A technical review of the National Marine Fisheries Service Leslie matrix model of Snake River spring and summer chinook populations

*Prepared by*

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Executive Summary

Snake River salmon and steelhead have undergone precipitous declines in the last three decades. Since the completion of the Snake River hydrosystem, coho salmon have become extinct, and in the 1990s the remaining species were listed under the Endangered Species Act (ESA). As required by the ESA, management actions (including operation of the Federal Columbia River Power System) are subject to biological assessments to determine whether they jeopardize the listed populations. The National Marine Fisheries Service (NMFS) judges whether proposed actions pose unacceptable risk to listed salmon and steelhead populations through the Biological Opinion (BiOp) process. To make these assessments, NMFS has developed two analytical approaches, the Plan for Analyzing and Testing Hypotheses (PATH) and the Cumulative Risk Initiative (CRI).

The PATH forum is an inclusive, regional analytical work group developed to provide technical analysis of biological parameters affected by fish passage through the hydrosystem and impacts on other portions of their life cycle. The process began in 1995 and was developed to support the 1999 (delayed until 2000) BiOp. The majority of the analyses for spring/summer chinook (the species of focus in this document) were completed in 1998. NMFS announced the beginning of its CRI in July of 1999. NMFS needed an analytical tool that allowed them to evaluate management options for many salmon and steelhead Evolutionarily Significant Units (ESU) in the greater Northwest region with consideration of the effects of potential improvements in all H’s (habitat, harvest, hydropower, and hatcheries). The CRI used a Dennis-type extinction model to estimate probability of extinction. In addition, they developed an age structured Leslie matrix model to characterize survival over the life cycle and estimate the average annual population growth rate. NMFS is now using results from CRI analyses to support the biological recommendations for the 2000 BiOp and the Draft Lower Snake River Juvenile Salmon Migration Feasibility Report/Environmental Impact Statement (DEIS).

Where comparisons are possible, some of these NMFS CRI conclusions conflict with those based on the PATH analysis. CRI concluded that there was enough potential to improve survival in the egg to smolt stage to avoid short-term extinction. In contrast, PATH analyses indicated that there was not a feasible set of actions that could improve freshwater habitat (egg-to-smolt) enough to provide a significant improvement in survival overall. In addition, PATH predicted that the dam breach scenarios yielded a much larger benefit than observed with CRI matrix model predictions. Based on available analyses to date, decision makers may be faced with conflicting conclusions regarding the role of habitat improvements and the degree of improvement in survival that can be expected under a dam breach scenario. In order to understand why PATH and CRI came to these different conclusions for spring/summer chinook, the States, Tribal, and U.S. Fisheries Agencies (STUFA) PATH participants conducted a technical analysis of the CRI matrix.

The overall goals of this analytical effort were to: (1) investigate and evaluate the structure of the CRI matrix model and the assumptions used in it; (2) compare analytical methods and results of
the CRI matrix using information utilized by PATH, using variations on the CRI matrix model for Snake River spring and summer chinook; and (3) evaluate conclusions indicated by these modifications. We first used a stepwise approach to make modifications to the CRI matrix, changing as little as possible in the basic matrix, in order to make clear how each modification impacts the CRI analyses and conclusions. We next created a version of the CRI matrix model that explicitly incorporated delayed mortality (both for in-river fish [extra mortality] and transported fish [‘D’]) assumptions used for modeling other critical uncertainties (e.g., estuary and ocean survival). We then created a matrix model that could be used to model the alternative management actions described in the DEIS, and finally, a matrix that could evaluate the relative impacts of variation and uncertainty in the matrix parameters.

NMFS CRI analyses are continually being revised and updated. The analyses reviewed here are those discussed primarily in the DEIS (USACE 1999). We realize that further changes may occur to the CRI analyses.

One of the goals of the CRI approach was to develop a simple model that other scientists could duplicate. We were, in fact, able to duplicate, modify, and understand the CRI matrix model. Another goal of the CRI model was to develop a transparent process with all assumptions and methods explicitly stated, allowing others to follow the logic of their approach. Although the model structure was simple, we do not believe the derivation of the model parameters was transparent. For example, survival values through the hydrosystem were based on a reconfiguration of the passage models used in PATH that are not easily reproduced. Also, CRI used literature values of survival for other species over different life stages to represent estuary and early ocean survival of spring/summer chinook in their matrix model.

The use of survival values for different species, over different portions of their life history, and in different geographical locations is puzzling given that CRI has excluded historical information and has criticized PATH for using this information. Also, CRI has criticized PATH for utilizing information from lower Columbia River stocks (stocks that migrate through three or fewer dams and are not transported as opposed to the eight dam migration or transportation that Snake River stocks face). Although these stocks have similar life histories (migrate, share the estuary and ocean, and return at the same time), CRI does not believe these stocks are comparable because they are classified as different ESUs. We believe that using unrelated information rather than information related to spring/summer chinook stocks may be responsible for discrepancies between the CRI configuration of the matrix and empirically based recent and historical data.

To test the CRI method and assumptions, we compared the CRI model estimates of survival rates over different life stages and different time periods to empirical estimates. The CRI matrix estimated smolts-to-adult survival rates (SAR) three times higher than current observed SARs. Because the CRI matrix is calibrated to observed estimates of overall life cycle survival, an overestimated survival rate must be compensated for by underestimating a survival rate in another life stage. The high SAR values produced by the CRI model indicates that egg-to-smolt survival must have been too low. This was verified when CRI estimated that egg-to-smolt

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survival was less than half of the observed egg-to-smolt survival.

We also used the CRI matrix to estimate historic (1957-1967) SAR values from the time period before most of the lower Snake River dams were present. We adjusted for differences in harvest rates, adult passage, and downstream survival rates through the hydrosystem to values used by NMFS for this time period. According to the CRI approach, which ignores extra mortality, during this period when populations were relatively healthy and these stocks migrated through only three to five dams rather than eight dams, SAR values were substantially lower than present SAR values, and also much lower than empirically estimated SAR values over that same time period. Also, for the 1957-1967 period, the CRI model estimated an egg-to-smolt survival rate as much as eight times higher than the recent period (estimated by fitting the model to recent data). This analysis strongly suggests that mortality in some life stage, most probably the stages after juveniles have migrated to below the hydrosystem, is higher now than it was in the 1960s.

Instead of using assumed values from coho and pink salmon for estuary survival, we estimated survival in the estuary using SARs observed for these stocks. We then estimated egg-to-smolt survival using the CRI model with this new estuary survival rate. We found model estimates compared well to recent observed egg-to-smolt survival rate. However, the slightly modified model could still not estimate SAR or egg-to-smolt survival rates consistent with the historic observations of these survival rates over the 1957-1967 time periods.

The information that we believe was crucial to explaining differences not only between historical and present observations but also differences in results between PATH and CRI, was delayed mortality, or mortality that occurs in one life stage due to an experience in an earlier life stage. We incorporated this information into our matrix model expressed, as in PATH, as the delayed mortality of transported fish relative to non-transported fish (incorporated in ‘D’), and delayed mortality of non-transported fish below Bonneville Dam (extra mortality).

We also incorporated another important modification to the CRI approach by directly addressing the impact of alternative management actions. The CRI evaluated potential management actions by asking what would be the benefit to the population by decreasing mortality 10% in each life stage. Because these “numerical experiments” do not necessarily correspond to biologically and logistically feasible actions aimed at improving the health of these stocks, we do no believe this approach is very informative. In fact, this approach will always demonstrate that life stages with the lowest assumed survival will always provide the largest benefit to the population. Because evolutionary constraints to the life history of this species are ignored, and the model does not compartmentalize the life stages over similar time scales, the results of these numerical experiments are simply a mathematical artifact of the default model structure. Therefore, we explicitly modeled feasible alternative management actions. The management actions were also similar to some of the management actions modeled in PATH and allowed for a general comparison between the results of the two analytical approaches. The management actions we modeled were as follows:
1) **Baseline**: “Average”, status quo conditions from 1980 to present (similar to the A1 scenario in PATH).

2) **Maximize transport**: Maximizing the number of smolts transported at each collector project (similar to the A2 scenario in PATH).

3) **Dam breach/delayed mortality reduced**: Four lower Snake River dams are breached and delayed mortality is assumed to be linked to the hydrosystem and is thus reduced (similar to the A3/Hydro scenario in PATH).

4) **Dam breach/delayed mortality remains**: Four lower Snake River dams are breached, but delayed mortality of non-transported fish is assumed to unrelated to the hydrosystem and remains (similar to the A3/BKD scenario in PATH).

5) **Everything but dam breach**: All feasible management actions except dam breach. Maximize transport plus zero harvest, improvements in habitat, and reduction in estuary smolt mortality via Caspian tern relocation.

6) **Everything including dam breach**: All feasible management actions including dam breach. Includes zero harvest, improvements in habitat, and reduction in smolt mortality via Caspian tern relocation, and dam breach (with delayed mortality reduced).

We used our modified matrix model (including estimates of delayed mortality for transported and non-transported fish) to evaluate the benefit of management actions 1-4 on the average annual population growth rate and the improvement in SARs. We evaluated these actions with both pessimistic and optimistic passage/transportation scenarios (the FLUSH and CRiSP/NMFS passage models) to incorporate uncertainty in how smolt survival rates are characterized through the hydrosystem. We assumed, as did CRI, that the parameter values do not exhibit environmental variability or measurement error. We refer to this model to as the STUFA deterministic matrix.

