

Assessing Hydrosystem Influence on Delayed Mortality of Snake River Stream-Type Chinook Salmon

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Abstract.—Snake River stream-type Chinook salmon *Oncorhynchus tshawytscha* exhibited substantial delayed mortality despite recent improvements in oceanic and climatic conditions. These salmon declined sharply with the completion of the Columbia River hydrosystem in addition to other anthropogenic impacts and changes in oceanic conditions. Previous analytical approaches have compared management options for halting the population decline. The predicted benefits of these options on salmon recovery hinged on whether the source of the mortality that takes place in the estuary and during early ocean residence is related to earlier hydrosystem experience during downstream migration (i.e., delayed hydrosystem mortality). We analyzed the spatial and temporal patterns of mortality for Chinook salmon populations to determine whether delayed mortality for the Snake River populations decreased during the recent period of favorable oceanic and climatic conditions. We found that Snake River stream-type Chinook salmon populations continued to exhibit survival patterns similar to those of their downriver counterparts but survived only one-fourth to one-third as well. The hypothesis that delayed mortality decreased and became negligible with more favorable oceanic conditions appears inconsistent with the patterns we observed for the common year effect and our estimates of delayed mortality of in-river migrants. A plausible explanation for this persistent pattern of delayed mortality for Snake River populations is that it is related to the construction and operation of the hydrosystem.

The success of recovery actions for Snake River stream-type Chinook salmon *Oncorhynchus tshawytscha* hinges on whether delayed mortality is substantial and linked to their hydrosystem experience during seaward migration. Delayed mortality is the component of mortality that takes place in the estuary and during early ocean residence that is related to earlier life stage anthropogenic impacts. All populations of Snake River salmon *Oncorhynchus* spp. substantially declined since completion of the hydroelectric projects of the Federal Columbia River Power System (FCRPS) and were subsequently listed under the U.S. Endangered Species Act (ESA). The declines in survival rates of Snake River stream-type Chinook salmon, coincident with completion of the hydrosystem projects, were considerably sharper than those of downriver populations (Schaller et al. 1999; Deriso et al. 2001). Most survival rate declines were in the smolt-to-adult life stage rather than in the spawner-to-smolt life stage (Petrosky et al. 2001). Previous large-scale analytical assessments (Karieva et al. 2000; Peters and Marmorek 2001; Wilson 2003) evaluated management options for

halting the decline of these populations. These results depended on whether the source of mortality that takes place in the estuary and during early ocean residence is related to earlier hydrosystem experience during downstream migration.

Delayed mortality is expressed after fish pass through the hydrosystem and therefore is presently impractical to measure directly. There are a number of reasons why delayed mortality would be associated with FCRPS development and operation. Specific impacts from the FCRPS have been identified as possible causes of delayed mortality in the literature, such as injuries or stress from migration through juvenile bypass systems, turbines, or spill at dams; stress or transmission of disease resulting from concentration of fish in bypass systems or transportation barges; changes to migration rates and timing; depletion of energy reserves from prolonged migration; and altered conditions in the estuary and plume as a result of FCRPS construction or operation (Bottom et al. 2001; Williams 2001; Budy et al. 2002; Congleton et al. 2002; Williams et al. 2005; Schreck et al. 2006). At the same time that there were impacts from the hydrosystem, there were also changes in oceanic and climatic conditions (Francis and Mantua 2003) as well as possible hatchery and other freshwater habitat effects. These potential impacts make it difficult to

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Received March 9, 2006; accepted December 7, 2006
Published online July 5, 2007

reach consensus on the relative influence of different factors in elevating mortality levels. However, a number of reviews have found evidence in various forms that links delayed mortality to the construction and operation of the FCRPS (Budy et al. 2002; Marmorek et al. 2004; Muir et al. 2006).

The agencies that operate the FCRPS and a National Marine Fisheries Service study (Williams et al. 2005) have hypothesized that delayed mortality has been low or nonexistent in recent years, when oceanic conditions were favorable to high ocean survival rates. Williams et al. (2005) asserted that hydrosystem-related delayed mortality under the oceanic conditions that juveniles experienced in 1999 and 2000 would not prevent populations from returning to abundance levels observed before completion of the hydrosystem.

In response to the salmon declines and ESA listings in the Snake and Columbia rivers, the region has embarked on one of the most costly and administratively complex fishery restoration programs in the world (NRC 1996). The large-scale analytical processes described above address the policy and management question of whether adequate life cycle or smolt-to-adult survival can be achieved without breaching Snake River dams (Peters and Marmorek 2001). More recent salmon recovery policy and decisions for the Snake and Columbia rivers emphasize tributary habitat restoration actions to improve survival in the smolt-to-adult life stage to offset mortality caused by migration through the hydrosystem and variable oceanic conditions (NMFS 2000, 2004; NPCC 2003). The effectiveness of these complex and costly restoration strategies will be determined, ultimately, by the extent to which direct and delayed hydrosystem mortality limit smolt-to-adult return rates (SARs).

In this study, we assessed whether the delayed mortality of Snake River stream-type Chinook salmon decreased substantially during the recent period of favorable oceanic and climatic conditions. Because of the difficulties that presently exist for directly measuring delayed mortality, our assessment followed three steps.

First, we estimated the difference in mortality rates between Snake River populations and downriver stream-type Chinook salmon populations that migrate through fewer dams (Schaller et al. 1999; Deriso et al. 2001). These differential mortality rates were estimated, taking into consideration a common mortality pattern (common year effect) exhibited among Snake River and downriver populations. Following Deriso et al. (2001), we attributed to the FCRPS those relative shifts in productivity and survival rates that were associated in time and space with FCRPS impacts. We also evaluated other methods and data types to corroborate the estimates of differential mortality rates

between Snake River and downriver populations. We then subtracted estimates of measurable juvenile passage mortality (Berggren et al. 2005b; Williams et al. 2005) from total FCRPS mortality to estimate delayed mortality of Snake River populations (Peters and Marmorek 2001).

Second, we evaluated whether downriver population performance was a reasonable control for Snake River populations. The common year effect is a measure of the covariation of survival rates between upriver and downriver stream-type Chinook salmon in the Columbia River. Snake River and downriver stream-type Chinook salmon have similar smolt migration timing when leaving the tributaries and share common estuary and early-ocean conditions (Schaller et al. 1999; Berggren et al. 2005a). We evaluated whether the variation captured by the common year effect for Snake River and downriver populations was similar to the variation in survival rates for salmon species across a wide geographic range outside the Columbia River. We then evaluated how well the common year effect correlated with oceanic and climatic environmental variables. These assessments were also used to evaluate the validity of previous criticisms for using downriver populations as controls for Snake River population performance (Zabel and Williams 2000; Williams et al. 2005).

Last, an evaluation was performed to determine whether delayed mortality decreased and became negligible for the Snake River populations during the recent period of favorable oceanic and climatic conditions.

