In contrast, John Day River populations exhibited higher recent life cycle survival compared with the Snake River populations that migrate through five additional dams. The recent John Day SARs have averaged about 4%, similar to historical levels for the Snake River, and the recent John Day SRIs are relatively closer to their historical levels.

Poor SARs are also related to the marine environment when the PDO index values and sea surface temperatures are warmer and the nearshore upwelling volumes are less. Pacific salmon populations experienced wide variations in PDO index values in both the base period and the post-1974 period. The top models in Schaller et al. (2014) identified the September PDO index values as the most influential marine variable in explaining variation in SRI. However, Snake River SRI declines began in the early 1970s (while the PDO index values were still low) and SRIs remained depressed when Snake River salmonids experienced cooler ocean conditions in the late 1990s and mid-2000s (Schaller and Petrosky 2007; Figure 2).

Snake River populations experience substantial delayed mortality in the marine environment as a result of their out-migration experience through the FCRPS (Williams et al. 2005; Buchanan et al. 2011; Marmorek et al. 2011; Schaller et al. 2014). The out-migration experience results in an accumulation of injuries, multiple stress events, and alteration of estuary arrival timing: mechanisms that may explain delayed mortality (Budy et al. 2002; Muir et al. 2006; Scheuerell et al. 2009; Rechisky et al. 2012). Decreased water velocity and an increased number of powerhouse passages have been related to large increases in the time required for juveniles to migrate to sea and reductions in SRI, SAR, and marine survival rates for Snake River Chinook Salmon (Petrosky and Schaller 2010; Buchanan et al. 2011; Haeseker et al. 2012; Schaller et al. 2014). The avoidance of powerhouse passages has been assessed by directly evaluating spill levels (Haeseker et al. 2012) or through calculating powerhouse passages, which are the compliment of spill levels (Petrosky and Schaller 2010; Schaller et al. 2014). John Day River populations have fewer powerhouse encounters than Snake River populations and hence are impacted less by the FCRPS.

John Day River and Snake River populations have many similar characteristics. Populations in the John Day River and Grande Ronde–Imnaha River MPGs share a

TABLE 4. Regression results for SRI versus ln(SAR) for Snake River populations, Snake River and John Day River MPGs, and for combined Snake River and John Day River data. Abbreviations for MPGs are defined in Table 1.

Population group	n	a	SE(α)	P(α)	β	SE(β)	P(β)	R^2
Snake River								
USR	41	3.2350	0.5151	<0.0001	1.0816	0.1174	<0.0001	0.69
MFS	41	3.5162	0.6024	<0.0001	1.2699	0.1373	<0.0001	0.69
SFS	41	1.9981	0.3510	<0.0001	0.6647	0.0800	<0.0001	0.64
GRIM	41	2.6846	0.4458	<0.0001	0.9583	0.1016	<0.0001	0.70
All Snake River MPGs	41	2.8907	0.3504	<0.0001	1.0082	0.0799	<0.0001	0.80
John Day River								
JDA	13	1.4417	0.5187	0.0179	0.5720	0.1569	0.0038	0.55
All MPGs	54	2.6536	0.2600	0.0000	0.9516	0.0626	<0.0001	0.82

TABLE 5. Predicted percent of historical productivity (95% prediction interval in parentheses) at different SAR levels for Snake River populations, Snake River and John Day River MPGs, and for combined Snake River and John Day River data. Predicted productivity is estimated from the regression parameters for SRI versus ln(SAR) for the population groups (Table 4). Abbreviations for MPGs are defined in Table 1.

