ARTICLE

Evaluating river management during seaward migration to recover Columbia River stream-type Chinook salmon considering the variation in marine conditions

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Abstract: Evidence suggests Snake River stream-type Chinook salmon (*Oncorhynchus tshawytscha*) experience substantial delayed mortality in the marine environment as a result of their outmigration experience through the Federal Columbia River Power System (FCRPS). We analyzed mortality patterns using methods that incorporated downriver reference populations passing fewer dams, and temporal approaches that were independent of reference populations. Our results from the alternative spatial and temporal methods consistently corroborated with spawner–recruit residuals and smolt-to-adult survival rate data sets, indicating that Snake River salmon survived about one quarter as well as the reference populations. Temporal analysis indicated that a high percentage (76%) of Snake River juvenile salmon that survived the FCRPS subsequently died in the marine environment as a result of their outmigration experience. Through this and previous studies, it is evident that delayed hydrosystem mortality increases with the number of powerhouse passages and decreases with the speed of outmigration. Therefore, a promising conservation approach would be to explore management experiments that evaluate these relationships by increasing managed spill levels at the dams during the spring migration period.

Résumé : Des données semblent indiquer que le saumon quinnat (*Oncorhynchus tshawytscha*) de type dulcicole de la rivière Snake présente une importante mortalité différée dans le milieu marin découlant de son avalaison par l'intermédiaire du réseau fédéral d'installations hydroélectriques du fleuve Columbia (FCRPS). Nous avons analysé la distribution de la mortalité en faisant appel à des méthodes qui tiennent compte des populations de référence des parties aval du réseau, qui traversent moins de barrages, ainsi qu'à des approches temporelles indépendantes des populations de référence. Nos résultats pour les différentes méthodes spatiales et temporelles étaient uniformément en accord avec les ensembles de données de résidus de relations géniteurs-recrues et de taux de survie associés à la transition saumoneau-adulte, qui indiquent un taux survie pour les saumons de la rivière Snake d'environ le quart de celui des populations de référence. L'analyse temporelle indique qu'un fort pourcentage (76 %) de saumons juvéniles de la rivière Snake ayant survécu au FCRPS sont morts plus tard dans le milieu marin des suites de leur avalaison. Cette étude et d'autres études antérieures démontrent clairement que la mortalité retardée associée aux installations hydroélectriques augmente parallèlement au nombre de passages par des centrales électriques et est plus faible pour de plus grandes vitesses d'avalaison. Une approche de conservation prometteuse consiste donc à examiner des expériences de gestion qui évaluent ces relations en accroissant les niveaux de déversements contrôlés aux barrages durant la migration printanière. [Traduit par la Rédaction]

Introduction

Numerous operational changes and technological approaches have been employed over the years to reduce the negative impacts of the Federal Columbia River Power System (FCRPS) on salmon populations. While there is evidence that these approaches have yielded incremental improvements in survival, Snake River salmon (*Oncorhynchus* spp.) populations have substantially declined since completion of the hydroelectric projects of the FCRPS and were subsequently listed under the U.S. Endangered Species Act. A key question has been how the seaward migration experience through the hydrosystem affects survival rates at later life stages in the marine environment (Budy et al. 2002).

Pacific salmon exhibit complex life histories and variable levels of survival rates as a result of conditions in freshwater and ocean environments. The relative influence of the freshwater versus marine conditions is a subject of ongoing debate throughout the range of Pacific salmon, and it is of particular importance in regulated river systems such as the Columbia River, as well as watersheds throughout the Pacific Rim, with anthropogenic disturbances to the landscape that impact salmon populations. For many of the salmon populations along the west coast of North America, overall life-cycle survival appears to be regulated by conditions of both the freshwater and marine environments (Bradford 1995; Bisbal and McConnaha 1998; Levin et al. 2001). The Northwest Power and Conservation Council highlighted the need to identify the effects of ocean conditions on anadromous fish survival so that broad conservation and management 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). While distinguishing between the influence of ocean and freshwater factors on salmon survival is difficult and requires long time series of life stage specific demographic data because of possible confounding factors, the knowledge is critical to predict best

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what potential inland protection and restoration actions are needed to conserve and recover depressed populations of salmon and steelhead. Budy and Schaller (2007) provide examples of the importance of understanding demographic vital statistics of animals that require and occupy large geographic ranges at different stages in their lives, if conservation planning and implementation initiatives are most likely to succeed. Specifically, they assess the potential for tributary habitat protection and restoration efforts in the Snake River basin to restore salmon and steelhead populations to viable levels, with emphasis on the importance of knowing when limiting factors at subsequent life stages constrain the survival to adulthood and successful reproduction, following improvements to survival at earlier stages of life. They use data on Snake River stream-type Chinook salmon survival and freshwater spawning and rearing habitat condition. Petrosky and Schaller (2010) found that survival rates during the smolt-to-adult and first-year ocean life stages of Snake River Chinook salmon and steelhead were associated with both river and ocean conditions. In addition, Haeseker et al. (2012) demonstrated that both freshwater and marine factors are important to characterize variation in Snake River salmonid survival rates and found that, across a range of marine conditions, improvements in stage-specific and life-cycle survival may be achievable through improved river outmigration conditions by increasing the proportion of river flow spilled over crests of dams and (or) water velocity. Within the Snake River basin, Petrosky et al. (2001) found that potential improvements to survival occurring only at the freshwater spawning and rearing life stage are unlikely to increase survival to a level that ensures recovery of stream-type Chinook salmon populations. Relying only on tributary habitat restoration to mitigate for mortality imposed at later life stages, such as seaward migration through the FCRPS, is risky with a low probability of success (Budy and Schaller 2007). Here, we narrow our focus to restoration potential within the FCRPS.

Transporting a majority of out-migrating Snake River spring–summer (stream-type) Chinook salmon (*O. tshawytscha*) past the FCRPS began in 1977, and it was the primary effort used by the U.S. Army Corps of Engineers to mitigate the effect of the hydrosystem on juvenile salmon outmigration (Raymond 1988). Spring migrating smolts are now collected and transported, primarily by barge, from the uppermost three of four lower Snake River FCRPS dams (Williams et al. 2005). Transported smolts avoid most of the direct mortality of in-river migrants but experience the injuries and stresses of collection systems at the transport dam, crowding and exposure to pathogens in holding raceways and barges, and altered estuary arrival timing (Budy et al. 2002; Van Gaest et al. 2011). There are numerous lines of evidence that barged fish may incur additional mortality after release as a result of these stresses of collection and transport and the altered estuary arrival timing (Budy et al. 2002; Schaller et al. 2007; Tuomikoski et al. 2011).

A preponderance of evidence suggests that Snake River fish migrating in-river through the FCRPS also experience delayed mortality in the estuary and during early ocean residence (Williams et al. 2005; Marmorek et al. 2011), although not all investigators have detected such evidence (Rechisky et al. 2013). This outmigration experience results in an accumulation of injuries and stress events and alters estuary arrival timing, which are mechanisms that may explain delayed mortality (Muir et al. 2006; Scheuerell et al. 2009; Rechisky et al. 2012).

Numerous studies investigated 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. Spatial evaluations have contrasted survival rate patterns of Snake River populations with those of reference populations that pass fewer FCRPS dams. These evaluations have generally found that the survival rate of the Snake River population group was a small fraction of that for the reference group (Peters and Marmorek 2001; Schaller and Petrosky 2007; Hinrichsen

and Fisher 2009). However, the relevance of upriver and downriver spatial population comparisons that infer common climatic influences to estimate FCRPS impacts was questioned by Zabel and Williams (2000), Levin and Tolimieri (2001), and Williams et al. (2005). A primary criticism was that because of genetic or behavioral differences, the two evolutionarily significant units (ESUs) might not respond identically to estuary and ocean conditions, and the Snake River survival rate patterns might be driven primarily by environmental conditions. The counter argument emphasized that any such between-region differences would need to explain the systematic change in relative population performance coincident with, but unrelated to, development and operation of the FCRPS (Marmorek et al. 1998; Schaller et al. 2000; Deriso et al. 2001).

Temporal approaches have evaluated time series of survival rates for various life stages of Snake River populations, contrasting increasing impacts of the hydrosystem through time (Petrosky et al. 2001; Wilson 2003; Scheuerell et al. 2009), and in some cases, concurrently evaluating the influence of varying ocean conditions (Schaller et al. 2007; Petrosky and Schaller 2010; Haeseker et al. 2012). These temporal approaches avoid a number of the criticisms and caveats posited against the spatial analyses (Williams et al. 2005).