The STUFA deterministic model indicated that little improvement in population growth rates or changes in SAR over current conditions (**Baseline**) would be expected under the **Maximize transport** management scenario. The greatest improvement occurred under three of the four breach scenarios where average annual population growth rates were positive and increased by approximately 30% and SARs increase 205 to 235%. Improvements were not as great under dam breach if transport delayed mortality was assumed low (‘D’ assumed high) and extra mortality of non-transported fish remained after dam breach (**Dam breach/delayed mortality remains** using CRiSP/NMFS passage/transport model); however, improvements were still higher than **Maximize transport** scenarios.

A major shortcoming of the STUFA deterministic matrix and the CRI matrix is the assumption that survival rates and other parameters are certain and do not vary. In general, demographic models that incorporate variability around model parameters tend to produce more pessimistic results about population growth rates than models that assume parameters are fixed. Therefore, we created another matrix that incorporated a distribution of potential values for each model parameter. This model is referred to as the STUFA stochastic matrix. In addition to the...
management scenarios evaluated with the STUFA deterministic model, we also explored the impacts of management actions 5 and 6.

As expected, the median annual population growth rates under all scenarios evaluated by the STUFA stochastic matrix were lower than the population growth rates determined from the STUFA deterministic and CRI matrix for a given scenario. Again, the Maximize transport scenario did not provide much benefit over Baseline, with the probability of a positive population growth rate of just 25%. The Everything but dam breach scenario yielded little improvement over the Maximize transport scenario alone. The Dam breach had the greatest benefit to the stocks with three of the four scenarios having a 65 to 75% probability of a positive population growth rate. Only under the Dam breach/delayed mortality remains using CRiSP/NMFS passage model did breaching have less of a benefit, though it was still greater than the Maximize transport scenarios. Finally, the greatest improvement occurred when Everything including dam breach was implemented; however, the population growth rates only increased approximately 4% over the dam breach alone scenario.

Although CRI did not explicitly model management actions, results from their numerical experiments suggest that the management action that would likely provide the greatest benefit to these stocks is to implement all proposed management actions including dam breaching. Our analyses led us to the same conclusion; however, in our analysis, the improvements over dam breaching alone were not as great. Both the CRI and our model also suggest that breaching the dams provided a large benefit if the delayed mortality was reduced when the dams were removed. We also can agree with the CRI conclusion that improvements in transportation and the hydrosystem short of breaching will not provide much benefit to these stocks. Finally, our modeling results agree with CRI that reduction in harvest will not provide much benefit to spring/summer chinook because harvest is already minimal.

From our analysis we cannot concur with the CRI analyses that greatest benefits to these stocks would occur through improvements to spawning/rearing habitat, and estuary/early ocean habitat (independent of influences from juvenile hydrosystem migration). The benefits from spawning and rearing habitat that CRI suggests would come from improvements are purely hypothetical, unless fish are taken into a hatchery for spawning and the eggs are kept till release as smolts. We came to this conclusion by restricting the amount of these improvements in spawning and rearing habitat survival by limiting stock productivity to the highest productivity estimate observed from all the stocks. We also restricted the benefit of improvements in the estuary (other than delayed mortality) to the improvement attainable from reduction in Caspian tern predation, which is the only potentially feasible management action proposed. Differences in the CRI and model results highlight the importance of incorporating feasibility into modeled management scenarios. Without this crucial step we believe the numerical experiments are misleading because this method simply reflects what life stage is assumed to have the lowest survival rate rather than where in the life cycle mortality is actually limiting these stocks.

We also differ from CRI in our conclusion of the impact that dam breaching alone will have on
the growth rate of Snake River spring/summer chinook. CRI has determined that dam breaching alone will have a large benefit to these populations only if delayed mortality caused by the dams is substantial. Since they ignore evidence that indicates that delayed mortality is substantial they do not explicitly include this source of mortality in their model. However, both the PATH analyses and the historical matrix analysis presented here (which did not use PATH results or downstream stock comparisons) agree that extra mortality is currently substantial. We believe NMFS needs to address the magnitude and causes of extra mortality rather than simply state what they believe is reasonable.

By incorporating the delayed mortality component into our matrix we found that the relative rank of expected benefits from management actions evaluated in PATH and in this analysis were consistent. Dam breaching provided a much greater benefit to Snake River spring/summer chinook under a wide range of uncertainties than did the maximized transportation options. Also, feasible improvements in egg-to-smolt survival or a reduction of predators in the estuary did not provide a large benefit to these stocks. The significance of the consistency of PATH results and results of our analysis is that the conflicting conclusions of PATH and CRI are not a result of the different models employed but rather due to the underlying assumptions that go into the models.

In both the PATH and the CRI analyses, the efficacy of dam breaching to recover Snake River spring/summer chinook is largely dependent on whether or not, and the degree to which, delayed mortality is related to hydrosystem experience. We believe there are empirical data and several lines of evidence that strongly suggest that delayed mortality is a result of a smolt’s experience through the hydrosystem. Because CRI does not discuss the magnitude and the possible mechanisms for delayed mortality, determining the importance of this critical information is left to the decision makers. We believe that this issue is best resolved, to the extent possible, by the scientists who are providing the biological information to aid decision makers in their task. We suggest conducting a formal weight of evidence for and against the factors hypothesized to be responsible for delayed mortality. This would provide the best biological advice on the ability of alternative management actions to recover Snake River salmon.

We are aware that CRI has made several changes to their approach based on the input from external comments. Some of the concerns we have highlighted in this report already may have been partially addressed. CRI participants have also stated that the CRI approach is still young and constantly evolving. Although we have concerns about inconsistencies and questionable assumptions in applying these models to these stocks, there are several merits to the CRI approach. However, this analysis suggests that the current configuration of the CRI matrix cannot accurately estimate current and historical observations of survival across different life stages. Also, no hypothesis in the CRI matrix can resolve differences between recent and historical observations. We believe this is a result of not incorporating the delayed mortality component into the CRI matrix model. When this component is included in the CRI matrix, and management actions are explicitly modeled, the matrix produces results similar to the PATH analyses. Because of these concerns we believe it is premature to base the biological assessment of a BiOp or EIS on the CRI analyses.

A technical review of the National Marine Fisheries Service Leslie matrix model of Snake River spring and summer chinook population.
1. Introduction

1.1 Background

In response to sustained declines in Columbia Basin salmon and steelhead returns in the 1970’s, federal, state, and tribal managers implemented or planned numerous large-scale conservation initiatives that focused on: (1) reducing mortality to juvenile and adult fish passing by dams and through reservoirs; (2) reducing mortality of adult fish by restricting harvest; (3) augmenting wild populations through artificial propagation; and (4) stabilizing or improving tributary spawning and rearing habitats. Yet despite sincere efforts to stabilize and recover Snake River salmon and steelhead populations, the number of spawners returning to the basin continued to decline precipitously through the 1980s and into the 1990s. As a result, all species of Snake River salmon and steelhead were listed under the federal Endangered Species Act (ESA) in the 1990s. As required by the ESA, fisheries, hatchery programs, and land use practices are subject to biological assessments of the potential jeopardy they pose to the survival and recovery of listed populations. A biological assessment is also required for proposed operations of the hydropower system. The National Marine Fisheries Service (NMFS) then passed judgment on whether proposed actions pose unacceptable risk to listed salmon and steelhead populations through the Biological Opinion (BiOp) process.

Current management of the hydropower system is based on a Biological Opinion for the 1994 to 1998 operation of the Federal Columbia River Power System and its supplement for listed steelhead (1995 BiOp). The 1995 BiOp contains specific measures for operating and improving the configuration of the hydropower system in the near term. However, NMFS deferred decisions about the long-term future operation and configuration of the hydropower system until late 1999 (deferred to 2000), when it anticipated completion of a formal and deliberate assessment of management actions required to meet ESA standards. To make these assessments, NMFS has developed two analytical approaches, the Plan for Analyzing and Testing Hypotheses (PATH) and the Cumulative Risk Initiative (CRI).

1.2 PATH Analyses

The PATH process was developed through a collaborative process and adopted by NMFS in 1995 to support the hydropower system biological opinion concerning the listed salmon, and most PATH analyses were completed in 1998. The PATH forum is an inclusive, regional analytical work group\(^1\) developed to provide technical analysis of biological parameters affected

\(^1\) PATH participation is broadly represented by as many as 25 scientists from state, tribal, federal, and private institutions including NMFS, U.S. Fish and Wildlife Service, U.S. Geological Survey, U.S. Army Corps of Engineers, Bonneville Power Administration, Columbia River Inter-Tribal Fisheries Commission, Idaho Department of Fish and Game, Washington Department of Fish and Wildlife, Oregon Department of Fish and Wildlife, Columbia Basin Fish and Wildlife Authority, University of Washington, and other private firms.

A technical review of the National Marine Fisheries Service Leslie matrix model of Snake River spring and summer chinook population.
by fish passage through the hydrosystem and impacts on other portions of their life cycle. The basic structure of PATH modeling and analysis is a life cycle model based on historical estimates of mortality at different life stages and spawner and recruit counts.

PATH efforts were divided into retrospective analyses, to generate parameter values and basic model structure based on historical information, and prospective modeling, where future stock performance was predicted under different proposed management actions (e.g., dam breaching). Retrospective models used historical data on spawner and recruits, dam passage mortality, harvest, and climatic or environmental variation to account for the overall pattern of survival. By first performing retrospective analyses, PATH ensured that the current status of the listed stocks could be put in context, by helping to narrow down in which areas and life stages survival rates appeared to have declined from the more healthy, pre-listing years, thereby suggesting where improvements might be made. Once the impacts of trends in natural and human-caused factors on the listed stocks were assayed, it allowed PATH to focus on critical uncertainties in predicting the fate of these stocks in the future, given the interaction of proposed management actions with natural variability in environmental conditions.