Population group	SAR level				
	1%	2%	4%	6%	8%
Snake River					
USR	18 (5–60)	37 (11–127)	78 (22–275)	121 (34–436)	165 (45–608)
MFS	10 (2–41)	23 (5–99)	57 (13–246)	95 (21–42)	136 (30–624)
SFS	35 (15–80)	55 (24–127)	87 (37–205)	114 (48–272)	138 (57–334)
GRIM	18 (6–52)	35 (12–100)	67 (23–199)	99 (33–300)	130 (42–402)
All Snake River MPGs	17 (8–40)	35 (15–81)	70 (30–165)	106 (44–252)	141 (58–342)
John Day River					
JDA	30 (12–75)	45 (20–102)	67 (31–146)	85 (38–187)	100 (44–226)
All MPGs	18 (8–41)	34 (15–78)	66 (29–152)	98 (42–226)	128 (55–299)

dominant geology and biome. Impairment of spawning and rearing habitat quality for John Day River populations is similar to that of the Lostine–Wallowa River, Catherine Creek, and upper Grande Ronde ESA-listed populations (Table 1), yet the relative population performance is vastly different. Performance of the John Day River populations, with uniformly impaired habitat quality, exceeds that of Snake River populations within the Middle Fork Salmon MPG, which has high-quality habitat (Table 1). Stray hatchery influence is low in the John Day River populations and the Snake River populations in the Minam and Wenaha rivers, the Middle Fork Salmon MPG, the Secesh River population, and three populations in the Upper Salmon River (Table 2). Survival and productivity of the Snake River populations with minimal hatchery influence have decreased compared with the John Day River populations, despite their generally better habitat and lower harvest pressure.

Our results are consistent with previous studies of the relative influences of tributary habitat and hatcheries on life cycle survival of Snake River Chinook Salmon. Budy and Schaller (2007) concluded that a “large gap remains between how much survival improvement is needed versus what is likely to occur” in Snake River spawning and rearing habitats. Venditti et al. (2018) found that hatchery supplementation had no apparent lasting influence on adult-to-adult productivity in Snake River populations.

Managers are unlikely to restore productivity of Snake River stream-type Chinook Salmon without major increases in SARs. Incremental improvements in FCRPS passage to date have been insufficient to achieve SAR goals for Snake River Chinook Salmon. A recent court order (Simon 2016) has compelled FCRPS managers and regulators to evaluate the feasibility and efficacy of spill and Snake River dam removal through an Environmental Impact Statement under the National Environmental Policy Act. The potential benefits of actions such as spill and dam removal to ameliorate FCRPS impacts are being evaluated for increasing SARs (CSSOC 2017; USACE et al. 2020). Decreasing the time required for smolts to migrate downstream through the FCRPS and reducing the number of times they are forced to encounter powerhouses should increase SARs for Snake River stream-type Chinook Salmon and for salmonids from other natal rivers of the Columbia River basin. Evaluation of approaches to experimental spill management (CSSOC 2017) estimated that increasing spill for fish passage within safe limits (125% total dissolved gas) had a high probability of improving SARs. We acknowledge there are uncertainties surrounding the efficacy of spill and researchers have varying interpretations of the data underlying arguments for the benefit of avoiding powerhouse encounters (e.g., Faulkner et al. 2019). However, meaningful management actions are only available to affect conditions within the FCRPS that have a potential to increase SARs. The current basinwide marking of representative groups of juvenile salmonids will allow evaluation of the spill program (CSSOC 2017).

Regional management goals emphasize the restoration of healthy and harvestable Pacific salmon populations (NPCC 2014; CBPTF 2019) in the face of variable marine conditions. Projected climate changes that warm oceans and increase variability in environmental conditions suggest that Columbia River basin Pacific salmon may face less favorable future marine survival conditions (Lijing et al. 2019). Those predictions emphasize the need to greatly improve migration conditions through the FCRPS in concert with other actions being implemented to protect and improve freshwater spawning and rearing habitats, improve hatchery practices, and maintain harvest regulations. Our study, including the synthesis of past studies, highlights the importance of considering river management options in the face of increasingly variable and warming ocean conditions.