In this paper, we explored the influence of both river conditions during seaward migration and ocean conditions on life-cycle survival rates of Snake River and John Day River stream-type Chinook salmon. We first estimated differential mortality between the Snake River target populations and the John Day River reference populations that migrate through fewer dams. We also estimated differential mortality temporally within these groups as the relative change in mortality over the history of development and operation of the FCRPS. We compared these differential mortality estimates with those from previous spatial and temporal analyses. Synthesizing these studies with additional analyses, we assessed the magnitude of mortality affecting these populations in the estuary and ocean from the delayed effect of their earlier hydrosystem experience. Finally, we evaluated the specific river conditions and related hydrosystem operations that influenced life-cycle survival rates and delayed mortality while accounting for the influence of marine conditions. This approach can be broadly applied to evaluating river regulation and inland restoration activities for many Pacific salmon populations while considering the variation in marine conditions that affect them.

Materials and methods

Subject populations

We compiled spawner and recruit (SR) data from 21 populations within the Snake and John Day rivers (Fig. 1). We used SR data for wild stream-type Chinook salmon populations in the Snake River spring–summer Chinook salmon ESU compiled for viable salmon population analyses by the Interior Columbia Technical Recovery Team (ICTRT 2007) and recently updated through the NOAA Fisheries five-year review process (Ford et al. 2011). We identified 18 Snake River populations, across four major population groups (MPG), with continuous SR data spanning comparable years. These populations include seven original index populations in three MPGs used with intention to develop conservation plans during the mid to late 1990s (e.g., Marmorek 1996; National Marine Fisheries Service 2000). The addition of 11 populations to the seven index populations greatly increases the geographic scope to include multiple populations within each of the four MPGs of the Snake River ESU upstream of Lower Granite Dam. For populations downstream from the Snake River, we updated the SR data for three John Day River populations from the mid-Columbia ESU with unpublished information provided by Oregon Department of Fish and Wildlife, following the convention employed in Schaller and Petrosky (2007).

Fig. 1. The Columbia and Snake rivers showing the spawning and rearing area currently accessible to Snake River spring–summer Chinook salmon (light shaded) and John Day spring Chinook salmon (dark shaded). The subject populations are within the following five major population groups: John Day River, Grande Ronde/Imnaha (GRIM), South Fork Salmon (SFS), Middle Fork Salmon (MFS), and Upper Salmon River (USR). 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).
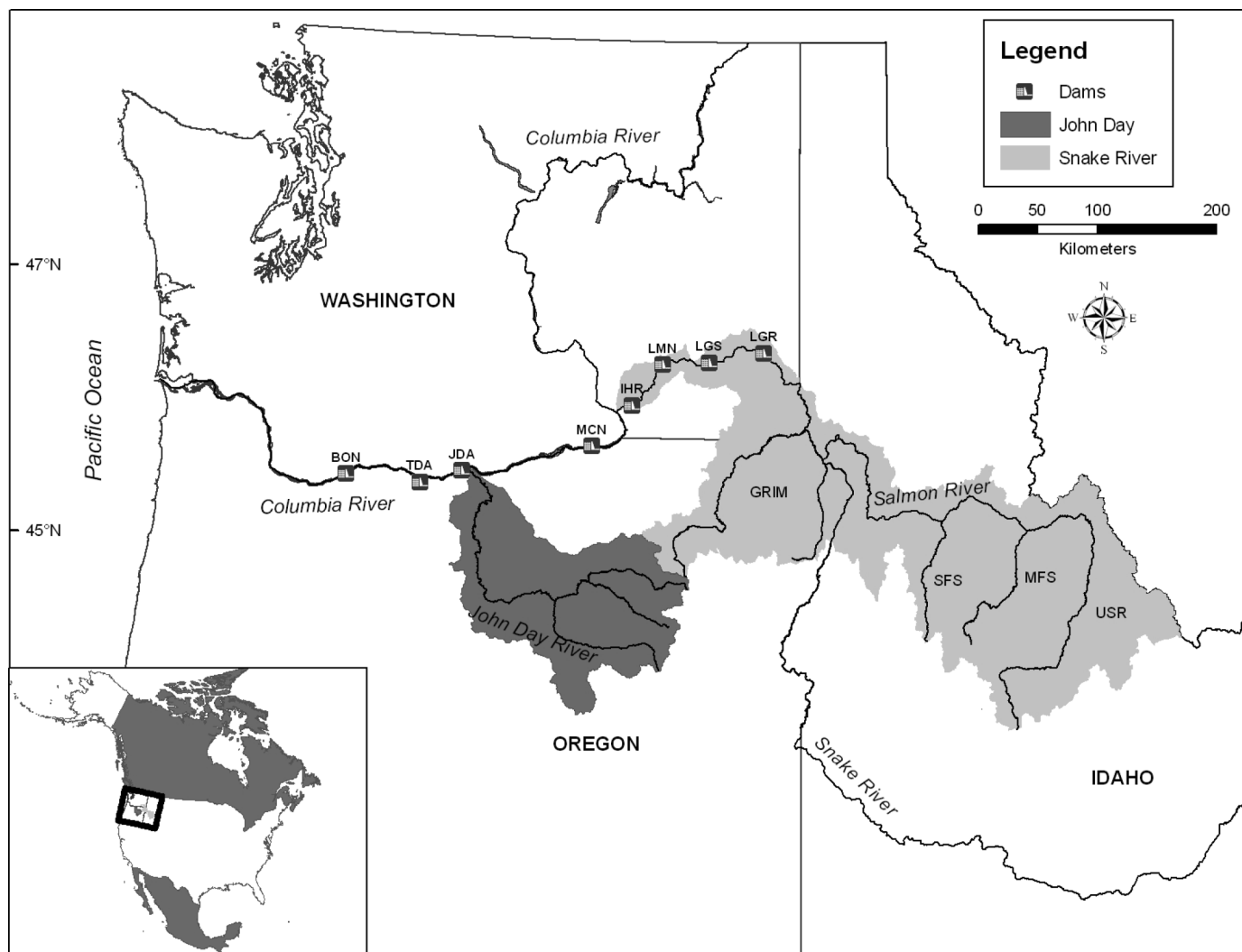
Adult spawners were age 4 and older fish that spawn in nature, including any hatchery-origin fish. Recruits were estimated at the Columbia River mouth. Recruits were assigned to brood year using age-structured estimates of wild spawner abundance and include wild age 3 (jacks) and older progeny; adults collected during recent years for hatchery broodstock (where applicable); prespawn mortality and harvest in terminal subbasins; harvest between the mouth of the Columbia River and subbasin of origin in Columbia mainstem commercial, recreational, and treaty Indian fisheries; and other losses due to upstream passage mortality and straying.

Age-structured recruits on the spawning grounds were expanded back to the Columbia River mouth, using estimates of upstream passage success rates from Bonneville to Lower Granite dams. For return years after 2001 these rates were based on detections of wild adult Chinook salmon marked with passive integrated transponder (PIT) tags reported in Tuomikoski et al. (2011). For adult return years prior to 2002, we based our upstream adult passage success rates on the long time series of historical adult counts at the FCRPS dams and harvest estimates in the mainstem fisheries compiled by the Joint Staffs of Oregon and Washington

and the U.S. versus Oregon Technical Advisory Committee (ODFW and WDFW 2012; TAC 2008). We followed the approach of Petrosky and Schaller (2010) to adjust the pre-2002 upstream adult passage success rate estimates to accommodate greater accuracy of the contemporary PIT tag based estimates, while maintaining the temporal patterns of the historical longer time series.

Survival rate indices

Survival rate indices provide estimates of changes in life-cycle survival rates over time, and they are the deviations of observed recruits–spawners from those expected for a period before completion of the FCRPS (see below). We analyzed survival rate indices for different periods and populations in the Snake and mid-Columbia River regions, updating and expanding the analysis of Schaller et al. (1999) and Schaller and Petrosky (2007). For each population, SR data were classified into two primary periods defined by FCRPS development and operations affecting the threatened Snake River populations (Schaller et al. 1999). The first period, pre-1970 brood years, was before completion of the final two Snake River dams. The second period, post-1974 brood years

(1975–2004), was characterized by completion of the full eight-dam complex, collection and transportation of smolts around dams in barges and trucks, turbine screening programs, and other management actions to improve passage at the dams (Budy et al. 2002). The 1970–1974 period was excluded from fitting of the recruitment functions because it was a period of construction and of changing operations in the Snake River that caused extremely high levels of atmospheric gas supersaturation in high-flow years (Raymond 1979) before mass transportation of smolts had begun.

