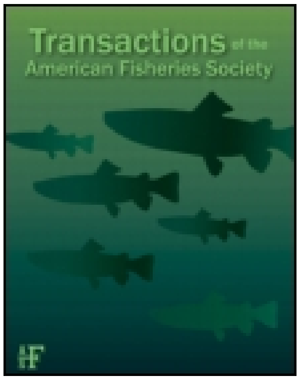

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Assessing Freshwater and Marine Environmental Influences on Life-Stage-Specific Survival Rates of Snake River Spring-Summer Chinook Salmon and Steelhead

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ARTICLE

Assessing Freshwater and Marine Environmental Influences on Life-Stage-Specific Survival Rates of Snake River Spring–Summer Chinook Salmon and Steelhead

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Abstract

Pacific salmon *Oncorhynchus* spp. from the Snake River basin experience a wide range of environmental conditions during their freshwater, estuarine, and marine residence, which in turn influence their survival rates at each life stage. In addition, researchers have found that juvenile out-migration conditions can influence subsequent survival during estuarine and marine residence, a concept known as the hydrosystem-related, delayed-mortality hypothesis. In this analysis, we calculated seasonal, life-stage-specific survival rate estimates for Snake River spring–summer Chinook salmon *Oncorhynchus tshawytscha* and steelhead *O. mykiss* and conducted multiple-regression analyses to identify the freshwater and marine environmental factors associated with survival at each life stage. We also conducted correlation analyses to test the hydrosystem-related, delayed-mortality hypothesis. We found that the freshwater variables we examined (the percentage of river flow spilled over out-migration dams and water transit time) were important for characterizing the variation in survival rates not only during freshwater out-migration but also during estuarine and marine residence. Of the marine factors examined, we found that the Pacific Decadal Oscillation index was the most important variable for characterizing the variation in the marine and cumulative smolt-to-adult survival rates of both species. In support of the hydrosystem-related, delayed-mortality hypothesis, we found that freshwater and marine survival rates were correlated, indicating that a portion of the mortality expressed after leaving the hydrosystem is related to processes affected by downstream migration conditions. Our results indicate that improvements in life-stage-specific and smolt-to-adult survival may be achievable across a range of marine conditions through increasing spill percentages and reducing water transit times during juvenile salmon out-migration.

The adult abundance of Pacific salmon *Oncorhynchus* spp. is determined by survival across multiple life stages and a high degree of variation exists at each life stage (Bradford 1995), across-years (Peterman 1987; Pearcy 1992) and within-years (Scheuerell et al. 2009). Pacific salmon experience a wide range of environmental conditions during periods of freshwater, estuarine, and marine residence, which in turn influence survival rates at each life stage. However, quantifying the relative importance of freshwater and marine factors on survival is often complicated by the lack of life-stage-specific survival data for many salmon populations (Greene et al. 2005). Improving the understanding of the environmental factors that affect salmon survival is especially important for prioritizing and implementing conservation and recovery actions for stocks listed as threatened or endangered under the U.S. Endangered Species Act (Good et al. 2005).

Within the Columbia River basin, Snake River spring–summer Chinook salmon *O. tshawytscha* and steelhead *O. mykiss* declined dramatically in the 1970s, which coincided with development and operation of the Federal Columbia River

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Power System (FCRPS) (Raymond 1988; Marmorek et al. 1998; Schaller et al. 1999). The development and operation of the FCRPS dams and reservoirs has drastically altered freshwater migration habitat conditions, which has resulted in reduced freshwater survival and delayed migration timing of juvenile Chinook salmon and steelhead (Raymond 1988; Williams et al. 2001; Budy et al. 2002; Muir et al. 2006; Williams 2008). For both species, measures of smolt-to-adult survival rates (SARs) also decreased coincident with development and operation of the FCRPS (Raymond 1988; Schaller et al. 1999; Schaller and Petrosky 2007; Petrosky and Schaller 2010).

Beginning in 2003, after these declines in abundance and smolt-to-adult survival became evident, the Northwest Power and Conservation Council (NPCC) adopted a goal of achieving SARs averaging 4% and a minimum of 2% for listed Snake River and upper Columbia River salmon and steelhead (NPCC 2003, 2009). The NPCC (2009) highlighted the need for identifying the effects of ocean conditions on anadromous fish survival so that this information can be used to evaluate and adjust inland actions. The NPCC recognized that a better understanding of the conditions that salmon face in the ocean can suggest which factors will be most critical to survival. New data could be used to determine which actions taken inland will provide the greatest benefit in terms of improving the likelihood that Columbia River basin salmon can survive varying ocean conditions (NPCC 2009).

In addition to the environmental factors that influence survival at each life stage, Budy et al. (2002) presented and discussed evidence that some of the mortality that occurs during the period of estuary and early ocean residence is related to earlier hydrosystem experience during downstream migration, a concept known as the hydrosystem-related, delayed-mortality hypothesis (Schaller and Petrosky 2007). This delayed mortality is thought to be due to the cumulative effects of stress and its effects on energetic condition, predation vulnerability, disease, and physiology of migrating smolts, which eventually influence levels of delayed mortality. Because the same hydrosystem factors that cause direct mortality during downstream migration also impose stress on those fish that do survive, under the Budy et al. (2002) hypothesis mortality rates during downstream migration are expected to be positively correlated with mortality rates at later life stages.

The overall goals of this analysis were to evaluate the Budy et al. (2002) hydrosystem-related, delayed-mortality hypothesis and to quantify the influences of freshwater and marine environmental factors on life-stage-specific survival rate estimates of Snake River spring–summer Chinook salmon and steelhead. To accomplish these goals, we used fish tagged with passive integrated transponder (PIT) tags (Prentice et al. 1990a, 1990b, 1990c) along with the detection system infrastructure located at Columbia and Snake river dams. The PIT-tag detection systems for smolts and adults, when combined with mark–recapture survival estimation models (Burnham et al. 1987; Skalski et al. 1998; Muir et al. 2001a), allow for estimates of survival over several key life stages: (1) during smolt out-migration through a series of hydropower dams and reservoirs; (2) during the period of estuarine and marine residence through adult return; and (3) cumulative smolt-to-adult survival, from the period of smolt out-migration through adult return (Figure 1).

To accomplish these goals, this research effort had four primary objectives. Our first objective was to measure cumulative smolt-to-adult survival to determine whether the NPCC SAR goal (SARs averaging 4% with a minimum of 2%) was being met. Our second objective was to estimate and test the degree of correlation between freshwater survival during juvenile out-migration and subsequent marine survival for each species in order to evaluate the hydrosystem-related, delayed-mortality hypothesis of Budy et al. (2002). Our third objective was to evaluate which environmental factors were most important for characterizing variation in survival rates at each life stage and in terms of cumulative smolt-to-adult survival. Finally, our fourth objective was to identify which actions taken inland would be most critical for improving cumulative smolt-to-adult survival rates (NPCC 2009) and to identify the corresponding freshwater survival rates that may be necessary to achieve the NPCC SAR goal. To accomplish these objectives, we used mark–recapture models (Burnham et al. 1987) with PIT-tagged Snake River spring–summer Chinook salmon and steelhead in combination with information-theoretic and multimodel inference methods (Burnham and Anderson 2002).

METHODS

Study Area

Our study focused on spring and summer Chinook salmon (hereafter Chinook salmon) and steelhead populations originating from the Snake River basin within the Columbia River basin (Figure 1). The Chinook salmon populations are stream-type (Healey 1991) composed of yearling smolts of wild and hatchery origin. The steelhead populations examined in this study produce multiple smolt ages and also were of wild and hatchery origin. Smolts of both species out-migrate through a series of eight hydropower dams and reservoirs (Lower Granite Dam [LGR], Little Goose Dam [LGS], Lower Monumental Dam [LMN], Ice Harbor Dam [IHR], McNary Dam [MCN], John Day Dam [JDA], The Dalles Dam [TDA], and Bonneville Dam [BON]) during the spring, primarily in April and May. A proportion of the out-migrating smolts were collected at the dams and placed onto transportation barges for release downstream of Bonneville Dam, the lowermost dam in the system. The remaining smolts, which migrate in-river through the FCRPS, were the focus of this study.

Tagging with Passive Integrated Transponders

Juvenile Snake River Chinook salmon and steelhead were tagged with PIT tags during the fall in the year before their out-migration and during the spring in the year of out-migration as smolts at traps, at hatcheries, and at Lower Granite Dam