For prospective analyses, different hypotheses about the likely effect of the management actions to mortality in each life stage were applied. PATH used a biological decision analysis framework to incorporate the different hypotheses about key uncertainties and environmental variability when predicting the response of alternative management actions. The impact of management actions was assessed over a large range of assumptions and variability resulting in a range of potential responses relative to survival or recovery thresholds and to alternative management actions. Thus, management actions can be ranked not only by the mean response, but across the range of uncertainties. The range of responses provides a measure of risk.

Prospective PATH analyses for spring/summer and fall chinook salmon indicated that the “dam breach” actions had higher probabilities of achieving the three survival and recovery elements of the jeopardy standard than the “transportation” actions. Dam breach actions met the standard over a wide range of assumptions (i.e., these actions are robust to remaining uncertainties). In fact, the “dam breach” actions met the 100-year survival and the 48-year recovery elements of the jeopardy standard for spring/summer chinook even under the most pessimistic set of assumptions. The dam breach actions were also more robust than the “transportation” actions (i.e., model projections had relatively little variability over the full range of assumptions).

1.3 NMFS CRI Analyses

NMFS announced the beginning of its Cumulative Risk Initiative (CRI) in July of 1999. NMFS needed an analytical tool that allowed them to evaluate management options for many salmon and steelhead ESUs in the greater Northwest region with consideration of the effects of potential improvements in all H’s (habitat, harvest, hydropower, and hatcheries). Many workshops have been held, and several documents describing CRI modeling and the results from those modeling
efforts have been issued. In addition, a website (http://research.nwfsc.noaa.gov/cri/) has been set up containing working versions of the models used in the CRI analysis. NMFS CRI analyses are continually being revised and updated, so it is important to note that this paper addresses NMFS CRI analyses discussed primarily in the Draft Lower Snake River Juvenile Salmon Migration Feasibility Report/Environmental Impact Statement (DEIS; USACE 1999).

For CRI analyses, current conditions under status quo are first summarized in two ways: through Dennis-type extinction models that assess the urgency of the situation, and through Leslie matrix life-tables that summarize stage-specific demography and consequent average potential for population growth. Second, to the extent that data used by CRI allow, numerical sensitivity experiments were conducted to see what “hypothetical” changes in life-stage survival estimates elicit the greatest improvement in annual population growth. This mathematical exercise represents “what if experiments”. For example, “What if we could increase downstream survival of salmon? How much would that increase annual rates of population growth?” The point of these experiments was to direct attention towards life stages that provide the greatest opportunities for reversing population declines, based on NMFS's estimation of how mortality is distributed across the life cycle. NMFS does not model management scenarios in terms of expected improvements in survival and does not attempt to gauge the feasibility of most management actions. This paper provides a critical analysis of the NMFS matrix model used for numerical sensitivity analyses, but does not consider the Dennis-type extinction models used to determine the improvement that is necessary.

Mortality is distributed across several life stages in the NMFS matrix model used for their numerical sensitivity analyses: egg-to-smolt survival ($S_1$), downstream survival and survival through the estuary and early ocean ($S_2$), survival in the ocean to age-3, age-4, and age-5 ($S_3$, $S_4$, and $S_5$, respectively; Figure 1.1), and upstream survival through freshwater to spawn ($1-\mu$). To parameterize the NMFS matrix model, NMFS first assigns survival values to all life stages except $S_1$ (egg-to-smolt), then, using the spawner and recruitment data, $S_1$ is solved for as a residual. In other words, after mortality has been assigned to the different life stages (except $S_1$), and given the overall mortality observed in the spawner and recruit data, the remaining portion is assigned to the egg-to-smolt stage. Using this approach, NMFS estimated $S_1$ using passage models for downstream survival, ocean survival of coho salmon for estuary and early ocean survival, sockeye salmon data for later ocean survival, and estimates of harvest, upstream survival, age, and fecundity from PATH data for Snake River spring/summer chinook adults.

NMFS CRI analyses indicated that the risk of extinction for Snake River spring/summer chinook stocks is very high, based on Dennis-type model predictions. Numerical sensitivity analyses performed using the NMFS matrix model indicated that improvements in transportation and passage survival will not prevent quasi-extinction. According to their analysis, the largest potential benefits would result from improving spawning and rearing habitat (i.e. improving egg-to-smolt survival in the freshwater stage). NMFS concluded that dam breaching alone will not likely prevent quasi-extinction, and that improvements in all H’s (including dam breach) will have the best chance of avoiding quasi-extinction.

A technical review of the National Marine Fisheries Service Leslie matrix model of Snake River spring and summer chinook population.
1.4 The problem

To the degree that direct comparisons are possible, some of these NMFS CRI conclusions conflict with those based on the PATH analysis. PATH analysis did not indicate that improvements in egg-to-smolt survival, expressed through feasible improvements to habitat, provided a significant improvement in survival overall. In addition, PATH predictions under the dam breach scenarios yielded a much larger increase in survival than that observed with NMFS matrix model predictions. Based on available analyses to date, decision makers could potentially be faced with conflicting conclusions regarding the role of habitat improvements and the degree of improvement in survival that can be expected under a dam breach scenario. Thus despite the numerous workshops that NMFS has held and the incorporation of many suggestions into their most recent analyses, many critical scientific issues have not been resolved. In addition, after reviewing the NMFS matrix model and related CRI analyses, it became clear that many of the parameters and assumptions were not as transparent as the authors claimed. In order to understand the behavior of the CRI model, particularly for spring/summer chinook, we have completed a technical analysis, which investigated the influence of underlying assumptions on the model results.

1.5 Goals and approach

The overall goals of this analytical effort were to: (1) investigate and evaluate the structure of the Leslie matrix model developed by NMFS and the parameter values used in it; (2) compare analytical methods and results of the NMFS Leslie matrix with PATH assumptions, using variations on the NMFS Leslie matrix model for Snake River spring and summer chinook; and (3) evaluate conclusions indicated by these modifications. We first used a stepwise approach to make modifications to the NMFS Leslie matrix, changing as little as possible in the basic matrix, in order to make clear how each modification impacts CRI analyses and conclusions. We next created a version of the NMFS matrix model that explicitly incorporated delayed mortality (both for in-river fish [extra mortality] and transported fish [‘D’]) assumptions used for modeling other critical uncertainties (e.g., estuary and ocean survival). Finally, we created a stochastic version that can be used to model the alternatives described in the DEIS, and evaluate the relative impacts of variation and uncertainty in the matrix parameters.

This approach has many limitations, due primarily to the limitations of the Leslie matrix model structure. Perhaps most important is the fact that CRI analyses focus almost exclusively on lambda ($\lambda$, average annual population growth rate) when some fairly strict requirements are met. Burgman et al. (1993) indicate that because most threatened and endangered species populations are in accelerating declines, often due to habitat degradation, $\lambda$ is a questionable output variable. Nonetheless, for comparative purposes, the analyses in this paper also rely on the same output variable ($\lambda$). Although this approach required us to adopt some problematic assumptions used in the NMFS matrix model, it allowed us to investigate and compare the CRI approach and results, to those of PATH.
In addition, we are concerned that the CRI approach for Snake River spring/summer chinook assumes values of survival and other life history attributes for some life stages for which estimates are relatively weak, while allowing the model to fit values in cells for which relatively robust, independent estimates are available. At the outset it should be noted that there is no “right” way to parameterize a Leslie matrix because data for salmon stocks are not collected in ways compatible with the cells of the matrix, nor are data available for all life stages. However, it is generally safest to use the best available data where possible and make estimates when necessary. We are concerned that CRI did not adequately follow this guideline and instead we present some alternative approaches which we believe make better use of available data for model calibration and validation.
Figure 1.1. Allocation of survival rates to the spring/summer chinook life cycle. Survival estimates are those used in the NMFS CRI Leslie matrix model.
2. Step-by-step modifications to the NMFS Leslie matrix model

In the NMFS CRI matrix model, the average annual growth rate of the population ($\lambda$) is calculated for the Baseline scenario using given spawner and recruitment data, the generation time, and $S_1$ (egg-to-smolt survival). Hypothetical improvements in survival at certain life stages are modeled to see which life stage shows the greatest potential for increasing $\lambda$. Increases in $\lambda$ that result from the hypothetical changes to life stage survival values are then compared to the percentage of increase in population growth, as estimated in the NMFS Dennis model, necessary to minimize extinction. It is important to note that $\lambda$’s estimated using the Dennis-type model may not be directly comparable to $\lambda$’s estimated from the NMFS matrix model.

In the CRI calculations, $\lambda$ is not actually calculated using the Leslie matrices, but instead by using estimates of recruits per spawner (R/S), average generation length ($T$), and first year survival ($S_1$), following the method of (Ratner et al. 1997). The approach described by Ratner et al. essentially fits the R/S record to a Ricker equation, in order to estimate the average finite rate of increase per generation at low population density, $e^a$, where $a = \text{average} \left[ \ln(R/S) \right]$. In the CRI spreadsheet models, mortality estimates (or survival rates) are then supplied for all life stages and variables, except $S_1$. Following Ratner's approach, all the parameters are defined except $S_1$, and the Ricker assumption and Euler equation are used to simultaneously solve for $\lambda$, $T$, and $S_1$. Once the matrix parameters have been assigned, mortality not allocated to one life stage must be allocated to some other stage(s) in order to be consistent with the R/S estimates. Therefore, if survival rates for other stages are inaccurate, any remaining mortality, by default, ends up in $S_1$.