Productivity and survival rate indices were estimated for pre-1970 and post-1974 periods for each population in the Snake and mid-Columbia ESUs. Productivity is defined as the natural logarithm (ln) of the ratio of recruits to spawners in the absence of density-dependent mortality. The SR data can be fit to the Ricker recruitment function (Ricker 1975) with the equation

$$(1) \qquad R = \exp^{a} S \exp^{-\beta S}$$

where R is the number of recruits, S is the number of spawners, a is the intrinsic productivity, and β is a capacity parameter. The a and β parameters are estimated by the ln transformation of equation 1. Productivity is measured as the intercept, or Ricker a. Survival rate indices provide a time series of density-independent mortality estimates through deviations of observed ln(R/S) from those predicted by the fitted stock–recruitment function for a specified period. Previous analysis (Schaller et al. 1999) concluded that a temporal change in density-independent mortality, such as that imposed by hydroelectric development and operation, or an oceanic regime shift, was reflected primarily in the intercept (Ricker a) rather than in the slope (β) of the regressions. To account for nonstationarity in the recruitment functions (Hilborn and Walters 1992), we followed the Schaller et al. (1999) and Schaller and Petrosky (2007) analysis of covariance (ANCOVA) method to examine differences in the intercepts (Ricker a)

$$(2) \qquad \ln(R_{ij}/S_{ij}) = T_i + a - \beta(S_{ij} - \overline{S}_{..}) + \varepsilon_{ij}$$

where T_i is the class effect (period), a is the intercept, β is the slope, $\overline{S}_{..}$ is the average spawners for all observations during both time periods, ε_{ij} is the normally distributed residual, i is the class (period), and j is the observation (brood year).

We tested homogeneity of slopes for significant interaction between the treatment (period) and the covariate (spawners). We then used ANCOVA to estimate the period effect on ln(R/S), taking into account spawner abundance. The measure of productivity by period was estimated with $T_i + a$ from the ANCOVA results (eq. 2). This is equivalent to the Ricker a parameter by period (assuming a common slope for both periods).

We calculated survival rate indices (SRIs) as the residuals about the predictions of ln(R/S), based on Ricker coefficients for the pre-1970 time period (Schaller et al. 1999; Schaller and Petrosky 2007). Annual SRIs for each population were averaged for each ESU and MPG for use in temporal analyses to evaluate the influence of various river and ocean variables on the survival rate variation within the Snake River ESU, within four Snake River MPGs, and within the John Day MPG of the mid-Columbia ESU. SRIs were generated for brood years 1954–2004 for the Snake River ($n = 51$), and 1959–2004 for the John Day River ($n = 46$). We also used the SRIs from each ESU in a spatial comparison to calculate differential mortality between ESUs for the post-1974 period. Finally, we compared inferences about differential mortality between the alternative temporal and spatial approaches (see below).

Survival rate model

We used analytical and statistical tools to make inferences about the effects of broad scale ocean, near shore ocean, and river conditions on Snake River and John Day River wild Chinook salmon survival rates following the approach of Petrosky and Schaller (2010). Specifically, our approach was (*i*) to estimate life-cycle SRI, (*ii*) to use correlation and regression techniques to statistically evaluate candidate parameters that best explain the variation in survival rates, (*iii*) to statistically evaluate various combinations of the parameters using multivariate regression techniques to produce a multivariate model with a high level of fit to the survival rate data series, and (*iv*) to use our best-fit models to isolate the influence of ocean and river conditions on overall survival rates.

We evaluated a number of independent variables to assess both the influence of broad scale and near shore ocean conditions, as well as conditions in the Snake and Columbia rivers, on life-cycle survival rates of Snake River and John Day River Chinook salmon.

River variables

We incorporated five river variables (Table 1) associated with the juvenile seaward migration (brood year + 2): water travel time (WTT); the expected number of powerhouse passages (N_Powerhouse) and turbine passages (N_Turbine) for juveniles migrating through the FCRPS; the mean temperature (MeanMaxT or MCN_Temp, °C) where smolts enter the FCRPS; and the proportion of juveniles arriving at the upper most dam that were collected and transported around dams (pT). All variables were expressed as annual estimates for the spring migration period (April 16 – May 31).

River velocity affects juvenile fish travel time (FTT) through a river reach and is expressed as WTT (Schaller et al. 2007). The river reach for Snake River Chinook salmon is defined from the head of Lower Granite Reservoir on the Snake River at the mouth of the Clearwater River to Bonneville Dam and for John Day Chinook salmon extends from the forebay of John Day Dam to Bonneville Dam (Fig. 1). We obtained historic annual estimates of WTT from the Fish Passage Center (Portland, OR). Juvenile migrants that are not spilled over the dam enter the powerhouse and pass through the turbines or through collection–bypass systems. Route of passage, which also affects FTT and has been found to be influential in Columbia River juvenile survival rate studies (e.g., Schaller et al. 2007), is affected by the proportion of water spilled. Because the number of dams changed during the 1956–2006 time period (and differs between Snake and John Day regions), we expressed the effects of spill in terms of N_Powerhouse, which is a function of the number of dams, the proportion spill at each dam, and spill passage efficiency. Juvenile migrants that enter the powerhouse, but do not pass through the collection–bypass systems, pass through turbines. We estimated N_Turbine, which is a function of the number of dams, the proportion spill at each dam, spill passage efficiency, and the efficiency of screens to guide fish away from the turbine intakes. The effect of water temperature during the juvenile migration on recruitment success of Snake River and John Day River Chinook salmon was evaluated with available temperature data collected at locations near where each ESU entered the FCRPS. For Snake River Chinook salmon, MeanMaxT was calculated from data at the USGS Anatone gauge station on the Snake River and Spaulding gauge station on the Clearwater River, migration years 1960–2006. For John Day Chinook salmon, we used the daily forebay scrollcase temperature at McNary Dam (MCN_Temp) obtained from the U.S. Army Corps of Engineers, migration years 1962–2006. The majority of Chinook salmon smolts entering the powerhouse collection systems of Lower Granite, Little Goose, or Lower Monumental dams on the Snake River was transported during 1977–2006. The pT varies with spill and indirectly with WTT and is a function of probability of powerhouse passage, fish guidance efficiency, and annual management operations.

Table 1. Candidate predictor variables for river conditions during seaward migration and broadscale and near shore ocean conditions for Snake River and John Day River survival rate indices (SRIs), brood years 1954–2004.

Predictor variable	Short name	Source
River variables		
Water travel time, the average time in days it takes a water particle to travel through a river reach	WTT	Petrosky and Schaller 2010
Expected number of powerhouse passages	N_Powerhouse	Petrosky and Schaller 2010
Expected number of turbine passages	N_Turbine	Petrosky and Schaller 2010
Mean maximum daily temperature of Snake River (Snake populations only)	MeanMaxT	Petrosky and Schaller 2010
Mean daily temperature at McNary Dam (John Day populations only)	MCN_Temp	http://www.cbr.washington.edu/dart/river_com.html
Proportion of juveniles transported (Snake populations only)	pT	Petrosky and Schaller 2010
Ocean variables		
Monthly Pacific Decadal Oscillation index	JanPDO, FebPDO, … DecPDO	http://jisao.washington.edu/pdo/PDO.latest
Mean Pacific Decadal Oscillation index, May, June, and July	PDO_MJJ	Rupp et al. 2011
Four-year running average Pacific Decadal Oscillation index, May, June, and July (Four-year running mean corresponds to the year of ocean entry and the three preceding years.)	PDO_MJJ-4	Rupp et al. 2011
Multivariate El Niño/La Niña-Southern Oscillation index, October and November	MEI_ON	Rupp et al. 2011
Monthly sea surface temperature, 45°N, 2 degree grid	JanSST, FebSST, … DecSST	http://dss.ucar.edu/datasets/ds540.1
Mean sea surface temperature, 45°N, April, May, and June	SST_AMJ	Rupp et al. 2011
Monthly upwelling index, 45°N	JanUP, FebUP, … DecUP	http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html
Mean upwelling index, 45°N, July, August, and September	UWI_JAS	Rupp et al. 2011
Mean upwelling index, 45°N, September, October, and November	UWI_SON	Rupp et al. 2011
Spring transition date (extended back to 1956, see text)	SPR.TRN	Rupp et al. 2011

Ocean variables

Salmon recruitment success in the ocean environment is generally believed to occur largely during the first critical months at sea (Ricker 1976; Mueter et al. 2002; Pyper et al. 2005). We explored the relationships between SRIs and a number of long-term indices (Table 1) to evaluate whether variation in broad scale and in near shore oceanic conditions during the year of ocean entry (brood year + 2) influenced survival rate patterns of the Snake River and John Day River Chinook salmon populations (Petrosky and Schaller 2010; Rupp et al. 2012).