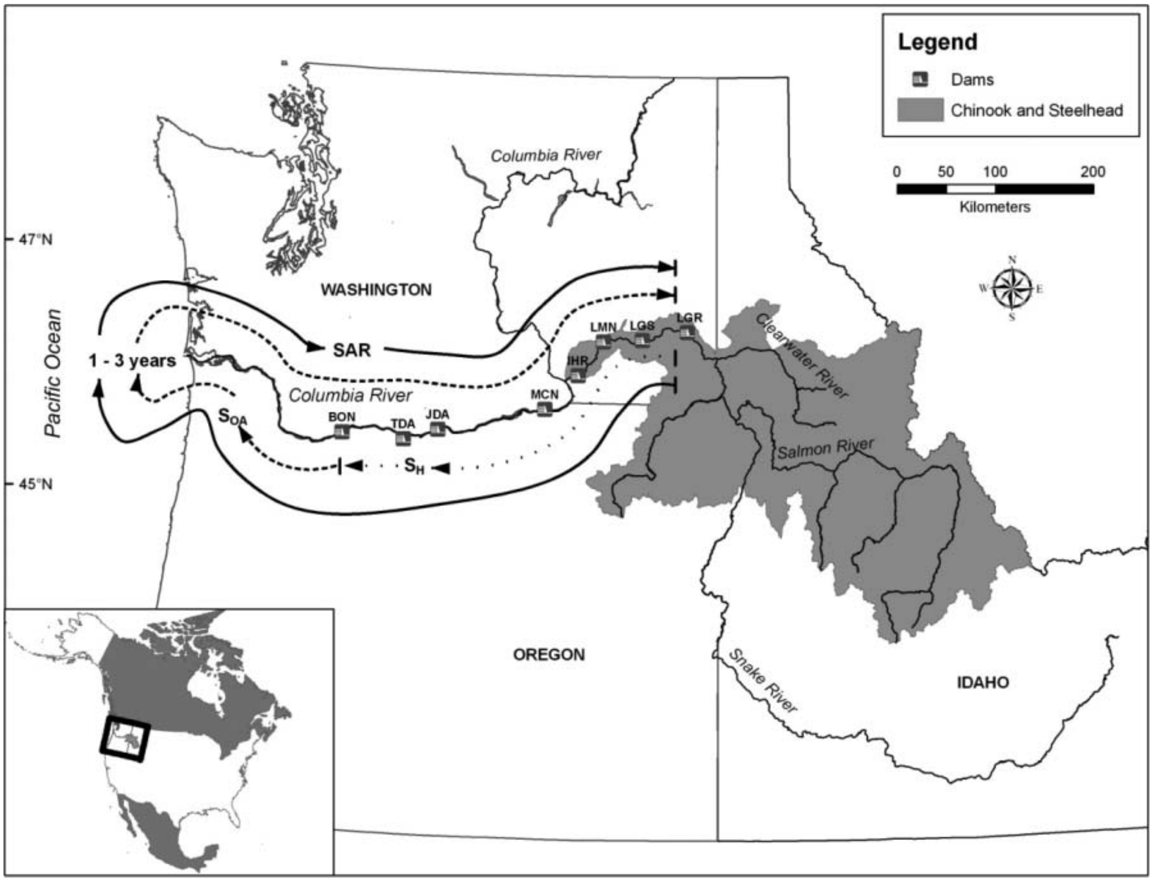

FIGURE 1. The Columbia and Snake rivers showing the spawning and rearing area currently accessible to Snake River spring–summer Chinook salmon and steelhead (shaded). The locations of eight hydropower dams on the lower Snake River and Columbia River are also shown: Lower Granite Dam (LGR), Little Goose Dam (LGS), Lower Monumental Dam (LMN), Ice Harbor Dam (IHR), McNary Dam (MCN), John Day Dam (JDA), The Dalles Dam (TDA), and Bonneville Dam (BON). The life stages that were assessed included freshwater survival (S_H, defined as survival from the tailrace of LGR to the tailrace of BON), ocean-adult survival (S_{OA}, defined as survival from the tailrace of BON as a smolt to adult detection at LGR), and life cycle survival (smolt-to-adult survival or SAR, defined as survival from the tailrace of LGR as a smolt to detection as an adult at LGR).

(Figure 1) as part of ongoing monitoring and evaluation programs, including the Smolt Monitoring Program (DeHart 2009), the Comparative Survival Study (Schaller et al. 2007), and smolt survival and transportation evaluations (Muir et al. 2001a, 2006; Marsh et al. 2004). Smolts with PIT tags can be detected at Lower Granite, Little Goose, Lower Monumental, McNary, John Day, and Bonneville dams, as well as downstream from Bonneville Dam by using specialized trawl equipment (Ledgerwood et al. 2004) for PIT-tag detection (Figures 1, 2). Adult fish with PIT tags migrating upriver can be detected at Bonneville, McNary, and Lower Granite dams.

Juvenile Fish Survival in Reaches

We applied the Cormack–Jolly–Seber (CJS) multiple mark–recapture model (Cormack 1964; Jolly 1965; Seber 1965) to estimate survival rates, detection probabilities, and their associated variances during smolt out-migration through the FCRPS over migration years 1998–2006. Details of the CJS model are fully described in Burnham et al. (1987), Skalski et al. (1998), and Muir et al. (2001a). The CJS model has been routinely and extensively applied to mark–recapture data for PIT-tagged fish throughout the Columbia River basin (Skalski et al. 1998; Muir et al. 2001a; Smith et al. 2002) and can produce accurate and valid survival estimates as well as reliable estimates of uncertainty in the survival estimates (Skalski et al. 1998; Muir et al. 2001a). The Cormack–Jolly–Seber model has four main assumptions: (1) all fish in a cohort have the same probability of recapture; (2) fish in a cohort have the same probability of survival from each sample site to the next; (3) marks are not lost or missed; (4) all samples are instantaneous and release is immediately after the sample. Goodness-of-fit tests showed that for most cohorts analyzed the data were mildly overdispersed, which suggests that assumptions 1 and 2 may have been violated. To account for issues with overdispersion, we used $\hat{c}$-adjustments (described below) to account for this potential violation (White et al. 2001).

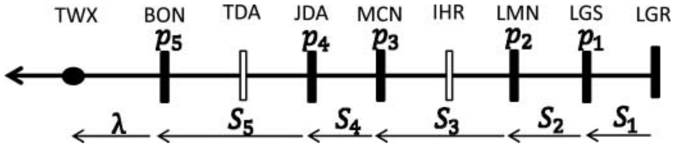

FIGURE 2. Graphical representation of the 11 Cormack–Jolly–Seber mark–recapture model parameters estimated in this analysis. Survival probabilities (S_i) are defined from release in the tailrace until the tailrace of the next subsequent dam with PIT-tag detection capability. Detection probabilities (p_i) are estimated for each of the dams with PIT-tag detection capability. Downriver from Bonneville Dam (BON), a PIT-tag detection trawl (TWX) operates as a terminal detection site, with the joint probability of survival and detection estimated by λ. See Figure 1 for the abbreviations for the dams.

Release groups.—We used a cohort-based approach for estimating life-stage-specific and cumulative smolt-to-adult survival rates (Figure 2). Cohort-based approaches allow for increased sample sizes (i.e., more than one survival rate per year) and allow for finer-scale attribution of environmental conditions experienced during out-migration (Muir et al. 2001a; Smith et al. 2002). Cohorts consisted of PIT-tagged smolts that were detected and released into the tailrace at LGR using a PIT-tag diversion system (Marsh et al. 1999) as well as smolts that were PIT-tagged at LGR (Muir et al. 2001a; Marsh et al. 2004) and subsequently released into the tailrace over four 2-week periods in each year: April 8–21, April 22–May 5, May 6–19, and May 20–June 2. Hatchery-reared and wild smolts of each species were combined in the analyses, but we recorded the percentage of hatchery-origin smolts for each release cohort in order to examine the effects of hatchery proportion on survival at each life stage (described below). To increase sample sizes of the PIT-tagged smolts that were released at LGR we augmented the detection histories for each cohort with smolts that were PIT-tagged and released upriver from LGR but were first detected at LGS. Assignment of smolts that were first detected at LGS to a release cohort at LGR was based on the median travel time between LGR and LGS for each cohort in each year. For example, if the median travel time between LGR and LGS for the first steelhead release cohort in 1998 was 4 d, the detection history data set for that cohort was augmented with steelhead that were first detected at LGS during April 12–25. Following passage at LGS, we assumed that the LGR-releases and the first-time detected smolts at LGS were effectively mixed and shared identical survival rates and detection probabilities downriver from LGS. Because the CJS model survival (S) and detection probabilities (p) are conditioned upon first release, only the LGR releases are used to estimate S_1 and p_1 (Figure 2), while both releases (i.e., LGR releases and first-time detected smolts at LGS) are used to estimate the remaining survival and detection probabilities.

Theoretically, the LGR releases could be augmented with first-time detections at all of the downriver dams. However, owing to the variation in travel times of individual smolts and increasing variability with migration distance (Zabel 2002), it becomes more and more difficult to assign first-time detections to the appropriate release cohort timing at LGR as migration distance increases. In our judgment, we determined that first-time detections at LGS could be reliably assigned to the appropriate release cohort timing at LGR owing to the relatively narrow variation between individuals, but that first-time detections at LMN or below could not.

Survival estimates.—After their release, PIT-tagged smolts could be detected at five downriver dams or the PIT-detection trawl operating downriver from Bonneville Dam (Figures 1, 2). At each site, smolts could be detected and returned to the river (Marsh et al. 1999), detected and removed from the tagged population (e.g., for smolt transportation or for biological sampling), or undetected at that site. The series of event histories at each site (i.e., detection, nondetection, or removal) constituted a detection history record for each tagged smolt suitable for survival estimation in the multiple-recapture CJS model. In our application, the CJS model is applied to these detection history data to estimate five reach survival parameters ($S_1, S_2, \ldots, S_5$), five detection probability parameters ($p_1, p_2, \ldots, p_5$) and one parameter (λ) representing the joint probability of survival and detection at the PIT-detection trawl (Figure 2).

Cumulative smolt survival estimates through the hydropower dams and reservoirs (S_H) and associated error estimates were produced for PIT-tagged Chinook salmon and steelhead that out-migrated during the years from 1998 to 2006 in the river reach between LGR and BON dams (Figures 1 and 2) by using the CJS methodology as described by Burnham et al. (1987) and implemented within the MARK program (White and Burnham 1999). Cumulative smolt survival was estimated as the product of the five, reach-specific survival rates:

$$\hat{S}_H = \hat{S}_1\hat{S}_2\hat{S}_3\hat{S}_4\hat{S}_5. \tag{1}$$

To account for potential overdispersion in the mark–recapture data (i.e., extrabinomial variation), we used the program RELEASE implemented within MARK to estimate $\hat{c}$, the variance adjustment factor. The variance–covariance matrix for $\hat{S}_1, \hat{S}_2, \ldots, \hat{S}_5$ was multiplied by $\hat{c}$ (Burnham and Anderson 2002), and we used the delta method (Burnham et al. 1987) to calculate the variance of $\hat{S}_H$ from the $\hat{c}$-adjusted variance–covariance matrix. This process was repeated for each of the four release cohorts per year and for each species over 9 years for a total of 36 possible cohort-year cases for each species.

Smolt-to-Adult Survival

As a measure of overall survival, smolt-to-adult-return survival estimates (SARs; Figure 1) were produced for PIT-tagged Chinook salmon and steelhead release cohorts that out-migrated during the years 1998 to 2006. The SARs are defined as the number of adults that return to LGR divided by the number of smolts that were released at LGR. However, as mentioned previously, a portion of the PIT-tagged smolts after release are subsequently removed from the tagged population owing to biological sampling at the dams or to placement on transportation barges at Lower Granite, Little Goose, Lower Monumental, or McNary dams. Those fish that are removed, along with the mortality that occurs before removal, must be accounted for when the number of smolts that are actually migrating in-river are calculated, otherwise a bias could occur.

In this study we adopted a similar approach to that described in Schaller et al. (2007) for estimating the number of PIT-tagged smolts at Lower Granite Dam that are expected to migrate in-river without being removed, termed "Lower Granite equivalents." The number of Lower Granite equivalent smolts was calculated as

$$\widehat{N}_{\mathrm{LGR}} = R_{\mathrm{LGR}} + \frac{n_{0_1}}{\hat{S}_1} - \sum_{i=1}^{5} \frac{d_i}{\prod_1^i \hat{S}_i}, \tag{2}$$

where R_{LGR} is the number of PIT-tagged smolts released at LGR, n_{01} is the number of PIT-tagged smolts released upriver of LGR that were first-detected at LGS (i.e., having a "01" detection history at LGR and LGS), $\hat{S}_1, \hat{S}_2, \ldots, \hat{S}_5$ are the five, reach-specific CJS survival estimates (Figure 2), and $d_1, d_2, \ldots, d_5$ are the numbers of PIT-tagged smolts that are removed at LGS, LMN, MCN, JDA, and BON, respectively. The method accounts for the cumulative survival that occurs before the arrival and removal of smolts at downriver dams and augments the number of original releases (R_{LGR}) with the effective number of smolts passing LGR but were first detected at LGS.