Methods

Spawner–recruit (SR) information was analyzed for seven Snake River spring–summer Chinook salmon populations and three lower Columbia River spring Chinook salmon populations (Figure 1) to evaluate patterns of survival rate indices and between-region similarities and differences in mortality rates from the 1950s through brood year 1998. Snake River SR data began with 1949 data for the Imnaha River, 1954 data for the Minam River, and 1957 data for the Bear Valley Creek, Marsh Creek, Sulphur Creek, Poverty Flat, and Johnson Creek populations (Schaller et al. 1999). Downriver SR data began with 1959 data for the upper main stem and North Fork John Day River and 1960 data for the Middle Fork John Day River.

All populations in the analysis are stream-type Chinook salmon (Healy 1991), producing yearling smolts that migrate seaward in the spring (primarily April and May). The Snake River populations migrate as smolts through eight dams and reservoirs, and a large portion of the smolts are collected and transported

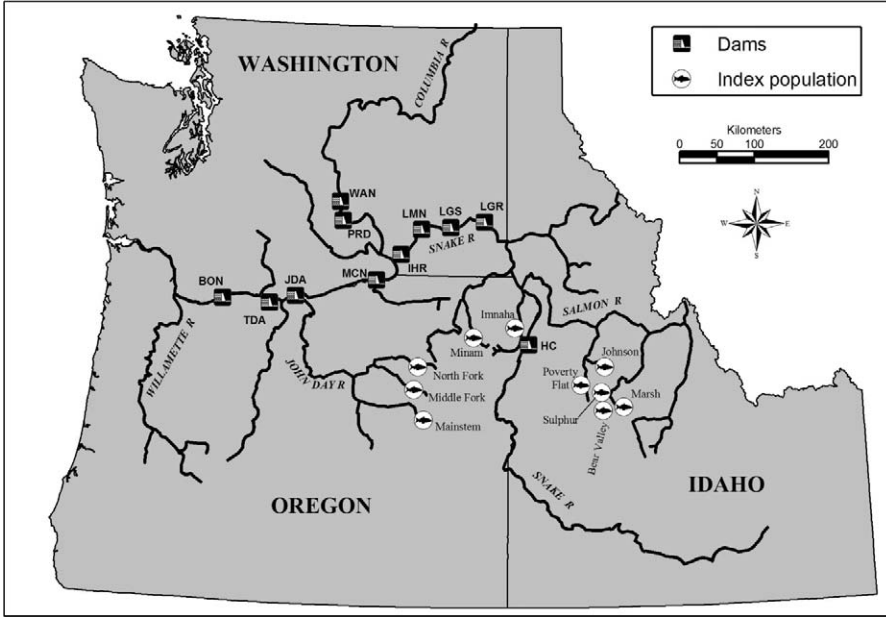


FIGURE 1.—Distribution of index populations of spring and summer Chinook salmon in the Snake and lower Columbia rivers. Main-stem dams include Bonneville (BON), the Dalles (TDA), John Day (JDA), and McNary (MCN) on the lower Columbia River and Ice Harbor (IHR), Lower Monumental (LMN), Little Goose (LGS), and Lower Granite (LGR) on the Snake River. For reference we included Priest Rapids (PRD) and Wanapum (WAN) of the upper Columbia River.

past most of the dams on barges or trucks (Figure 1). The last of these eight dams, Lower Granite Dam, was completed in 1975. The upriver and downriver populations are all interior Columbia River basin Chinook salmon and have similar life history characteristics as juveniles and adults (Schaller et al. 1999, 2000).

The seven Snake River and three downriver populations were previously the subject of intensive SR analyses through brood year 1990 (e.g., Schaller et al. 1999; Deriso et al. 2001; Peters and Marmorek 2001; Paulsen and Hinrichsen 2002). The spawners and recruits were defined and estimated according to methods in Beamesderfer et al. (1997) and Schaller et al. (1999). Spawners represented adults age 4 and older on the spawning ground; recruits were age-3 jacks and adults returning to the Columbia River.

Productivity and survival rate indices.—Productivity and survival rate indices were analyzed for different periods and populations in the Snake and lower Columbia River basin, updating the analysis of Schaller et al. (1999). We then evaluated whether productivity and survival rate indices declined more for Snake River populations than for downriver populations after hydrosystem development with the use of the updated SR data.

For each index population, SR data were classified

into two primary time periods (and a transition period) 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 primary period, post-1974 brood years (1975–1998), was marked by initiation of mass transportation of smolts around the Snake River dams in barges and trucks and gradual passage improvement at the dams. The transition period, 1970–1974, 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-1975 periods for each index population in the Snake and lower Columbia rivers. Productivity is defined as the natural logarithm 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

$$R = e^a S e^{-\beta S}. \tag{1}$$

The a and β parameters are estimated by the \log_e transformation of equation (1). Productivity is mea-

sured as the intercept, or Ricker a . Schaller et al. (1999) found that the Ricker recruitment function provided a better fit to the first-period data than a Beverton–Holt function. Survival rate indices provide a time series of density-independent mortality estimates through deviations of observed $\log_e(R/S)$ from those predicted by the fitted stock–recruitment function for a specified time period. We would expect a temporal change in density-independent mortality, such as that imposed by hydroelectric development and operation or an oceanic regime shift, to be 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) analysis of covariance (ANCOVA) using the SAS; SAS version 8.02 (SAS 2002) general linear model (GLM) to examine differences in the intercepts (Ricker a) of the relationship of $\log_e(R/S)$ versus S in the equation

$$\ln(R_{ij}/S_{ij}) = \tau_i + a - \beta(S_{ij} - \bar{S}_{..}) + \varepsilon_{ij}, \quad (2)$$

where τ_i is the class effect (period), a is the overall intercept, β is the overall slope, \bar{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).

First, the homogeneity of slopes was tested for significant interaction between the treatment (period) and the covariate (spawners). An ANCOVA was then run to estimate the period effect on $\log_e(R/S)$, taking into account spawning level. The measure of productivity by period was estimated with $\tau_i + a$ from the ANCOVA results (equation 2). This is equivalent to the Ricker a parameter by period (assuming a common slope [β] for all periods).

We tested whether survival rate indices declined more for Snake River populations than for downriver populations in the post-1974 period. Survival rate indices are defined as the life cycle survival rate after accounting for density-dependent mortality. Using the ANCOVA fit (equation 2) to survival rate indices (SRI-1s) for pre-1970 data (Schaller et al. 1999), SRI-1s are estimated from $\log_e[(\text{observed } R/S)/(\text{predicted } R/S)]$. These SRI-1s are the residuals about the predictions of recruits per spawner based on Ricker coefficients for the pre-1970 time period. Period differences in survival rate indices were tested between population groups from the two regions with one-way classification analysis of variance (ANOVA) under the GLM procedure of SAS (SAS 2002).