The Pacific Decadal Oscillation (PDO) index is a broad scale climate index based on patterns of variation in sea surface temperature (SST) of the North Pacific from 1900 to the present (Mantua et al. 1997). The PDO data were from updated standardized values of the PDO index derived as the leading principal component of monthly SST anomalies in the North Pacific Ocean. We used as candidate predictor variables the monthly PDO index (Petrosky and Schaller 2010), the mean May–June–July PDO, and a four-year running mean of the May–June–July PDO (Rupp et al. 2012) describing a multiyear ecosystem effect for Oregon coho salmon recruitment. The other broad scale ocean index we considered as a candidate predictor variable was the El Niño/La Niña-Southern Oscillation (ENSO). ENSO is a periodic climate pattern that describes a warm oceanic phase, El Niño, accompanied by high air surface pressure in the western Pacific, and a cold phase, La Niña, accompanied by low air surface pressure in the western Pacific. Specifically, we employed the multivariate ENSO index for October and November (Rupp et al. 2012).

For the near shore ocean environment, we used indicators of SST, monthly upwelling indices (UWI), and the index of Logerwell et al. (2003) of the timing of spring transition between downwelling and upwelling favorable winds. To capture the influence of near shore temperature on survival (e.g., Mueter et al. 2005), SST candidate predictor variables included the mean monthly SST (Petrosky and Schaller 2010) and the mean April–May–June SST (Rupp et al. 2012) at 45°N latitude. The UWI (cubic meters/second/100 meters of coastline at 45°N latitude) variables considered to capture the influence of strength of upwelling of nutrient rich water in the spring or downwelling in the fall were the mean monthly UWI (Petrosky and Schaller 2010), the mean July–August–September UWI, and the mean September–October–November UWI (Rupp et al. 2012). We used the Logerwell et al. (2003) index of spring transition date (SPR.TRN) for migration years 1969–2006 and a predicted SPR.TRN for earlier migration years 1954–1968 (Table 1). The SPR.TRN is based on the first day when the value of the 10-day running average for upwelling is positive and the 10-day running average for sea level is negative. The spring transition date requires daily estimates of upwelling, which are only available beginning in 1969. Because the Logerwell SPR.TRN index was related to the mean March–April UWI during 1969–2006 ($r = 0.60$), we used the relationship between the two indices as a predictor for the SPR.TRN for the earlier migration years.

Independent variable selection

Following methods of Petrosky and Schaller (2010), we evaluated the strength of the associations between 49 candidate predictor variables (48 for the John Day populations) and SRIs in univariate analyses using correlation coefficients that rounded to at least $|0.4|$ as a preliminary screen. We calculated significance of the correlations (one-tailed t test) by adjusting degrees of freedom to account for autocorrelation in the time series using the methods of Pyper and Peterman (1998). Candidate variables were then selected for multiple regression analysis using correlation criteria (rounded $r \geq |0.4|$, $P \leq 0.05$).

Multiple regression model selection

We used multivariate regression to evaluate predictive capability of combinations of selected covariates on SRIs. Multiple linear regression procedures (SAS Institute, Inc. 2002) were used to run all combinations of alternative models among the covariates. The degree of model fit was evaluated based on adjusted R^2 values, Akaike's information criteria (AIC), and Bayesian information criteria (BIC) scores (Burnham and Anderson 2002). Our multiple

264

Can. J. Fish. Aquat. Sci. Vol. 71, 2014

regression models for various river and ocean variables took the form

$$(3) \qquad \text{SRI}_t = B0 + B river_i * river_{i,t} + B ocean_j * ocean_{j,t} + \varepsilon_t$$

where t is the smolt year; $B0$ is the intercept; $B river$ is the coefficient for each river variable, i; $B ocean$ is the coefficient for each ocean variable, j; and ε_t is the normally distributed residual. We evaluated the patterns of overall normalized residuals and the normalized residuals versus the independent variables to determine if the assumptions of regression were violated in the best-fit models. We also tested for presence of autocorrelation in the residuals of the multiple regression analysis by applying a Durbin-Watson test (Draper and Smith 1998). Generally, a Durbin–Watson statistic (D-W) < 1.0 indicates strong positive autocorrelation of regression residuals, indicating the assumption of no time effect may be violated.

We presented multiple regression results in the following three ways: (1) tables with coefficients for selected, best-fit models based on adjusted R^2, AIC, and BIC score; (2) plots of BIC score versus R^2 for all possible models containing river variables only, ocean variables only, and both river and ocean variables (Petrosky and Schaller 2010); and (3) plots of relative variable importance (Burnham and Anderson 2002). The more consistently a variable is included in alternative models with low AIC scores, the higher the relative variable importance (Burnham and Anderson 2002).

Differential and delayed mortality estimates

We used three alternative approaches to estimate differential mortality. First, we employed a spatial approach by calculating the mean difference in SRIs between the Snake River ESU and the mid-Columbia River ESU (as represented by the John Day MPG) to estimate differential mortality between regions in the post-1974 period (method 1). We also used method 1 to estimate differential mortality from the natural logarithm of smolt to adult return rates (SARs) of wild Chinook salmon of the Snake and John Day rivers for brood years 1998–2006 (Tuomikoski et al. 2011).

Second, we employed a temporal approach to estimate changes in mortality from average river conditions during the pre-1970 period to average river conditions during the post-1974 period, consistent with the approach used for fitting the spawner–recruit models. We predicted the change in mortality for the Snake River ESU from the pre-1970 river conditions to the post-1974 river conditions, using coefficients for river variables from the best BIC regression model (method 2). We then applied the same approach to the mid-Columbia River region.

Lastly, we compared the estimated differential mortality attributable to FCRPS impacts from spatial and temporal analyses (method 3). We estimated the change in FCRPS impacts from the pre-1970 to the post-1974 period for each region, using the coefficients for river variables from the best model based on BIC scores, while holding the ocean effect constant. Differential mortality from method 3, $\mu_{s/t}$, was calculated as follows:

$$(4) \qquad \mu_{s/t} = (m_{\text{SNK,post-1974}} - m_{\text{SNK,pre-1970}})$$
$$- (m_{\text{JDA,post-1974}} - m_{\text{JDA,pre-1970}})$$

where $m_{\text{SNK,post-1974}}$ and $m_{\text{SNK,pre-1970}}$ are FCRPS mortality for Snake River populations for post-1974 and pre-1970 periods, and $m_{\text{JDA,post-1974}}$ and $m_{\text{JDA,pre-1970}}$ are FCRPS mortality for John Day River populations for post-1974 and pre-1970 periods, respectively.

Our various estimates for hydrosystem-related mortality for the Snake River populations include both the direct and delayed effects of the FCRPS on the juvenile outmigration experience. We estimated hydrosystem-related delayed mortality by partitioning system survival (juvenile passage survival) estimates from the to-

tal (direct and delayed) FCRPS mortality estimate obtained from our temporal approach. Specifically, the predicted total FCRPS mortality for the Snake River Chinook salmon ESU was estimated from the mean Post-1974 river conditions, using coefficients for river variables from the best BIC regression model (method 2). We used the mean of system survival estimates (0.357; range 0.335–0.374) from previous analyses (Deriso et al. 2001; Schaller and Petrosky 2007; Hinrichsen and Fisher 2009; Petrosky and Schaller 2010) to partition delayed mortality from the total FCRPS mortality.

We compared our alternative differential mortality estimates with those from previous spatial analyses of SRIs and SARs (Schaller et al. 1999, 2007; Deriso et al. 2001; Schaller and Petrosky 2007; Hinrichsen and Fisher 2009), as well as temporal analysis of SARs (Petrosky and Schaller 2010).