By following the calculation of $\widehat{N}_{\mathrm{LGR}}$, smolt-to-adult survival (SAR) estimates were calculated as

$$\widehat{\mathrm{SAR}} = \frac{N_{\mathrm{adult}}}{\widehat{N}_{\mathrm{LGR}}}, \tag{3}$$

where N_{adult} is the number of PIT-tagged fish that were detected as adults at LGR and were not removed during juvenile out-migration. Precocial male Chinook salmon may return as "mini-jacks" after 0 years in the ocean (Larsen et al. 2004) or as jacks after 1 year in the ocean. Full-term adults return after 2 or 3 years in the ocean. For Chinook salmon, mini-jacks and jacks (0-ocean and 1-ocean, respectively) were not included in the adult return numbers, while for steelhead 1-ocean and older returns were considered adults. We used a bootstrapping procedure (Efron and Tibshirani 1993) to estimate the variance of $\widehat{\mathrm{SAR}}$. The procedure consisted of randomly sampling (with replacement) the detection history records from N' individual smolts, where N' is the number of detection history records in the original data set, creating a bootstrap sample data set. Using this bootstrap sample data set, we calculated $\hat{S}_1, \hat{S}_2, \ldots, \hat{S}_5$ by using the closed-form CJS equations (Burnham et al. 1987), $\widehat{N}_{\mathrm{LGR}}$ by using equation (2), and $\widehat{\mathrm{SAR}}$ by using equation (3). This process was repeated 1,000 times to produce 1,000 bootstrap estimates of $\widehat{\mathrm{SAR}}$. Our estimate of the variance of $\widehat{\mathrm{SAR}}$ was the variance of these 1,000 bootstrap estimates of $\widehat{\mathrm{SAR}}$. As with $\hat{S}_H$, the $\widehat{\mathrm{SAR}}$ estimation and variance calculation process was repeated for each of the four release cohorts per year and for each species over 9 years for a total of 36 possible cohort-year cases for each species.

Ocean-Adult Survival

Given estimates of smolt survival from Lower Granite Dam to Bonneville Dam ($\hat{S}_H$) and survival from Lower Granite Dam as smolts back to Lower Granite Dam as adults ($\widehat{\mathrm{SAR}}$), we estimated ocean-adult survival ($\hat{S}_{\mathrm{OA}}$, Figure 1) as

$$\hat{S}_{\mathrm{OA}} \frac{\widehat{\mathrm{SAR}}}{\hat{S}_H}. \tag{4}$$

Survival estimates from this life stage encompass all survival processes during the period following passage at Bonneville Dam as a smolt through the time when adults migrate past Lower Granite Dam. As such, $\hat{S}_{\mathrm{OA}}$ includes survival down the remaining portion of the Columbia River from Bonneville Dam, survival through the estuary and nearshore ocean, survival during the 1–3 years spent in the ocean, and survival during the upriver migration from the ocean and through the FCRPS to Lower Granite Dam. For simplicity, we refer to this as ocean-adult survival. Because $\hat{S}_{\mathrm{OA}}$ is calculated as the quotient of two random variables ($\widehat{\mathrm{SAR}}$ and $\hat{S}_H$), we used the approximation for the variance of the quotient of two random variables provided by Mood et al. (1974) to estimate the variance of $\hat{S}_{\mathrm{OA}}$:

$$\mathrm{var}(\hat{S}_{\mathrm{OA}}) = \mathrm{var}\left(\frac{\mathrm{SAR}}{S_H}\right) \cong \left(\frac{\mathrm{SAR}}{S_H}\right)^2 \times \left(\frac{\sigma^2_{\mathrm{SAR}}}{\mathrm{SAR}^2} + \frac{\sigma^2_{S_H}}{S_H^2} - \frac{2\hat{r}(\mathrm{SAR}, S_H) \cdot \sqrt{\sigma^2_{\mathrm{SAR}} \sigma^2_{S_H}}}{\mathrm{SAR} \cdot S_H}\right), \tag{5}$$

where $\hat{r}(\mathrm{SAR}, S_H)$ is the estimated correlation between SAR and S_H across cohorts, and σ^2_{SAR} and $\sigma^2_{S_H}$ are the cohort-specific variance estimates for SAR and S_H, respectively. We estimated $\hat{S}_{\mathrm{OA}}$ and its variance for all Chinook salmon and steelhead cohorts that we had estimates of both freshwater survival ($\hat{S}_H$) and smolt-to-adult survival ($\widehat{\mathrm{SAR}}$) during 1998–2006.

Correlation Analyses

We used correlation analyses to examine patterns of covariation in the life-stage-specific survival rate estimates for Chinook salmon and steelhead. Budy et al. (2002) provided a review of the evidence supporting the hypothesis that a portion of the mortality expressed after passage at Bonneville Dam is related to earlier hydrosystem experience during downstream migration. Their paper synthesized the evidence documenting that the hydrosystem causes direct mortality during juvenile out-migration and imposes cumulative stress on those fish that survive, which can lead to delayed mortality. By using survival rates as a measure of the degree of cumulative stress (or alternatively, the lack thereof), under the Budy et al. (2002) hypothesis we would expect a positive correlation between measures of hydrosystem (S_H) and post–Bonneville Dam (S_{OA}) survival. In addition, we were interested in assessing the degree to which shared environmental processes may be influencing survival rates between these two species, as indicated by patterns of positive correlation between the two species in their life-stage-specific survival rates (Pyper et al. 2005). A priori, we hypothesized that correlations in survival rates between the two species would be highest during juvenile out-migration (S_1H), when the two species shared the same migration pathway through the FCRPS and would be lowest during the period of ocean residence through adult return (S_{OA}) because of potential differences in ocean distributions and ocean ecology. We hypothesized that correlations between the two species for SAR would be intermediate between the S_H correlation (hypothesized to be high) and the S_{OA} correlation (hypothesized to be low) because the SAR is the product of S_H and S_{OA}.

To evaluate these hypotheses, we conducted a series of comparisons between life-stage-specific survival rates by using Pearson's product-moment correlation coefficient. Pearson's product-moment correlation coefficient is a measure of the degree of linear relationship between two variables. In preliminary bivariate plots of the life-stage-specific survival rates we noticed heteroscedasticity in some of the plots, which could reduce the power to detect positive correlations. Therefore, we used a logit transformation on the stage-specific survival rates to reduce heteroscedasticity and improve measurement of the degree of linear relationship between the stage-specific survival rates:

$$\mathrm{logit}(S_i) = \log_e\left(\frac{S_i}{1 - S_i}\right), \tag{6}$$

where S_i is the life-stage-specific survival rate (S_H, S_{OA}, or SAR) for release cohort i. We calculated Pearson's product-moment correlation coefficient for five pairs of logit-transformed survival rates: ($S_{H,\mathrm{CHN}}$, $S_{\mathrm{OA,CHN}}$) and ($S_{H,\mathrm{STH}}$, $S_{\mathrm{OA,STH}}$) for evaluating the hydrosystem-related, delayed-mortality hypothesis, and ($S_{H,\mathrm{CHN}}$, $S_{H,\mathrm{STH}}$), ($S_{\mathrm{OA,CHN}}$, $S_{\mathrm{OA,STH}}$) and ($\mathrm{SAR}_{\mathrm{CHN}}$, $\mathrm{SAR}_{\mathrm{STH}}$) for evaluating patterns of covariation shared across species.

To account for positive autocorrelation evident in the survival rate time series, we conducted significance tests for all correlations by using the method recommended by Pyper and Peterman (1998). Their recommended method consists of approximating the "effective" degrees of freedom (N^*) in correlation tests by using

$$\frac{1}{N^*} \approx \frac{1}{N} + \frac{2}{N}\sum_{j=1}^{\infty} \rho_{XX}(j)\rho_{YY}(j), \tag{7}$$

where N is the sample size, and $\rho_{XX}(j)$ and $\rho_{YY}(j)$ are the autocorrelation parameters of X and Y at lag j. Sample autocorrelation coefficients were calculated with the estimator

$$r_{XX}(j) = \frac{N}{N - j}\,\frac{\sum_{t=1}^{N-j}(X_t - \bar{X})(X_{t+j} - \bar{X})}{\sum_{t=1}^{N}(X_t - \bar{X})^2}. \tag{8}$$

Sample correlations between series X and Y ($\hat{r}_{XY}$) were compared to a critical value (r_{crit}), based on the standard normal distribution (Z)

$$r_{\mathrm{crit}} = Z_a\sqrt{1/(N^* - 2)}, \tag{9}$$

to determine the statistical significance of the tests (one-tailed tests; H_0: $r_{XY} = 0$, H_A: $r_{XY} > 0$, $\alpha = 0.05$).

