Delayed Mortality of Columbia River Salmon

Exploring evidence concerning delayed hydrosystem mortality for Snake River spring/summer Chinook

A draft technical document developed for the
Framework/Policy Work Groups
Federal Columbia River Power System
Salmon Biological Opinion Remand

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Executive Summary:

The hypothesis that a portion of the mortality that occurs in the estuary and ocean life stage is due to cumulative impacts of the Federal Columbia River Power System (FCRPS) is examined and the rationale described. Multiple analytical approaches are presented addressing this delayed or latent mortality for Snake River spring/summer Chinook. Water travel time and ocean/climatic conditions are considered in describing the variation in survival rates. In all results water travel time proved to be a significant factor in explaining the variation in survival. The FCRPS has delayed migration of in-river fish; with later arriving components of the population exhibiting lower SARs. The results of these multiple analyses provide compelling evidence that passage through the FCRPS strongly influences levels of delayed mortality of in-river migrants for these populations.

- The paper summarizes the hypothesis of delayed (latent) mortality relative to development and operation of the FCRPS, the mechanisms and the lines of evidence for this hypothesis, and variants of this main hypothesis.
- Past analyses are updated and expanded addressing upriver and downriver population comparisons and the development and operation of the FCRPS as a key factor in delayed mortality of Snake River spring/summer Chinook.
- New analyses are presented on survival of Snake River stocks alone that do not rely on upriver and downriver population comparisons.
- The analysis of Snake River populations alone included ocean/climatic variables, and water travel time relative to spawner-recruit residuals, smolt-to-adult return rates (SARs) and survival during the first year of ocean residence. Water travel time increased as the FCRPS was developed, and populations experienced a wide range of ocean/climatic conditions during the study period.
- Evaluation of the spawner-recruit residuals, SARs and early ocean survival showed that survival was related to water travel time, providing supporting evidence that there is a significant component of the survival during early ocean residence that is accounted for by delayed mortality, and related to construction and operation of the FCRPS. These analyses compliment the results from the upriver/downriver population performance model and did not rely on an assumption that downriver populations can serve as controls for Snake River populations.
- There is a delayed mortality component to survival during early ocean residence that is related to construction and operation of the FCRPS; however survival rates are also strongly related to the PDO and upwelling indices (measures of oceanic climatic conditions). The magnitude of delayed mortality may be modified by ocean conditions.
- Additional support for delayed mortality associated with passage through the FCRPS is provided by within-season patterns of SARs for in-river migrants, SARs of bypassed vs. true in-river migrants, and the relatively higher SARs of John Day wild Chinook when they experience the same arrival timing at Bonneville Dam as Snake River wild Chinook.
- Some delayed mortality of transported fish is well established by D-values less than 1.0, indicating ocean survival of transported smolts is less than that of in-river fish, which also experience delayed mortality.

I. Introduction

The Federal Columbia River Power System (FCRPS) Biological Opinion Remand Policy Work Group (PWG) provided direction in early May 2006 to the Framework Group participants to clarify issues related to delayed hydrosystem mortality for in-river migrants of Snake River spring/summer Chinook salmon. The PWG directed the Framework Group participants to develop clear statements of the differing hypotheses related to delayed mortality, and provide supporting rationale and evidence by May 31. Due to the short time-frame for this assignment, the draft document has not received complete agency or Framework Group review.

This technical draft document describes one hypothesis implemented in the Framework process that indicates substantial delayed (latent) mortality of juvenile salmon in the estuary or early ocean as a consequence of the hydrosystem experience. We also explored a variation on this hypothesis that delayed hydrosystem mortality may be influenced by ocean and climatic conditions. The rationale for the delayed mortality hypothesis is briefly described, and evidence from a number of existing and new analyses is presented.

II. Definition and Background for delayed mortality of Columbia River salmon

Development of the FCRPS from 1968 through 1975 resulted in a doubling of the number of dams, from four to eight, through which Snake River salmon migrate. This development was accompanied by severe declines in all Snake River anadromous salmon and their listing under the Endangered Species Act (ESA) in 1992.

A key remaining uncertainty for evaluating recovery options for upper basin salmon populations relates to the source of mortality that fish experience while in the estuary and early ocean. Sources of estuary and early ocean mortality include not only elements of the natural ocean environment, but also delayed effects of earlier life-stage experiences. One hypothesis for this delayed (or latent) mortality is that although this mortality occurs in the estuary and early ocean, it may be related to a fish's earlier experience through the hydrosystem. Because this mortality may be caused by the cumulative impacts of the hydrosystem during downstream migration as juveniles, a portion of the mortality that occurs in this life stage is called delayed mortality. In the case of Snake River salmon, fish may die in the estuary or ocean after exiting the hydrosystem, but as a result of the cumulative impacts from negotiating up to eight hydroelectric dams. Hereafter, in order to synthesize the terminology and emphasize its anthropogenic source, we refer to this type of mortality as delayed hydrosystem mortality. Identifying the magnitude of delayed hydrosystem mortality of Snake River salmon populations is crucial to estimate the distribution of mortality among the Hs and the predicted the outcome of recovery scenarios. The relative utility of different recovery actions for Snake River stream-type Chinook salmon hinges in part on whether post-Bonneville smolt-to-adult survival rate is influenced by hydrosystem experience during seaward migration. Previous analytical assessments (2000 BiOp, Peters and Marmorek 2001; Karieva et al. 2000; Wilson 2003) evaluated management options for halting the decline of these populations. Investigators found that model results of management actions are sensitive to assumptions about the degree to which mortality that takes place in the estuary and ocean is related to earlier hydrosystem experience during downstream migration.

To standardize the discussion, we introduce the following notation (Figure 1) in use by the COMPASS modeling group. First, we designate survival terms using S and mortality terms using $L = 1 - S$. Terms for in-river migrants are denoted by the subscript I and terms for transported fish by the subscript T. We partition survival and mortality into the following life stages: downstream migration through the hydropower system (subscript ds), estuary/ocean (subscript e/o), and upstream migration through the hydropower system (subscript us). We further partition the estuary/ocean stage to reflect mortality that would occur independent of the hydropower system ($1-S_{e/o}$), and hydropower system-related delayed (latent) mortality (L), which applies to both transported fish and in-river migrants. This partitioning of estuary/ocean survival reflects an assumption that for in-river fish, delayed mortality is essentially entirely expressed in the estuary/ocean stage. In previous studies, latent mortality (L) was termed delayed hydrosystem mortality and denoted as 1-λn (Peters and Marmorek 2001). We use this earlier terminology when discussing updated estimates of delayed mortality.

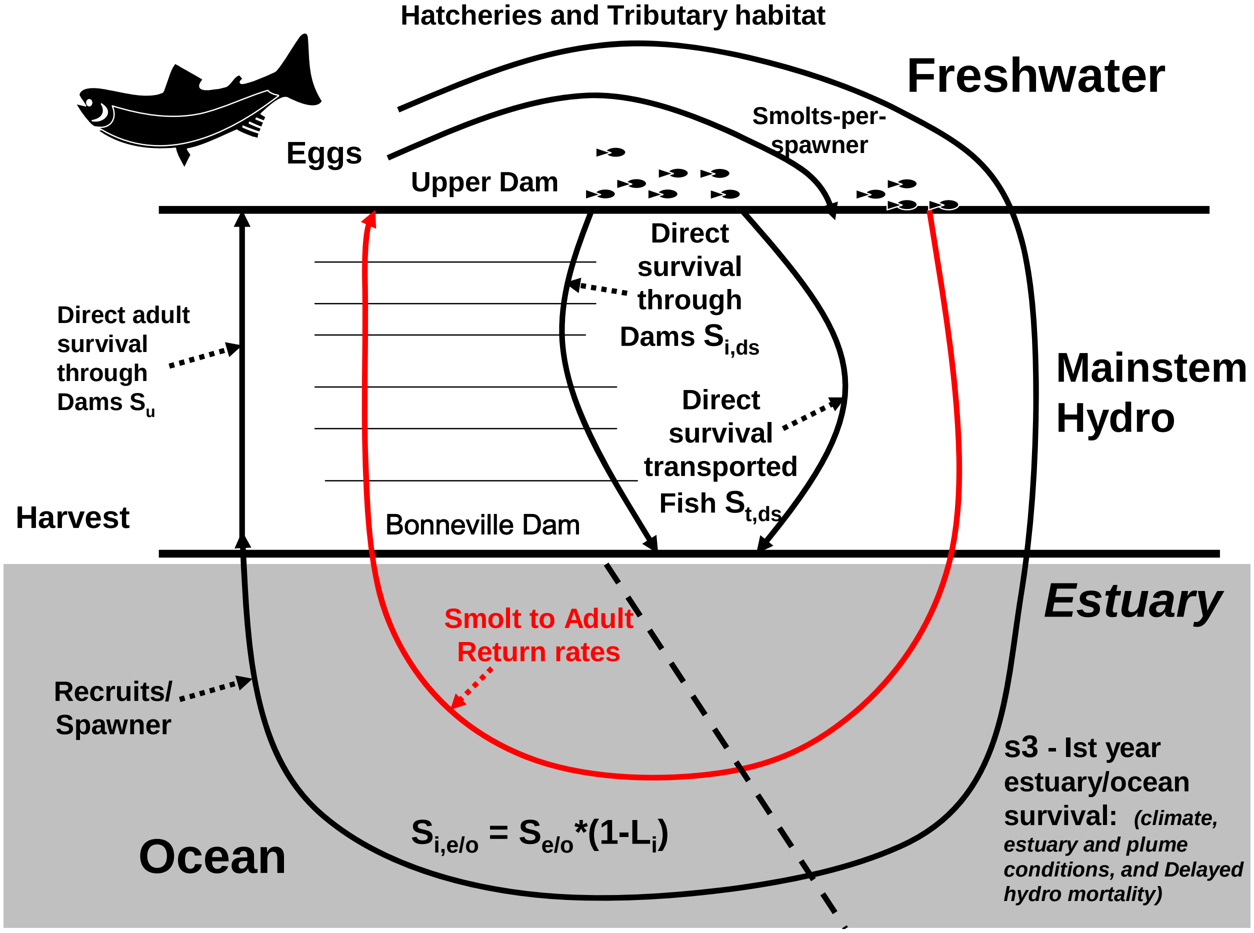

Figure 1. Survival and mortality terms used by the COMPASS work group for migration through the hydrosystem, and estuary/ocean survival partitioned into natural survival and hydrosystem latent mortality (L) components. Survival (*S*) and mortality (*L*) affecting Snake River anadromous salmonids migrating in-river (denoted by subscript *I*) at various life stages. The life stages are downstream migration through the hydropower system (*ds*), estuary/ocean (*e/o*), and upstream migration through the hydropower system (*us*). The estuary/ocean survival is partitioned into survival that would occur in the absence of the hydropower system ($s_{e/o}$) and latent mortality associated with the passage through the hydropower system (L_I). Transported fish (denoted by subscript *T*) are affected by the same survival and mortality processes and are represented by changing the subscript *I* to *T*. In previous literature, L = 1-λn.