The significance of this approach is that all the variables in the Leslie matrix are assumed known, except for $S_1$. Thus, different assumptions of age-specific survival rates will also influence $S_1$ (or whichever survival variables the user chooses to absorb the residual mortality). We evaluated the appropriateness of the survival rates, fecundity rates, sex ratios, and age structuring used by CRI and how alternative partitioning of survival rates to different stages, using information utilized by PATH and the U.S. Army Corps of Engineers (USACE), would affect CRI results and conclusions.

Although the latest CRI spreadsheet models available at the start of this analysis ("12-13-99matrix.xls" found at internet website http://research.nwfsc.noaa.gov/cri/xlsfiles/) use only 1980-1990 brood year data, we used 1980-1993 brood year data for all the analyses in this section. Earlier CRI models used the 1980-1993 brood year data, and we expected that NMFS would soon update their models to make use of the full range of data available. Unless otherwise noted, all the settings for each of these analyses were the same used by CRI (Table 2.1).

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2 The NMFS CRI recently submitted a new spreadsheet model (3-20-00matrix.xls). The analyses reviewed here are those discussed primarily in the DEIS (USACE 1999).

A technical review of the National Marine Fisheries Service Leslie matrix model of Snake River spring and summer chinook population.
Table 2.1. CRI settings adjusted to include all brood years 1980-1993.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Source (NMFS 1999b)</th>
<th>Marsh</th>
<th>Johnson</th>
<th>Imnaha</th>
<th>Bear</th>
<th>Poverty</th>
<th>Sulphur</th>
<th>Minam</th>
</tr>
</thead>
<tbody>
<tr>
<td>$S_1$</td>
<td>Calculated as residual</td>
<td>0.0135</td>
<td>0.036</td>
<td>0.0163</td>
<td>0.0168</td>
<td>0.0314</td>
<td>0.0209</td>
<td>0.0149</td>
</tr>
<tr>
<td>$p_t$ = Fraction barged</td>
<td>None provided</td>
<td>0.7745</td>
<td>0.7745</td>
<td>0.7745</td>
<td>0.7745</td>
<td>0.7745</td>
<td>0.7745</td>
<td>0.7745</td>
</tr>
<tr>
<td>$S_b$ = Juvenile survival, barged fish</td>
<td>PATH</td>
<td>0.98</td>
<td>0.98</td>
<td>0.98</td>
<td>0.98</td>
<td>0.98</td>
<td>0.98</td>
<td>0.98</td>
</tr>
<tr>
<td>$S_d$ = Juvenile survival, non-barged fish</td>
<td>PATH</td>
<td>0.3225</td>
<td>0.3225</td>
<td>0.3225</td>
<td>0.3225</td>
<td>0.3225</td>
<td>0.3225</td>
<td>0.3225</td>
</tr>
<tr>
<td>$S_e$</td>
<td>2% to 10% for Oregon coastal coho (Nickelson 1986, Pearcy 1992)</td>
<td>0.07</td>
<td>0.07</td>
<td>0.07</td>
<td>0.07</td>
<td>0.07</td>
<td>0.07</td>
<td>0.07</td>
</tr>
<tr>
<td>$S_2$</td>
<td>Calculated ($S_2 = ((1-p_t)<em>S_d + p_t</em>S_b) * S_e$)</td>
<td>0.058</td>
<td>0.058</td>
<td>0.058</td>
<td>0.058</td>
<td>0.058</td>
<td>0.058</td>
<td>0.058</td>
</tr>
<tr>
<td>$S_3$, $S_4$, $S_5$</td>
<td>Ratner et al. 1997 (citing Ricker 1976)</td>
<td>0.8</td>
<td>0.8</td>
<td>0.8</td>
<td>0.8</td>
<td>0.8</td>
<td>0.8</td>
<td>0.8</td>
</tr>
<tr>
<td>Fecundity</td>
<td>Myers et al. 1998</td>
<td>5607</td>
<td>4100</td>
<td>4927</td>
<td>5607</td>
<td>4100</td>
<td>5607</td>
<td>4086</td>
</tr>
<tr>
<td>Fraction female by age, used in “propensity to breed” calculations</td>
<td>Subbasin planning estimates</td>
<td>0, 0.49, 0.67</td>
<td>0.11, 0.28, 0.58</td>
<td>0.11, 0.28, 0.58</td>
<td>0, 0.49, 0.67</td>
<td>0.11, 0.28, 0.58</td>
<td>0, 0.49, 0.67</td>
<td>0.11, 0.28, 0.58</td>
</tr>
<tr>
<td>Fraction female, Leslie matrix</td>
<td>Arbitrary</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>$P_s$ = Pre-spawning survival</td>
<td>Not given, but consistent with PATH run reconstructions 1980-1990 brood years (Beamesderfer et al. 1997)</td>
<td>0.9</td>
<td>0.9</td>
<td>0.9</td>
<td>0.9</td>
<td>0.9</td>
<td>0.9</td>
<td>0.9</td>
</tr>
<tr>
<td>$\mu$ = total adult passage mortality</td>
<td>Calculated from $P_s$, sub-basin harvest rates, conversion rates, and mainstem harvest rate for brood years 1980-1990 (Beamesderfer et al. 1997)</td>
<td>0.496</td>
<td>0.420</td>
<td>0.458</td>
<td>0.496</td>
<td>0.420</td>
<td>0.496</td>
<td>0.496</td>
</tr>
<tr>
<td>$\lambda$ = average annual population growth rate</td>
<td>$12\text{-}13\text{-}99\text{matrix.xls}$ spreadsheet (CRI 1999)</td>
<td>0.898</td>
<td>1.017</td>
<td>0.926</td>
<td>0.939</td>
<td>1.033</td>
<td>0.983</td>
<td>0.861</td>
</tr>
</tbody>
</table>
With the exception of $S_f$, and the $S_d$ and $S_b$ components of $S_2$, all other CRI survival estimates were based on literature values. Because it was not clear from the CRI documentation how these survival estimates were determined, we tried to reconstruct the same survival estimates using the same references. These literature values are discussed in Appendix A.

### 2.1 Effect of SAR on $S_e$

Using the parameter definitions from the CRI matrix, smolt-to-adult return (SAR) values can be estimated and compared to recent published estimates of SARs. SAR values (estimated from the number of Lower Granite Dam smolts to the number of adults returning to the Columbia River mouth, adjusting for harvest and adult conversion rates) have been less than 1% since the early 1980s (NMFS 1999a). We also estimated SAR for run years 1980-1997, which produced a geometric mean value of 0.0096, across a range of assumptions about hatchery influence and fish guidance efficiencies (FGEs; see Appendix B).

![Figure 2.1. Probability tree used to calculate SARs for the Marsh Creek population.](image)

In the CRI, the SARs that can be calculated from the Leslie matrices (Lower Granite Dam smolt-to-river-mouth adult) ranged from 0.031 to 0.033. The CRI matrices assumed SARs that are more than three times as high as recent estimates.

The assumption of $S_e = 0.07$ for chinook may be problematic (see Appendix A). Therefore, we estimated $S_e$ based on our best estimate of SAR. Setting SAR = 0.0096, but otherwise using all the CRI default settings, we solved for $S_e$. SAR calculations were carried out using a probability tree as in Figure 2.1.

The probability tree can be expressed algebraically as follows:

$$A \text{ technical review of the National Marine Fisheries Service Leslie matrix model of Snake River spring and summer chinook population.}$$
\[ F_{s3} = S_2 * S_3 * b_3 \]
\[ F_{s4} = S_2 * S_3 * (1-b_3) * b_4 * S_4 \]
\[ F_{s5} = S_2 * S_3 * (1-b_3) * (1-b_4) * S_4 * S_5 \]
\[ SAR = F_{s3} + F_{s4} + F_{s5} \]

Where:

- \( b_i \) = maturation rate (“propensity to breed” in CRI terms) for age \( i \) fish
- \( F_{s3} \) = Fraction of smolts that will survive and return to the Columbia River mouth as 3-year olds
- \( F_{s4} \) = Fraction of smolts that will survive and return to the Columbia River mouth as 4-year olds
- \( F_{s5} \) = Fraction of smolts that will survive and return to the Columbia River mouth as 5-year olds

The survival probabilities shown in the probability tree (e.g., \( S_2, S_3, S_4, S_5 \)) are the values used in the CRI spreadsheet models, and any one of them can be solved for, using Excel’s Solver. In this case, the probability tree and Excel Solver were used to calculate what \( S_e \) would have to be in order to make SAR add up to 0.0096. This resulted in a \( S_e \) that was less than half of CRI’s value of 0.07 (average 0.024, range 0.023 to 0.026).

### 2.2 Effect of SAR and \( S_e \) on \( S_1 \)

The method the CRI uses for finding \( \lambda \) and \( S_1 \) forces mortality not allocated to one stage to be allocated to another. We conducted exercises to see how mortality rates would be reallocated from one stage to another, under different assumptions. CRI calculated \( S_1 \) (using the Euler equation) assuming that all other survival rates, maturation rates, fecundity rates, and sex ratios are known. Because \( \lambda \) is calculated using the R/S record and solving simultaneously for average generation length and \( S_1 \), mortality rates not accounted for in \( S_2, S_3, S_4, \) and \( S_5 \) are lumped into \( S_1 \). PATH retrospective analyses provided estimates for the 1980s of smolts-per-spawner and SARs for aggregate wild Snake River spring/summer chinook (NMFS 1999a, p. A4-7 and A2-7). Egg-to-smolt survival probability estimates (\( S_1 \)) derived from these numbers averaged 4.8% (range 2.8% to 6.6%) for the aggregate population. The CRI method of calculating \( S_1 \) produces an average that is less than half of that, 2.1% (range 1.35% to 3.6%).