Freshwater Environmental Indices

Within the freshwater environment of the Columbia River basin hydropower system, freshwater survival and mortality rates of salmon have been associated with water transit time and the percentage of water spilled at dams (spill), along with seasonal effects indexed by release day of the year (Muir et al. 2001a; Schaller et al. 2007). Water transit time is a measure of the number of days it takes an average water particle to transit the length of a reservoir and is calculated by dividing a reservoir volume by the outflow rate (Petrosky and Schaller 2010). When water transit times are high (i.e., low water velocity), freshwater mortality rates of salmon and measures of their migration delay tend to increase (Raymond 1988; Berggren and Filardo 1993; Schaller et al. 2007). The provision of spill increases the proportion of smolts passing the dams by nonturbine routes and reduces migratory delays through dam forebays and tailraces. Estimates of smolt survival are often highest through spillways compared with estimates of smolt survival through juvenile bypass systems or turbines (Muir et al. 2001b). Given these findings, we developed two indices to characterize conditions within the freshwater environment during the period of juvenile out-migration of each cohort during each year. Average spill percentage and total water transit time (WTT) indices were calculated for each cohort based on timing and fish travel time through the hydrosystem. The median fish travel time between dams was estimated for each cohort and used to determine the period over which to calculate the average spill percentages and WTT indices. Conditions at downstream dams were averaged over a 2-week period by using the travel time to the next dam to adjust the start date of the calculations. The overall reach (LGR–BON) index for average spill percentage was the average of the dam-specific spill percentage values across the seven intermediary dams, while for water transit time the indices were the summation of the water transit times across the seven intermediary reservoirs. In addition to these two indices characterizing the out-migration conditions through the hydrosystem, we also used release day of the year for each cohort to examine changes in survival rates that may occur over the migration season. The day of the year for each release cohort was set at the midpoint (day 7) of each 2-week cohort. To account for

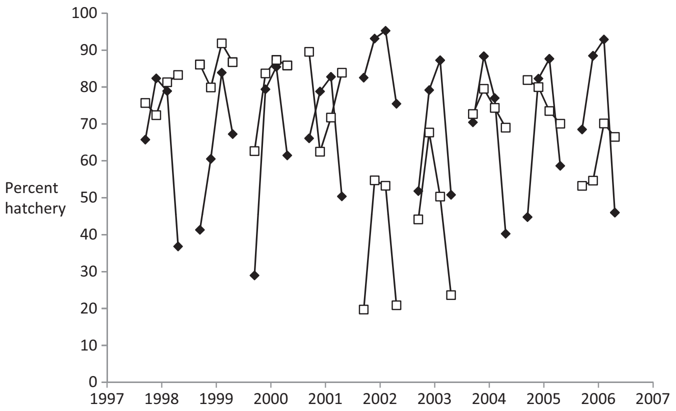

FIGURE 3. Percent of the release cohorts that were of hatchery origin for spring–summer Chinook salmon (filled diamonds) and steelhead (open squares).

and evaluate potential differences in survival between wild and hatchery-reared individuals, we recorded the percentage of individuals within each cohort that was of hatchery origin. Figure 3 provides the percentage of the Chinook salmon and steelhead releases that were hatchery origin across the release cohorts, while Figure 4 provides the average spill percentages and water transit times across release cohorts.

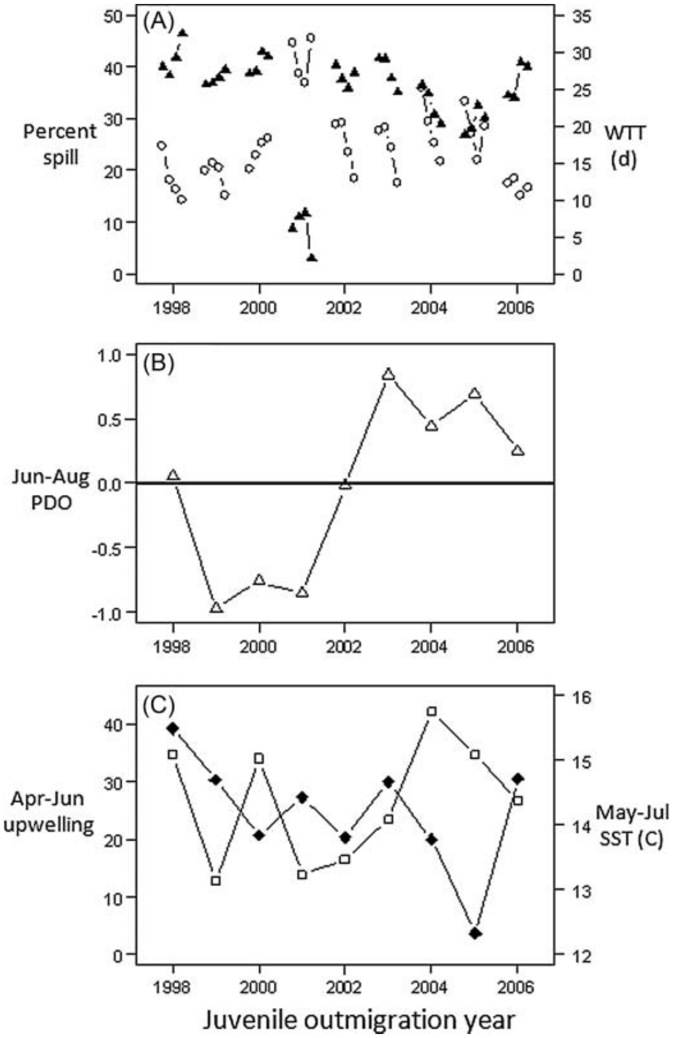

FIGURE 4. Freshwater and marine environmental variables used in the analysis: (**A**) average percent spill (filled triangles) and LGR–BON water transit time (WTT, open circles); (**B**) average June–August Pacific Decadal Oscillation (PDO, open triangles); and (**C**) average April–June upwelling (filled diamonds) and average May–July sea surface temperature (SST, open squares).

Ocean Environmental Indices

We examined three ocean indices that have previously been identified as being associated with salmon survival rates. Both Scheuerell and Williams (2005) and Petrosky and Schaller (2010) found that Chinook salmon ocean survival rates were positively associated with spring upwelling. Schaller and Petrosky (2007) and Petrosky and Schaller (2010) found that Chinook salmon ocean survival rates were negatively associated with the Pacific Decadal Oscillation (PDO) during June–August. The PDO is a large-scale index of ocean temperatures in the North Pacific Ocean (Mantua et al. 1997). Mueter et al. (2005) found that salmon survival indices were either positively or negatively associated (depending on latitude) with coastal sea surface temperature (SST) during the period of smolt entry into the ocean and Emmett and Sampson (2007) found that jack counts of Columbia River spring and summer Chinook salmon were related to May–June SST. Similarly, Petrosky and Schaller (2010) found that spring SST was positively associated with estimates of ocean mortality for Chinook salmon and steelhead from the Snake River basin. We considered each of these indices (upwelling, PDO, and SST), either individually or in combination, to be plausible factors that may be associated with survival rates of both the Chinook salmon and steelhead examined in this study. Instead of selecting individual months for characterizing upwelling, PDO, and SST (Scheuerell and Williams 2005; Petrosky and Schaller 2010), which may not reflect the general prevailing conditions during the extended period of ocean entry and residence, we chose to average monthly values over 3-month windows corresponding to the time periods that have previously been identified as being associated with Columbia River basin Chinook salmon and steelhead survival or mortality rates.

We obtained data on monthly values for upwelling, SST, and PDO from public databases available online. Data on average April–June upwelling at 45°N latitude and 125°W longitude were obtained from the National Oceanic and Atmospheric Association (NOAA) Pacific Fisheries Environmental Laboratory (www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html). Data on average May–July SST came from the Comprehensive Ocean Atmospheric Data Set (COADS) from within a 1° cell extending from 45–46°N and from 124–125°W (near the mouth of the Columbia River) and were obtained from the University Corporation for Atmospheric Research website (https://dss.ucar.edu/cgi-bin/login). Data on average June–August PDO were obtained from the

Joint Institute for the Study of the Atmosphere and Ocean (http://jisao.washington.edu/pdo/). Figure 4 summarizes the freshwater and marine environmental variables used in the analysis.

Multivariate Regression and Multimodel Inference

Similar to the approach of Greene et al. (2005), we used multivariate regression and multimodel inference techniques based on information theory (Burnham and Anderson 2002) to characterize associations between the freshwater and ocean indices and the life-stage-specific survival rates of Chinook salmon and steelhead. In all analyses we used a logit transformation (equation 3) of the life-stage-specific survival rates as dependent variables. All environmental indices were standardized to have a mean value of zero and a SD of one by subtracting the mean and dividing by the SD. The full model for examining survival during juvenile out-migration through the hydrosystem was

$$\begin{aligned}\text{logit}(S_H) = {} & \beta_0 + \beta_1 \cdot \text{Day} + \beta_2 \cdot \text{WTT} + \beta_3 \cdot \text{Spill} \\ & + \beta_4 \cdot \text{Hat.\%} + \varepsilon, \end{aligned} \tag{10}$$

where $\beta_0, \beta_1, \ldots, \beta_4$ are estimated regression coefficients and $\varepsilon \approx N(0, \sigma^2{}_{SH})$. In this model we assume that only the freshwater (WTT and spill), seasonal (Day) and rearing-type composition (hatchery percentage) indices may contribute to variation in freshwater survival rates. The full model for examining ocean-adult survival rates was

$$\begin{aligned}\text{logit}(S_{\text{OA}}) = {} & \beta_0 + \beta_1 \cdot \text{Day} + \beta_2 \cdot \text{WTT} + \beta_3 \cdot \text{Spill} \\ & + \beta_4 \cdot \text{Hat.\%} + \beta_5 \cdot \text{PDO} + \beta_6 \cdot \text{Up.} \\ & + \beta_7 \cdot \text{SST} + \varepsilon, \end{aligned} \tag{11}$$

where $\beta_0, \beta_1, \ldots, \beta_7$ are estimated regression coefficients and $\varepsilon \approx N(0, \sigma^2{}_{\text{SOA}})$. In this model we assume that the freshwater, seasonal, rearing-type composition, and ocean indices may contribute to variation in ocean-adult survival. By allowing for potential freshwater influences on ocean-adult mortality, this model represents another means of evaluating the Budy et al. (2002) hypothesis that freshwater migration experiences influence subsequent survival after passage at Bonneville Dam. The full model for examining cumulative smolt-to-adult survival rates was:

$$\begin{aligned}\text{logit}(\text{SAR}) = {} & \beta_0 + \beta_1 \cdot \text{Day} + \beta_2 \cdot \text{WTT} + \beta_3 \cdot \text{Spill} \\ & + \beta_4 \cdot \text{Hat.\%} + \beta_5 \cdot \text{PDO} + \beta_6 \cdot \text{Up} \\ & + \beta_7 \cdot \text{SST} + \varepsilon, \end{aligned} \tag{12}$$

where $\beta_0, \beta_1, \ldots, \beta_7$ are estimated regression coefficients and $\varepsilon \approx N(0, \sigma^2{}_{\text{SAR}})$. In this model we assumed that the freshwater, seasonal, rearing-type composition, and ocean indices may contribute to variation in the cumulative smolt-to-adult survival rates.

We calculated Akaike's information criterion (AIC) for small sample sizes (AIC$_c$) for all possible model combinations of the predictor variables (all subsets regression). For the S_H regressions, there were 16 possible combinations of the four predictor variables and for the S_{OA} and SAR regressions, there were 128 possible combinations of the seven predictor variables. To account for differences in the relative precision of the individual survival rate estimates, each model was estimated with an inverse-coefficient of variation weighting of the observations. The models were ranked according to AIC$_c$, the model with the minimum AIC$_c$ was identified, and Akaike weights (w_i) were calculated for each model (Burnham and Anderson 2002). To assess our assumption that residuals were normally distributed, we conducted Shapiro–Wilk tests on the residuals for the best-fitting models (best-fitting as determined by minimum AIC$_c$) for each life stage and species. Similarly, to assess our assumption that residuals were uncorrelated (i.e., independent), we used the Durbin–Watson test statistic (Draper and Smith 1998). Durbin–Watson test statistics less than 1.0 are indicative of strong, positive autocorrelation of regression residuals.