III. **Rationale for delayed mortality and mechanisms:**

Because, by definition, delayed mortality is expressed after fish pass through the hydrosystem, it is impossible to measure directly. Delayed mortality associated with the FCRPS might result from changes in migration timing; injuries or stress incurred during migration through juvenile bypass systems, turbines, or spill at dams that does not cause direct mortality; disease transmission or stress resulting from the artificial concentration of fish in bypass systems or barges (Williams 2001, Williams et al. 2005, Budy et al. 2002; Schreck et al. 2006); depletion of energy reserves from prolonged migration (Congleton et al. 2004); altered conditions in the estuary and plume as a result of FCRPS construction or operation; or disrupted homing mechanisms. Nevertheless, changes in the hydrosystem over time were concurrent with changes in ocean conditions, hatchery smolt releases, and etc., making direct inference about relative influence of different factors in elevating mortality difficult. However, a number of reviews have found evidence in various forms linking the delayed mortality to the construction and operation of the FCRPS (Budy et al. 2002; Marmorek et al. 2004).

a. *Stress and injury at the dams*: Problems associated with collection and mechanical bypass systems at the dams include: 1) delay of fish in the forebay; 2) a large pressure change experienced by fish going through the collection and bypass system; 3) mechanical injury during collection and bypass; and 4) concentration of fish at the bypass outflow where predators tend to congregate. Fish that pass via turbines are also delayed in forebays and are exposed to similar extreme pressure changes and mechanical injuries while going through the turbines (Long et al. 1968; Mathur et al. 1996; Navarro et al. 1996; Ferguson et al. 2006; *see review by* Bickford and Skalski 2000).

b. *Stress and delayed mortality*: In addition to the stress smolts experience at the dam, the reservoirs behind the dams may also create stressful conditions. Water velocity has been greatly reduced as a result of the dams, and thus the time and energy expended to get through the reservoirs has increased over that experienced in the free flowing conditions for which these fish evolved (Williams and Mathews 1995). The concept of increased vulnerability to predators as a result of acute or chronic stress is ubiquitous in ecology (see Budy et al. 2002).

c. *Delayed mortality and arrival timing to the estuary*: During their seaward migration smolts are undergoing physiological changes in order to make the transition to saltwater. The increased freshwater residence time may result in premature physiological changes for saltwater that are not optimally suited for the freshwater environment. Also, the delay in reaching the estuary may result in arriving during a period of suboptimal conditions for survival. The combination of disrupting the timing of physiological readiness and arrival to the estuary during suboptimal conditions could cause increases in delayed mortality levels. The decrease in water velocity has also resulted in an increase in the residence time of the water, stressing fish energetically and allowing water temperatures to increase to higher than optimal levels for these cool water species (Raymond 1979; Budy et al. 2002; Congelton et al. 2004).

IV. Hypothesis: *Passage of seaward migrating juvenile fish through and around the FCRPS causes delayed mortality to salmon populations that may not be expressed until the estuary and ocean life-stage.*

a. *Evidence*

Delta model results from updated spawner-recruit (SR) analysis indicates that differential mortality between upriver and downriver populations increased during development of the FCRPS and remained high after completion of the FCRPS (Deriso et al. 2001; Marmorek et al. 2004; Schaller and Petrosky *in review*). In addition, delayed mortality estimates (using the methods of Peters and Marmorek 2001) also increased during development of the FCRPS and remained high after completion of the FCRPS.

i. Differential mortality between upriver and downriver populations.

Differential mortality is an estimate of the difference in the instantaneous mortality rate between Snake River and downriver (John Day River) population groups, accounting for common ocean climatic influence on both groups. Retrospective life-cycle analysis provided evidence of increases in mortality in Snake River spring/summer Chinook coincident with the development of the FCRPS (Schaller et al. 1999; Deriso et al. 2001; Marmorek et al. 2004; Schaller and Petrosky *in review*). The declines in survival rate of Snake River stocks were considerably sharper than those of downriver stocks over the same time period. Further, most Snake River survival rate declines were in the smolt-to-adult life stage, rather than the spawner-to-smolt stage (Petrosky et al. 2001). Differential mortality (μ), using model 1 from Deriso et al. (2001), has averaged about 1.47 since hydrosystem completion (Fig. 2). An alternative SR method compares Ricker residuals from Snake River and downriver stocks, which results in differential mortality estimates of about 1.15 (Fig. 3; Schaller et al. 1999; Schaller and Petrosky *in review*). Thus, life cycle survival rates ($e^{-\mu}$) of Snake River population averaged only ¼ to 1/3 those of downriver populations since FCRPS completion.

PIT-tagged fish provide an independent measure of survival rates from smolt to adult stage, which incorporates variation in hydrosystem experiences and environmental conditions in the estuary and (early) ocean. Spatial and temporal contrasts of survival rates from different life stages (adult-to-adult, adult-to-smolt, and smolt-to-adult) provide valuable information to diagnose where mortality rates have increased in the salmon life-cycle, and allow indirect inferences about alternative causes. The Comparative Survival Study (CSS; Berggren at al. 2005) started a consistent time series of PIT-tag SARs for Snake River and downriver wild spring/summer Chinook (John Day River) beginning in smolt year 2000. SAR estimates of differential mortality generally agree with those from spawner and recruit information (Fig. 2, 3), and indicate Snake River stocks survived 1/3 as well as downriver stocks during smolt years 2000-2002 (Berggren et al. 2005). The close correspondence of the SAR and SR estimates of differential mortality provides additional evidence that the relative survival difference occurred during the smolt- to-adult life stage. Lastly, this SAR analysis of differential mortality provides a measure that is independent of μ estimated from SR data.

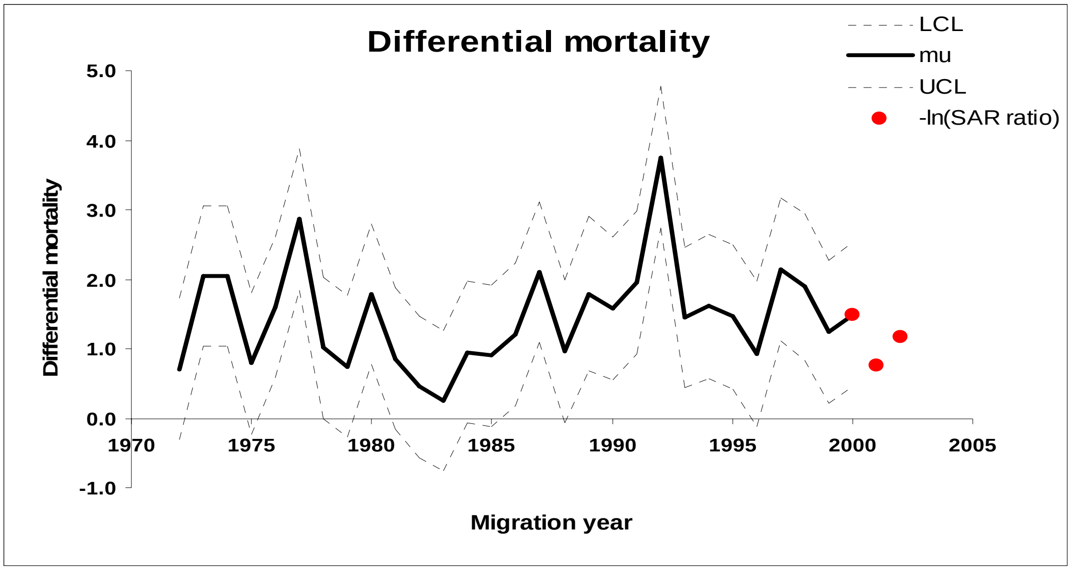

Figure 2. Differential mortality estimates (mu) from the Deriso et al. (2001) model updated through smolt year 2000 (Marmorek et al. 2004; Schaller and Petrosky *in review*) compared to estimates based on SARs of wild Snake River and John Day River spring/summer Chinook (-ln(SAR ratio)), smolt years 2000-2002 (Berggren et al. 2005).

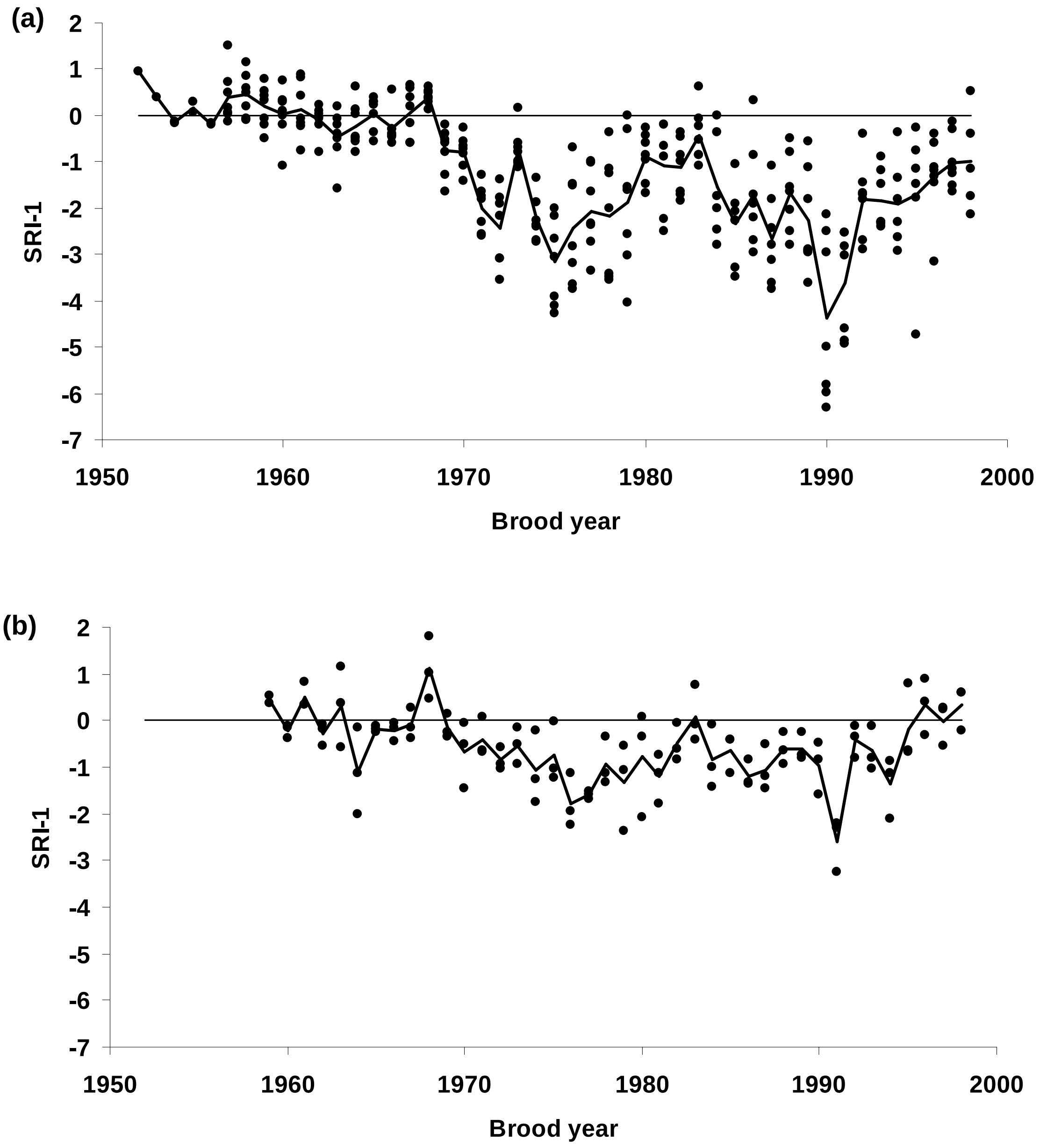

Figure 3. Deviations of ln[(observed R/S)/(predicted R/S)] from ANCOVA fit to the pre-1970 period (SRI-1) for the (a) Snake, and (b) downriver regions, brood years 1952-1998 (Schaller and Petrosky *in review*). Average SRI-1 values represented by solid line.

ii. Estimating delayed mortality. The magnitude of delayed mortality is estimated by partitioning direct juvenile passage survival and the differential delayed transportation mortality factor, *D*, from the estimated total mortality (m) of the Snake River populations (Peters and Marmorek 2001; see Fig. 1). Total mortality (m) is estimated by spawner-recruit methods described in Deriso et al. (2001; model 1). Tagging studies (Williams et al. 2005; Berggren et al. 2005, Zabel et al. 2006) and retrospective juvenile passage modeling (Peters and Marmorek 2001) can be used to generate historical estimates of the juvenile passage survival, direct hydrosystem mortality (M) and *D*.