We compared our estimate of delayed mortality with those from previous studies and evaluated the level of supporting evidence used in the various alternative approaches. We then further assessed the supporting evidence by comparing the assumptions for various survival rates and stock productivity, made in the alternative delayed mortality methods, with independent estimates for these parameters from empirical information.

Results

Productivity and survival rate analysis

Survival rates declined more for Snake River Chinook salmon than for John Day River Chinook salmon after FCRPS completion (post-1974). SRI values averaged –2.16 for Snake River populations and –0.85 for John Day River populations (Table 2; Fig. 2) for brood years 1975–2004. In other words, R/S declined to 12% of the pre-FCRPS productivity for Snake populations and 43% for John Day populations. The average correlation of SRIs from individual MPGs with the Snake River ESU average was 0.92; the correlation among MPGs was 0.81. We found little evidence that the presence of hatchery spawners in Snake River populations significantly influenced the survival rate patterns (Table 2); average SRIs in the post-1974 period for populations with >10% hatchery fraction in the spawning population (–2.18, SE = 0.16) were not significantly (paired t test, $P = 0.23$) lower than those with low hatchery fractions (–2.11, SE = 0.17).

SRI variable selection

Snake River SRIs were correlated with 13 variables at a level of at least |0.4| and significance of $P \leq 0.05$ (Table 3). For multiple regression analyses, we selected the following nine variables: May PDO, September PDO, April Upwelling, October Upwelling, April SST, PDO_MJJ, WTT, N_Powerhouse, and pT. We rejected March PDO, April PDO, July PDO, and August PDO for model analysis, as they were highly correlated with May PDO values. The nine variables that we accepted for the Snake River ESU resulted in 511 alternative regression models with all combinations of river and ocean variables. In general, the correlation results for the ocean and river variables were similar across the four Snake River MPGs (Table 3).

John Day River SRIs were correlated with 10 variables at a level of at least |0.4| and significance of $P \leq 0.05$ (Table 3). For multiple regression analyses, we selected the following five variables: May PDO, October PDO, April Upwelling, PDO_MJJ, and N_Powerhouse. We rejected June PDO, July PDO, August PDO, September PDO, and November PDO for model analysis, as they were highly correlated with May PDO or October PDO values. The five variables that we accepted for the John Day River populations resulted in 31 alternative regression models with all combinations of river and ocean variables. In general, the correlation results for the ocean variables were similar between the John Day and the Snake River populations.

Table 2. Analysis of covariance results for Ricker recruitment functions (eq. 2) that used period (treatment) and spawners (covariate) for stream-type Chinook salmon major population groups (MPG) and populations from the Snake River and John Day River regions, brood years 1954–2004.

		Fraction of hatchery spawners (post-1974)	Intercept						
Region, MPG	Population		T1 + a pre-1970	T2 + a post-1974	T1 − T2	Intercept H0: T1 = T2, P	Slope (−B)	H0: −B < 0, P	R^2
Snake River									
Middle Fork Salmon (MFS)	**Bear Valley**	0.00	3.9995	1.0326	2.9668	<0.0001	−0.00168	0.0001	0.40
	Marsh	0.00	3.8725	0.6973	3.1753	<0.0001	−0.00224	0.0002	0.46
	Sulphur	0.00	3.5699	0.5576	3.0123	<0.0001	−0.00401	0.0002	0.46
	Big	0.00	2.6974	0.9454	1.7520	0.0011	−0.00236	0.0006	0.28
South Fork Salmon (SFS)	**Mainstem**	0.23	1.7163	0.6976	1.0187	0.0029	−0.00038	0.0024	0.25
	East Fork South Fork	0.04	2.5528	0.9608	1.5920	<0.0001	−0.00267	0.0000	0.53
	Secesh	0.02	1.6764	1.1836	0.4928	0.0679	−0.00156	0.0001	0.31
Upper Salmon (USR)	Lemhi	0.00	2.5395	0.4166	2.1229	0.0006	−0.00084	0.0086	0.27
	Upper Salmon	0.15	3.4158	1.1485	2.2673	<0.0001	−0.00100	0.0002	0.37
	East Fork	0.11	3.2066	1.0852	2.1215	0.0005	−0.00124	0.0003	0.30
	Valley	0.00	2.9375	0.8419	2.0956	0.0003	−0.00252	0.0002	0.34
Grande Ronde/Imnaha (GRIM)	**Imnaha**	0.29	2.4367	0.6950	1.7416	<0.0001	−0.00061	0.0000	0.55
	Big Sheep	0.26	1.7178	−0.7791	2.4968	0.0819	−0.00098	0.2972	0.23
	Wenaha	0.21	2.5661	0.4025	2.1636	<0.0001	−0.00082	0.0133	0.41
	Lostine	0.21	3.7156	1.1477	2.5680	<0.0001	−0.00234	0.0000	0.65
	Minam	0.15	2.5039	0.7222	1.7817	<0.0001	−0.00112	0.0000	0.47
	Catherine	0.27	2.7399	0.0640	2.6759	<0.0001	−0.00091	0.0018	0.45
	Upper Grande Ronde	0.24	3.2572	0.4797	2.7775	<0.0001	−0.00330	0.0000	0.56
Snake River mean		0.12	—	—	2.1568	—	—	—	—
John Day River									
John Day (JDA)	Upper Mainstem	0.02	1.9346	1.2056	0.7289	0.0102	−0.00136	0.0004	0.47
	Middle Fork	0.02	1.8733	1.2855	0.5878	0.0964	−0.00158	0.0003	0.46
	North Fork	0.02	2.6916	1.4550	1.2366	<0.0001	−0.00072	0.0001	0.63
John Day mean		0.02	—	—	0.8511	—	—	—	—

Note: Historic index populations are bolded.

Fig. 2. Survival rate index (SRI) patterns for Snake River (solid line) and John Day River (dashed line) stream-type Chinook salmon, brood years 1950s–2004.
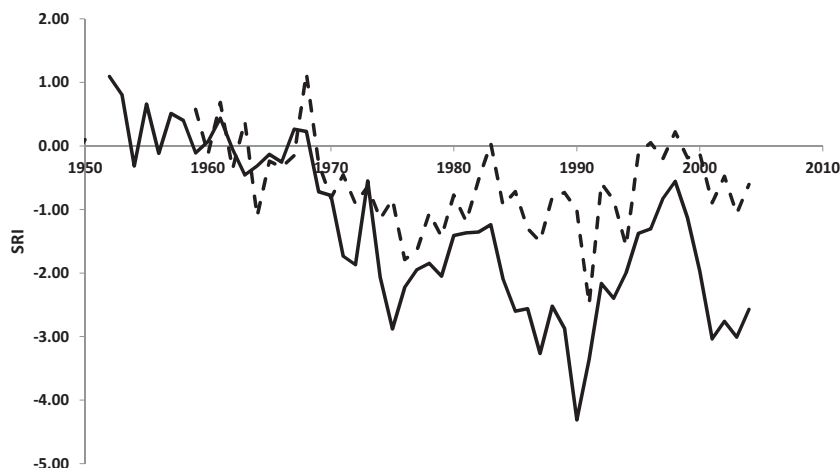
SRI regression

Best-fit simplest models for Snake River SRIs included both river and ocean variables (Fig. 3a), whereas models that contained only ocean variables or only river variables had little statistical support. These results imply that both river conditions during seaward migration, as well as ocean conditions, influence life-cycle survival rates. The best-fit model based on BIC for Snake River SRIs included one ocean variable, N_Powerhouse, and pT (Table 4). The best-fit model based on AIC for Snake River SRIs included two ocean variables, WTT, and pT (Table 4). Coefficients from the top models indicate that lower survival rates are associ-

ated with warmer ocean conditions, weaker downwelling in the fall, slower water velocities, multiple powerhouse passages, and high proportion of transported juvenile fish. The relative variable importance to best-fit models for Snake River populations indicated for ocean variables that September PDO was most important, followed by October upwelling and April upwelling (Fig. 4a). Proportion transported was the most important river variable in the top models, followed by water travel time and number of powerhouse passages (Fig. 4a).

Best-fit simplest models for John Day SRIs included both river and ocean variables (Fig. 3b). The statistical support for models

Table 3. Correlations of variables with survival rate indices (SRI) – 1 for Snake River region, four Snake River major population groups (MPGs), and John Day River Chinook salmon.