By using the AIC$_c$-ranked set, we calculated model-averaged predictions for the life-stage-specific survival rates of each species. Model-averaged predictions were calculated with the equation

$$\hat{\hat{\theta}} = \sum_{i=1}^{R} w_i \hat{\theta}, \tag{13}$$

where $\hat{\hat{\theta}}$ denotes the model-averaged prediction of θ (i.e., S_H, S_{OA}, or SAR) across the R models and w_i denotes the Akaike weight for model $i = 1, 2, \ldots, R$ (Burnham and Anderson 2002). In addition to model-average predictions of the life-stage-specific survival rates of each species, we also used equation (13) to calculate model-averaged parameter coefficients for each of the environmental indices (substituting β for θ in equation 13). We calculated the unconditional variance estimates for $\hat{\hat{\beta}}$ with the equation

$$\widehat{\text{var}}\left(\hat{\hat{\beta}}_i\right) = \left[\sum_{i=1}^{R} w_i \sqrt{\widehat{\text{var}}\left(\hat{\beta}_i | g_i\right) + \left(\hat{\beta}_i - \hat{\hat{\beta}}\right)^2}\,\right]^2, \tag{14}$$

where $\hat{\hat{\beta}}$ is the model-averaged estimate of β determined from equation (13) and $\widehat{\text{var}}(\hat{\beta}_i | g_i)$ is the variance of $\hat{\beta}_i$ conditional on model g_i (Burnham and Anderson 2002). To help understand the directionality and strength of the associations (effect sizes) between the environmental variables and survival rates, we constructed and plotted 95% confidence intervals (CIs) for the $\hat{\hat{\beta}}$ by using the unconditional variance estimates. We interpreted an environmental variable as having a strong effect if its 95% CI did not contain zero. We interpreted an environmental variable as having a moderate effect if the value of zero was within, but near the tail of the 95% CI. We interpreted an environmental variable as having a weak effect if the $\widehat{\widehat{\beta}}$ was near zero.

The sets of best-fitting models were also used to evaluate the relative importance of each predictor variable used in the regressions (Burnham and Anderson 2002). The relative variable importance is a quantitative measure of the degree to which variables are consistently included among the best-fitting models based on AIC$_c$ relative to the other variables that were considered. The relative variable importance for variable j among a set of R models is calculated as

$$\sum_{i=1}^{R} w_i I_j(g_i), \tag{15}$$

where w_i is the Akaike weight for model i and $I_j(g_i)$ is an indicator variable equal to one if variable j is in model i (g_i) and equal to zero otherwise. Variables with relative variable importance values near one are consistently in the top-fitting models while variables with relative variable importance values near zero are rarely, if ever, included in the top-fitting models.

Assessing Inland Actions under Variable Ocean Conditions

As mentioned previously, our objectives included identifying which actions taken inland would be most critical for improving cumulative smolt-to-adult survival rates across variable ocean conditions (NPCC 2009) and identifying the corresponding freshwater survival rates that may be necessary to achieve the NPCC SAR goal of SARs averaging 4% and having a minimum of 2% (NPCC 2003, 2009). To accomplish these objectives, the effects of variable ocean conditions and their influences on smolt-to-adult survival rates must be accounted for. We accounted for variable ocean conditions by first determining which ocean environmental index (upwelling, SST, or PDO) had the highest relative variable importance in the SAR regressions for each species. We then classified each year as having favorable, neutral, or unfavorable ocean environmental conditions based on the sign of the model-averaged parameter coefficient for the selected ocean index variable and the ocean index value in each year. To determine which actions inland would be most critical for improving SAR, we graphically examined associations between WTT, spill, and SAR and identified which SAR observations occurred under favorable, neutral, or unfavorable ocean environmental conditions. Similarly, to identify freshwater survival rates that may be necessary to achieve the NPCC SAR goal, we graphically examined associations between S_H and SAR and identified which *SAR* observations occurred under favorable, neutral, or unfavorable ocean environmental conditions.

RESULTS

We were able to estimate SARs for all 36 release cohorts of each species (Figure 5). However, owing to a combination of low sample sizes and low detection probabilities, we were able to estimate S_H for only 33 of the Chinook salmon and 22 of the steelhead release cohorts. Likewise, because calculation of S_{OA} required an estimate of SAR and S_H, we were able to estimate S_{OA} for only 33 of the Chinook salmon and 22 of the steelhead release cohorts. Low sample sizes or low detection probabilities, or both, also influenced the precision of the S_H, with the highest precision for both species occurring in 2001 when detection probabilities were high owing to the elimination of spill for fish passage in that year (Figure 4). Several of the S_H estimates had SE values exceeding 0.3.

Across release cohorts and years, survival rates during juvenile out-migration tended to be higher for Chinook salmon than for steelhead, with an average S_H of 0.53 for Chinook salmon and 0.39 for steelhead (Figure 5). The lowest estimates of S_H for Chinook salmon occurred in 2001, 2004, and 2005, averaging 0.28, 0.43, and 0.48, respectively, across cohorts within those years. Similarly, the lowest estimates of S_H for steelhead occurred in 2001, 2004, and 2005 and averaged 0.03, 0.12, and 0.33, respectively, across cohorts in those years. These years of low S_H corresponded with the 3 years with the longest water transit times and the lowest average percent spill levels (Figure 4). Within-year changes in S_H were variable and had increasing, decreasing, or relatively stable seasonal patterns in S_H, depending on the year for both species.

Across release cohorts and years, the average S_{OA} was 1.01% for Chinook salmon and 1.64% for steelhead (Figure 5). For Chinook salmon, the lowest estimates of S_{OA} occurred in 2001 and 2003–2005, while the lowest estimates for steelhead S_{OA} occurred in 2001 and 2004–2005. These years of low S_{OA} corresponded with the 3 years with the longest water transit times and the lowest average percent spill levels (Figure 4). The highest estimates of S_{OA} occurred in 1999 and 2000 for Chinook salmon and 2000 for steelhead. Within-year changes in S_{OA} were variable for Chinook salmon and had increasing, decreasing, or relatively stable seasonal patterns, depending on the year. In contrast, steelhead generally exhibited a decreasing seasonal trend in S_{OA} within years.

The SAR estimates for both species were well below the NPCC (2009) goal of SARs averaging 4% and a minimum of 2%. The average SAR for Chinook salmon was 0.59% and the average SAR for steelhead was 0.61%. Only 1 of the 36 SAR estimates for Chinook salmon was above the 2% minimum and only 1 of the 36 SAR estimates for steelhead was above the 2% minimum. Within-year changes in SAR were variable for Chinook salmon and had increasing, decreasing, or relatively stable seasonal patterns, depending on the year. Steelhead SARs consistently declined over the migration season, with the exception of 2001 when low SARs (average = 0.02%) were exhibited throughout the migration season.

When we accounted for autocorrelation in the logit-transformed time series' of S_H, S_{OA} and SAR the original sample sizes were reduced from 22–36 observations to 15–21 effective samples (Table 1). After we accounted for this autocorrelation, we identified significant positive correlations between the S_H

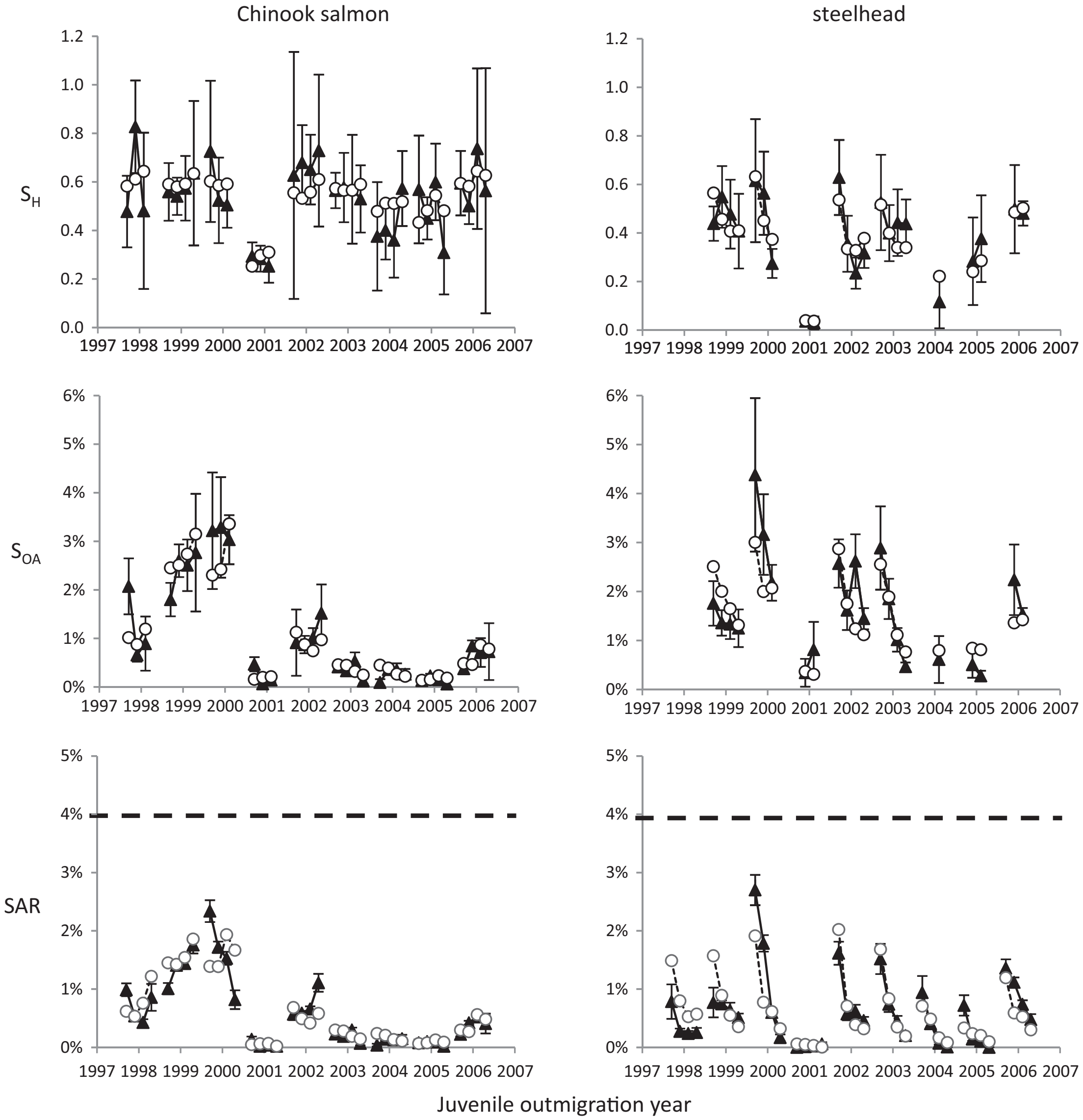

FIGURE 5. Estimates of S_H, S_{OA}, and SAR (filled triangles, ±1 SE) and model-averaged predictions of S_H, S_{OA}, and SAR (open circles) for Chinook salmon (left column) and steelhead (right column). A horizontal dashed line at 4% on the SAR graphs denotes the Northwest Power and Conservation Council SAR goal.