Common year effect and differential mortality.—Deriso et al. (2001) evaluated alternative SR models using the same SR data set used in Schaller et al. (1999) and three additional downriver populations

(Klickitat, Warm Springs, and Wind rivers); the SR data for these populations began in 1966, 1969, and 1970, respectively. The best empirical models evaluated by Deriso et al. (2001) included an estimate of a common year effect (δ) for Snake River and downriver stream-type Chinook salmon populations. Their primary model (delta model) was

$$\ln(R_{ti}/S_{ti}) = (a_i + \delta_t - m_{ti}) - \beta_i S_{ti} + \varepsilon_{ti}, \quad (3)$$

where R_{ti} is the Columbia River recruitment originating from spawning in year t and population i , S_{ti} is the spawners in year t and population i , a_i is the Ricker a value for population i , δ_t is the common year effect in year t , m_{ti} is the total passage mortality (direct plus delayed mortality) for population i in year t , β_i is the regression slope for population i , and ε_{ti} is the normally distributed process error and sampling error.

The differential mortality (μ_t for a given year t) experienced by Snake River populations relative to the downriver populations can be indirectly estimated from the delta model output for a given year t . Differential mortality is the difference between model-estimated total mortality for the Snake River populations (m_{ti}) and juvenile passage mortality (M_{ti}) experienced by the downriver populations (equations 4–6 in Deriso et al. 2001). Note that equation (3) estimates the same mortality rates (m_{ti}) for populations (i) within a region for a given year (t) because these populations pass the same number of dams (equations 5 and 6 in Deriso et al. 2001).

We used Paulsen and Hinrichsen’s (2002) ordinary least squares (OLS) method to fit the delta model to all years of SR data updated through brood year 1998. We used the same Snake River populations as Deriso et al. (2001), but for the downriver populations we only used the three John Day River populations in these analyses because updated estimates for the other downriver populations were not available. We performed sensitivity analyses to the Deriso et al. (2001) approach by excluding the other downriver populations. We compared the μ (for convenience, the t subscript is dropped when generally referring to a differential mortality) between the OLS fit through brood years 1990 and 1998 with those reported by Deriso et al. (2001) through brood year 1990.

An analogous measure of differential mortality was calculated between Snake River and downriver populations based on the SARs of Snake River and John Day River wild stream-type Chinook salmon. The SAR data provided independent information to help identify the life stage that primarily influences the SR model estimates of μ . This analog to μ was estimated as

$$\mu_{\text{SAR},t} = -\log_e(\text{SAR}_{\text{Snake},t}/\text{SAR}_{\text{John Day},t}), \quad (4)$$

where $SAR_{Snake} = (\text{smolts arriving at the first dam encountered or Lower Granite Dam})/(\text{adult returns to Bonneville Dam})$, $SAR_{John\ Day} = (\text{smolts arriving at the first dam encountered or John Day Dam})/(\text{adult returns to Bonneville Dam})$, and t is brood year. The estimates of SAR_{Snake} and $SAR_{John\ Day}$ were available from passive integrated transponder (PIT)-tag studies for smolt migration years 2000–2004 (Berggren et al. 2006), where the John Day River PIT-tagging studies started in migration year 2000. We estimated the mean and 95% confidence interval (Ott 1977; paired-difference experiment approach) for $\mu_{SAR,t}$.

Comparison of estimates for differential mortality.—Estimates of differential mortality between Snake River and downriver populations were compared for alternative methods and time periods. We compared our updated μ estimate with the μ estimated by Deriso et al. (2001) in their primary model (equation 3). We also compared our μ estimate (mean and the 95% confidence interval) with alternative differential mortality estimates, such as (1) changes in productivity between time periods (using $\tau_1 - \tau_2$ from equation 2) and (2) regional differences in survival rate indices (average period difference of SRI-1 values for Snake River and downriver populations). The final comparison was between the differential mortality estimated from SAR ratios (equation 4) with estimates from the above SR-based methods.

Variation in survival rates.—There is considerable evidence that populations going through a steep decline (such as that caused by large bottlenecks) exhibit increased variation in survival rates (or population growth rates; Schaller et al. 1999; Morris and Doak 2002). A population's health is directly related to the performance of individuals through birth, death, and growth rates. Explicitly considering the variability in these demographic rates is critical in determining population growth and persistence (Morris and Doak 2002). Therefore, we contrasted the temporal patterns of variation in survival rates for Snake River populations with the downriver populations. We then assessed whether these patterns of variation in survival for Snake River populations were similar to those exhibited by salmon populations across a wide geographic range along the U.S. West Coast.

Using an F -test, we evaluated the change in SRI-1 variance between period 1 and period 2 for each population. We then evaluated whether survival rates for Snake River populations recently became more variable than for downriver populations.

The variances of δ and the SRI-1 for Snake River and downriver stream-type Chinook salmon populations were compared with the variances of the residuals from other salmon population groups. We obtained

residuals of Beverton–Holt SR fits for population groups of pink salmon *O. gorbuscha*, chum salmon *O. keta*, and sockeye salmon *O. nerka* for brood years 1950–1996 (Pyper et al. 2001, 2002, 2005) from R. M. Peterman and B. J. Pyper (Simon Fraser University, personal communication). We calculated the variance of the Oregon production index (OPI) for hatchery populations of coho salmon *O. kisutch* for brood years 1969–2003 from \log_e transformed SARs (Appendix B in PFMC 2005). Spawner–recruit residuals for three lower and mid-Columbia River populations of ocean-type Chinook salmon (brood years 1964–1991) were obtained from Peters et al. (1999). We standardized our SRI-1s for stream-type Chinook salmon to a mean of zero by subtracting the average residual and designated the standardized parameter as SRI-1* to graphically contrast with other populations. We used F -tests to determine differences between the variance of δ and the SRI-1s for Snake River and downriver Chinook salmon as well as population groups for the other salmon species at a significance level of 0.05.

Correlation of survival indices with environmental variables.—To evaluate whether variation in oceanic conditions influenced the survival patterns of Snake River and downriver populations similarly, we correlated the measure of salmon mortality rates in common with Snake River and downriver populations to several oceanic environmental variables that have been linked to (or hypothesized to influence) salmon survival. We also correlated SRI-1 values for Snake River and downriver populations with these oceanic and climatic environmental variables to determine whether there was independent support for a common influence on survival from oceanic conditions on these populations. These included Pacific decadal oscillation (PDO), regional sea surface temperature (SST) conditions, and upwelling indices. All correlations corresponded to the year of ocean entry (brood year + 2) for stream-type Chinook salmon.

The PDO is a large-scale measure of SST variability. We correlated δ s and SRI-1s with the winter PDO (December–February average before smolt out-migration) and summer PDO (June–August average after out-migration), consistent with Hare and Mantua (2000), as well as the PDO during smolt out-migration (April–May). 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 (Mantua et al. 1997). The PDO indices were obtained from the Joint Institute for the Study of the Atmosphere and Ocean Web site: jisao.washington.edu/pdo/PDO.latest.

Mueter et al. (2005) found that regional averages of SSTs were better predictors of survival rates across a

wide geographic range than large-scale measures of SST variability such as the PDO. We correlated δs and SRI-1s with the monthly SST anomalies at three latitudes: 41, 45, and 47°N. The SST values were obtained from the National Oceanic and Atmospheric Administration (NOAA; nomad2.ncep.noaa.gov/upwelling_data/).