We also estimated \( S_1 \) in the matrix using our \( S_e \) adjusted to the observed SAR rather than the literature generated \( S_e \) used by CRI. To do this, we replaced the nominal 0.07 with the \( S_e \) calculated using a SAR of 0.0096. Then we used the Euler equation to solve for \( S_1 \) as in CRI. This approach produced \( S_1 \) values that average 5.7% (range 4.0% to 8.7%; Figure 2.2). We also repeated the analysis assuming that the Ricker \( a \) equaled the averaged ln(R/S) instead of the median (as the CRI does). There was no significant difference in the resulting average \( S_1 \)'s (paired \( t \) test \( p = 0.47 \)). It is interesting to note that neither our \( S_1 \) nor the CRI \( S_1 \) survival probabilities vary with habitat quality (see Appendix B). \( S_1 \)'s calculated for populations that
Egg-to-smolt survivals (S1) versus habitat quality

Based on SAR=.0096
CRI

Index populations, ordered by increasing habitat quality

Figure 2.2. Egg-to-smolt survival $S_I$ versus rearing habitat quality: values used in the CRI Leslie matrix and values corrected for under-estimated SARs. POV=Poverty Flat, BEA=Bear Valley, JOH=Johnson Creek, MAR=Marsh Creek, IMN=Imnaha River, SUL=Sulphur Creek, MIN=Minam River.

Estimated $S_I$'s do not vary with habitat quality for several reasons. First, the calculations are driven partly by R/S estimates, and although the geometric mean R/S estimates do vary somewhat with habitat quality (Figure 2.3), they vary in the opposite direction than expected. Second, two of the worst habitats, Johnson Creek and Poverty Flat, are summer chinook runs. Without these two summer chinook populations, there is no particular trend in survival rates with habitat quality for spring chinook (Figure 2.3). Third, habitat quality for the five spring chinook populations ranges from poor to excellent, yet no discernible trend in median R/S is evident. If population dynamics were being controlled primarily by factors outside the spawning and rearing habitat, one would not expect to have much power with which to detect spawning and rearing habitat influences. Finally, ignoring density dependence could mask differences in productivity between the stocks, especially if depensation affects productivity at small spawner abundance levels.
2.3 Summary of impacts of shifting mortality rates

Because the CRI model and our model both estimate $\lambda$ from the R/S record using the Euler equation, reallocating mortality rates will have a negligible effect on $\lambda$. However, the reallocation of mortality rates will have an impact on the conclusions drawn by NMFS from their sensitivity analyses and numerical experiments.

The CRI assumed SARs that are more than threefold higher than current data support, and egg-to-smolt survival rates that are about one third the estimates described by USACE and PATH (NMFS 1999a; Figure 2.4). When the empirical estimates for SARs are used to calculate estuary survival $S_e$, as discussed above, estuary/early ocean survival drops to less than one third the value assumed by CRI (Figure 2.5). Because $\lambda$ is constrained by the R/S record, and the CRI calculates $S_I$ rather than using an empirically-based estimate (used in PATH), an inflated SAR leads to an underestimate of $S_I$.
Figure 2.4. SARs calculated with the CRI matrices compared to empirically-derived SARs used by the USACE and PATH.

Figure 2.5. Estuary/early ocean survival $S_e$ used in the CRI compared to an empirically-based estimate.
Figure 2.6. Egg-to-smolt survival rates ($S_1$) estimated in the NMFS CRI Leslie matrix for the seven indicator stocks compared to an empirically-based estimate.

Figure 2.7. Proportions of mortality allocated to different life stages by the CRI versus proportions that result when observed survival rates are used.
Although CRI acknowledges that both $S_1$ and $S_e$ are important phases, the sensitivity analysis method favored by CRI indicates that improvements in survival in the life phase with the lowest survival rate will provide the biggest benefit to the population growth rate. Thus, the answer to the question "what should we do?" depends on how mortality rates are allocated over the life cycle. If the lowest survival rate is in the egg-to-smolt stage (as in the CRI analyses) then the emphasis will be on freshwater survival. If the lowest survival rate is in the estuary/early ocean phase, then a larger emphasis will be on improving survival below Bonneville Dam (for both barged and in-river smolts).

For example, CRI concluded that reducing egg-to-smolt mortality by 10% will increase the average annual population growth rate ($\lambda$) by 20% to 30% (average 28.5%), whereas a 10% reduction in estuary and first-year ocean mortality would increase $\lambda$ by an average of 19.8% (Kareiva et al. 1999).

However, when $S_e$ values are derived from current observed (empirical) SARs the sensitivity analysis conclusions are reversed. Reducing egg-to-smolt mortality by 10% increases $\lambda$ by 14.2% to 27.4% (average 22.4%), whereas reducing estuary mortality by 10% increases $\lambda$ by 39.4% (range 38.8% to 40.6%). This suggests that improving survival in the estuary and early ocean phase could yield a 75% greater benefit to the population growth rate than would improving egg-to-smolt survival alone.

The point here is not that habitat restoration efforts should focus on the estuary rather than the freshwater, but rather that the results of the numerical experiments are highly dependent on how the variables are arranged.

### 2.4 Effects of $D$ on $S_1$ and $S_e$

Although fish generally appear to survive reasonably well while in the trucks and barges, it is harder to gauge how well transported fish survive below Bonneville Dam after they are released and continue their life cycle in the estuary and ocean. Some of the mortality experienced by transported fish in the estuary and the ocean is natural or due to factors in these environments (e.g., predation). Another component of mortality in the estuary and ocean may be a result of their experience in trucks or barges and not realized until after they are released below Bonneville Dam. This mortality would be referred to as delayed mortality of transported fish. Although the absolute delayed mortality component for transported fish cannot be measured, the relative difference between the delayed mortality of fish that were transported versus those that migrated in-river can be estimated. The differential survival rate of transported fish relative to fish that migrate in-river, as measured from Bonneville Dam tailrace to adult returning to Lower Granite Dam, is referred to as the ‘$D$’ value. This is estimated by comparing the SARs (Lower Granite Dam smolts to adults returning to Bonneville Dam) for transported fish to the SARs of non-transported fish while accounting for the direct survival through the hydrosystem for both groups of fish. A ‘$D$’ equal to one indicates that there is no difference in survival rates (after
hydrosystem passage), while a ‘$D$’ less than one indicates that transported fish die at a higher rate after release than fish that have migrated through the hydrosystem.

We incorporated ‘$D$’ into the CRI matrix by modifying the equation for $S_2$. The CRI equation for $S_2$ is:

$$S_2 = ((1-p_t) \cdot S_d + (p_t \cdot S_b)) \cdot S_e$$

Where:

$p_t$ = fraction of smolts entering the hydrosystem destined to be barged
$S_d$ = probability of non-barged fish surviving to below Bonneville
$S_b$ = probability of barged fish surviving from placement on barge to below Bonneville
$S_e$ = probability of surviving from below Bonneville to third birthday

The modification we made in order to incorporate ‘$D$’ and more explicitly describe the downstream passage routing is:

$$S_2 = ((1-p_t) \cdot S_d + (p_t \cdot V_t \cdot S_b \cdot D)) \cdot S_e$$

Where:

$p_t$ = fraction of smolts entering the hydrosystem destined to be barged
$S_d$ = probability of non-barged fish surviving to below Bonneville Dam
$S_b$ = probability of barged fish surviving from placement on barge to below Bonneville
$S_e$ = probability of surviving from below Bonneville to third birthday
$V_t$ = probability of survival of transported fish up to the point of transport. Average from passage models over 1980-1990 brood years
$D$ = differential survival of transported fish from below Bonneville relative to non-transported fish. Average from FLUSH (using its default transport model) over 1980-1990 brood years or from NMFS estimates for recent PIT-tag data.

Using the probability trees as before, we calculated what $S_e$ would have to be to achieve the observed SAR value (0.0096) from 1980-1992 brood years from Lower Granite Dam to mouth of the Columbia River.

Incorporating an average $D$ of 0.286 and $V_t$ of 0.865 (both from FLUSH) into $S_2$ would decrease our original $S_2$. Unless we changed $S_3$, $S_4$, and $S_5$, $S_2$ would have to remain the same in order to achieve the same observed SAR of 0.0096. We used Excel Solver to adjust $S_e$ to offset the decrease in the other components of $S_2$. The result is that $S_e$ increased an average of 15.2%, from the CRI-assumed 7.0% to an average of 8.1% (range 7.8% to 8.2%; Figure 2.8).
Figure 2.8. Estuary survival $S_e$ calculated assuming average FLUSH estimates for $D$ and $V_t$.

Because $S_e$ was adjusted to allow $D$ to be incorporated into $S_2$, and $S_2$ was kept consistent with the empirical SAR, $S_2$ did not change compared to what it was without $D$. Since $S_2$ does not change, $S_1$ will not change either.

Incorporating $D$ and empirically-derived survival estimates therefore affects distribution of survival rates (Figure 2.9). As noted previously, survival distributions drive the sensitivity analysis and thus CRI's answer to the question of what should we do to save Snake River salmon.
Figure 2.9. Survival distributions of CRI matrices and distributions using empirically-derived freshwater ($S_f$) and estuary ($S_e$) survival with and without $D$.