	Snake	MFS MPG	SFS MPG	USR MPG	GRIM MPG	John Day
WTT	−0.70**	−0.68**	−0.48**	−0.65**	−0.69**	−0.24
N_Powerhouse	−0.78**	−0.76**	−0.53*	−0.73**	−0.76**	−0.46*
N_Turbine	−0.43	−0.42	−0.37	−0.39	−0.37	−0.20
MeanMaxT	−0.32*	−0.29*	−0.10	−0.24	−0.41**	NA
MCNTemp	NA	NA	NA	NA	NA	−0.08
pT	−0.73*	−0.68*	−0.39	−0.66*	−0.74*	NA
JanPDO	−0.32	−0.22	−0.11	−0.15	−0.39*	−0.05
FebPDO	−0.32	−0.28	−0.09	−0.23	−0.36*	−0.15
MarPDO	−0.41*	−0.42*	−0.21	−0.34	−0.45*	−0.17
AprPDO	−0.44*	−0.44*	−0.27	−0.37	−0.44*	−0.31
MayPDO	−0.53*	−0.59*	−0.45*	−0.52*	−0.52*	−0.52**
JunPDO	−0.33*	−0.42*	−0.31*	−0.34*	−0.32	−0.42**
JulPDO	−0.50*	−0.51*	−0.48**	−0.48*	−0.49*	−0.49**
AugPDO	−0.51**	−0.61**	−0.52**	−0.48**	−0.50**	−0.47**
SepPDO	−0.37*	−0.47**	−0.55**	−0.42*	−0.34*	−0.41**
OctPDO	−0.30*	−0.41*	−0.38*	−0.32*	−0.25	−0.47**
NovPDO	−0.31*	−0.35*	−0.25*	−0.23	−0.29*	−0.42**
DecPDO	−0.29*	−0.31*	−0.24	−0.23	−0.28	−0.31*
PDO_MJJ	−0.49*	−0.55*	−0.45*	−0.48*	−0.48*	−0.51**
PDO_MJJ-4	−0.43	−0.33	−0.14	−0.32	−0.52	−0.29
MEI_ON	−0.02	0.04	0.14	0.05	−0.09	0.13
JanSST	0.09	0.10	0.09	0.12	0.07	0.04
FebSST	−0.05	−0.03	−0.01	0.06	−0.06	0.08
MarSST	−0.35*	−0.39*	−0.21	−0.38*	−0.32*	−0.24
AprSST	−0.38*	−0.38*	−0.30	−0.43*	−0.35*	−0.26
MaySST	−0.29	−0.43*	−0.39**	−0.38*	−0.26*	−0.11
JunSST	0.01	−0.18	−0.08	−0.12	0.03	−0.24
JulSST	0.11	0.00	0.01	0.01	0.11	−0.13
AugSST	0.30*	0.17	0.19	0.21	0.29	0.10
SepSST	0.31*	0.23	0.07	0.23	0.34	0.01
OctSST	0.17	0.05	−0.06	0.12	0.19	−0.12
NovSST	0.07	0.02	−0.03	0.07	0.07	−0.12
DecSST	0.07	0.04	0.06	0.09	0.01	0.14
SST_AMJ	−0.24	−0.40*	−0.31	−0.37*	−0.20*	−0.26
JanUP	0.14	0.13	−0.04	0.19	0.18	0.04
FebUP	−0.06	−0.02	−0.04	−0.05	−0.08	−0.06
MarUP	0.04	−0.02	−0.03	0.01	0.05	0.07
AprUP	0.36*	0.39**	0.38**	0.32*	0.30*	0.39**
MayUP	0.13	0.16	0.01	0.05	0.18	0.04
JunUP	0.10	0.14	−0.04	0.14	0.15	0.17
JulUP	0.09	0.06	0.08	0.03	0.11	0.05
AugUP	−0.12	−0.05	−0.15	−0.02	−0.12	−0.05
SepUP	−0.14	−0.02	0.02	−0.09	−0.18	0.09
OctUP	−0.38*	−0.41*	−0.32*	−0.36*	−0.37*	−0.27
NovUP	−0.09	−0.15	−0.29*	−0.22	−0.07	−0.20
DecUP	−0.08	−0.02	0.01	−0.02	−0.11	−0.05
UWI_JAS	−0.07	0.00	−0.03	−0.02	−0.07	0.04
UWI_SON	−0.29	−0.30	−0.36*	−0.37*	−0.28*	−0.25
SPR.TRN	−0.25*	−0.24	−0.32*	−0.18	−0.20	−0.28*

Note: *, $P < 0.05$; **, $P < 0.01$; adjusted for autocorrelation. Variables with underlined correlations were incorporated into multiple regressions.

that contained only ocean variables or only river variables was weak. These results imply that both river conditions during seaward migration and ocean conditions influence life-cycle survival rates. The best-fit (BIC, AIC) model for John Day SRIs included two ocean variables and N_Powerhouse (Table 4). Coefficients from the top models indicate that lower survival rates are associated with warmer ocean conditions, weaker upwelling in the spring, and multiple powerhouse passages for juvenile fish. The relative variable importance to best-fit models for John Day River populations indicated for ocean variables that October PDO was most important, followed by April upwelling (Fig. 4b). The number of powerhouse passages was the most important river variable in the top models (Fig. 4b). However, the best-fit models for John Day River populations explained less of the variation in SRIs than did the models for Snake River populations.

The normalized overall residual patterns and the normalized residual patterns for each of the independent variables for the Snake River and John Day River populations' best-fit models did not appear to violate the assumptions of regression. Slight positive serial correlation of residuals of the best-fit regression models for both the Snake River and John Day River populations was evident, based on the D-W statistic. Autocorrelation of residuals did not appear extreme for either Snake or John Day populations (D-W range 1.28–1.99).

Differential and delayed mortality

The results from the three methods for estimating differential mortality (from SRIs) indicated substantial differences in mortality between the Snake River populations and their downriver

Fig. 3. Multiple regression fits (R^2 and BIC) to ocean and river variables (cross), river only (black circle), and ocean only (shaded square) classes of independent variables for (a) Snake River Chinook salmon SRIs (plotted for four or fewer variable models) and for (b) John Day River Chinook salmon SRIs.
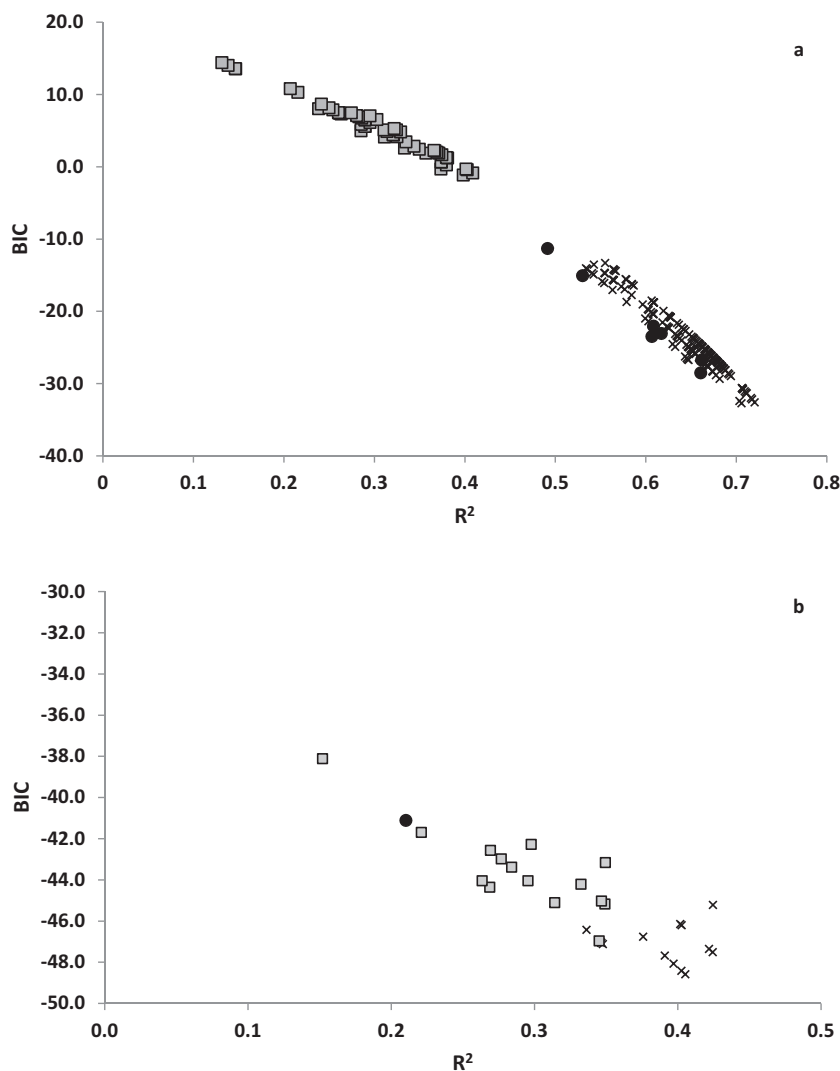
counterparts from the John Day River. Our estimate of differential mortality, using the spatial approach (method 1) for the post-1974 brood years, was 1.33. In other words, the Snake River Chinook salmon survival rates on average were 26% of those for the John Day River (Table 5). The differential mortality estimate from the temporal method (method 2) for the post-1974 brood years was 1.90, indicating that the Snake River Chinook salmon survival rates on average were 15% of those for the John Day River. Using the spatial and temporal approach (method 3), differential mortality was 1.40, indicating that the Snake River Chinook salmon survival rates on average were 25% of those for the John Day River.