Delayed mortality is estimated as 1-λn ("lambda_n" in Table 1; Peters and Marmorek 2001). Estimates of delayed mortality averaged 0.59 for smolt migration years 1977-1993 (Peters and Marmorek 2001; Fig. 4), using passage model in-river survival estimates and an average D = 0.53 (Table 1). Updated estimates of delayed mortality, using PIT-tag estimates of in-river survival and D, averaged 0.67 for smolt years 1994-2000 (Marmorek et al.2004, Schaller and Petrosky *in review*; Fig. 4).

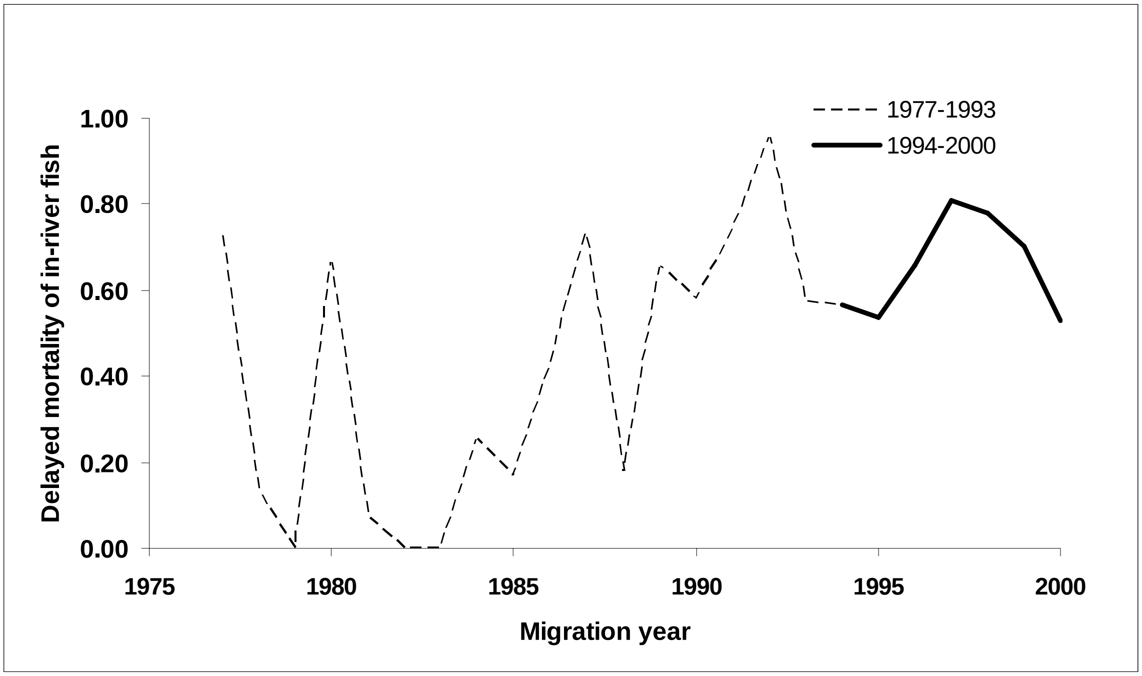

Figure 4. Delayed mortality estimates for smolt migration years 1977-2000 (Schaller and Petrosky *in review*).

Table 1. Estimates of instantaneous mortality rates, and survival rates attributed to delayed hydrosystem mortality for Snake River spring/summer Chinook, post FCRPS completion. Estimated parameters from Peters and Marmorek (2001), updated through brood year 1998 (Marmorek et al. 2004). Differential mortality estimates for 1999 from SARs of Snake River and John Day River spring Chinook (Berggren et al. 2005). Estimates of D before brood year 1992 sampled from 1993-2003 distribution (Berggren et al. 2005), except brood year 1999 value of D (2001 smolt year) applied to other low flow years (brood year 1975).

Brood year	M	Pbt	D	m	Delta_m	Sem	**Lambda n**	Delta	Mu
1975	1.252	0.984	2.20	3.176	1.924	0.146	0.07	-0.198	2.860
1976	0.632	0.900	0.48	1.327	0.695	0.499	0.94	-1.137	1.011
1977	0.514	0.936	0.47	1.060	0.546	0.580	1.00	-1.046	0.744
1978	0.427	0.939	0.47	2.104	1.678	0.187	0.37	-0.341	1.789
1979	0.511	0.938	0.47	1.169	0.658	0.518	1.00	-0.727	0.853
1980	0.616	0.732	0.49	0.767	0.150	0.860	1.00	-0.100	0.451
1981	0.738	0.703	0.49	0.569	-0.169	1.000	1.00	-0.523	0.254
1982	0.542	0.746	0.48	1.266	0.724	0.485	0.79	0.151	0.950
1983	0.466	0.922	0.48	1.220	0.754	0.470	0.90	0.800	0.905
1984	0.444	0.880	0.49	1.527	1.083	0.339	0.62	-0.157	1.211
1985	0.492	0.958	0.48	2.425	1.933	0.145	0.29	0.027	2.109
1986	0.470	0.969	0.48	1.276	0.807	0.446	0.90	-0.573	0.961
1987	0.497	0.892	0.49	2.106	1.609	0.200	0.37	-0.642	1.790
1988	0.430	0.957	0.48	1.893	1.463	0.231	0.46	-0.105	1.577
1989	0.339	0.942	0.48	2.274	1.935	0.144	0.29	0.008	1.958
1990	0.322	0.979	0.48	4.072	3.750	0.024	0.05	-0.337	3.756
1991	0.320	0.943	0.48	1.759	1.439	0.237	0.47	-1.892	1.443
1992	0.210	0.973	0.32	1.925	1.715	0.180	**0.53**	0.128	1.609
1993	0.159	0.939	0.40	1.775	1.616	0.199	**0.46**	-0.186	1.460
1994	0.180	0.874	0.86	1.244	1.063	0.345	**0.39**	-0.733	0.928
1995	0.198	0.862	0.39	2.450	2.251	0.105	**0.22**	0.581	2.134
1996	0.178	0.882	0.54	2.210	2.032	0.131	**0.22**	0.901	1.894
1997	0.121	0.912	0.74	1.555	1.433	0.239	**0.31**	0.585	1.239
1998	0.218	0.859	0.36	1.808	1.590	0.204	**0.45**	1.025	1.492
1999	0.027	0.990	2.20	0.947	0.919	0.399	**0.18**		0.756
							0.44	geomean lambda n (BY78-98)	

M = direct mortality of Snake stocks
m= total annual mortality of Snake stocks
Delta_m = m - M
Sem = exp(-Delta_m)
Lambda_n = Sem/(D*Pbt+1-Pbt)

Lambda_n is survival rate attributed to delayed hydrosystem mortality of in-river migrants
Delayed mortality = 1 - Lambda_n

D = differential delayed mortality of transported smolts
Pbt = proportion of migrants below Bonneville Dam that were transported
Delta = common year effect (common mortality patterns between Snake and downriver populations)
Mu = differential mortality (difference in mortality between Snake and downriver populations)

Average Mu = 1.47, i.e., Snake River populations surviived 23% as well as downriver populations

M, m, Delta and Mu are defined in Deriso et al. (2001)
Delta_m, D, Pbt and Lambda_n are defined in Peters and Marmorek (2001)

iii. Common year effect. In the Delta model, differential mortality is estimated with an assumption of a common climatic influence on the different population groups (Deriso et al. 2001); the best fit empirical models included an estimate of a common year effect (δ). The estimated common year effect ranged from -1.89 to 1.49 for smolt years 1954-2000 (Fig. 5; Marmorek et al. 2004; Schaller and Petrosky *in review*). This range of mortality equates to relative annual changes (e^{δ}) from 15% to 444% of the long-term average survival rate.

The relevance of upriver/downriver population comparisons to infer common climatic influences and to estimate 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 stock complexes may have considerable genetic differences and would not respond identically to estuary and ocean conditions. Arguments in support of such a framework appeared in Schaller et al. (1999, 2000), Marmorek et al. 1998, Deriso et al. (2001) and Schaller and Petrosky *in review*. These papers stressed that the stock differences would need to explain the systematic change in relative stock performance coincident with, but unrelated to, the development and operation of the hydrosystem.

The common year effect, δ, appears to be a reasonable description of co-variation between upriver and downriver stream-type Chinook salmon in the Columbia River. Snake River and John Day River stream-type Chinook have similar smolt migration timing and share common estuary conditions (Schaller et al. 1999; Berggren et al. 2005). Elsewhere, co-variation in survival rates within and between species has been 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 SR residuals for the downriver stream-type Chinook populations fell within a range similar to that observed for pink, chum, sockeye and coho salmon from other regions, and Columbia River ocean-type Chinook (Fig. 6a,b; Schaller and Petrosky *in review*). In contrast, the variance in Snake River SR residuals significantly exceeded that in 36 out of 40 other salmon population groups (Fig. 6c). This larger variation in Snake River SR residuals relative to other salmon population groups is consistent with the Schaller et al. (1999) and Deriso et al. (2001) hypotheses of large mortality impacts due to hydrosystem development and operation, which is in addition to environmental variation (captured by the common year effect).

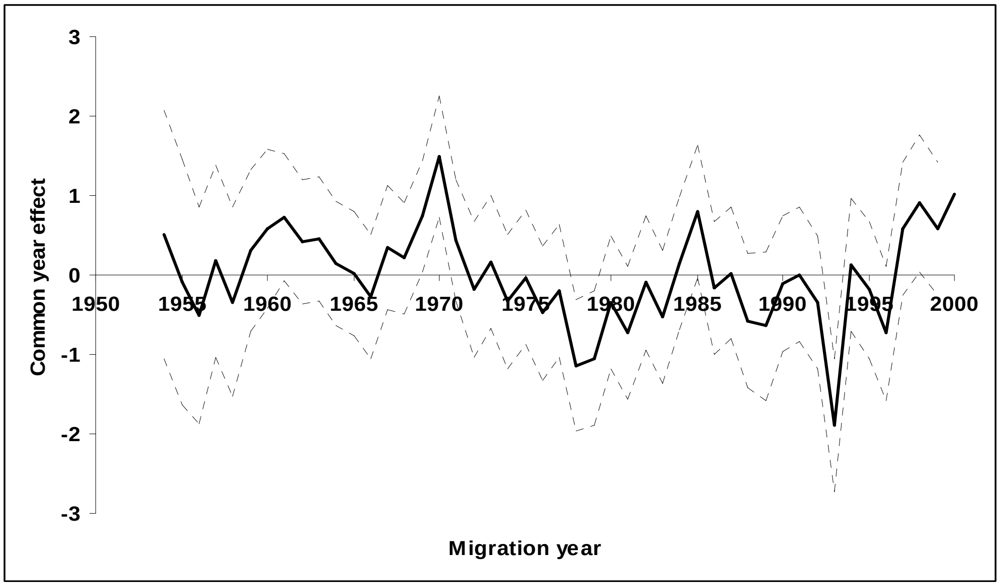

Figure 5. Common year effect estimates from the Deriso et al. (2001) model updated through smolt year 2000 (Marmorek et al. 2004; Berggren et al. 2005).