Upwelling indices have also been linked to ocean survival for Columbia River stream-type Chinook salmon (Scheuerell and Williams 2005) and Oregon coastal coho salmon (Nickelson 1986). We correlated δs and SRI-1s with the monthly upwelling anomalies at three latitudes: 42, 45, and 48°N. Upwelling indices were obtained from the NOAA Pacific Fisheries Environmental Laboratory (www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html).

Direct and delayed mortality.—Past decision analysis showed that hypotheses related to the cause of mortality in the estuary and ocean life stages (either delayed hydrosystem mortality or “extra” mortality unrelated to the dams) had the most influence on projected outcomes of actions to recover Snake River stream-type Chinook salmon populations (Peters and Marmorek 2001). In light of recently increased recruitments, improved oceanic conditions, and empirical estimates of juvenile passage mortality, we tested the hypothesis that delayed hydrosystem mortality substantially decreased with improved oceanic conditions.

Retrospective juvenile passage modeling (Peters and Marmorek 2001) generated historical estimates (for brood years 1952–1990) of four parameters related to the passage of smolts through the migration corridor: (1) the direct passage survival rate (e^{-M} , where M is the direct mortality rate through the migration corridor) measured from the top of the reservoir of the first dam encountered (Lower Granite since 1975) to below the last dam (Bonneville), including transportation; (2) the survival rate of in-river smolts from the head of Lower Granite reservoir to below Bonneville Dam (V_c); (3) the proportion of smolts arriving below Bonneville Dam that were transported (P_{bt}); and (4) the estuary and ocean survival rate of transported fish relative to that of in-river fish (this ratio is called D). The ratio D is estimated as

$$D = (\text{SAR}_t/\text{SAR}_r)/(V_c/V_r), \quad (5)$$

where SAR_t is the smolt-to-adult survival rate for groups transported from the point of collection and placement in a barge (or truck) back to that point as adults, SAR_r is the smolt-to-adult survival rate of in-river migrants back to that point as adults, V_t is the survival rate of transported fish in the barge (assumed

to be 0.98) times in-river survival to the point of collection and transport, and V_c is the survival rate of in-river fish from the top of the hydrosystem to below Bonneville Dam.

The juvenile passage parameters are used to estimate system survival (ω), defined as the number of in-river-equivalent smolts below Bonneville Dam (i.e., adjusting for the relative estuary and ocean survival of transported fish) divided by the population at the head of the first reservoir. System survival (ω) is calculated as

$$\omega = e^{-M}(\text{DP}_{bt} + 1 - P_{bt}). \quad (6)$$

From the four passage parameters and m_{ti} from equation (3), we can derive an estimate of the post-Bonneville survival factor for nontransported smolts, λ_n , which is an estuary and ocean survival rate of the in-river fish after accounting for a common year effect that is estimated as

$$\lambda_n = e^{-m - \log_e(\omega)}, \quad (7)$$

where m is defined in equation (3; see the appendix in Peters and Marmorek 2001 for details). Delayed mortality is defined as $1 - \lambda_n$.

Wild Chinook salmon PIT-tag studies provided empirical estimates for V_c , P_{bt} , and D in brood years 1991–1998 (Berggren et al. 2005b). Estimates of total direct mortality, M , also included survival through the Lower Granite Dam pool (Williams et al. 2005). Before brood year 1991, partitioning estimates of m_{ti} into direct and delayed mortality components required the use of passage models for V_c and P_{bt} (Peters and Marmorek 2001), coupled with use of the brood year 1992–1998 average D -value (0.53; Berggren et al. 2005b) for all years before brood year 1992. Input values for M , P_{bt} , and D are shown in the appendix.

We evaluated whether the level of delayed mortality was significant in years with better-than-average oceanic or climatic conditions (positive common year effect) with a two-tailed t -test to determine whether 95% of the values were greater than a 10% mortality rate. In other words, we evaluated whether the delayed mortality of in-river migrants became negligibly small when oceanic or climatic conditions improved.

Results

Productivity and Survival Rate Indices

Using all of the brood years (including updated brood years 1991–1998), productivity declined significantly from period one to period two for all but two populations (Poverty Flat and Middle Fork John Day River). However, declines were substantially greater for Snake River populations relative to downriver populations from the first to the second period (average

TABLE 1.—Analysis of covariance results for Ricker recruitment functions that used period (treatment) and spawners (covariate) for stream-type Chinook salmon index populations from the Snake River and downriver (lower Columbia River) regions, brood years 1949–1998. See equations (1) and (2) for variable definitions.

Regions and subbasin	Index stock	Intercept		$\tau_1 - \tau_2$	$H_0: \tau_1 = \tau_2$			$H_0: \beta \leq 0$		P (homogeneity of slope)
		$\tau_1 + a$ (pre-1970)	$\tau_2 + a$ (post-1974)		P	SE(β)	Slope (β)	P	R^2	
Snake River										
Middle Fork Salmon	Bear Valley	3.8606	1.2113	2.6493	0.0017	0.7789	0.001608	0.0029	0.25	0.1065
	Marsh	3.7044	0.8559	2.8486	0.0001	0.6260	0.002876	0.0016	0.39	0.1030
	Sulphur	3.5181	0.9034	2.6147	0.0001	0.5573	0.003760	0.0005	0.42	0.4271
South Fork Salmon	Poverty	1.4073	0.6043	0.8030	0.0661	0.4224	0.000378	0.0630	0.10	0.0494
	Johnson	2.0160	0.7533	1.2628	0.0050	0.4211	0.001847	0.0139	0.21	0.7732
Imnaha	Main stem	2.0356	0.5396	1.4980	0.0001	0.2383	0.000657	0.0002	0.51	0.5587
Grande Ronde	Minam	2.8082	0.9332	1.8751	0.0001	0.4158	0.002484	0.0003	0.38	0.0058
Downriver										
John Day	Main stem	2.0414	1.3558	0.6856	0.0217	0.2842	0.002085	0.0017	0.43	0.0652
	Middle Fork	1.9637	1.5207	0.4430	0.2361	0.3667	0.002216	0.0005	0.43	0.0389
	North Fork	2.7330	1.4518	1.2812	0.0001	0.2409	0.000764	0	0.56	0.7410

difference between τ_1 and τ_2 between regions = 1.13; Table 1).

The pattern of survival rates as measured by SRI-1s for Snake River populations exhibited a marked decline in the post-1974 brood years. Snake River survival rates for the 1991–1998 brood years continued to remain below those observed in the pre-1970 period (Figure 2A). Survival rates of downriver populations showed a smaller decline and returned to the level observed in the pre-1970 period for the most recent brood years (Figure 2B). Survival rates declined significantly more for Snake River populations than for downriver populations ($F = 45.39$; $P < 0.0001$).

Common Year Effect and Differential Mortality

Estimates of the common year effect (δ) ranged from -1.89 to 1.49 for brood years 1952–1998 (Figure 3). The range of δ equated to changes from 15% to 444% of the long-term average density-independent survival rate (e^δ). Estimates of δ for the updated time period indicated a shift from poor oceanic or climatic conditions in 1991–1994 to good conditions in brood years 1995–1998 (Figure 3). Except for the 1991 brood year, which exhibited the strongest negative value in the full time series, updated δ estimates fell within the range observed in previous years.