and S_{OA} life-stage survival rates for both species (Table 1). For Chinook salmon, the estimated correlation between S_H and S_{OA} was $\hat{r} = 0.49 (P = 0.0085)$. For steelhead, the estimated correlation between S_H and S_{OA} was $\hat{r} = 0.55 (P = 0.0215)$. These results demonstrated that there are significant positive correlations between survival during juvenile out-migration through the hydrosystem and subsequent survival during the ocean-adult life stage. Also, these sample correlation coefficients are probably underestimates of their true values. Because of the measurement error in each of the life-stage-specific survival rates (especially for S_H), the estimated correlation coefficient is biased to some degree towards zero (Buonaccorsi 2010).

In addition to positive correlations between life stages, we also found significant positive correlations in the life-stage-specific survival rate estimates between species (Table 1). The highest correlations between the two species occurred during juvenile out-migration through the hydrosystem (S_H) ($\hat{r} = 0.75$, $P = 0.0015$) and during the ocean-adult life stage (S_{OA}) ($\hat{r} = 0.75$, $P = 0.0020$). The correlation between the two species for smolt-to-adult survival was lower, but was statistically significant ($\hat{r} = 0.61$, $P = 0.0040$). While the high correlation between species during juvenile out-migration was consistent with our expectation, we were surprised by the equivalently high correlation between species during the ocean-adult life stage (S_{OA}). We hypothesized that the correlation between SARs of the two species would be intermediate between the S_H and S_{OA} correlations, but instead it was the lowest among the three.

TABLE 1. Sample size (N), effective sample size (N^*), Pearson's product-moment correlation coefficient ($\hat{r}$), the correlation coefficient critical value ($r_{\text{crit.}}$), and P-value for life-stage-specific survival rate pairs of Chinook salmon (CHN) and steelhead (STH).

Survival rate pair	N	N^*	$\hat{r}$	$r_{\text{crit.}}$	P-value
$S_{H,\text{ CHN}}$, $S_{H,\text{ STH}}$	22	18	0.75	0.42	0.0015
$S_{OA,\text{ CHN}}$, $S_{OA,\text{ STH}}$	22	17	0.75	0.43	0.0020
SAR_{CHN}, SAR_{STH}	36	21	0.61	0.38	0.0040
$S_{H,\text{ CHN}}$, $S_{OA,\text{ CHN}}$	33	25	0.49	0.34	0.0085
$S_{H,\text{ STH}}$, $S_{OA,\text{ STH}}$	22	16	0.55	0.44	0.0215

Examinations of the residuals from the best-fit (based on AIC$_c$) multiple-regression models indicated that assumptions of independence and normality were largely met. Shapiro–Wilk tests for normality indicated no significant departures from normality among the residuals for all of the models except for the SAR model for steelhead, where two residuals were large enough for the Shapiro–Wilk test to indicate a departure from normality. There was only slight evidence of autocorrelation in the residuals based on the Durbin–Watson test statistics, with values of 1.53–1.88 for models of S_{OA} and SAR of both species. For the S_H models, the Durbin–Watson test statistics were 2.18 and 2.25 for Chinook salmon and steelhead, respectively.

The model-averaged predictions captured a high proportion of the variation in S_H, S_{OA}, and SAR (Figure 5; Table 2). The life-stage-specific survival rate with the highest amount of variation explained by the model-averaged predictions was S_{OA} for Chinook salmon ($r^2 = 0.87$) followed by S_H for steelhead ($r^2 = 0.81$). The model-averaged predictions explained a higher proportion of the variability in S_{OA} and SAR for Chinook salmon ($r^2 = 0.87$ and $r^2 = 0.78$) than for steelhead ($r^2 = 0.66$–0.67 for both life stages), but the proportion of variation explained by the model-averaged estimates for S_H was considerably higher for steelhead than for Chinook salmon ($r^2 = 0.81$ versus $r^2 = 0.53$). Visual inspection of the model-averaged predictions in Figure 5 shows that the models were capable of capturing a high degree of the variation in the life-stage-specific survival rates.

Model-averaged parameter coefficients for the environmental indices provide information on the directionality and strength of their associations with survival at each life stage (Figure 6). During juvenile out-migration through the hydropower system (S_H), average percent spill had a strong positive effect on survival rates of both species. The negative effect of increased water transit time on juvenile survival was strong for steelhead and moderate for Chinook salmon. We found a strong negative effect of increasingly later day of release on steelhead survival during the juvenile life stage, but there was only a weak negative effect of day of release on Chinook salmon survival. During the ocean-adult life stage (S_{OA}), average percent spill had a strong positive effect on survival rates of both species. There was a strong negative effect of PDO on Chinook salmon survival during the ocean-adult life stage. Pacific Decadal Oscillation had a moderate negative effect, and day of release had a strong negative effect, on steelhead survival during the ocean-adult life stage. For cumulative smolt-to-adult survival (SAR), spill had a strong positive effect on the SAR of both species. Increasing water transit time had a moderate negative effect on the SAR of both species. Day of release had a strong negative effect on the SAR of steelhead, while the effect of day of release on the SAR of Chinook salmon was moderate and negative. Pacific Decadal Oscillation had a strong negative effect on the SAR of Chinook salmon, while PDO had a moderate negative effect on the SAR of steelhead. Sea surface temperature had a moderate negative effect on the SAR of steelhead, but SST had a weak effect on the SAR of Chinook salmon. Upwelling had weak effects on the SAR of both species. The effect of rearing-type composition (percent hatchery) was weak across all three life stages of both species.

TABLE 2. Proportion of the variation explained (r^2 values) using model-averaged estimates of survival to hatch (S_H), ocean-adult survival (S_{OA}), and survival to adult return (SAR) of Chinook salmon and steelhead.

Species	S_H	S_{OA}	SAR
Chinook salmon	0.53	0.87	0.78
Steelhead	0.81	0.66	0.67

The relative variable importance values for the environmental variables were consistent with the information provided by the model-averaged parameter coefficient estimates (Figure 7). During juvenile out-migration, the most important variables for characterizing variation in S_H were spill and WTT for Chinook salmon, while day of release, spill and WTT were the most important variables for steelhead. During the ocean-adult life stage (S_{OA}), spill and PDO were important for both species, while day of release was also important for steelhead. For cumulative smolt-to-adult survival (SAR), spill had a high relative variable importance for both species. For Chinook salmon SAR, PDO had high relative variable importance, with moderate importance of day and WTT. For steelhead SAR, day of release had high relative variable importance, while WTT, PDO, and SST were moderately important. The relative variable importance of rearing-type composition (percent hatchery) was low for all three life stages of both species.

Of the three marine environmental indices examined (upwelling, SST, and PDO), PDO had the highest relative variable importance in the SAR regressions for both Chinook salmon and steelhead. The sign of the model-averaged parameter coefficient for PDO was negative for both species, indicating that positive values for PDO were associated with reduced smolt-to-adult survival, while negative values for PDO were associated with increased smolt-to-adult survival (Figure 6). Over the 1998–2006 time frame that we analyzed, we observed a wide range of ocean conditions in terms of PDO values