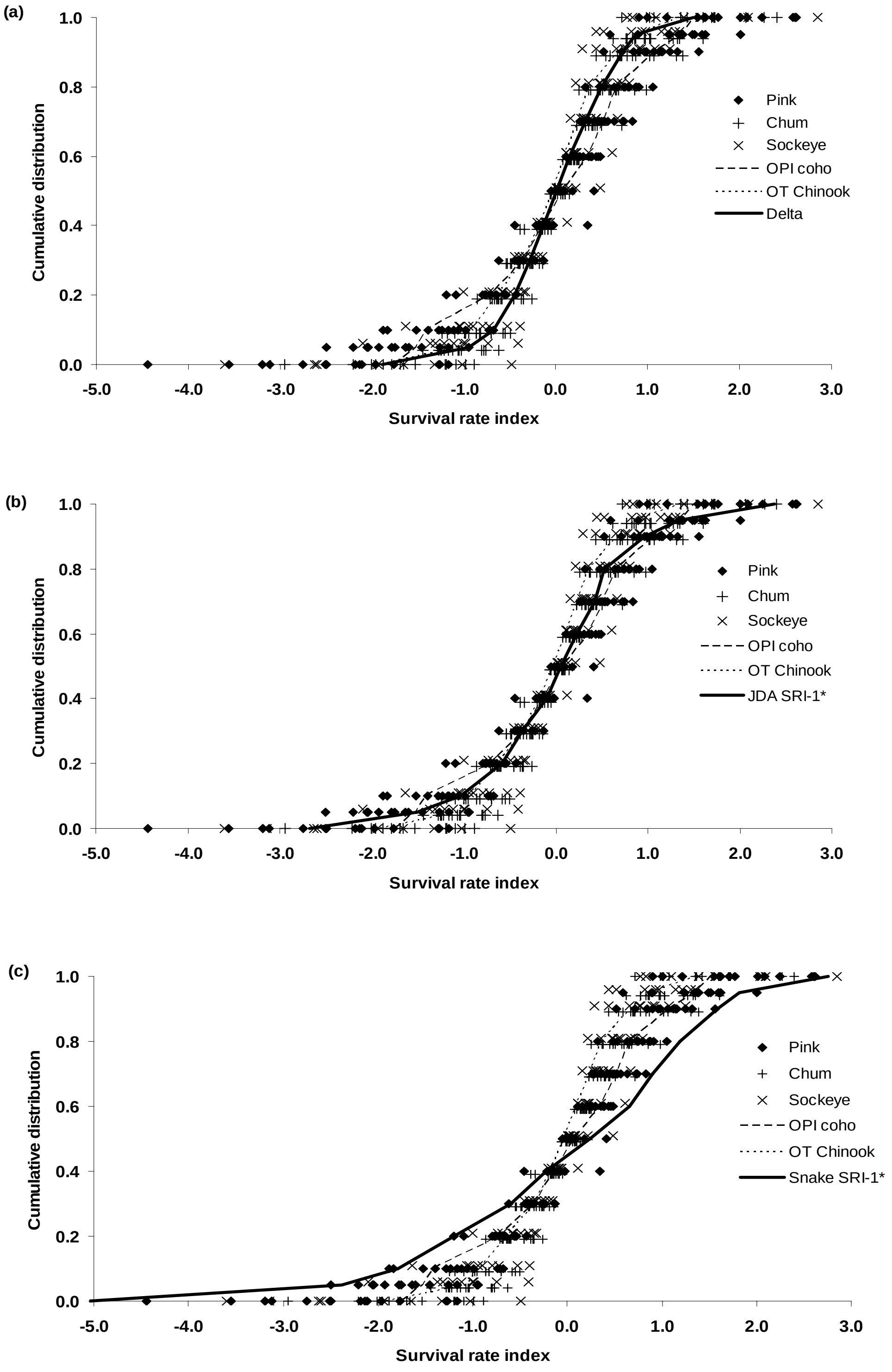

Figure 6. Distribution of δ (a), SR residuals for John Day River populations (b) and SR residuals for Snake River populations (c) of stream-type Chinook compared with SR residuals for other salmon population groups (Schaller and Petrosky *in review*).

iv. Analyses excluding downriver stocks. The preceding delayed mortality analyses relied on upriver/downriver population performance to determine annual mortality differences between population groups, and then partitioned this annual mortality by the measured (or model estimated) direct passage mortality and *D*.

Other analytical methods, which rely only on the Snake River population response, also point to large mortality impacts from the FCRPS in the SAR life-stage. First, Wilson's (2003) matrix modeling analysis also concluded that a sharp decline in estuarine and ocean survival, associated with dam construction and operation, was the primary reason for the population declines. We explored alternative approaches, using just the Snake River populations, including multiple regression of the SR residuals (Schaller et al. 1999; Schaller and Petrosky *in review*), the SARs and the 1st year ocean survival (s3 - Zabel et al. 2006) against environmental conditions experienced during the smolt migration and in the ocean (Petrosky and Schaller *in prep*.).

Linear multiple regression was used to relate SR residuals (an index of survival) for Snake River spring/summer Chinook populations (Schaller et al. 1999; Schaller and Petrosky *in review*) to water travel time (WTT) during the smolt migration and ocean climatic variables experienced during the first year at sea. WTT is a measure of the average number of days for water particles to travel from the confluence of Clearwater and Snake Rivers to Bonneville Dam (April 15-May 31 flow). Ocean climatic variables investigated included: Pacific Decadal Oscillation Index (PDO), Sea Surface Temperatures (SST) and wind induced coastal upwelling index (Mantua et al. 1997, Pacific Fisheries Environmental Laboratory 2006). WTT increased substantially as the number of dams increased, and varied as a function of flow (Fig. 7). WTT was about 2 days during pristine conditions and increased to an average 19 days (range 10-40 days) with 8 dams. WTT was a significant independent variable in the top regression models (Table 2), suggesting some of the life cycle survival variation was associated with the juvenile migration conditions. The best 3 variable model included WTT, April Upwelling and September PDO. The expected response for (R/S) to changes in WTT (holding ocean climatic variables constant) is shown in Fig. 8. For average climate conditions the expected ln(R/S) residual was 0 at 2.8 days WTT, decreasing to -1.79 at 19 days WTT. In other words, with increased WTT survival (recruits/spawner residuals) would decrease to 17% ($e^{-1.79}$) of survival expected under historic WTT conditions. For the good and poor climate conditions considered here (Sep PDO -1 or +1, April Upwelling +40 or -40), the expected recruits/spawner was 2 fold higher or lower, respectively (Fig. 8). The increase in instantaneous mortality after FCRPS completion predicted by the WTT regression (1.79) corresponded closely with the Delta model estimates of annual instantaneous mortality (average m = 1.75; Table 1). In other words, both methods (upstream/downstream comparison and Snake River population performance only) estimate that, on average, current survival has decreased to 17% of the average historic level.

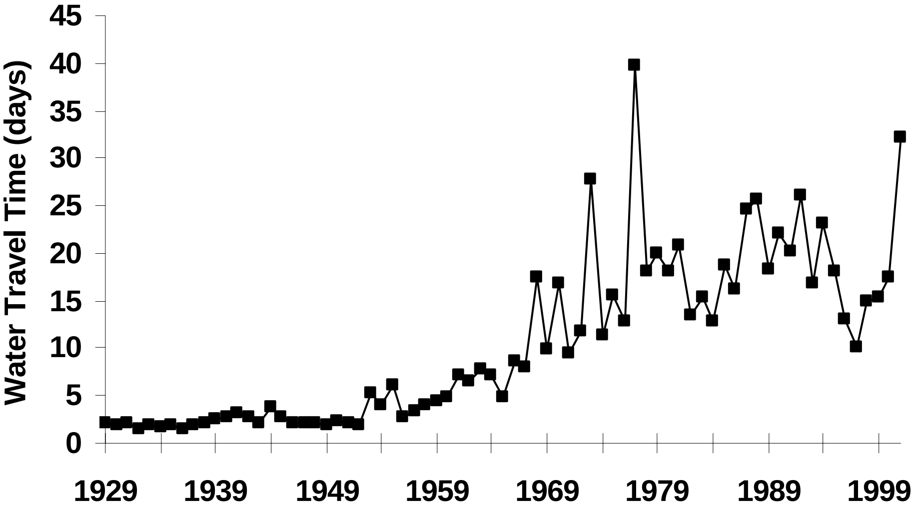

Figure 7. Water Travel Time (days for water particles to travel from the confluence of Clearwater and Snake Rivers to Bonneville Dam), 1929-2001. FCRPS dams were constructed in 1938 (BON), 1953 (MCN), 1957 (TDD), IHR (1961), JDA (1968), 1969 (LMN), 1970 (LGS), and 1975 (LGR).

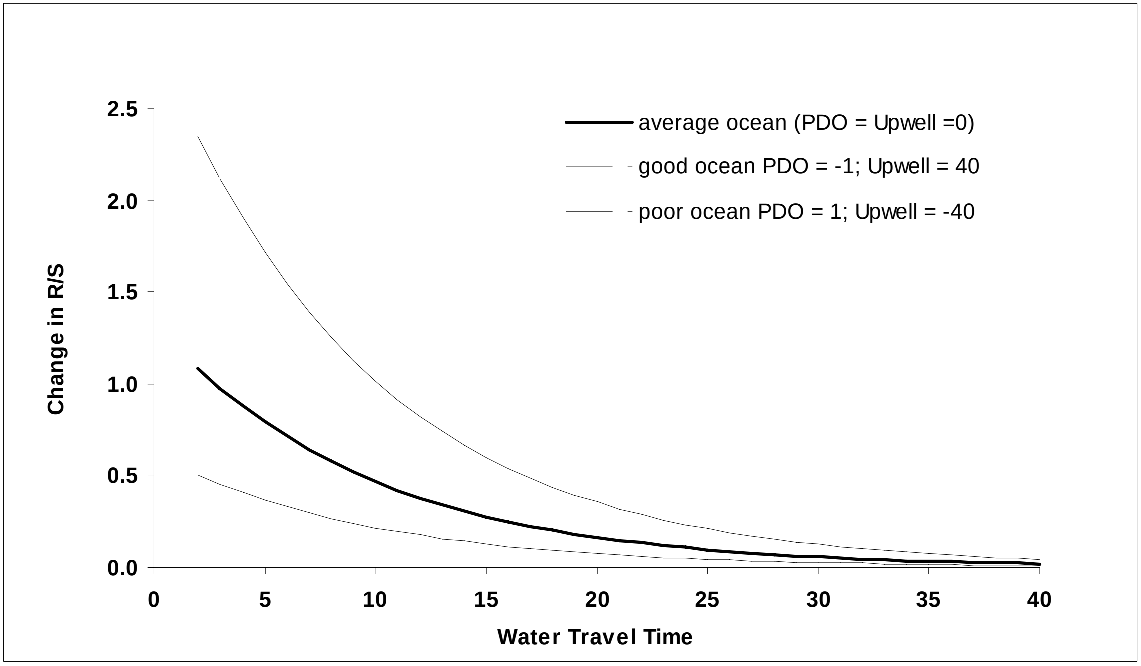

Figure 8. Expected change in Recruit/Spawner vs. Water Travel Time (WTT) for average ocean conditions (Sep PDO = 0; April Upwelling = 0), good ocean conditions (Sep PDO = -1; April Upwelling = 40), and poor ocean conditions (Sep PDO = 1, April Upwelling = -40). Historic WTT was 2 days, recent average (range) with 8 dams is 19 days (10-40 days).