The differential mortality (μ) of Snake River stream-type Chinook salmon remained high through brood year 1998 (Figure 4). Estimates of μ averaged 1.47 for brood years 1975–1998. Snake River populations survived only 23% ($e^{-\mu}$) as well as downriver populations for brood years 1975–1998. Estimates of μ for the updated brood years (1991–1998) fell well within the range of previous years (Figure 4).

Comparison of Estimates for Differential Mortality

Estimates of differential mortality ranged from 1.1 to 1.5 when different methods and time periods were used (Table 2). Our updated delta model estimate of μ of 1.47 was similar to the previous estimate made by Deriso et al. (2001). Sensitivity analysis indicated that use of only John Day River populations as downriver indicators produced a similar estimate of μ (1.42)

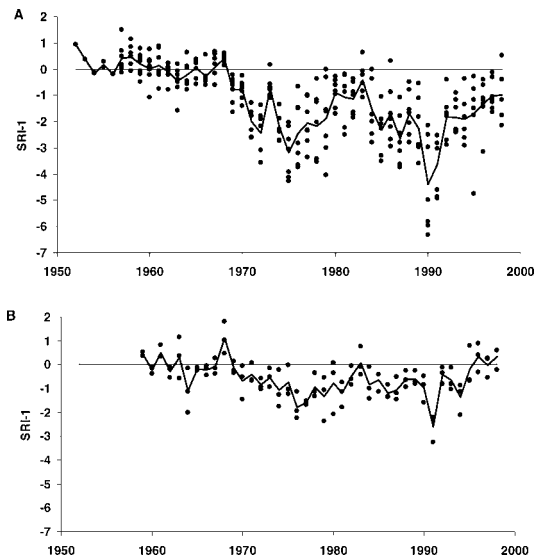


FIGURE 2.—Deviations of $\log_e([\text{observed recruits } \{R\}/\text{spawners } \{S\}]/[\text{predicted } R/S])$ of stream-type Chinook salmon from analysis of covariance fit to survival rate indices from the pre-1970 period (SRI-1s) for (A) the Snake River and (B) the downriver (lower Columbia River) regions, brood years 1952–1998. The average SRI-1 values are represented by the solid lines.

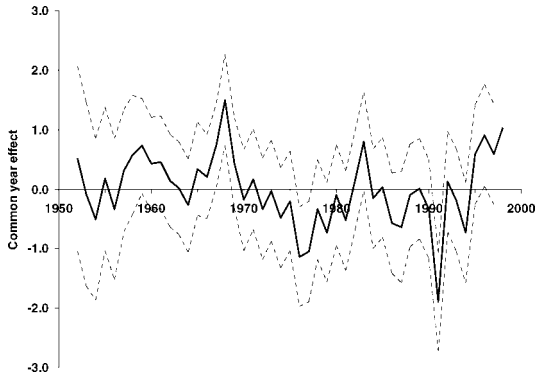


FIGURE 3.—Estimates (solid line) and 95% confidence intervals (dashed lines) of the common year effect for Snake River and downriver stream-type Chinook salmon, brood years 1952–1998.

compared with the Deriso et al. (2001) estimate (1.44) when using the same brood years (1970–1990). This result is not surprising because of the limited time series for the three additional downriver populations. Our updated estimate of μ was somewhat higher than estimates of μ from the alternative SR methods (changes in productivity between time periods and regional differences in survival rate indices). John Day River population SARs ranged from 0.025 to 0.119 for brood years 1998–2002. In contrast, Snake River population SARs ranged from 0.004 to 0.027 for brood years 1998–2002. Our estimate of μ based on the ratio of SARs was 1.48, which was similar to our SR estimates of μ from the delta model. The 95% confidence intervals for all μ estimates excluded zero, except for those based on $\tau_1 - \tau_2$ (Table 2).

Variation in Survival Rates

Survival rates became more variable (post-1974) for a majority of Snake River populations, which was in contrast to the patterns for downriver populations. This pattern was similar to the results of Schaller et al. (1999). Variance increased significantly in the second period for all Snake River populations, except Poverty Flat (Table 3). For downriver populations, only the North Fork John Day River showed a significant increase in variance in the second period.

The distribution of the common year effect appeared generally similar to the distributions of residuals for pink, chum, sockeye, coho, and ocean-type Chinook salmon population groups (Table 4; Figure 5A). The *F*-tests indicated that, compared with the variance of 40 population groups of other salmon, the variance of δ was significantly less than 19, not different from 18, and significantly greater than 3 (Table 4). The variance of δ was most similar to the variance of chum and

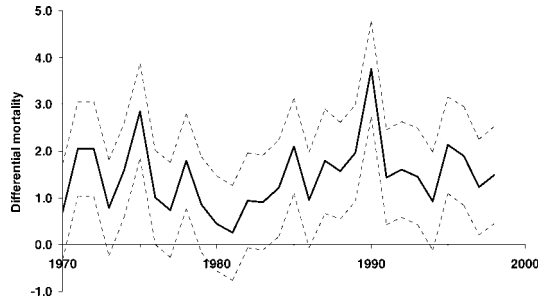


FIGURE 4.—Estimates (solid line) and 95% confidence intervals (dashed lines) of differential mortality between Snake River and downriver stream-type Chinook salmon populations, brood years 1970–1998.

sockeye salmon and less than that for most of the pink salmon population groups.

The distribution of downriver SR residuals also appeared generally similar to those of other salmon population groups (Table 4; Figure 5B). The *F*-tests indicated that, compared with the variance of 40 population groups of other salmon, the variance of John Day River SRI-1s was significantly less than 6, not different from 18, and significantly greater than 16 population groups (Table 4).

In contrast to the common year effect and downriver SR residual patterns, the Snake River SR residuals were more variable than the residuals for other salmon population groups (Table 4; Figure 5C). The Snake River SRI-1s were significantly more variable than 12 of 14 pink salmon population groups, 14 of 15 chum salmon population groups, 8 of 9 sockeye salmon population groups, the OPI for coho salmon, and Columbia River ocean-type Chinook salmon. In no cases were Snake River SR residuals significantly less variable than any population group for any other salmon species.

Correlation of Survival Rate Indices with Environmental Variables

We found modest correlations between SRI-1s and oceanic and climatic variables. The common year effect and the SRI-1s for Snake River and downriver populations correlated similarly with environmental variables. The summer PDO correlated negatively with δ (−0.37), SRI-1s for Snake River (−0.48), and SRI-1s for John Day River (−0.52), whereas the winter and spring PDO showed less correlation with SRI-1s (Figure 6C). At the latitude closest to the point of ocean entry for Columbia River populations (45°N), there were positive correlations with April upwelling (Figure 6A) and negative correlations with both October upwelling (Figure 6A) and SSTs during the

TABLE 2.—Comparison of differential mortality estimates (μ ; 95% confidence intervals in parentheses) and differential survival ($e^{-\mu}$) for stream-type Snake River Chinook salmon using alternative methods and time periods; SRI-1 = survival rate index; SAR = smolt-to-adult return rate.