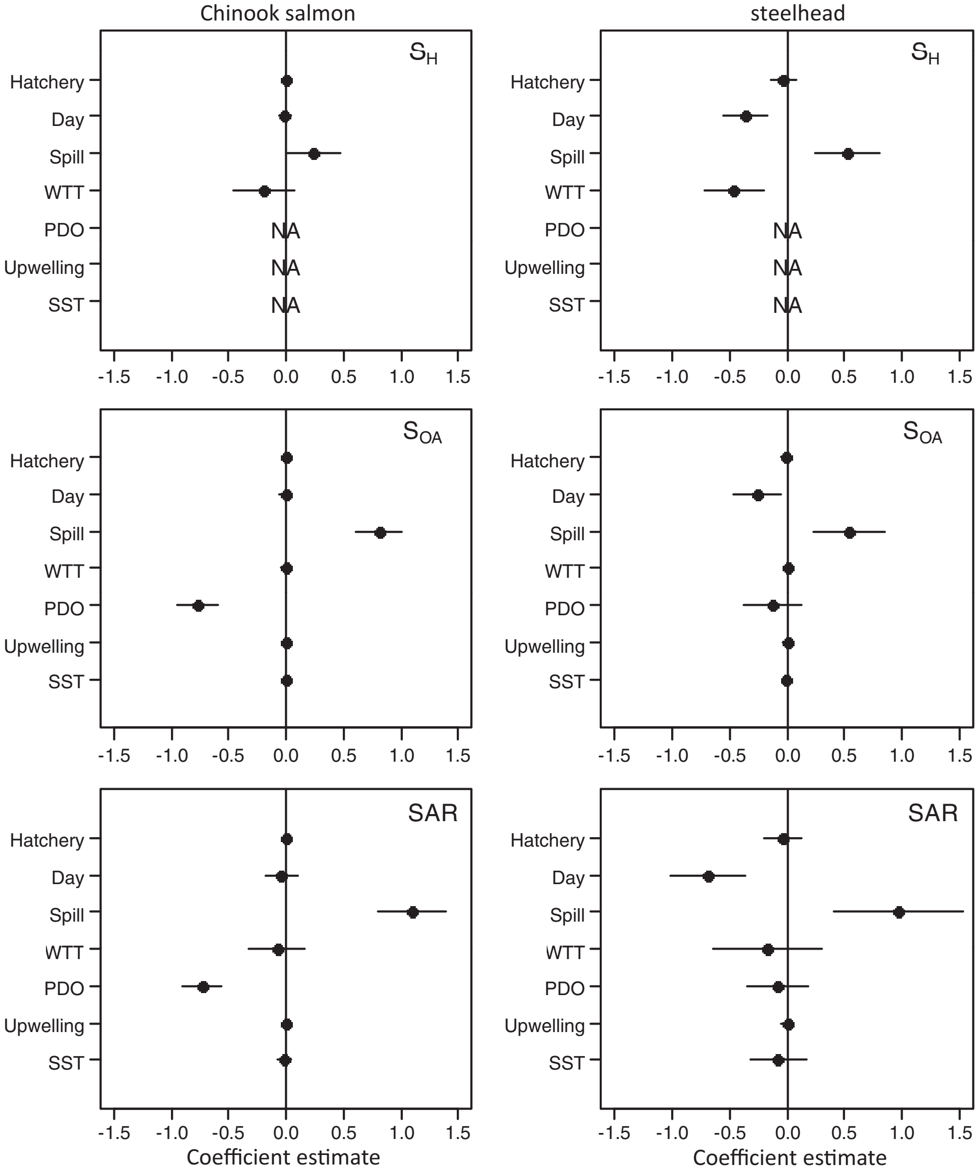

FIGURE 6. Model-averaged parameter coefficients with 95% confidence limits for percent hatchery composition (Hatchery), day of release (Day), average percent spill (Spill), water transit time (WTT), Pacific Decadal Oscillation (PDO), upwelling, and sea surface temperature (SST) across S_H, S_{OA}, and SAR models for Chinook salmon (left column) and steelhead (right column).

(Figure 4). We classified years 1999–2001 as having favorable ocean conditions for Chinook salmon and steelhead owing to the negative PDO values in those years, years 1998 and 2002 as having neutral ocean conditions owing to PDO values near zero in those years, and years 2003–2006 as having unfavorable ocean conditions owing to positive PDO values in those years (Figure 4).

Plots of SAR versus WTT, spill and S_H show that SARs increase with decreases in WTT, increases in spill, and increases in S_H across the range of ocean conditions indexed by PDO (Figure 8). The highest SARs occurred when water transit times were short, when spill percentages were high, or when S_H was high in combination with negative PDO values. The lowest SARs occurred when water transit times were long, when spill levels were low, or when S_H was low, regardless of PDO values. The effects of variable ocean conditions were most apparent when spill levels were high, when water transit times were low, or when S_H was low. When spill levels were low, when water transit times were long, or when S_H was low, the presence of favorable ocean conditions did not result in high SARs. These results demonstrated that favorable ocean conditions did not compensate or mitigate for poor freshwater migration conditions characterized by long water transit times, low spill levels, or low S_H. During years with high spill levels, short water

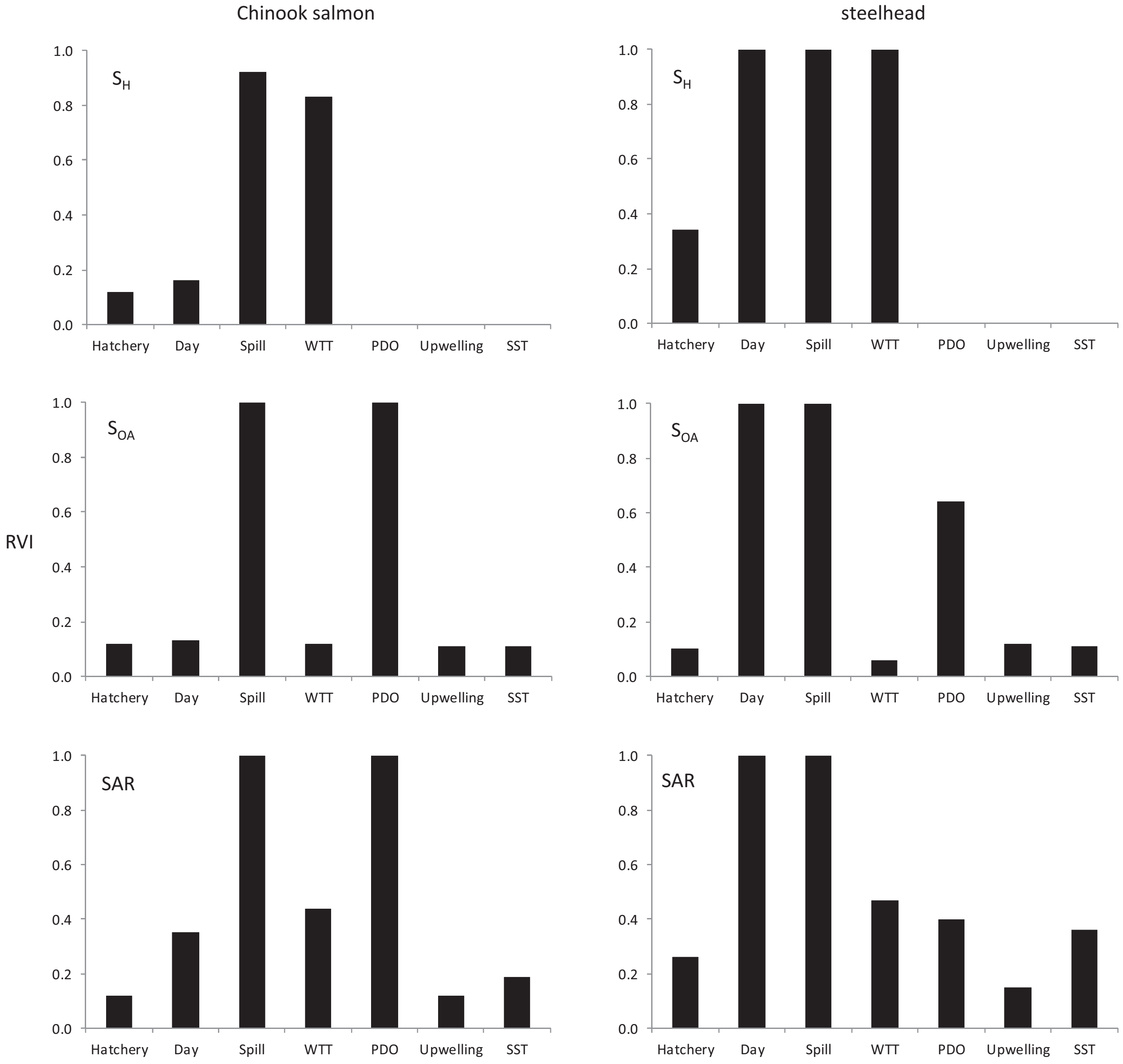

FIGURE 7. Relative variable importance (RVI) values for the environmental variables that describe variation in S_H, S_{OA}, and SAR for Chinook salmon (left column) and steelhead (right column). See Figure 6 for the environmental variable abbreviations.

transit times, or high values of S_H, the presence of moderate or unfavorable ocean conditions was associated with reduced SARs.

These results (Figure 8) provide an indication of the water transit times, spill levels, and freshwater survival rates that may be necessary to achieve the NPCC goal of SARs averaging 4% and with a minimum of 2%. In terms of spill percentages, the data indicate that spill percentages of 50% or greater may be necessary to have a reasonable chance of meeting the NPCC SAR goal. In terms of water transit times, the data indicate that WTTs of less than 5 d may be necessary to have a reasonable chance of meeting the NPCC SAR goal. In terms of freshwater survival rates, the data indicate that S_H values of 0.80 or greater may be necessary to have a reasonable chance of meeting the NPCC SAR goal. Without large changes in either WTT, spill levels, or S_H, it appears unlikely that the NPCC SAR goal will be achieved.

DISCUSSION

The high degree of covariation in the survival rate estimates suggests that shared environmental factors are influencing survival rates of both Chinook salmon and steelhead (Pyper et al. 2005). The high degree of covariation in S_H between species