Table 2. Regression model results (selected) for SR residuals of Snake River spring/summer Chinook versus environmental variables, Water Travel Time (days), PDO, Upwelling and Sea Surface Temperature (selected months), smolt migration years 1954-2000.

Number in model	**Adjusted R^2**	**R^2**	**AIC**	**BIC**	**Variables in model**	**Comments**
8	0.733	0.780	-37.46	-30.37	WTT, May PDO, JunPDO, AprUP, OctUP, MarPDO, AugPDO,SepPDO	highest R^2_{adj}
4	0.721	0.745	-38.62	-35.48	WTT, AprUP, OctUP, SepPDO	best AIC, BIC
3	0.695	0.715	-35.36	-33.37	WTT, AprUP, SepPDO	best 3 variable model
3	0.689	0.709	-34.39	-32.56	WTT, AprUP, AugPDO	
3	0.688	0.708	-34.32	-32.50	WTT, OctUP, SepPDO	
3	0.687	0.707	-34.10	-32.32	WTT, OctUP, AugPDO	
2	0.668	0.682	-32.30	-30.94	WTT, AugPDO	best 2 variable model
1	0.540	0.550	-17.93	-17.67	WTT	
3	0.524	0.555	-14.44	-15.58	WTT, MarSST, MarPDO	lowest R^2_{adj} including WTT
4	0.464	0.511	-7.99	-10.52	MayPDO, JunPDO, OctUP, AugUP	highest R^2_{adj} excluding WTT

Parameter estimates SR residuals = WTT, AprUP, OctUP, SepPDO

Variable	Estimate	Pr > [t]
Intercept	0.0600	0.7909
WTT	-0.0974	<0.0001
AprUP	0.0106	0.0183
OctUP	-0.0111	0.0311
SepPDO	-0.3147	0.0019

Parameter estimates SR residuals = WTT, AprUP, SepPDO

Variable	Estimate	Pr > [t]
Intercept	0.2916	0.1691
WTT	-0.1051	<0.0001
AprUP	0.0109	0.0201
SepPDO	-0.3368	0.0014

Linear multiple regression was also used to relate SARs for Snake River spring/summer Chinook populations to water travel time and the above ocean climatic variables (PDO, SST, upwelling index). SARs were transformed into mortality rates (-ln(SAR)) for the analysis. Two time series of SAR estimates were investigated, one using the estimates reported in Zabel et al. (2006) for all years (SARnmfs), and the other using the same estimates for the early years and PIT tag estimates (Berggren et al. 2005) for smolt years 1994-2001 (SARpit). Smolt years 1985-1991 were excluded from the SAR analyses because no estimates of wild smolts were available (Petrosky et al. 2001). WTT was a significant independent variable in the best fit regression models for both data series (Tables 3 and 4), suggesting ocean survival was also influenced by the juvenile migration conditions. The expected response of SARpit to changes in WTT (holding ocean climatic variables constant) is shown in Fig. 9. The regression suggests that at current average WTT (19 days), SARpit survival rate would decline to 35% of the value predicted from historic WTT (2 days).

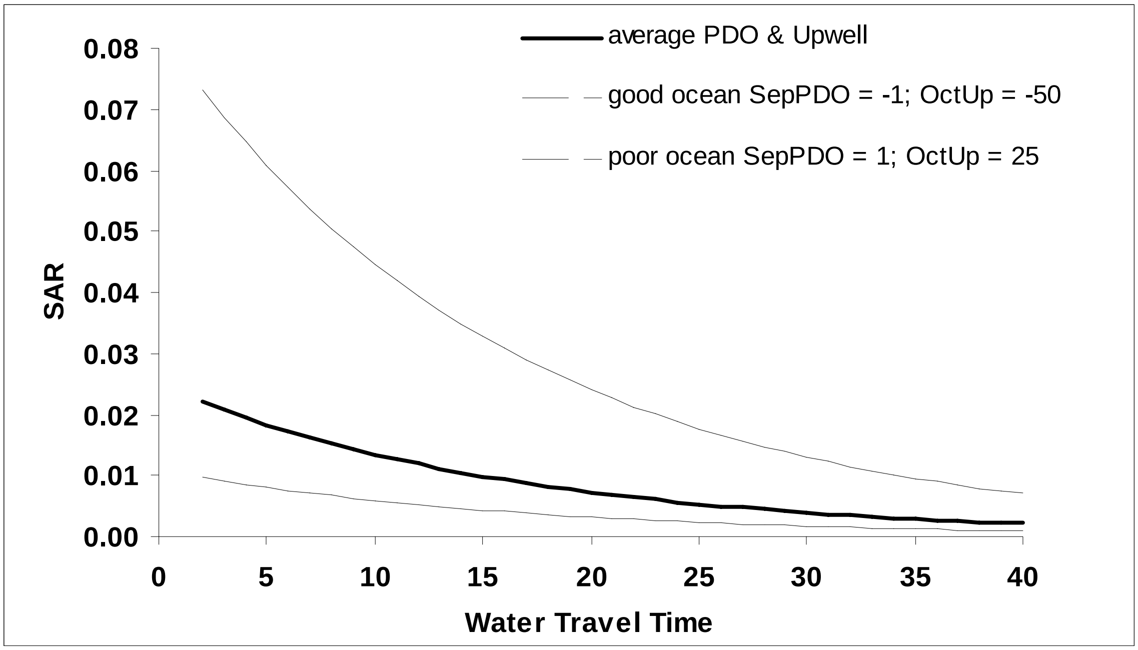

Figure 9. Expected SAR vs. Water Travel Time (WTT) for average ocean conditions (Sep PDO = 0; Oct Upwelling = 0), good ocean conditions ((Sep PDO = -1; Oct Upwelling = -50), and poor ocean conditions (Sep PDO = 1, Oct Upwelling = 25). Historic WTT was 2 days, recent average (range) with 8 dams is 19 days (10-40 days).

Table 3. Regression model results for SARs of Snake River spring/summer Chinook versus environmental variables, Water Travel Time (days), PDO, Upwelling and Sea Surface Temperature (selected months), smolt migration years 1966-1984, 1992-2001. SARs (SARnmfs) are from Zabel et al. (2006) based on run reconstruction from Williams et al. (2005).

Number in model	**Adjusted R^2**	**R^2**	**AIC**	**BIC**	**Variables in model**	**Comments**
5	0.706	0.755	-39.11	-33.46	WTT, SepPDO, OctUP, AugSST, AprUP	highest $R^2_{adj,}$ best AIC
4	0.680	0.723	-37.29	-33.67	WTT, SepPDO, AugSST, AprUP	best model from BIC
3	0.633	0.670	-33.85	-32.01	WTT, SepPDO, AugSST	best 3 variable model
4	0.577	0.633	-28.59	-27.80	MayPDO, SepPDO, OctUP, AugSST	highest R^2_{adj} excluding WTT
2	0.514	0.547	-26.03	-25.91	WTT, SepPDO	best 2 variable model

Parameter estimates -ln(SARnmfs) = WTT, SepPDO, OctUP, AugSST, AprUP

Variable	Estimate	Pr > [t]
Intercept	7.3010	<0.0001
WTT	0.0529	0.0003
SepPDO	0.5138	<0.0001
OctUP	0.0089	0.0823
AugSST	-0.2387	0.0099
AprUP	-0.0079	0.0654

Table 4. Regression model results for SARs of Snake River spring/summer Chinook versus environmental variables, Water Travel Time (days), PDO, Upwelling and Sea Surface Temperature (selected months), smolt migration years 1966-1984, 1992-2001. SARs (SARpit) through 1993 are from Zabel et al. 2006; SARs for 1994-2001 are from PIT tag estimates (Berggren et al. 2005).

Number in model	Adjusted R^2	R^2	AIC	BIC	Variables in model	Comments
6	0.690	0.752	-38.44	-31.84	WTT, SepPDO, OctUP, AprSST, AugSST, AprUP	highest R^2_{adj}
5	0.688	0.740	-39.00	-33.74	WTT, SepPDO, OctPDO, AugSST, AprUP	best model from AIC
4	0.665	0.709	-37.55	-34.10	WTT, SepPDO, OctUP, AugSST	best model from BIC
3	0.618	0.656	-34.32	-32.55	WTT, SepPDO, OctUP	best 3 variable model
4	0.536	0.598	-27.49	-27.24	MayPDO, SepPDO, OctUP, AugSST	highest R^2_{adj} excluding WTT
2	0.516	0.549	-27.91	-27.61	WTT, SepPDO	best 2 variable model

Parameter estimates -ln(SARpit) = WTT, SepPDO, OctUP, AugSST, AprUP

Variable	Estimate	Pr > [t]
Intercept	4.6836	0.0342
WTT	0.0562	0.0002
SepPDO	0.4452	0.0005
OctUP	0.0112	0.0316
AprSST	0.1599	0.2953
AugSST	-0.1709	0.0581
AprUP	-0.0058	0.1807

Parameter estimates -ln(SARpit) = WTT, SepPDO, OctUP

Variable	Estimate	Pr > [t]
Intercept	3.6911	<0.0001
WTT	0.0617	0.0002
SepPDO	0.4434	0.0002
OctUP	0.0151	0.0073

The time series of 1st year ocean survival (3rd year survival, s3) was estimated by methods similar to Zabel et al. (2006) from SARs of aggregate Snake River spring/summer Chinook for smolt years 1966-2001. Smolt years 1985-1991 were excluded from the s3 analyses[1] because no estimates of wild smolts were available (Petrosky et al. 2001). Estimates of s3 were derived by partitioning the SARs for each smolt migration year by estimates of direct passage survival and *D*, assuming the survival during the 2nd and 3rd ocean years is fixed at 0.8 (Zabel et al. 2006). This approach contains any latent or delayed hydrosystem mortality in the s3 estimate, rather than attempting to estimate the magnitude of delayed mortality as described above for the Peters and Marmorek (2001) method.

Linear multiple regression was used to relate s3 to water travel time (WTT), and several ocean climatic variables (PDO, SST, upwelling index). First year ocean survival was transformed to a mortality rate (-ln(s3)) for the analysis. WTT was a significant independent variable in the top s3 regression models (Table 5), suggesting some of the 1st year ocean survival was associated with the juvenile migration conditions. The simplest best fit model (best BIC score) selected the independent variables WTT, September PDO, and April Upwelling.