Method	Brood years	Differential mortality	Differential survival	Source
Updated μ	1975–1998	1.47 (1.15–1.80)	0.23	Equation (3)
Previous μ	1970–1990	1.44 (1.09–1.79)	0.24	Deriso et al. (2001)
Updated $\tau_1 - \tau_2$	1975–1998	1.13 (–0.01–2.27)	0.32	Equation (2)
Previous $\tau_1 - \tau_2$	1975–1990	1.16 (–0.04–2.35)	0.32	Schaller et al. (1999)
Updated SRI-1	1975–1998	1.13 (0.80–1.46)	0.32	This paper
Previous SRI-1	1975–1990	1.15 (0.75–1.56)	0.32	Schaller et al. (1999)
μ_{SAR}	1998–2002	1.48 (1.10–1.85)	0.23	Equation (4)

spring of ocean entry (Figure 6B). The correlations were generally consistent across the different SRI-1s (δ and SRI-1s for Snake River and John Day River populations) and latitudes investigated.

Direct and Delayed Mortality

For brood years 1991–1998, direct mortality (M) averaged 0.20 and ranged from 0.12 to 0.32 (Table A.1). For brood years 1991–1998, differential delayed mortality of transported fish (D) averaged 0.53 and ranged from 0.34 to 1.01. The proportion of Chinook salmon transported averaged 0.91 for this time period.

Estimates of delayed mortality of in-river migrants have remained high (Figure 7). For the updated brood years 1991–1998, delayed mortality ($1 - \lambda_n$) averaged 0.81 and ranged from 0.75 to 0.90. In contrast, delayed mortality estimates for brood years 1975–1990 averaged 0.64 and ranged from 0.06 to 0.98.

There was a weak positive correlation (0.28) between the common year effect and delayed mortality of in-river migrants. Delayed mortality of in-river migrants did not appear to decrease with the climatic improvements in the late 1990s (Figure 7). For the years with a positive common year effect, 95% of the distribution of delayed mortality estimates (two-tailed t -test) was greater than 65%. In addition, for the recent years with a positive common year effect (years with

PIT tags), 95% of the distribution of delayed mortality estimates (two-tailed t -test) was greater than 70%. In other words, for the years influenced by good oceanic and climatic conditions, the majority of the distribution (95%) of estimates for delayed mortality far exceeded a negligible mortality level of 10%.

Discussion

The hypothesis that delayed mortality levels decreased and became negligible during years with more favorable oceanic and climatic conditions appears inconsistent with the patterns we observed for the common year effect and our estimates of delayed mortality for in-river migrants. The hypothesis that this source of mortality that takes place in the estuary and during early ocean residence is related to earlier hydrosystem experience during downstream migration of juvenile Snake River stream-type Chinook salmon remains a plausible explanation.

Our spatial and temporal population performance comparisons provide additional support for delayed hydrosystem mortality. In addition, more recent tagging studies have demonstrated substantial delayed mortality of transported fish relative to in-river migrants (appendix; Berggren et al. 2005b; Williams et al. 2005). Substantial evidence from the literature demonstrates numerous mechanisms that would ex-

TABLE 3.—Results of F -tests for the change in variance of Snake River and downriver (lower Columbia River) region stream-type Chinook salmon survival rate indices (SRI-1s) between periods.

Region and subbasin	Index stock	Variance of pre-1970 SRI-1 deviations	Variance of post-1974 SRI-1 deviations	F	df	P	Direction of change
Snake River							
Middle Fork Salmon	Bear Valley	0.4581	1.2547	2.74	12, 23	0.0367	+
	Marsh	0.3099	1.5513	5.01	12, 22	0.0030	+
	Sulphur	0.2258	2.1958	9.73	12, 21	0.0001	+
South Fork Salmon	Poverty	0.3712	0.7767	2.09	12, 22	0.0934	0
	Johnson	0.2775	0.8608	3.10	12, 23	0.0228	+
Imnaha	Main stem	0.1770	0.4849	2.74	17, 22	0.0191	+
Grande Ronde	Minam	0.4612	1.5945	3.46	15, 23	0.0081	+
Downriver							
John Day	Main stem	0.4846	0.5301	1.09	10, 23	0.4631	0
	Middle Fork	0.9495	0.6433	1.48	9, 23	0.2152	0
	North Fork	0.0953	0.5216	5.48	10, 23	0.0041	+

TABLE 4.—Comparison of variance of the common year effect (δ) and spawner–recruit survival residuals for Columbia River stream-type Chinook salmon and other salmon species. The columns represent the number of population groups for which the variation of Columbia River stream-type Chinook salmon was less than (<), not different from (0), or greater than (>) the variation in other salmon species.

Variable	Comparison	<	0	>
δ	Pink salmon	10	4	0
	Chum salmon	5	9	1
	Sockeye salmon	3	4	2
	Coho salmon	1	0	0
	Ocean-type Chinook salmon	0	1	0
	Total	19	18	3
SRI-1 (John Day River)	Pink salmon	5	6	3
	Chum salmon	0	7	8
	Sockeye salmon	1	4	4
	Coho salmon	0	1	0
	Ocean-type Chinook salmon	0	0	1
	Total	6	18	16
SRI-1 (Snake River)	Pink salmon	0	2	12
	Chum salmon	0	1	14
	Sockeye salmon	0	1	8
	Coho salmon	0	0	1
	Ocean-type Chinook salmon	0	0	1
	Total	0	4	36

plain delayed mortality in relation to a fish’s experience passing through the hydrosystem (Budy et al. 2002; Marmorek et al. 2004). Petrosky et al. (2001) concluded that most of the Snake River populations’ survival rate declines were in the smolt-to-adult life stage (consistent with high levels of delayed hydro-system mortality) rather than in the earlier life stage from spawner to smolt. These conclusions should provide pause for implementing costly recovery strategies for Snake River stream-type Chinook salmon populations that rely on tributary restoration actions to improve life cycle survival rates with current or slightly modified hydrosystem actions (NMFS 2004).

Our estimates for differential mortality between Snake River and downriver stream-type Chinook salmon ranged from 1.1 to 1.5; these results are consistent with the values estimated by previous studies (Schaller et al. 1999; Deriso et al. 2001). Thus, the relative survival of Snake River populations since FCRPS development continues to average one-fourth to one-third that of downriver populations, despite operational and structural changes to the hydrosystem. The estimate of differential mortality from μ_{SAR} agreed with those from the SR estimates, providing additional evidence that the relative survival difference occurred during the smolt-to-adult life stage. Wilson (2003) explored a number of lines of evidence in his analysis and also concluded that the elevated mortality (over historical levels) in the smolt-to-adult life stage (rather than in the egg-to-smolt life stage) was responsible for

the depressed status of Snake River stream-type Chinook salmon.