These exercises demonstrate the importance of validating the CRI model. Presently, CRI does not validate their models, therefore raising concerns about the predictive ability of such an approach. By using information specific to these stocks for $S_e$, such as the observed SAR values accepted by NMFS, the USACE, and PATH, we arrived at $S_f$ values consistent with $S_i$ values specific to Snake River spring/summer chinook estimated independently from the model. Our estimates of $S_f$ compare well to PATH’s $S_f$ estimates, which range from 2.8% to 6.6% for the aggregate index populations (Petrosky and Schaller 1996, see Appendix B). Our estimates are also consistent with non-PATH literature values for Columbia River basin spring/summer chinook egg-to-smolt survivals (Lindsay et al.1982, Smith et al. 1983, Lindsay et al. 1989, BPA 1992, Mullan et al. 1992, Bradford 1995). In contrast, egg-to-smolt survival probabilities estimated by the CRI Leslie matrix are significantly lower (1.5% to 3.6%).

3. The STUFA matrix

Several steps were required to change the structure and assumptions of the CRI matrix to make it sufficiently compatible with PATH, thereby justifying comparisons of analytical experiments performed by CRI and PATH.

1) CRI models used to date have no way of handling what PATH calls "extra mortality." (see Appendix D).

2) CRI analyses assume the same fecundity for all age fish, though CRI uses different fecundity
values for different populations (see Table 3.1 comparison).

3) For juvenile passage variables, CRI analyses use average estimates, although a more appropriate statistical estimate of expected value for proportions is the geometric mean (Sokal 1995). There is little difference between the average and the geometric mean for proportions that exhibit little variability, but if they exhibit significant variability, the geometric mean will be considerably less than the average.

4) The way CRI treats sex ratios by age is inconsistent. In the "propensity to breed" calculations, CRI adjusts the spawner counts by an assumed fraction of males to females. For example, most of the fish that return in their third year are male, but most that return in their fifth year are female. However, in the Leslie matrix itself, CRI assumes spawners at each age are 50% female.

5) The CRI analyses are also inconsistent in that they use slightly different numbers for spawners and recruits in the "propensity to breed" calculations than they do for the R/S numbers they use in calculating $\lambda$.

In the analyses described in previous sections, we used the same 1980-1993 brood year data that the CRI did, not modifying the model in order to address any of these inconsistencies or problems, so that results could be compared to the available CRI analyses. In the following sections, we resolved the above inconsistencies and modified the matrices to include factors and hypotheses found to be important in PATH’s analysis of Snake River spring/summer chinook.

3.1 Incorporation of extra mortality

Rather than using $D$ as the only expression of delayed mortality (post-Bonneville Dam), as done in the previous section, we incorporated "total extra mortality" into the Leslie matrix model. In PATH, life-cycle mortality was separated into two components, direct and extra mortality. Direct mortality occurs immediately and as a result of some cause in that life stage (e.g., predation). A portion of direct mortality occurs while juvenile and adult salmon and steelhead pass by dams and travel through reservoirs that comprise the hydrosystem. PATH used overall life-cycle mortality (from spawner and recruit data) and direct mortality to define a second component of mortality, called extra mortality. Extra mortality occurs in the Columbia River downstream from Bonneville Dam and into the ocean and is difficult to model because it is not directly measurable. This mortality is also called delayed or latent mortality (see Appendix D).

In PATH analysis, extra mortality for the delta model (used in this analysis) was estimated as any mortality that occurs from the time smolts arrive below Bonneville Dam to when the adults return to the river mouth, that is different from that represented by in-common climatic effects (e.g., ocean upwelling) shared with downstream counterparts.

To incorporate extra mortality, we modified equations (1) and (2) by incorporating $D$ and extra mortality of non-transported fish into a variable representing extra mortality of the population as
a whole: extra mortality survival probability (or simply survival rates based on extra mortality) $S_{em}$:

\[ S_2 = ((1-p_t) * S_d + p_t * V_t * S_b) * S_{em} \]

Where:

- $p_t = \text{fraction of population encountering the hydrosystem (at the head of Lower Granite Dam reservoir) destined to be barged equal to the geometric mean from FLUSH or CRiSP over 1980-1990 brood years}$
- $S_d = \text{probability of non-barged fish surviving from emigration to below Bonneville equal to the geometric mean from FLUSH or CRiSP over 1980-1990 brood years}$
- $V_t = \text{survival of transported fish up to the point of transport equal to the geometric mean from FLUSH or CRiSP.}$
- $S_b = \text{probability of barged fish surviving from emigration to below Bonneville (0.98)}$
- $S_{em} = \text{post-Bonneville survival probability adjustment due to any mortality that occurs from the time smolts arrive below Bonneville to when the adults return to the river mouth, that is not accounted for by in-common climatic effects (e.g., ocean upwelling) shared with downstream counterparts (see Appendix D). Geometric mean over 1980-1990 brood years derived using FLUSH or CRiSP. To estimate $S_{em}$ with the CRiSP passage/transport model parameters, rather than using the CRiSP predicted $D$ values used in PATH, we used NMFS’s latest geometric mean value of $D$ (approximately 0.8). NMFS estimated $D$ past Lower Granite Dam from PIT tag data for migration years 1994-96. We did this to cover the widest range of proposed effectiveness of transportation-based strategies, from least optimistic (FLUSH default) to most optimistic (CRiSP with NMFS $D$-value).}$

We used the geometric mean of $V_t$, $p_t$, $S_d$, and $S_{em}$ estimates from 1980-1990 brood years. Although 1991-1994 brood year data was available for FLUSH, we did not have access to CRiSP output for these years, and it seemed appropriate to use the same time frame for passage parameters in order to make comparisons between results for the two passage/transport models as directly as possible. Additionally, in the PATH analyses that allow estimation of extra mortality, the last brood year used was 1990.

### 3.2 Making age and sex structure consistent

To calculate $\lambda$ using the Leslie matrix or the Euler equation, the CRI assumes that half of any category modeled in the matrix is female (e.g., half of the spawners for all ages are female and males). $^3$

---

$^3$ The terminology is a bit awkward because the focus is actually on extra mortality, which is $1-S_{em}$, but to be consistent, the model uses survival rates rather than mortality rates. It is important to keep in mind that these "survival" rates are actually probability of surviving from one point in time to the next. $S_{em}$ represents an additional mortality imposed on the post-Bonneville period, which may be caused by factors above or below Bonneville Dam.

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*A technical review of the National Marine Fisheries Service Leslie matrix model of Snake River spring and summer chinook population.*
half of the adults remaining in the ocean are female). However, the maturation schedule used by CRI ("propensity to breed") is calculated from non-uniform sex ratios, as follows:

1) For Marsh, Bear Valley, and Sulphur Creek (tributaries of the Middle Fork Salmon River with spring chinook runs) none of the 3-year old spawners are female, 49% of the 4-year old spawners are female, and 67% of the 5-year old spawners are female.

2) For summer chinook populations in Johnson Creek and Poverty Flat (Idaho's South Fork Salmon River drainage), 11% of the 3-year old spawners are female, 28% of the 4-year old spawners are female, and 58% of the 5-year old spawners are female.

3) Of the Oregon populations, the Imnaha River population is spring/summer chinook and the Minam River (tributary to the Grand Ronde River in Oregon) population is spring chinook. For the Imnaha, latest reports show that none of the 3-year old spawners are female, 34% of the 4-year old spawners are female, and 66% of the 5-year old spawners are female. For the Minam, latest reports show that 1% of the 3-year old spawners are female, 56% of the 4-year old spawners are female, and 43% of the 5-year old spawners are female (Eric Tinus, ODFW, unpublished data).

We used the same non-uniform sex ratios for all the calculations, rather than just for the "propensity to breed" calculations as did the CRI (Table 3.2). Estimated spawners are partitioned into fraction female by age, using the same assumed fractions as the CRI (these fractions came from PATH originally). The maturation schedule (what CRI termed "propensity to breed") is calculated in the same manner as CRI, using survival probabilities ($S_3$, $S_4$, and $S_5$) and estimated observed fraction of spawners that are female by age. In the Leslie matrix, to get from spawners to eggs, the number of returning adults is first adjusted by the upstream survival rate ($1-\mu$) as performed by CRI. Then, in contrast to the CRI (i.e., assuming the population is half female and regardless of age), we calculated the number of female spawners by multiplying the sex ratios by age for that population.

For age fractions, we used the 1980-1999 run year age fractions from ODFW and IDFG data. These fractions were the same as used in the CRI except they included data from the most recent years.

### 3.3 Adjusting fecundity by age

To calculate $\lambda$ using the Leslie matrix, or the Euler equation, CRI assumes that fecundity (eggs per female) varies by subbasin (i.e., 5607 for Middle Fork Salmon River spring chinook, 4100 for South Fork Salmon River summer chinook, 4927 for Imnaha River spring/summer chinook, and 4086 for Minam River spring chinook). These subbasin variations in average fecundity result from different age structures, and length-at-age, between stocks during the period examined (Myers 1998). By using an average fecundity and fixed sex ratio, the CRI analyses ignored the impacts of varying age composition on recovery and extinction probability. However, the paper on which the CRI matrix model based its survival estimates (Ratner et al. 1997) used age-specific estimates of fecundity.
In contrast to the CRI, we used non-uniform sex ratios (from the Northwest Power Planning Council subbasin planning data sets) for all the calculations. Because age-3 fecundity data were not available, we used the ratio between age-4 and age-5 fecundity rates to estimate an age-3 fecundity rate. That value is approximately equal to the age-3 fecundity determined by WDFW in their lower Columbia River hatchery evaluation program at Klickitat and Speelyai hatcheries (J. Byrne, WDFW, personal communication). The ratio between age-3 and age-4, and between age-4 and age-5, for WDFW’s evaluation was nearly equal (approximately 0.85), and similar to the age-4 and age-5 ratio (approximately 0.80) calculated from Snake River stock data by IDFG (see Appendix B). The age-3 fecundity estimate is not a significant parameter, because the fraction female for age-3 is very low (0.00 to 0.11). Variability in the fecundity-at-age is taken from the relationship defined by the WDFW assessment (J. Byrne, WDFW, personal communication).