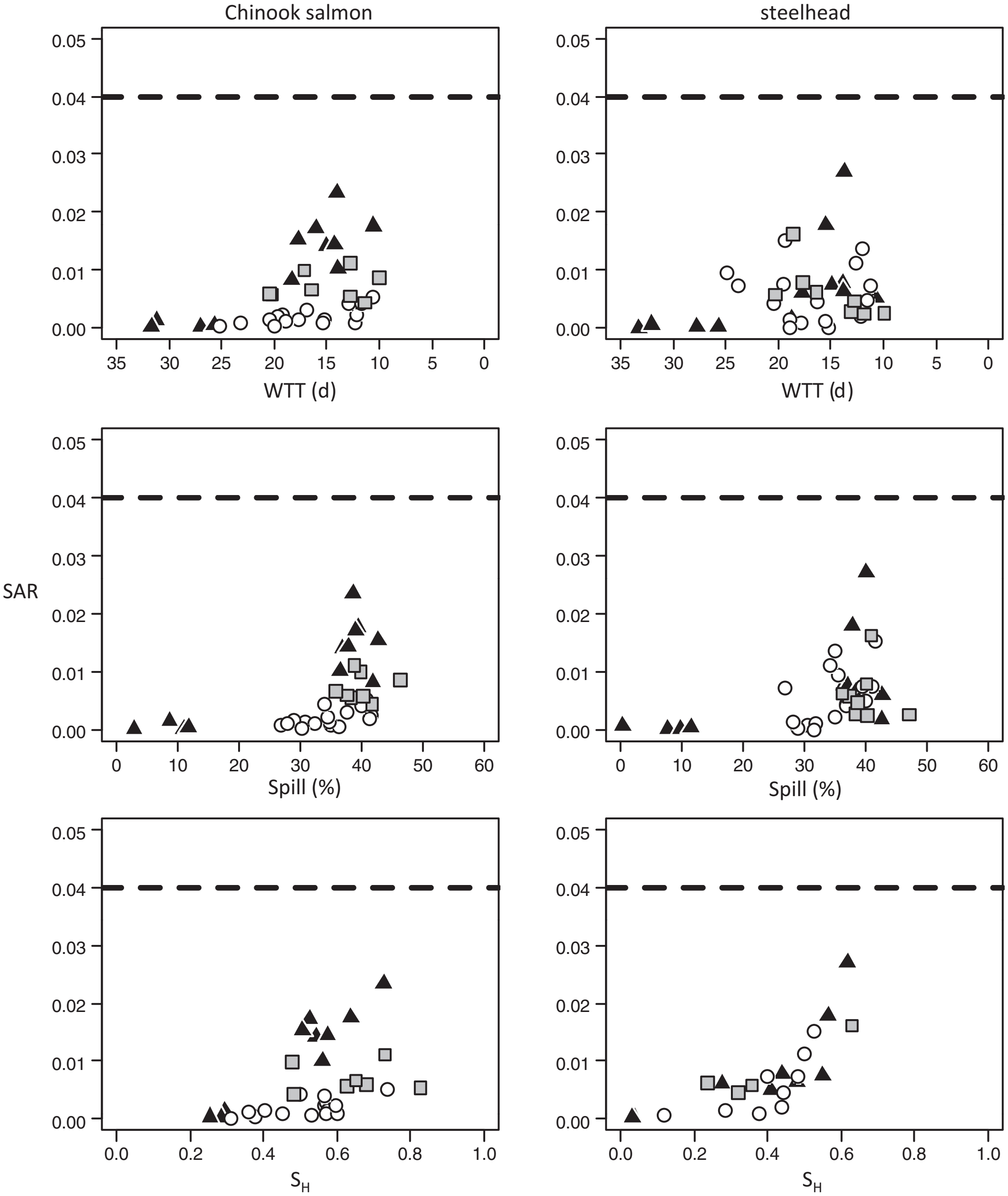

FIGURE 8. Bivariate plots of SAR against water transit time (WTT), average percent spill (Spill), and juvenile out-migration survival (S_H) for Chinook salmon (left column) and steelhead (right column). Years with negative June–August Pacific Decadal Oscillations (PDO) are denoted by black triangles, years with neutral PDO values near zero are denoted by gray squares, and years with positive PDO values are denoted by open circles. The horizontal dashed line at 4% denotes the Northwest Power and Conservation Council (NPCC 2009) SAR objective.

was not surprising given that the two species were migrating through the same corridor at nearly the same time. However, the two species also shared a surprisingly high degree of covariation in S_{OA}. Survival during this life stage represents the cumulative survival from the Bonneville Dam tailrace as a smolt until the fish's return as an adult at Lower Granite Dam, a period of 1–3 years during which time the fish had an opportunity to range anywhere in the Pacific Ocean. While relatively little is known about ocean distributions of Snake River spring–summer Chinook salmon and steelhead, the high degree of correlation in S_{OA} between the two species suggests that the habitats they occupy and the proximate factors that influence survival during the ocean-adult period is more similar than previously envisioned.

Our research provides two lines of evidence that support the hydrosystem-related, delayed-mortality hypothesis of Budy et al. (2002). First, we found significant, positive correlations between S_H and S_{OA} for both species. Under the hydrosystem-related, delayed-mortality hypothesis, mortality rates at later life stages are expected to be positively associated with mortality rates at previous life stages, and our results support this expectation. Second, we identified spill as having measureable effects not only on survival during juvenile out-migration, but also on survival during the ocean-adult period for both species. The identification of spill as a factor that accounts for variability across multiple life stages is consistent with the hydrosystem-related, delayed-mortality hypothesis because this factor, which explains variability in mortality in the later life stage (S_{OA}), also explains variability in the previous life stage (S_H). Therefore, our research provides two lines of direct evidence that a portion of the mortality expressed after Chinook salmon and steelhead leave the hydrosystem is related to processes that reflect downstream migration conditions.

Research continues to indicate that both freshwater and marine factors are important drivers of the observed variability in Chinook salmon and steelhead survival rates, particularly in river systems where freshwater habitat is highly influenced by anthropogenic factors (Lawson et al. 2004; Greene et al. 2005; Schaller and Petrosky 2007; Petrosky and Schaller 2010). Our study provides additional information on the influences of freshwater and marine factors, but we share the view, expressed by Bisbal and McConnaha (1998), that it is the cumulative effects of factors across the freshwater, estuarine, and marine environments that determine salmon survival and abundance. In addition to the factors that influence survival within each life stage, the positive correlations between freshwater and ocean-adult survival rates have important implications for improving the understanding of interactions between the freshwater and marine environments for Snake River Chinook salmon and steelhead. The potential for covariation between freshwater and marine survival rates was recognized by Bradford (1995), but to our knowledge our study is the first to quantify the degree of covariation. The significant, positive correlations between S_H and S_{OA} for both species demonstrates that survival within the ocean environment is not independent of survival within the freshwater environment. The evidence presented in this study indicates that a portion of the mortality expressed during the ocean-adult life stage is due to delayed mortality effects related to factors that occur during the freshwater life stage. Some of this covariation appears to be related to levels of spill, with spill affecting S_H and S_{OA} of both species. Thus, the effects of freshwater conditions are manifested across several life stages and are not limited to only affecting variation during the freshwater life stage.

From a modeling standpoint, these results also have important implications. Several researchers have conducted population projection analyses that examine how changes in survival during various life stages (e.g., egg to smolt, freshwater migration survival, early ocean survival, adult survival and harvest) would affect population growth rates (Kareiva et al. 2000; McClure et al. 2003; Wilson 2003). These are useful areas of research for prioritizing conservation actions at these life stages. However, the analyses that have been conducted to date have implicitly assumed that freshwater and ocean-adult survival rates are independent of each other. For example, Kareiva et al. (2000) conducted population projections under a hypothetical scenario where freshwater survival rates were increased to 100%, but without any function for characterizing how ocean-adult survival would be expected to change along with those assumed changes in freshwater survival. The identification of significant, positive correlation between S_H and S_{OA} for both species indicates that the independence assumption of Kareiva et al. (2000) is not consistent with the new available data. The correlation between freshwater and ocean-adult survival rates is a critical issue for properly characterizing and modeling the expected effects of changes in survival across various life stages, and the presence of correlation between life stages can have large effects on population growth models (Doak et al. 1994). From the perspective of prioritizing conservations actions, Kareiva et al. (2000) and Wilson (2003) both concluded that improving early ocean survival rates was critical for achieving Chinook salmon recovery objectives. Given the strong positive associations between spill and S_{OA}, our results indicate that increasing spill percentages may be a way to increase S_{OA}.

Although our results indicate that freshwater factors are important influences on freshwater, ocean-adult, and cumulative smolt-to-adult survival, our results clearly show that marine factors are also important. Of the three marine variables examined, PDO appeared to be the most important factor regulating ocean-adult and smolt-to-adult survival rates of Snake River Chinook salmon and steelhead. Consistent with Schaller and Petrosky (2007) and Petrosky and Schaller (2010), we found that warm-phase PDO values were negatively associated with ocean-adult and smolt-to-adult survival rates of Chinook salmon and steelhead. Warm SSTs were negatively associated with smolt-to-adult survival rates of steelhead, but had little measurable effect on ocean-adult or smolt-to-adult survival rates of Chinook salmon. In contrast to Scheuerell and Williams (2005) and Schaller and Petrosky (2007), we found that April–June upwelling generally had weak or inconsistent effects, or both, on ocean-adult and smolt-to-adult survival rates of Chinook salmon and steelhead. These differences may be due to the multivariate nature of the regressions, with spill and PDO explaining most of the variation in ocean-adult and smolt-to-adult survival, leaving little remaining variation to be explained by upwelling.

Large-scale climatic variables such as measures of ocean temperature anomalies (PDO and SST) and upwelling are linked to some degree with climatic conditions inland, and these inland conditions could affect the freshwater variables we evaluated, such as water transit time. Several researchers have found correlations between ocean indices, such as upwelling, SST, and PDO, and freshwater climate indices, such as flow and winter snowpack (Beamish 1993; Miller et al. 1994; Cayan 1996; Mantua et al. 1997). Mueter et al. (2005) speculated that correlations between wintertime ocean temperatures and sockeye salmon *O.*

nerka survival rates in British Columbia and Washington may have been due to the correlation between ocean climate conditions and inland climate conditions affecting freshwater habitat. However, the marine variables used in this analysis accounted for less than 7% of the variation in WTT and spill. Therefore, the observed correlations between freshwater and ocean survival do not appear to simply be the result of large-scale climatic factors that simultaneously influence survival within the freshwater and marine environments.

Some caution is warranted when comparing the SARs observed in this study to the NPCC SAR goals. First, the SARs reported in this study were derived from Chinook salmon and steelhead smolts that were detected at either Lower Granite Dam or Little Goose Dam. Several studies have found that fish that experience the bypass–detection systems at dams show negatively biased SARs compared with fish that migrate through undetected routes (Budy et al. 2002; Williams et al. 2005; Tuomikoski et al. 2009). Tuomikoski et al. (2009) found that the magnitude of the bias varies across years, but on average, SARs of undetected fish were estimated to be 23% greater than SARs of fish that experience the bypass–detection systems. Whether this bias remains constant or changes over the migration season is unknown. However, assuming the 23% bias is reasonable, multiplying the SARs in this study by 123% does not result in achieving the NPCC SAR goals. Second, a recent study by Knudsen et al. (2009) found that hatchery Chinook salmon from the Yakima River, Washington, that were only coded-wire-tagged had 33% higher SARs than those for fish that were tagged with both a PIT tag and a coded wire tag. Knudsen et al. (2009) were not able to identify when the bias occurred, though they suggested that it occurred within the first 6 months after release from the hatchery. In our study, some of the fish were tagged in the fall before the year of out-migration and migrated some distance within the Snake River basin before being detected at Lower Granite or Little Goose dams. These smolts may or may not have expressed a tagging bias by the time they arrived at Lower Granite and Little Goose dams. There are also questions as to whether the tagging bias is applicable to the wild and hatchery Chinook salmon and steelhead in the Snake River, or whether it is unique to the Yakima River hatchery Chinook salmon. Resolving these questions will require additional research. Assuming that both the detection and tagging biases are fully present and applicable in our study, we estimate that the SARs may be up to 64% higher than what we have reported ($123\% \times 133\% = 164\%$). Even assuming both biases are present, the Chinook salmon and steelhead SARs would remain substantially below the NPCC goals.

In conclusion, the models that were developed for characterizing variation in overall life cycle mortality rates indicate that increases in spill levels and reductions in water transit times are expected to increase stage-specific survival rates (S_H and S_{OA}) as well as cumulative smolt-to-adult survival rates. Across a range of ocean conditions, higher spill levels and reductions in water transit time are expected to result in higher SARs than would occur with lower spill levels and higher water transit times. At a minimum, the models developed here can predict the S_H, S_{OA}, and SAR that may result under various flow and spill alternatives. These predictions would provide quantitative, testable hypotheses on the predicted survival responses that could occur under a true adaptive management experiment (Walters 1986) conducted within the FCRPS, where spill and water transit times are extended beyond the range of available data and the resulting survival rates are monitored to determine whether the expected increases are realized.

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