The delayed mortality of Snake River stream-type Chinook salmon remained high, even as oceanic and climatic conditions improved in the late 1990s. The weak correlation we observed between delayed mortality and the common year effect was positive, opposite of the hypothesis evaluated. The common year effect was evident and influential in both the updated and previous SR data. Williams et al. (2005) stated that hydrosystem-related latent mortality under the oceanic conditions that juveniles experienced in 1999 and 2000 would not prevent populations from returning to abundance levels observed before completion of the hydrosystem. Our corresponding estimates of δ for these years (brood years 1997 and 1998) were 0.59 and 1.03 (Figure 3); in other words, the density-independent survival (e^δ) was 1.8–2.8 times the long-term average. It is unlikely that highly favorable oceanic conditions experienced by smolts in 1999 and 2000 would continue indefinitely.

The relevance of upriver and downriver population comparisons in inferring common climatic influences and estimating hydrosystem impacts, including delayed mortality, was questioned by Zabel and Williams (2000), Levin and Tolimieri (2001), and Williams et al. (2005). A primary criticism was that the two population groupings may have considerable genetic differences, are from different evolutionarily significant units (ESUs), and would not respond identically to estuary and oceanic conditions. Our analyses and previous published papers (Marmorek et al. 1998; Schaller et al. 1999, 2000; Deriso et al. 2001; Budy et al. 2002) stressed that the population differences would need to explain the systematic change in relative population performance coincident with, but unrelated to, the development and operation of the hydrosystem. The relevant issue is not whether there are any genetic differences between population groupings, but whether genetic differences manifest themselves in a systematic change in population performance coincident with, but unrelated to, hydrosystem development and operation. Another criticism against using the downriver populations as a control is that the Snake River populations have different arrival timing to the estuary. Snake River and John Day River stream-type Chinook salmon have similar smolt migration timing leaving the tributaries during the spring freshet (Schaller et al. 1999; Berggren et al. 2005b). The hydrosystem delays estuary arrival timing of in-river migrants and accelerates that of transported smolts, both likely mechanisms for delayed mortality (Budy et al. 2002). Shifts in arrival-timing patterns are largely a consequence of the hydrosystem; nonetheless, the upriver and downriver populations

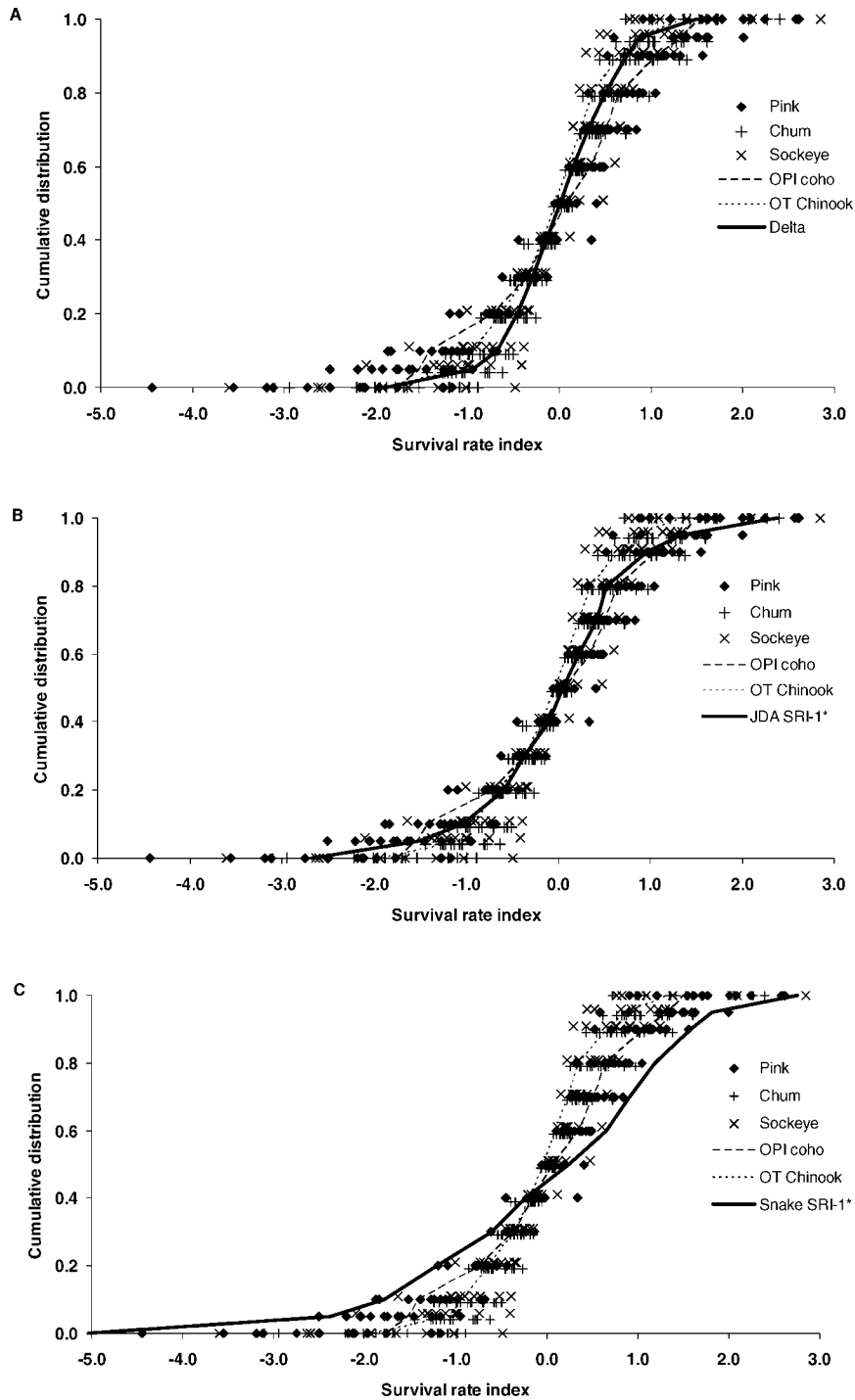


FIGURE 5.—Distributions of (A) the common year effect (delta), (B) the survival rate index (SRI-1*) for John Day River (JDA) populations, and (C) the SRI-1* for Snake River populations of stream-type Chinook salmon, compared with spawner–recruit residuals for other salmon population groups; OPI = Oregon production index for coho salmon (see text) and OT = ocean-type Chinook salmon).