The spatial comparison to estimate differential mortality from SARs (brood years 1998–2006) also indicated a substantial level of differential mortality of 1.30 (Table 5), indicating that the Snake River Chinook salmon SARs (on average) were 27% of those for the John Day River. This is similar to the above results for SRI analyses.

Finally, the result using the temporal approach (method 2) to estimate delayed mortality was 76% (Table 6). This indicates that three quarters of Snake River fish died later in the marine environment as a result of the FCRPS migration experience.

Discussion

Our analyses and previous studies provide a preponderance of evidence that the existence and operation of the FCRPS strongly influence survival rates of Snake River stream-type Chinook salmon during life stages in the marine environment. This result is consistent over a range of marine conditions. These findings add substantial information to the weight of evidence supporting the hydrosystem delayed mortality hypothesis posited by Budy et al. (2002).

Our analyses increased the number of populations in the Snake River basin from 7 to 18, expanded the time series of data by as many as 14 years, added an SR temporal approach, and added an SAR-based approach (that yields estimates that are more precise and does not rely on spawner–recruit models). Uncertainties and caveats have been identified for the approach that relies on contrasting SR results for Snake River populations with a reference population that migrates through fewer dams (Zabel and Williams 2000; Levin and Tolimieri 2001; Williams et al. 2005). Our enhanced approach enabled us to estimate the impacts of the hydrosystem and address past criticisms for these types of evaluations (Zabel and Williams 2000; Schaller et al. 2000). The expansion of the SR data from seven index populations in three MPGs to 18 Snake River populations in all of the MPGs upstream of Lower Granite Dam, with varying degrees of recent hatchery influence, substantially increased the geographic representation of the Snake River ESU. Updating the SR data through the 2004

Table 4. Regression model results (selected) for survival rate indices (SRIs) of Snake River (1954–2004) and John Day River (1959–2004) stream-type Chinook salmon versus river and ocean environmental variables.

Number of variables	Adjusted R^2	R^2	AIC	BIC	Variable	Estimate	SE	t	$P > [t]$	Selection criteria
Snake River										
6	0.7035	0.7391	−35.6178	−30.4361	Intercept	0.1381	0.2705	0.51	0.6123	Best adjusted R^2
					WTT	−0.0432	0.0266	−1.62	0.1120	
					N_Powerhouse	−0.1302	0.1080	−1.21	0.2342	
					pT	−0.9378	0.4359	−2.15	0.0370	
					SepPDO	−0.2773	0.1050	−2.64	0.0114	
					AprUP	0.0061	0.0049	1.26	0.2159	
					OctUP	−0.0082	0.0051	−1.62	0.1123	
4	0.6960	0.7203	−36.0692	−32.5940	Intercept	0.0151	0.2295	0.07	0.9479	Best AIC
					WTT	−0.0643	0.0163	−3.95	0.0003	
					pT	−1.3271	0.3819	−3.48	0.0011	
					SepPDO	−0.3555	0.0963	−3.69	0.0006	
					OctUP	−0.0084	0.0051	−1.66	0.1027	
3	0.6870	0.7058	−35.4864	−32.7425	Intercept	0.3558	0.2538	1.40	0.1675	Best BIC
					N_Powerhouse	−0.2678	0.0674	−3.97	0.0002	
					pT	−1.2619	0.4122	−3.06	0.0036	
					SepPDO	−0.2661	0.0993	−2.68	0.0101	
John Day River										
4	0.3683	0.4244	−50.9643	−47.5100	Intercept	0.1077	0.2998	0.36	0.7212	Best adjusted R^2
					N_Powerhouse	−0.3764	0.1470	−2.56	0.0142	
					OctPDO	−0.1393	0.0998	−1.39	0.1706	
					PDO_MJJ	−0.1226	0.1051	−1.17	0.2499	
					AprUP	0.0068	0.0044	1.55	0.1298	
3	0.3628	0.4053	−51.4608	−48.5827	Intercept	0.1829	0.2941	0.62	0.5373	Best AIC and BIC
					N_Powerhouse	−0.4325	0.1395	−3.10	0.0034	
					OctPDO	−0.1855	0.0920	−2.02	0.0502	
					AprUP	0.0085	0.0042	2.04	0.0480	

Fig. 4. The relative variable importance of river variables (black) and ocean variables (grey) to best-fit multiple regression models for (*a*) Snake River populations and (*b*) John Day River populations.
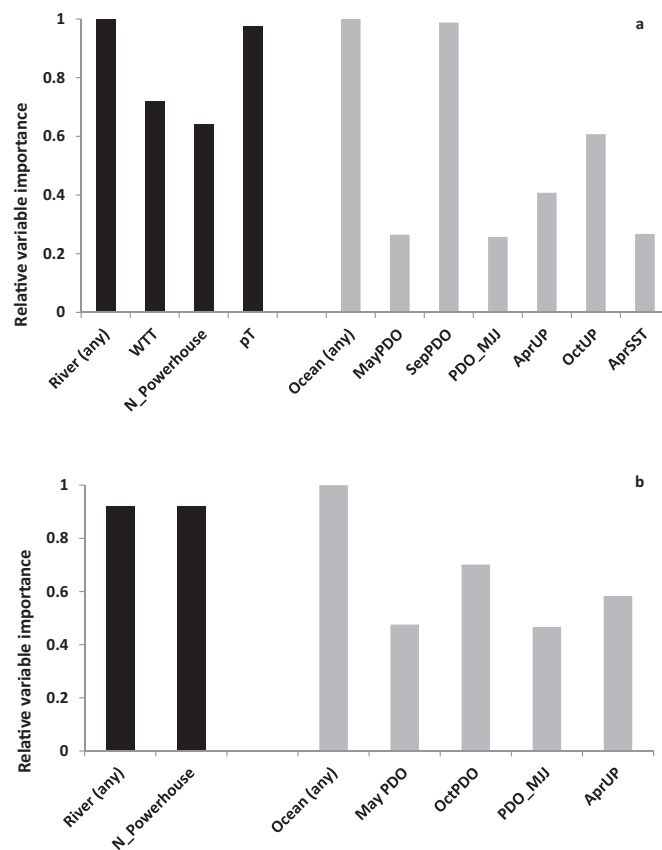
brood year made a longer time series to provide greater contrast in both river and ocean conditions. This assessment estimated the impacts of the FCRPS on Snake River populations with and without the use of downriver reference populations. Our analyses yielded similar results for the methods that relied on downriver reference populations and those that used a temporal approach independent of reference populations. We also estimated hydrosystem impacts using PIT tag estimated SARs of Snake River and downriver reference populations, which complemented the analyses based on SR data. Advancing the approach beyond relying solely on reference populations improved our ability to estimate the impacts of the hydrosystem while accounting for marine conditions.

Our use of the John Day River spring Chinook salmon populations as a reference in the spatial comparisons appears reasonable based on similarity of several life-history characteristics. The Snake River and John Day River Chinook salmon populations are generally similar in terms of adult return and spawn timing, smolt size, and emigration timing from their respective tributaries (Schaller et al. 2007). Although smolts from both regions had similar emigration timing from natal tributaries during the spring freshet, Snake River smolts arrived in the estuary 9–10 days after the downriver population as a consequence of the FCRPS (Schaller et al. 2007). Populations from both ESUs occupy a broad range of spawning and rearing habitats, and significant habitat disturbances mostly occurred prior to the beginning of the survival time series (Schaller et al. 1999). Exploitation by ocean fisheries is estimated to be 1% or less for populations from both regions based on a near absence of coded wire tagged hatchery stocks in catch sampling (Schaller et al. 2000; PFMC 2011).