The expected response of s3 to changes in WTT (holding ocean climatic variables constant) is shown in Fig. 10. Under average ocean conditions (Sep PDO = 0, April Upwelling = 0), predicted s3 was 20.5% at 2 days WTT and 4.1% at 19 days WTT. Under good ocean conditions (assumed Sep PDO = -1, April Upwelling = 40), predicted s3 was 55.7% at 2 days WTT and 11.1% at 19 days WTT. Under poor ocean conditions (assumed

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[1] Regression analyses using assumptions to generate wild smolts for 1985-1991 resulted in the same primary variables with similar coefficients.

Sep PDO = 1, April Upwelling = -40), predicted s3 was 7.6% at 2 days WTT and 1.5% at 19 days WTT.

The level of mortality for Snake River spring/summer Chinook populations, during their 1st year of ocean residence that can be attributed to the FCRPS configuration and operation is characterized by the s3 response to the change in WTT from average historic levels (2 days) to average present levels (19 days). Thus, under the current FCRPS configuration, 1st year ocean survival was expected to average only 20% of historic based on WTT change (2 to 19 days). The magnitude of delayed hydrosystem impact suggested by the s3 regression analysis is consistent with, and slightly greater than, the delayed mortality estimates (Table 1; $\lambda n = 0.33$) derived using upriver and downriver population performance.

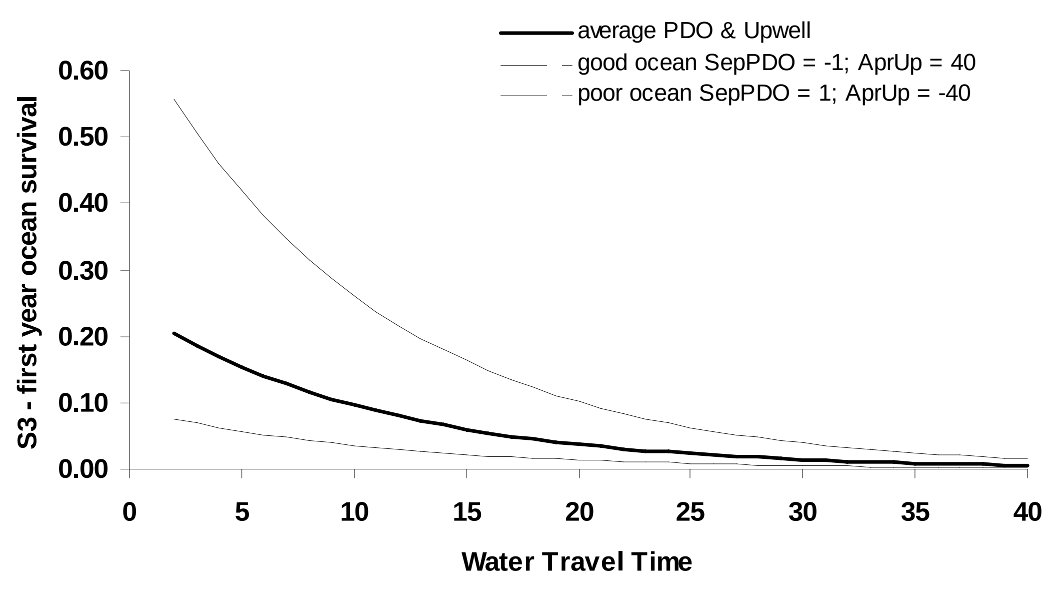

Figure 10. Expected 1st year ocean survival (s3) vs. Water Travel Time (WTT) for average ocean conditions (Sep PDO = 0; April Upwelling = 0), good ocean conditions ((Sep PDO = -1; April Upwelling = 40), and poor ocean conditions (Sep PDO = 1, April Upwelling = -40). Historic WTT was 2 days, average (range) with 8 dams is 19 days (10-40 days).

Table 5. Regression model results for 1st year ocean survival (s3) of Snake River spring/summer Chinook versus environmental variables, Water Travel Time (days), PDO, Upwelling and Sea Surface Temperature (selected months), smolt migration years 1966-1984, 1992-2001.

Number in model	**Adjusted R^2**	**R^2**	**AIC**	**BIC**	**Variables in model**	**Comments**
4	0.726	0.765	-33.99	-29.03	WTT, MayPDO, SepPDO, AprUP	highest $R^2_{adj,}$ best AIC
5	0.725	0.774	-33.08	-26.95	WTT, MayPDO, SepPDO, AugSST, AprUP	
3	0.712	0.743	-33.36	-29.82	WTT, SepPDO, AprUP	best 3 variable model, best BIC
3	0.705	0.737	-32.64	-29.31	WTT, MayPDO, AprUP	
2	0.655	0.680	-29.00	-27.21	WTT, AprUP	best 2 variable model
4	0.420	0.503	-12.23	-14.30	MayPDO, AprSST, AugSST, AprUP	highest R^2_{adj} excluding WTT

Parameter estimates S3 mortality (-ln(s3))= WTT, MayPDO, SepPDO, AprUP

Variable	Estimate	Pr > [t]
Intercept	1.4648	<0.0001
WTT	0.0865	<0.0001
MayPDO	0.1730	0.1437
SepPDO	0.2052	0.0988
AprUP	-0.0144	0.0088

Parameter estimates S3 mortality (-ln(s3)) = WTT, SepPDO, AprUP

Variable	Estimate	Pr > [t]
Intercept	1.3934	<0.0001
WTT	0.0947	<0.0001
SepPDO	0.2777	0.0204
AprUP	-0.0180	0.0006

Evaluation of the time series of SR residuals, SARs, and s3 showed that survival was related to water travel time – providing supporting evidence that there is a significant component of the survival during early ocean residence that is delayed mortality, and related to construction and operation of the FCRPS. These analyses compliment the results from the upriver/downriver population performance model, and did not rely on an assumption that downriver populations can serve as controls for Snake River population response.

V. **Modified delayed mortality hypothesis:** ***Passage of seaward migrating juvenile fish through and around the FCRPS causes delayed mortality to salmon populations that may not be expressed until the estuary and ocean life-stage. The magnitude of delayed effects related to the FCRPS may vary due to ocean/climate conditions.***

a. Evidence

The hypothesis that the magnitude of delayed mortality is modified by ocean conditions is plausible, because fish condition can be compromised by the effects of the hydrosystem and therefore the 1st year ocean survival moderated by ocean/climate conditions.

Williams et al. (2005) hypothesized that delayed mortality of Snake River spring/summer Chinook became negligible in the late 1990s as ocean conditions improved. Schaller and Petrosky (*in review*) found evidence that delayed hydrosystem mortality remained high even as climatic conditions improved (Figure 4).

Evaluation of the time series of s3 (early ocean survival), SARs, and SR residuals show that survival is related to water travel time – providing supporting evidence that there is a delayed mortality component to survival during early ocean residence that is related to construction and operation of the FCRPS. However, the survival rates are also strongly related to the PDO and upwelling indices (measures of ocean/climate conditions).

Figures 8-10 show the response of SR residuals, SARs and s3 from the multiple regression models to water travel time (WTT) for average, good and poor PDO and upwelling conditions. For a fixed WTT, the predicted survival rates vary widely across the ocean climatic conditions. The environmental variables that demonstrated a significant relation to these survival indices included Water Travel Time, April and October upwelling, May and September PDO, and on occasion August sea surface temperatures. These findings for the oceanographic indices were generally consistent with the work of Scheuerell and Williams (2005), Zabel et al. (2006), and Nickelson (1986). However, in addition we identified that survival rates have been strongly influenced by water travel time through the Columbia River mainstem projects and reservoirs.

b. *Sub Hypothesis: There is a differential delayed mortality for transported fish from those fish that migrate through the FCRPS inriver.*
   i. *D* refers to the ratio of smolt-adult survival (measured from below Bonneville Dam as juveniles to Lower Granite Dam as adults) of transported fish relative to that of in-river migrants. Using our earlier notation, the corresponding SARs are

$$SAR_{T,BON \to LGR} = S_{e/o}(1-L_T)S_{T,us} \text{ , and}$$

$$SAR_{I,BON \to LGR} = S_{e/o}(1-L_I)S_{I,us} \text{ .}$$

Therefore, *D* is simply

$$D = \frac{SAR_{T,BON \to LGR}}{SAR_{I,BON \to LGR}} = \frac{(1 - L_T)S_{T,us}}{(1 - L_I)S_{I,us}}$$

Note that we assume the same natural estuary/ocean survival ($S_{e/o}$) for both in-river and transported fish.

ii. *D* is typically below 1.0 for Snake River spring-summer Chinook salmon and steelhead, providing one measure of latent mortality for transported fish, but not an absolute measure--it is only relative to in-river fish. This latent mortality may result from stress experienced on the barge, disruption of timing to the estuary, or increased straying or fallback of adult migrants. While we cannot identify specific mechanisms that lead to *D* < 1.0, we can directly estimate *D*, because it relates to the juvenile survival and SAR for in-river migrants. Estimates of D for wild spring/summer Chinook are presented in the following table:

Migration year	NMFS (Williams et al. 2005)	CSS (Berggren et al. (2005)
1994	0.68	0.36
1995	0.46	0.42
1996	1.08	0.92
1997	0.50	0.40
1998	0.43	0.55
1999	0.64	0.72
2000	0.34	0.32
2001		2.16
2002		0.44
2003		0.69

D is not an absolute measure of the latent mortality of transported fish, because the overall amount of delayed mortality for transported fish is a consequence of both *D* and the level of hydropower-related delayed mortality of in-river migrants.

c. *Sub Hypothesis: Passage of seaward migrating juvenile fish through (inriver) and around (transportation) the FCRPS causes delayed mortality to salmon populations by delaying or accelerating arrival of smolts to the estuary.*

   i. Evidence

   1. Seasonal Trends in SARs: Previous analysis suggests that there may be seasonal trends in transport-inriver ratios (TIR) of SARs and D values for hatchery and wild yearling migrant Chinook. These analyses have suggested that TIR (and D) tends to increase over the migration season (e.g. see Figure C2 in Marmorek et al. (2004). Such a pattern may reveal one mechanism by which hydrosystem experience can affect survival below Bonneville dam, and it can have implications for transportation strategy. Patterns for steelhead are not as pronounced and average TIRs have tended to be above 1 across the migration season.

   Data from PIT-tagged wild spring/summer Chinook were used (Fish Passage Center unpublished data) to investigate the consistency of seasonal trend between years, from migration years 1998-2003. The method used to explore within-season variation was adapted from the method used in the Collaborative Systemwide Monitoring and Evaluation Project (CSMEP) Hydro Group Data Quality Objectives process (Porter et al. 2005) and in the post-Bonneville mortality work group for the NMFS COMPASS modeling process (P. Wilson). The method uses an assumption of binomial sampling error in the SAR estimates to remove measurement error variance from total variance to estimate inter-annual process error (environmental) variance. Instead of using data from each migration year in the aggregate to estimate environmental variance in

SARs and TIRs, here the data from each of three periods within the migration season is treated separately. The resulting distributions can then be used to derive estimates of, for instance, the frequency with which true TIR would be greater than one for each of the time periods. In this analysis, Lower Granite Dam (LGR) is the only transport project investigated (though the exercise could be performed for other projects). Unlike the CSMEP and post-Bonneville hypothesis analyses submitted to the post-Bonnneville group, the in-river fish used are "C1" fish—PIT-tagged fish detected at LGR dam. The "true control" (C0) fish used in previous applications of this method cannot be used to estimate season trends in SAR and TIR; since a C0 smolt is not detected at LGR (or any of the collector projects), a date of LGR passage cannot be accurately assigned to it. Because the C1 group has typically shown lower annual SARs than the "true controls" (Berggren et al. 2005) the seasonal TIRs calculated here likely have some positive bias.