We used age-specific fecundity rates obtained from Subbasin Planning data (S. Kiefer, IDFG, personal communication, June 1991; see Appendix B). Fecundity values for aggregate Snake River spring/summer chinook averaged 4095 (SD = 831) eggs/female for age-4 and 5149 eggs/female for age-5 (SD = 1031). Age-3 females represented a very small percentage (0.3%) of total spawners; using the ratio described above, their fecundity was assumed to be 3257 eggs/female (4095 * [4095/5149]).

We incorporated the above information into the Leslie matrix. We will refer to these modified matrices as the "STUFA" matrices.

3.4 Updating R/S numbers to use 1999 data

Estimates for adult recruits and spawners for all seven index populations were used to update the matrices for all brood years from 1980 through 1994 (E. Tinus, ODFW, and C. Petrosky, IDFG, unpublished data), so we could use run data through 1999. We also used the latest Bonneville to basin conversion rates and harvest rates (E. Tinus, ODFW, and C. Petrosky, IDFG, unpublished data).
Table 3.1. Summary of assumptions used in the CRI Leslie matrices and how they were handled in the STUFA matrices.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>CRI assumption</th>
<th>STUFA assumption</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fecundity</td>
<td>Same for all age spawners, but different fecundity values for different populations</td>
<td>Varies by age, using state agency estimates</td>
</tr>
<tr>
<td>Juvenile hydropower passage parameters</td>
<td>Averages</td>
<td>Geometric means (generally lower than the averages for these populations)</td>
</tr>
<tr>
<td>Sex ratios</td>
<td>Empirical estimates used in some places, 0.5 used in others</td>
<td>Empirical estimates used consistently throughout analyses</td>
</tr>
</tbody>
</table>

### 3.5 Effects of STUFA modifications on "propensity to breed"

The first step in understanding the effects of the STUFA matrix modifications was to find maturation schedules that correspond to the updated data. Next, FLUSH and CRiSP passage values for $p_r$, $S_d$, $V_t$, and $S_{em}$ were incorporated into the analyses. The other passage parameters were not changed. The maturation schedule—probability of leaving the ocean to return to the spawning grounds—refers to what CRI calls "propensity to breed" for age-3, age-4, and age-5 salmon ($b_3$, $b_4$, and $b_5$). The maturation schedules were nearly identical for CRiSP and FLUSH passage/transport models (Table 3.2). Incorporating these four recent brood years, extra mortality, and adjusting fecundity and fraction female by age, leads to an increase in $b_4$ by an average of 7.9% (paired $t$-test of means, $p < 0.004$). This increase in $b_4$ corresponds to a decrease in average age of spawners.
Table 3.2. "Propensity to breed" or maturation schedule using 1980-1990 and 1980-1994 brood year (BY) data.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>CRI (b_3)</td>
<td>CRI (b_4)</td>
</tr>
<tr>
<td>MAR</td>
<td>0.000</td>
<td>0.185</td>
</tr>
<tr>
<td>JOH</td>
<td>0.009</td>
<td>0.189</td>
</tr>
<tr>
<td>IMN</td>
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<td>BEA</td>
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<tr>
<td>POV</td>
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<tr>
<td>SUL</td>
<td>0.000</td>
<td>0.181</td>
</tr>
<tr>
<td>MIN</td>
<td>0.005</td>
<td>0.393</td>
</tr>
<tr>
<td>average</td>
<td>0.005</td>
<td>0.228</td>
</tr>
<tr>
<td>minimum</td>
<td>0.000</td>
<td>0.177</td>
</tr>
<tr>
<td>maximum</td>
<td>0.012</td>
<td>0.393</td>
</tr>
</tbody>
</table>

3.6 Effects of STUFA modifications on \(S_3\)

The variables we know the least about are ocean survival rates \(S_3\), \(S_4\), and \(S_5\). However, we do have reasonably good estimates for SAR (smolts at Lower Granite Dam to adults at the Columbia River mouth), which encompasses \(S_3\), \(S_4\), and \(S_5\) in addition to \(S_2\) (in this matrix \(S_2\) includes \(p_t\), \(S_d\), \(S_b\), \(V_t\), and \(S_{em}\), as described in Chapter 2). We used both CRISP and FLUSH passage/transport models to provide estimates for all the components of \(S_2\). Because survival probabilities generally increase with age of fish, we would expect age-3 fish to have a lower ocean survival rate than age-4 and age-5 fish. To simplify the analysis, we left \(S_4\) and \(S_5\) at 0.8. Using these values, we solved for \(S_3\) given our observed SAR of 0.0096. It is probably reasonable to expect that the greatest ocean mortality would affect the youngest fish, and it is also computationally easier to only vary one of the three adult mortality rates.

The resulting \(S_3\) (average 0.119, range 0.113 to 0.121)\(^4\) varied little regardless of whether we used FLUSH or CRI SP passage parameter values. This survival rate is considerably less than \(S_3\) assumed in the CRI (0.8). The reason for this is partly due to the model structure: the STUFA \(S_3\) includes CRI's \(S_e\), apart from the “extra mortality” represented by \(S_{em}\) in \(S_2\). We had concerns

\(^4\) This survival rate is skewed by the low \(S_3\) calculated for the Minam, which has a younger age structure than the other spring chinook populations (nearly 60% for 4-year olds, compared to Marsh (42%), Bear Valley (29.4%), and Sulphur Creek (29.2%). There is a higher percentage of 5-year olds in the other spring chinook populations.
about the applicability of the sources CRI cites in estimating their \(S_e\) value to Snake River spring and summer chinook salmon (see Appendix A). CRI's age-invariant 0.8 annual ocean survival rate assumption is based on a study of a different species, sockeye salmon (Ricker 1976).

### 3.7 Effects of STUFA modifications on \(S_1\)

The above exercise demonstrates that if estimates of post-Bonneville delayed mortality (extra mortality) are excluded from the estuary and ocean survival estimates, then the matrix is forced to put this mortality into earlier life stages; in the CRI matrix, it goes into \(S_1\). In a sense, CRI is incorporating extra mortality into \(S_1\) by default. By over-estimating post-Bonneville Dam survival, and in assigning the residual mortality to \(S_1\), the CRI matrix forced an under-estimation of egg-to-smolt survival (\(S_1\)). We investigated whether implementing alternative hypotheses of post-Bonneville Dam survival would produce a residual \(S_1\) that was more consistent with observed values of \(S_1\). Using what we believed were the most reasonable values for all the matrix entries except \(S_1\) (using both the FLUSH and CRiSP assumptions for \(p_t, S_d, V_t,\) and \(S_{cm}\)) we solved for \(S_1\), again using the Euler equation.

This resulted in an average \(S_1\) (egg-to-smolt survival) of 5.7% (range 4.2% to 7.2%; Figure 3.1). The average egg-to-smolt survival probability was more than double that of the CRI estimate, which calculated values for \(S_1\) averaging 2.1% (range 1.4% to 3.6%; Figure 3.1). Our calculated value is also more consistent with available data: PATH studies show that \(S_1\) for these populations averaged 4.8% (range 2.6% to 8.7%; see Appendix B), a range consistent with other studies of Columbia River spring/summer chinook survival, as noted previously.

![Egg-to-smolt survival S1](image)

**Figure 3.1.** Egg-to-smolt survival probability (\(S_1\)) estimated by CRI, STUFA, and the best SAR-based (empirical) estimate.

*An technical review of the National Marine Fisheries Service Leslie matrix model of Snake River spring and summer chinook population.*
4. Management Scenarios

4.1 CRI evaluation of potential management actions

CRI does not explicitly model the impact of management actions on population growth rate. Rather, CRI conducts “numerical experiments” to assess the potential benefit to the population by reducing mortality 10% in each life stage (which will be referred to here as the “constant percent” method). This approach does not identify when, where, how, and if this 10% reduction in mortality is achievable. Because these questions are not addressed, the usefulness of such an approach is extremely limited. CRI acknowledges the next step to this approach is to address the feasibility of achieving this reduction in mortality. However, CRI emphasizes that this approach is useful in identifying where management efforts to reduce mortality in specific life stages provides the greatest potential for improvement in population growth rates. We believe the conclusions from the constant percent method can be misleading for even this limited application.

The constant percent method will always demonstrate that a 10% reduction in mortality in the life stage with the lowest survival rate provides the greatest population benefit. The CRI matrix partitions the life history of a salmon into yearly age classes. Concerns over the impact that migrating through eight hydroelectric projects could have on salmon populations has led to several studies that have estimated the survival rate through this migration corridor. Changes in hydrosystem management have also been an obvious area to focus on ways to increase salmon survival. Because of these distinctions, CRI further divided the second-year age class into two stages: migration through the hydrosystem and the remainder of the second year (which CRI attributed to the estuary and early ocean). Therefore, CRI compartmentalized all portions of the life cycle into age classes, except for age-2, not because information (to best describe these populations) is collected over yearly increments or that management actions focus on yearly age classes but rather for model convenience. Using different criteria to partition survival across the life cycle has significant ramifications in assessing potential benefits to the population evaluated with the constant percent method.