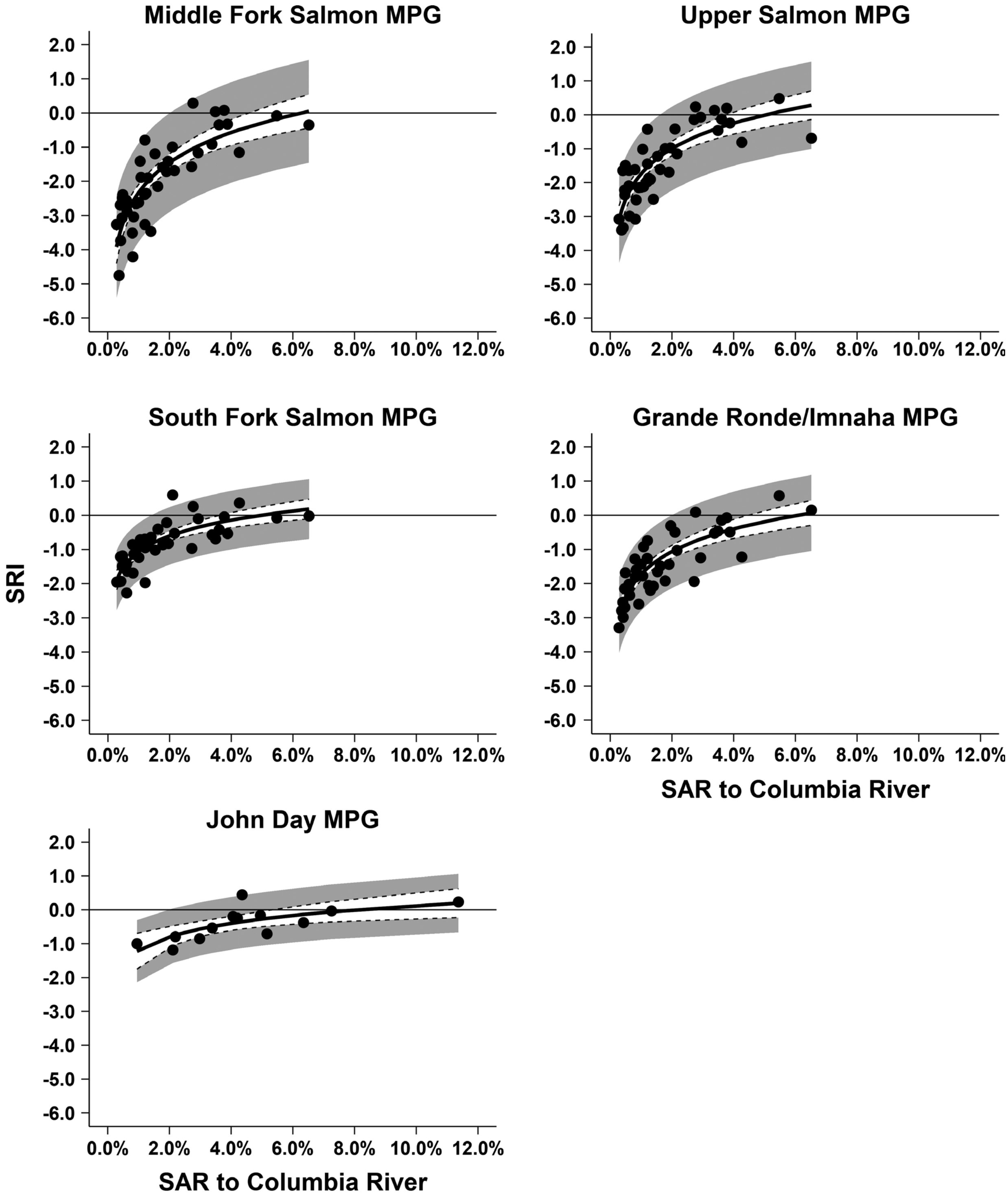

FIGURE 4. The SRI and SAR patterns by major population group (MPG) for Snake River and John Day River stream-type Chinook Salmon. The solid lines represent model estimates fit through the combined SAR data set. The shaded (gray) region represents 95% prediction intervals, and the dashed lines represent 95% confidence intervals.