Each migration year, the season was broken into three periods based on detection date at LGR: Before Apri1 26, April 26 to May 10, and after May 10. This resulted in approximately equal total numbers of PIT-tagged fish in each group, over the six year period. Summary information from the resulting TIR distributions is presented in the table below. It appears that TIR (and consequently, D) increases substantially over the season.

Period	T smolts	C1 smolts	Median TIR	Prob TIR > 1
Before 4/26	4059	15380	0.36	15%
4/26 – 5/10	2366	19568	1.29	59%
After 5/10	3022	15348	2.30	91%

Inspecting the distributions of transport and in-river SARs suggests that although transport SAR is modestly higher late in the season than earlier (Fig. 11a), the primary reason for the increasing trend in TIRs is that in-river (C1) SARs decline dramatically in the middle and end of the season

(Fig. 11b). The decline in SAR of in-river (C1) fish as the season progresses is consistent with the hypothesis that the protracted migration and late arrival in the estuary is in part responsible for elevated levels of post-Bonneville mortality as a consequence of the hydrosystem experience.

The seasonal TIRs contain some positive bias because the true controls (C0), which migrate through spill and turbine routes at collector dams, have shown higher SARs than fish bypassed at one or more of the collector dams (Berggren et al. 2005). The SAR distributions for true controls (C0) and smolts detected and returned to the river at LGR dam (C1) using the same method are shown in Figure 12. If in-river survivals are similar for C1 and C0 groups, as generally assumed, the differential SAR is evidence of delayed mortality for bypassed fish (see Budy et al. 2002). It is also possible that the trend in increasing TIRs may not be as pronounced for C0 fish as seen for C1 fish (Figure 11), particularly in years when the spill program is implemented.

A number of mechanisms may explain the temporal patterns of SARs. In-river migrants face migration delays through the FCRPS, which may have different consequences depending on seasonal timing. For example, later in-river migrants may:

- face increased exposure to elevated temperatures, contributing to poorer condition upon estuary arrival
- be further along in the smoltification process and be more vulnerable to migration delay
- miss the optimal window of estuary and early ocean environmental conditions
- face increased predation rates in the lower Columbia River mainstem, estuary and ocean

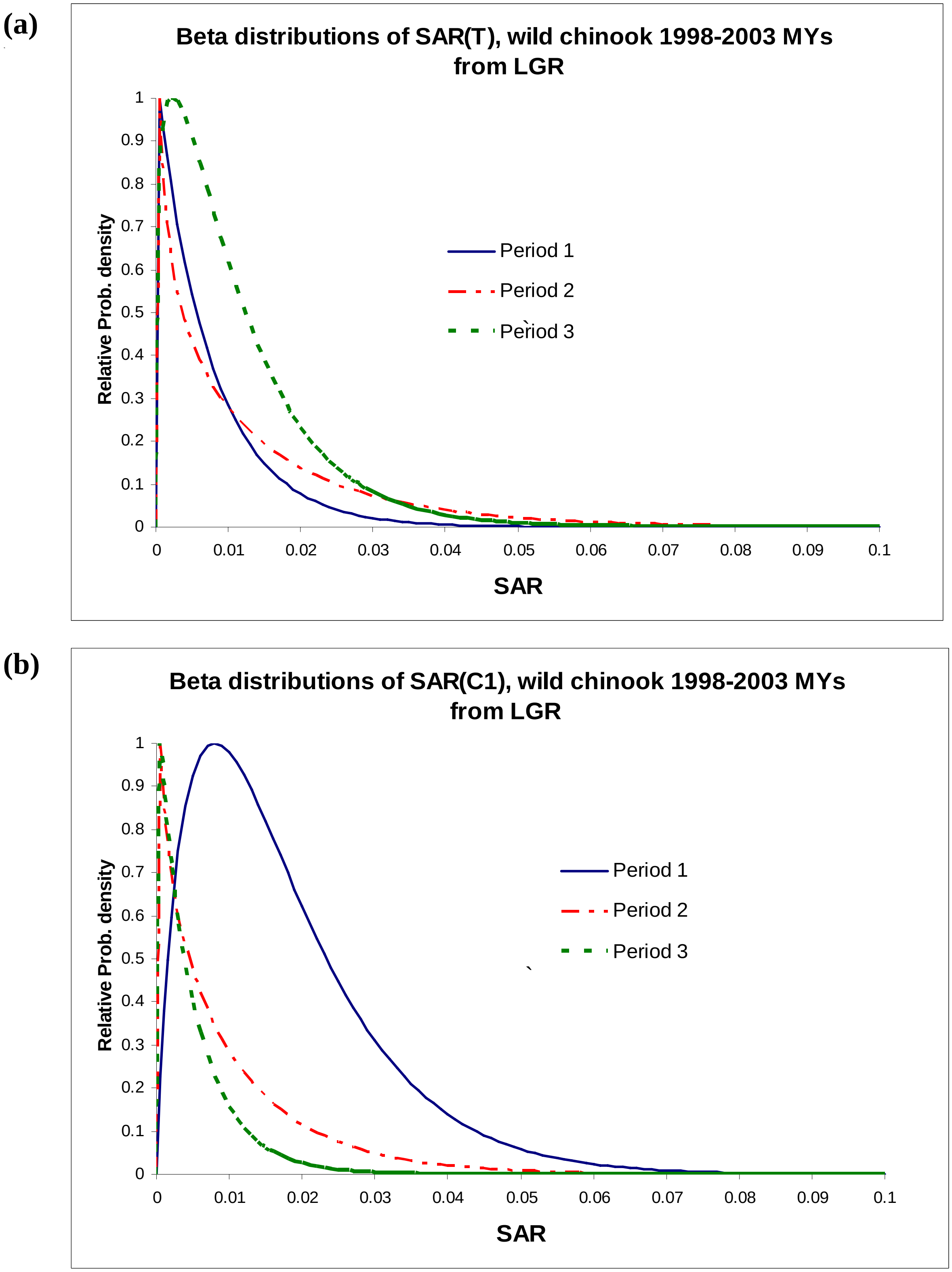

Figure 11. Distributions of SAR for smolts detected at Lower Granite and transported (a) or returned to the river (b), for the three migration periods.

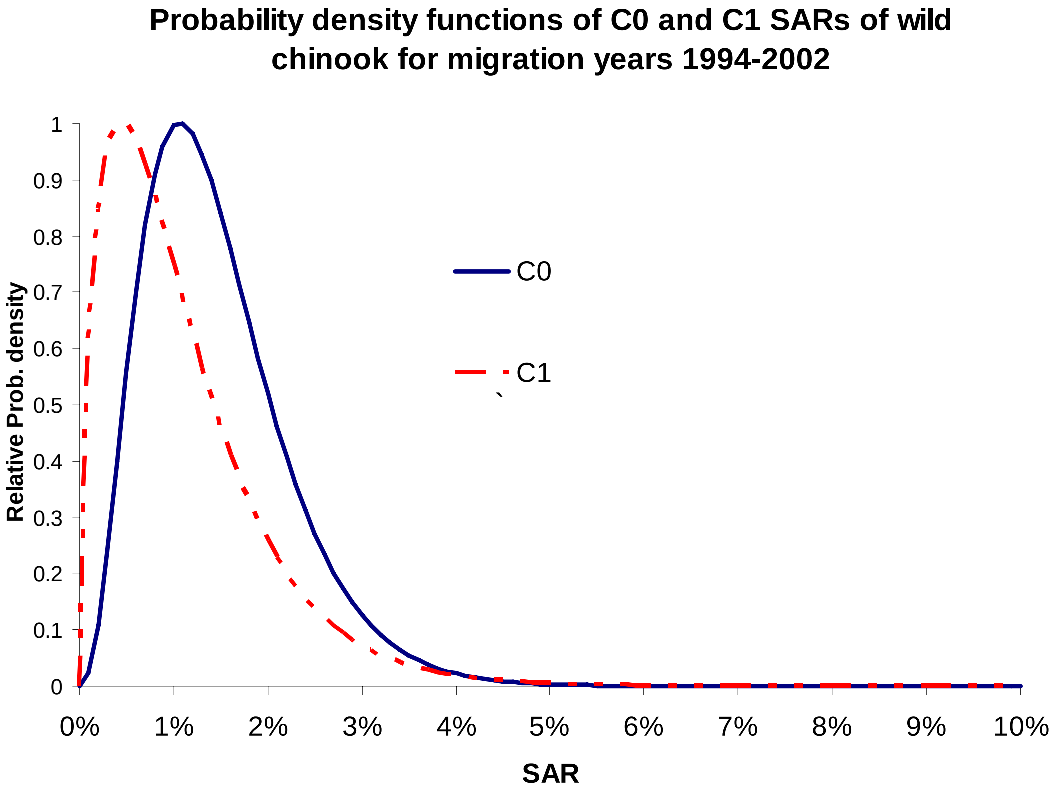

Figure 12. Distributions of SAR for true controls (C0) and smolts detected at Lower Granite and returned to the river (C1), 1994-2002 migration years.

2. SARs by Bonneville Arrival Timing: The numbers of Snake River wild spring/summer Chinook PIT-tagged smolts and returning adults from the CSS study groups T0, C0, and C1 were summarized for smolt arrival timing based on their detection at Bonneville Dam, at John Day Dam or trawl samples below Bonneville Dam (T. Berggren, pers. comm.), 2000-2003 migration years. Bonneville arrival dates for smolts detected only at John Day Dam or in the trawl were corrected for median travel times to or from the Bonneville detector. Numbers of PIT-tagged wild John Day River spring Chinook smolts and adults for the same arrival periods and years were included in the summary. SARs in this case represent smolts from Bonneville dam to adult returns to Bonneville dam.

The arrival timing of John Day wild smolts was primarily late April through May all years (similar to Snake River wild smolt timing at Lower Granite Dam). A combination of delayed migration of in-river smolts and transportation has altered the arrival timing of Snake River migrants to the lower Columbia River estuary. All groups of Snake River wild Chinook consistently experienced lower SARs (Bonneville to Bonneville) than John Day wild Chinook within the same arrival time period and for the season (Fig. 13, 14). In 2000 and 2001, SARs for the earliest transport Snake River groups apparently approached 10% (Fig. 13), but these were based on small sample sizes (n<70) and the pattern did not continue in subsequent years[2].

The disparity between SARs for John Day River and Snake River wild Chinook, when they arrive to the lower Columbia River at the same time, provides additional support for the hypothesis of delayed hydrosystem mortality, and may shed light on likely mechanisms. The Comparative

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[2] No adults returned from the earliest period from 68 transported smolts in 2002; and 1 returned from 661 transported smolts in 2003.

Survival Study analysts plan to more formally investigate the SAR patterns based on arrival timing and other factors in future years.