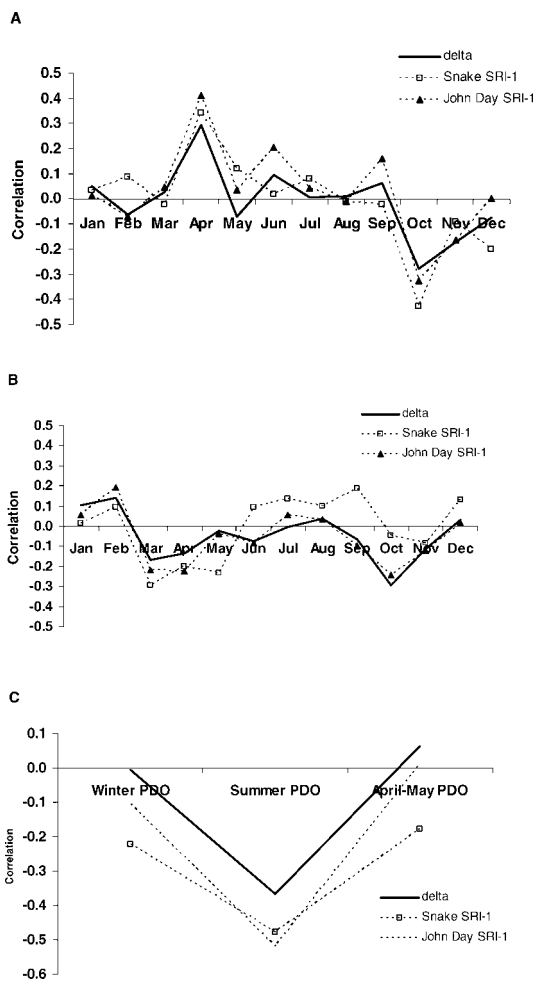


FIGURE 6.—Correlations of the common year effect (δ) and survival rate indices (SRI-1s) for John Day and Snake River stream-type Chinook salmon populations with three oceanic and climatic variables: (A) monthly upwelling anomalies at 45°N, (B) monthly sea surface temperature anomalies at 45°N, and (C) winter, summer, and April–May Pacific Decadal Oscillation (PDO) indices.

have overlapping estuary arrival timing and share common early ocean environmental conditions. These SR analyses did not assume that different ESUs (or population groupings) respond identically to environmental change. These analyses only assume that a portion of the overall survival rates for the population groups covary with common influences (e.g., estuary and early-ocean residence conditions).

The common year effect appears to be a reasonable description of the covariation of survival rates between upriver and downriver stream-type Chinook salmon in the Columbia River. Elsewhere, the covariation in survival rates within and between species has been

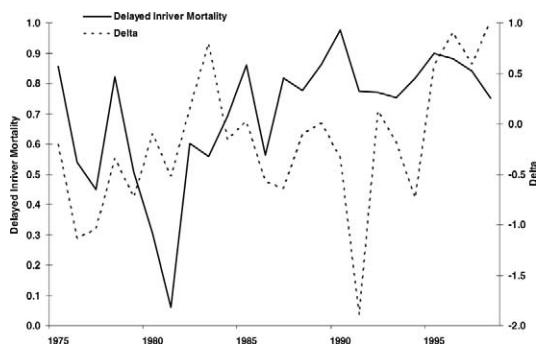


FIGURE 7.—Estimated delayed mortality of in-river migrant stream-type Chinook salmon compared with the common year effect, brood years 1975–1998, Snake and lower Columbia rivers.

described at regional scales up to 500 km from the point of ocean entry (e.g., Pyper et al. 2005). The variation in δ and in SR residuals for the downriver stream-type Chinook salmon populations fell within a similar range as that observed in pink, chum, sockeye, and coho salmon from other regions and in Columbia River ocean-type Chinook salmon (Table 4; Figure 5). In contrast, the variance in Snake River SR residuals significantly exceeded that observed in 36 out of 40 other salmon population groups. This larger variation in Snake River SR residuals relative to other salmon population groups is consistent with the large and variable mortality impacts caused by hydrosystem development and operation (Schaller et al. 1999). This larger variation in survival rates for Snake River populations has a critical impact on determining population growth rate and persistence (Morris and Doak 2002).

The common year effect and survival rate indices for Snake River and John Day River populations responded in a similar manner to oceanic and climatic variables. Our findings support previous conclusions that survival rates of salmon populations are influenced by broad-scale and local oceanic environmental conditions. These findings that the common year effect is positively correlated with the April upwelling index and negatively correlated with the October upwelling index are consistent with Scheuerell and Williams' (2005) correlations with SARs. This provides additional support that the common year effect is a reasonable index of oceanic conditions. However, survival rate indices for Snake River stream-type Chinook salmon populations were more variable than for other populations and considerably lower than for downriver populations. These patterns of survival are also consistent with the hypotheses of large mortality impacts caused by hydrosystem development and

operation, which are in addition to environmental variation.

Several Columbia River stream-type Chinook salmon populations and salmon population groups from other regions have exhibited increases in abundance since the late 1990s (BRT 2003; NMFS 2004; Good et al. 2005). While recognizing the positive trends, the West Coast Biological Review Team (BRT 2003) questioned how well the populations may fare in the future during periods of poor ocean survival combined with impacts in earlier life stages. Indeed, the 2005 and 2006 returns of Columbia River stream-type Chinook salmon were well below the recent average (see the Fish Passage Center Web site, <http://www.fpc.org/>), indicating poor ocean survival in 2003–2004. It is unknown how long poor climatic conditions may persist. Previous assessments (Peters and Marmorek 2001) indicated high risk for Snake River stream-type Chinook salmon during unfavorable climatic periods; global climate change will probably exacerbate these risks (Francis and Mantua 2003).

If both transported and in-river migrants experience substantial delayed mortality and the common year effect reasonably portrays the Snake River population's response to oceanic and climatic variation, as our results indicate, the risk to the persistence of Snake River stream-type Chinook salmon populations remains high. Recovery strategies must reduce both the direct and delayed components of hydrosystem mortality, regardless of the actions taken at other life stages.

Acknowledgments

We thank Randall Peterman and Brian Pyper for pink, chum, and sockeye salmon SR residual information, Eric Tinus for Oregon stream-type Chinook salmon updated SR data, and Joe Skalicky for creating the map. We would also like to recognize all of the efforts from the biologists of the Idaho Department of Fish and Game and the Oregon Department of Fish and Wildlife for collecting the spawning ground data. We greatly appreciate the reviews and comments of Don Anglin, Phaedra Budy, Margaret Filardo, Paul Wilson, and three anonymous reviewers. The findings and conclusions in this manuscript are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

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Appendix: Input Data

TABLE A.1.—Input data for estimating delayed mortality ($1-\lambda_n$) for Snake River stream-type Chinook salmon, brood years 1975–1998, where P_{br} is the proportion of all smolts arriving below Bonneville Dam that were transported, D is the ratio of the estuary and ocean survival rate of transported fish to that of in-river fish, and M is estimated total direct mortality.

Brood year	M	P_{br}	D
1975	1.252	0.984	0.530
1976	0.632	0.900	0.530
1977	0.514	0.936	0.530
1978	0.427	0.939	0.530
1979	0.511	0.938	0.530
1980	0.616	0.732	0.530
1981	0.738	0.703	0.530
1982	0.542	0.746	0.530
1983	0.466	0.922	0.530
1984	0.444	0.880	0.530
1985	0.492	0.958	0.530
1986	0.470	0.969	0.530
1987	0.497	0.892	0.530
1988	0.430	0.957	0.530
1989	0.339	0.942	0.530
1990	0.322	0.979	0.530
1991	0.320	0.943	0.530
1992	0.210	0.973	0.400
1993	0.159	0.939	0.390
1994	0.180	0.874	1.010
1995	0.198	0.862	0.480
1996	0.178	0.882	0.540
1997	0.121	0.912	0.780
1998	0.218	0.859	0.340