Natural spawner abundance levels of Snake River Chinook Salmon populations are far below ESA abundance thresholds (Table 2), and the Big Sheep Creek population became functionally extirpated by the early 2000s. The low abundance and perpetuation of low SARs, due in large part to FCRPS configuration and operations, pose

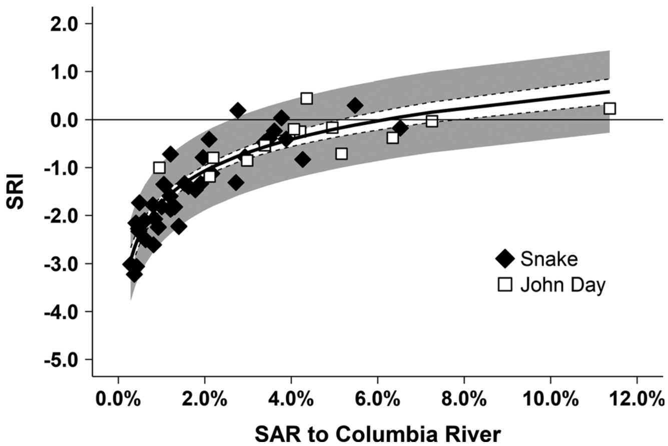

FIGURE 5. The SRI and SAR patterns for Snake River and John Day River stream-type Chinook Salmon. The regression line is fit through the combined SAR data set. The shaded (gray) region represents 95% prediction intervals, and the dashed lines represent 95% confidence intervals.

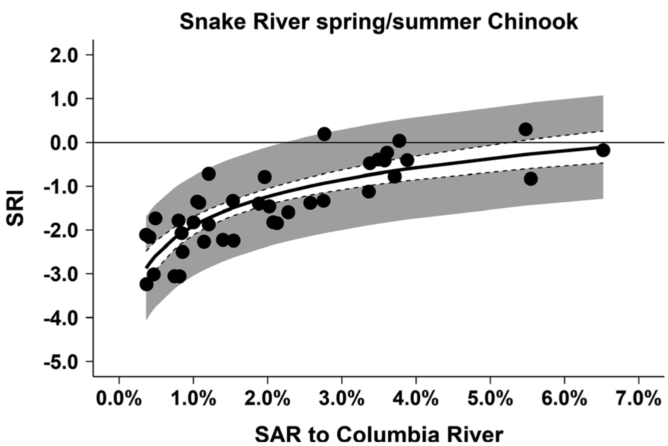

FIGURE 6. The SRI and SAR patterns for Snake River stream-type Chinook Salmon. The regression line is fit through the SAR data set based on run reconstruction. The shaded (gray) region represents 95% prediction intervals, and the dashed lines represent 95% confidence intervals.

both genetic and demographic risks that lead to a high extirpation risk (McElhany et al. 2000; ICTRT 2007; Thompson et al. 2019) to Snake River stream-type Chinook Salmon. The NPCC SAR objectives provide a readily measured metric that gauges whether life cycle survival rates can achieve ESA recovery goals and make progress toward broadscale salmonid restoration efforts (ISAB 2018).

Abundant stream-type Chinook Salmon populations are important socially, culturally, and legally to the Columbia River region to provide tribal, sport, and commercial fishing. Restored, healthy stream-type Chinook Salmon populations provide essential services to the ecosystem through the delivery of critical marine nutrients and as a food source for wildlife (ISG 1999). Restoring the ecosystem function requires a consistent and increased level of returning adults to the Snake and Columbia River stream-type Chinook Salmon populations affected by the FCRPS. Restoration activities should be focused where there is the greatest potential to increase productivity and where the level of risk to meet population recovery and rebuilding goals is lowest—an approach consistently supported in the peer-reviewed literature from scientific investigations of ecology (Crouse et al. 1987; Mangel et al. 2006; Budy and Schaller 2007).

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