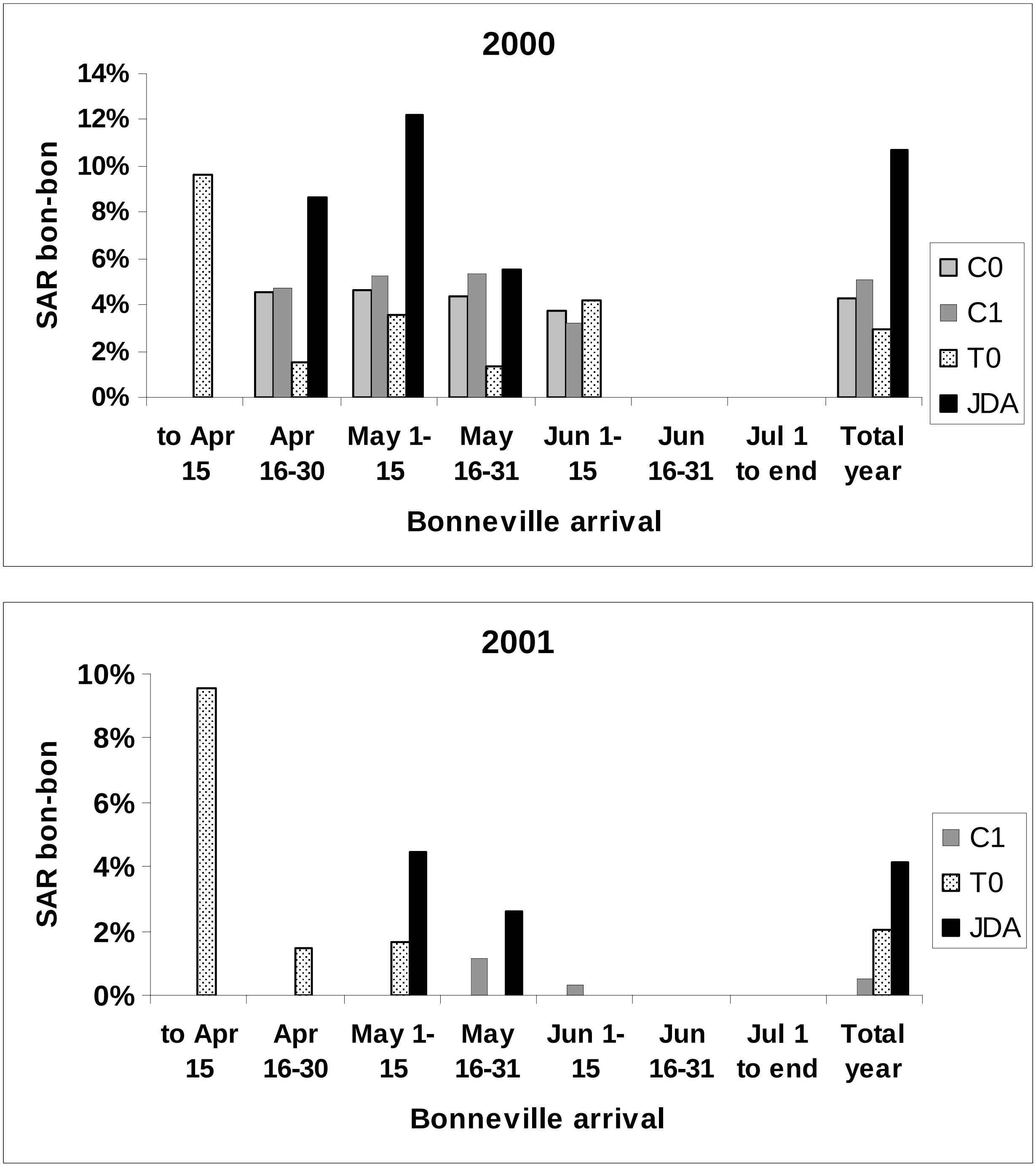
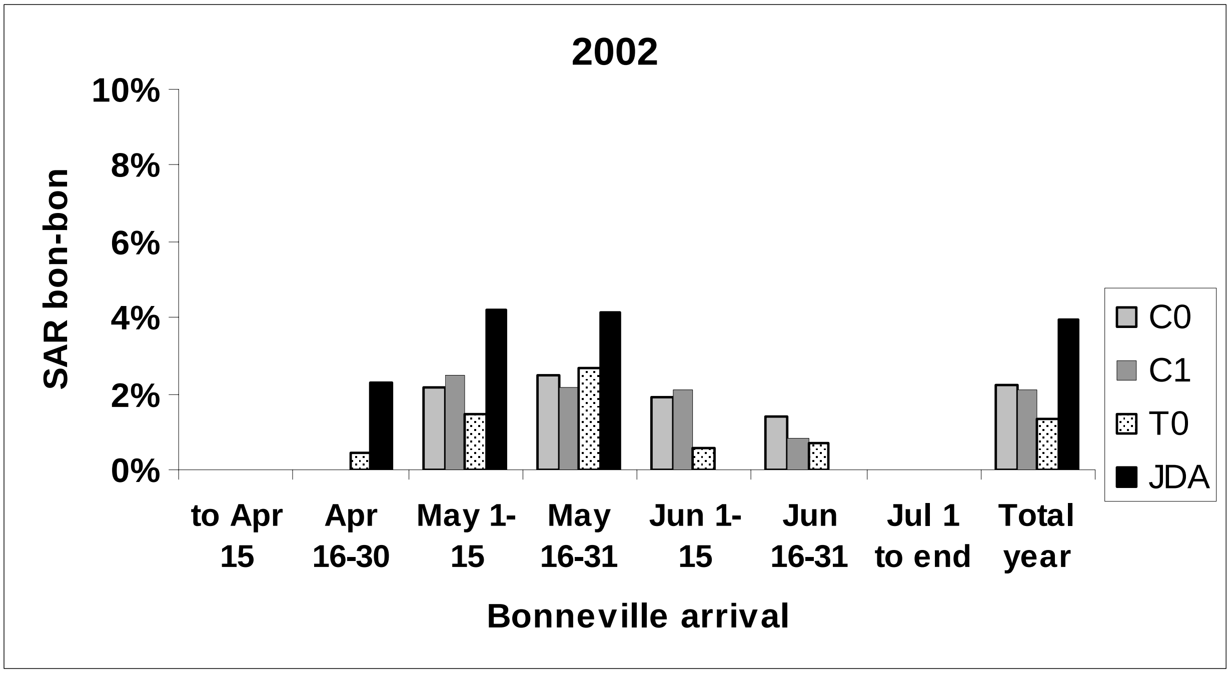


Figure 13. SAR by Bonneville arrival date and group for Snake River wild spring/summer Chinook (T0, C0, and C1) and John Day wild spring Chinook, 2000-2001. SARs calculated for all smolt groups > 50.



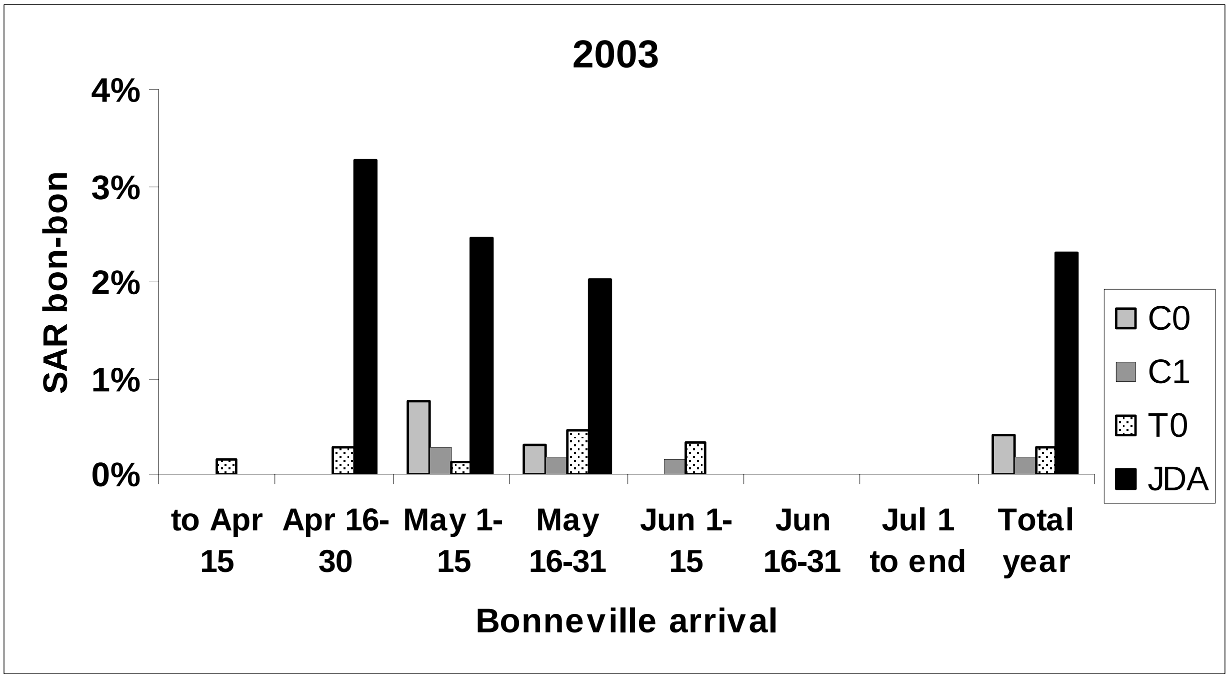


Figure 14. SAR by Bonneville arrival date and group for Snake River wild spring/summer Chinook (T0, C0, and C1) and John Day wild spring Chinook, 2002-2003. SARs calculated for all smolt groups > 50. Adult returns from 2003 complete only through 2-ocean returns.

VI. Summary and Conclusions

Based on our findings from multiple analyses, the hypothesis that a portion of the mortality that occurs in the estuary and ocean life stage is due to cumulative impacts of the FCRPS appears highly plausible. We explicitly described this hypothesis of delayed mortality relative to development and operation of the FCRPS and variants of this main hypothesis. We provided a summary, from the literature, for the mechanisms and the lines of evidence supporting this hypothesis.

We presented multiple analytical approaches addressing this delayed mortality for Snake River spring/summer Chinook. Results from updated and expanded analyses comparing upriver and downriver population performance continued to show that development and operation of the FCRPS was a key factor influencing levels of delayed mortality of Snake River spring/summer Chinook.

We developed new analyses relating survival rates for Snake River spring/summer Chinook to FRCPS and ocean/climate conditions, which did not rely on comparing upriver and downriver population performance. The analysis of Snake River populations alone included ocean/climatic variables, and water travel time relative to spawner-recruit residuals, smolt-to-adult return rates (SARs) and survival during the first year of ocean residence. Water travel time increased as the FCRPS was developed, and populations experienced a wide range of ocean/climatic conditions during the study period. Evaluation of the spawner-recruit residuals, SARs and early ocean survival showed that survival was related to water travel time, providing supporting evidence that there is a significant component of the survival during early ocean residence that is accounted for by delayed mortality, and related to construction and operation of the FCRPS. These analyses compliment the results from the upriver/downriver population performance model.

From this information there appears to be a delayed mortality component to survival during early ocean residence that is related to construction and operation of the FCRPS;

however survival rates are also strongly related to the PDO and upwelling indices (measures of oceanic climatic conditions). The magnitude of delayed hydrosystem mortality may be modified by ocean conditions.

The FCRPS has delayed migration of in-river fish; with later arriving components of the population exhibiting lower SARs. Additional support for delayed mortality associated with passage through the FCRPS is provided by within-season patterns of SARs for in-river migrants, SARs of bypassed vs. true in-river migrants, and the relatively higher SARs of John Day wild Chinook when they experience the same arrival timing at Bonneville Dam as Snake River wild Chinook.

The results of these multiple analyses provide compelling evidence that passage through the FCRPS strongly influences levels of delayed mortality of in-river migrants for these populations.

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