Our estimates for differential mortality between the Snake River populations and downriver reference populations (passing fewer dams) were similar to a majority of estimates of previous analyses (Table 5). Most of these estimates indicated that survival rate of Snake River populations was only 25% of the rate for

Table 5. Comparison of differential mortality estimates (95% CI) from current study and previous spatial and temporal analyses (see text for definition of methods).

Survival rate metric	Spatial (S), temporal (T)	Brood years	Differential mortality	Relative survival	Source and method
SRI	S	1954–2004	1.33 (1.13–1.52)	0.26	Method 1
SRI	T	1954–2004	1.90 (1.07–2.32)	0.15	Method 2
SRI	S/T	1954–2004	1.40 (0.51–2.30)	0.25	Method 3
SAR	S	1998–2006	1.30 (1.06–1.55)	0.27	Method 1
SRI	S	1954–1990	1.15 (0.75–1.56)	0.32	Schaller et al. 1999, method 1
SRI	S	1954–1990	1.44 (1.09–1.79)	0.24	Deriso et al. 2001, individual "a"
SRI	S	1954–1998	1.13 (0.80–1.46)	0.32	Schaller and Petrosky 2007, method 1
SRI	S	1954–1998	1.47 (1.15–1.80)	0.23	Schaller and Petrosky 2007, individual "a"
SRI	S	1954–1998	1.48	0.23	Hinrichsen and Fisher 2009, individual "a"
SRI	S	1954–1998	1.46	0.23	Hinrichsen and Fisher 2009, regional "a"
SRI	S	1954–1998	0.57	0.57	Hinrichsen and Fisher 2009, common "a"
SAR	S	1998–2002	1.48 (1.10–1.85)	0.23	Schaller and Petrosky 2007, method 1
SAR	T	1962–2004	1.09 (0.96–1.21)	0.34	Petrosky and Schaller 2010, method 2
All estimates			1.32	0.27	
Excludes common "a" method			1.39	0.25	

Table 6. Comparison of delayed mortality estimates from current study and previous spatial and temporal analyses (see text for definitions of methods).

Survival rate metric	Spatial (S), temporal (T)	Brood years	Delayed mortality	Source and method
SRI	T	1954–2004	76%	Method 2
SRI	S	1954–1990	56%	Deriso et al. 2001, individual "a"
SRI	S	1954–1998	70%	Schaller and Petrosky 2007, individual "a"
SRI	S	1954–1998	75%	Hinrichsen and Fisher 2009, individual "a"
SRI	S	1954–1998	76%	Hinrichsen and Fisher 2009, regional "a"
SRI	S	1954–1998	0%	Hinrichsen and Fisher 2009, common "a"
SAR	T	1962–2004	72%	Petrosky and Schaller 2010, method 2
All estimates			61%	
Excludes common "a" method			71%	

reference populations that passed through fewer dams. In addition, our temporal analyses found evidence that the downriver reference populations were also impacted by the FCRPS. Although there have been limitations identified for the spatial approach (ISAB 2007), the results from other methodologies and independent data sets (free of these limitations) were similar.

The corroboration of differential mortality estimates from this synthesis that incorporated downriver reference populations with estimates employing temporal approaches that are independent of reference populations, provides evidence for shared environmental conditions that influence survival rates of Snake and mid-Columbia River populations (common year effect; Deriso et al. 2001). The correlation patterns of the Snake and John Day SRIs in this study with marine environmental variables also provide evidence that a common year effect was supportable. Columbia River yearling Chinook salmon appear to move rapidly northward along West Coast Vancouver Island and southeast Alaska, after which their distribution is poorly understood (Tucker et al. 2011). Therefore, there is some uncertainty about the mechanism for a common year effect in the marine environment as the fish mature to adulthood.

The weight of evidence suggests that Snake River fish outmigrating through the FCRPS experience substantial delayed mortality in the estuary and during early ocean residence. Our estimate of delayed mortality, using the temporal method, was 76%. The average delayed mortality across all studies indicated that 61% of Snake River smolts surviving the FCRPS subsequently died in the estuary and early ocean phase as a result of the impacts of that migration experience (Table 6). The notable exception to analyses supporting substantial delayed mortality resulted from an analytical approach that assumed common productivity (Ricker *a*) among all Columbia basin populations and negligible

hydrosystem mortality to fish passing three dams (Hinrichsen and Fisher 2009). The assumptions for the outlier have little to no analytical support. Spawner–recruit analyses and different freshwater habitat conditions throughout the Columbia basin support the notion of variable intrinsic productivities among stream-type Chinook salmon populations (ICTRT 2007). In addition, recent PIT tag juvenile survival estimates (Tuomikoski et al. 2011) and multiple regression SR analysis for John Day populations (Table 4) contradict the assumption that downriver populations are unaffected by the FCRPS. The average delayed mortality estimate for Snake River populations, excluding the outlying estimate, was 71% (Table 6).

During the first month's migration through the estuary and coastal ocean, Rechisky et al. (2013) found no evidence that Snake River hatchery Chinook salmon smolts experienced lower survival rates than hatchery Chinook salmon from the Yakima River (mid-Columbia River) that migrated through fewer dams. However, the authors acknowledge these estimates represented tagged groups whose size, holding, and timing of release had been manipulated to accommodate acoustic tags that were large relative to fish size. One consequence was that the Yakima group's estuary arrival timing was changed to more closely match that of the group that migrated through all of the Snake River dams. In addition, the size distribution of the hatchery study fish was larger than all but a small fraction of the wild individuals. The study was short term (3 years), and the conditions study fish were exposed to differed dramatically from outmigration conditions experienced by wild fish. Therefore, the conclusion of Rechisky et al. (2013) that differential or delayed hydrosystem mortality for wild Snake River Chinook salmon is negligible is open to question.

In this paper, we extended previous studies to elaborate and further test the hypothesis (consistent with recommendations of the ISAB 2007) that increased delayed mortality in the Snake River Chinook salmon populations occurs as a consequence of outmigration through the hydropower system. Our SRI regression approach for Snake River populations indicated that reduced survival rates are associated with slower water velocities, multiple powerhouse passages, and a high proportion of transported juvenile fish. These results support the notion that the outmigration experience results in an accumulation of injuries and stress events and alters estuary arrival timing, which are mechanisms that explain these consistent observations of delayed mortality (Budy et al. 2002; Scheuerell et al. 2009; Marmorek et al. 2011). In addition, these lower survival rates were associated with warmer ocean conditions and weaker downwelling in the fall, which are linked to reduced food sources for salmon populations (Peterson et al. 2006).

Our study highlights the importance of considering river management options in the face of variable ocean conditions for Snake River Chinook salmon. In particular, our retrospective SRI regression results, and those of Petrosky and Schaller (2010) and Haeseker et al. (2012), suggest that hydrosystem-related direct and delayed mortality may be reduced substantially through actions (e.g., spill, surface passage, increases in water velocity through drawdown, or dam removal) that reduce the number of powerhouse passages, speed water velocity, and juvenile migrations, as well as reduce the reliance on juvenile collection and transportation. Substantially reducing hydrosystem-related delayed mortality should increase the probability of achieving the NPCC (2009) SAR objectives. A promising conservation approach would be to explore restoration actions that reduce the number of powerhouse passages and speed fish travel time through the FCRPS. A practical management experiment would be to evaluate increasing managed spill levels at the dams during the spring migration period and evaluate the population response based on the results of empirical survival estimates (Haeseker et al. 2012).

With the prospect of changing climate, migratory temperate zone animals could be pressured into smaller geographic ranges, making conservation initiatives and planning efforts even more important, and requiring more aggressive protective actions than currently planned. Maintaining the resiliency within metapopulations, such as Snake River stream-type Chinook salmon, demands a broad scale suite of protective actions within their inland freshwater environment. The spatial and temporal approaches used here for evaluating life-cycle survival rates can be applied broadly across Pacific salmon populations to evaluate river regulation and inland restoration activities (ISAB 2013) while considering variation in marine conditions.

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