Estimates of survival rates are not only a result of factors affecting survival, but also a result of time. Assuming that daily survival rates do not change, estimates of survival over very short time periods will be much higher than estimates over long time periods. For example, in the CRI matrix, $S_1$ represents the first year of life from the time eggs are deposited to the time smolts arrive at Lower Granite Dam, which more accurately occurs over approximately 550 days (Figure 4.1a). In contrast, the life stage migrating through the hydrosystem ($S_d$) occurs over an approximately 15- to 30-day time period, while the life-stage being transported ($S_b$) only occurs over a 2-day time period on average. If the daily survival were 0.99/day over both life stages then $S_1$ would be $0.99^{550} = 0.004$ and survival through the hydrosystem ($S_d$) would be $0.99^{15} = 0.86$ (ranging to $0.99^{30} = 0.74$). Therefore, because the constant percent method simply identifies what life stages has the lowest survival, this example would suggest that the greatest benefit in a 10% reduction in mortality would occur in $S_1$ only because it was estimated over a longer time scale, not because the fish are experiencing an unusual amount of mortality in this life stage.
If CRI explicitly stated over what portion of the life cycle a particular management action reduced mortality and made this statement for all feasible management actions for all life stages, then the constant percent method may be useful. Currently, however, CRI has only identified the portion of the life cycle that would be addressed by changes to the hydrosystem and harvest. Management actions were not identified in the other life stages so they cannot be assessed in the same units. For example, presently CRI suggests reducing mortality in spawning and rearing habitats by 10% would have the greatest benefit to the population growth rate. Even if habitat improvements were feasible in wilderness areas, where many of these listed populations spawn, the management action would have to decrease daily mortality rates by 10% for eggs, 10% for fry, 10% for parr, and 10% for pre-smolts over the entire 550 day $S_1$ period (during which fry, parr, and smolts move hundreds of kilometers). Similarly, CRI suggests that improvements in estuary survival are also extremely important in recovering these stocks. Daily mortality in the estuary would again have to be reduced over the 170-day (or greater) time period as modeled in CRI. If reducing predation by terns was the mechanism by which mortality was reduced in the estuary, then mortality would be reduced only over an approximately one-week period. Limiting the time frame for one life stage (the only life stage where a management action has been identified to occur) and constraining other life stages only out of model convenience (because the management actions have not been explicitly stated) does not provide consistent criteria with which to base advice on where management efforts will provide the greatest population benefit.

Another problem with the constant percent method is that it ignores the evolutionary life history strategy of salmon. Survival over the life history of salmon basically follows a Type III survivorship curve (Figure 4.1b). In other words, earlier life stages have a much lower daily survival rate than later stages. If survival over the life cycle of salmon follows the idealized curve, then the constant percent method will always demonstrate (even if evaluated over constant time periods) that management efforts should focus on the earlier life stages. What we believe is a more important question to ask is “At what life stage do salmon experience a higher percentage of mortality than that experienced in their evolutionary history?” For example, if survival in $S_1$ followed this idealized curve but human factors caused survival in the estuary ($S_e$) to be much lower than expected, then the greatest potential benefit would occur by reducing mortality in $S_e$ not in $S_1$ (Figure 4.1b). As state above, we would expect that daily survival rates should increase later in life. The daily survival rates used in the CRI matrix do not follow this idealized pattern because daily survival rates of $S_d$, $S_b$, and $S_c$ are lower than in $S_1$ (Figure 4.1c). One might conclude from this simple comparison that improving passage and estuary survival are potentially the most important life stages where mortality could be reduced.

As stated by NMFS, a major benefit of the CRI approach is the ability to address management actions on all H’s (see DEIS). However, the closest attempt to define a management action in the CRI is to identify what portion of the life history is directly affected by the hydrosystem. Because this has not been attempted for the other life stages (with the exception of harvest), and because the constant percent method ignores biological and logistical feasibility of achieving a 10% reduction in mortality across all life stages, we believe that the conclusions drawn from this approach simply represent a mathematical artifact that provides misleading advice regarding the life stages where management actions should focus.
Figure 4.1. (a) Time spent in each life stage as described by the CRI matrix, where $S_1$ is survival in the median date of year 1, $S_2$ in year 2, ..., $S_5$ in year 5; $S_e$ is the survival in the estuary; $S_d$ is survival during migration through the hydrosystem. (b) Theoretical survivorship curve (Type III) for salmon. (c) Daily survival rate for the median date of each life stage as described in the CRI matrix, where $S_b$ is survival during barging.
4.2 STUFA evaluation of management actions

In contrast to the “hypothetical” number experiments NMFS and CRI used to identify areas with the greatest potential for improving survival, we explicitly modeled six different management scenarios.

1. **Baseline**: “Average” status quo conditions from 1980-present. This is a best representation of actual conditions (similar to A1 in PATH).

2. **Maximize transport**: Maximizing the number of smolts transported at each collector project (similar to A2 in PATH)

3. **Dam breach/delayed mortality reduced**: Snake River dams are breached and delayed mortality is assumed to be linked to hydrosystem and is thus reduced (similar to A3/hydro in PATH).

4. **Dam breach/delayed mortality remains**: Snake River dams are breached but delayed mortality of non-transported fish is assumed to be unrelated to hydrosystem and remains (similar to A3/BKD in PATH).

5. **Everything but dam breach**: All possible management actions that are feasible except dam breach. Includes cessation of all harvest, improvements in spawning and rearing habitat, and reduction in smolt mortality via Caspian tern relocation.

6. **Everything including dam breach**: All possible management actions that are feasible including dam breach. Includes cessation of all harvest, improvements in spawning and rearing habitat, reduction in smolt mortality via tern relocation, and dam breach (with delayed mortality reduced).

The first scenario “Baseline” represents actual demographic and environmental conditions from 1980 to the present. This time period was originally chosen by NMFS to represent “so-called average conditions” as most of the major hydrosystem changes had been completed by then. Population growth rates from the “Baseline” are then compared to those observed under different management actions. The second scenario was the termed “Maximize transport” (similar to the “A2” scenario in PATH). Under the “Maximize transport” scenario, all possible actions (with the exception of surface collectors) are taken to maximize the number of smolts transported. This scenario represents the greatest improvement in survival we could hope for under the assumption that transportation is beneficial. The third scenario represents “Dam breach/delayed mortality reduced” (similar to “A3/hydro” in PATH). Under this scenario, the dams are breached, thereby reducing direct mortality through the Snake River projects, and delayed mortality, assumed to be related to experience through the hydrosystem, is reduced to the level experienced by the stocks under the historical 4-dam configuration of the Snake River/lower Columbia River hydrosystem. This scenario represents an optimistic view of survival improvement under a dam breach alone scenario. In addition, we also ran a “Dam breach/delayed mortality remains” scenario (similar to “A3/BKD” in PATH). Under this scenario, the direct mortality from dam passage is still
removed, but the delayed mortality of non-transported fish experienced in the recent (1980-1990 brood year) period is assumed to remain due to disease (BKD), or to depressed stock viability resulting from some cause or causes that will not be mitigated by dam breach. This scenario represents a more pessimistic representation of dam breach effectiveness. For the stochastic model, we also ran a “Everything but dam breach” scenario where all possible actions but breach are implemented and an “Everything including dam breach” option where all possible actions including breach are implemented.

Only scenarios 1-4 were modeled using the deterministic model. All scenarios were modeled under the stochastic model.

4.3 Development of the STUFA deterministic matrix

We used the STUFA matrices to evaluate the impact of alternative management actions on average annual population growth rates ($\lambda$) of Snake River spring/summer chinook. We evaluated these management actions across a range of inputs (pessimistic and optimistic) using FLUSH and CRiSP juvenile passage assumptions (see Table 4.1 for parameter settings). Because of time constraints, these experiments were not carried out for all seven index populations, but instead for a subset of three populations: Marsh Creek (spring chinook, Middle Fork Salmon River), Poverty Flat (summer chinook, South Fork Salmon River), and Imnaha (spring/summer chinook, mainstem Imnaha River).

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5 It is important to note, however, that since any delayed mortality of transported fish relative to non-transported fish is still eliminated (because transportation is halted), this scenario can result in substantial improvement in overall survival rates of the population if substantial delayed mortality of transported fish is assumed (‘D’ is low; see Appendix D).
Table 4.1. Summary of parameter values used in Baseline models.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>CRI</th>
<th>STUFA (FLUSH)</th>
<th>STUFA (CriSP)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$S_i$ (Average of MAR, JOH, IMN)</td>
<td>0.0219</td>
<td>0.0523</td>
<td>0.0523</td>
</tr>
<tr>
<td>$P_t$ = Fraction barged</td>
<td>0.7745</td>
<td>0.7389</td>
<td>0.6103</td>
</tr>
<tr>
<td>$S_b$ = Juvenile survival, barged</td>
<td>0.98</td>
<td>0.98</td>
<td>0.98</td>
</tr>
<tr>
<td>$S_d$ = Juvenile survival, non-barged</td>
<td>0.3225</td>
<td>0.1208</td>
<td>0.2335</td>
</tr>
<tr>
<td>$S_e$</td>
<td>0.07</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>$S_{em}$</td>
<td>n/a</td>
<td>0.1800</td>
<td>0.2133</td>
</tr>
<tr>
<td>$V_t$</td>
<td>n/a</td>
<td>0.858</td>
<td>0.7695</td>
</tr>
<tr>
<td>$S_3$</td>
<td>0.8</td>
<td>0.120</td>
<td>0.120</td>
</tr>
<tr>
<td>$S_d$ and $S_5$</td>
<td>0.8</td>
<td>0.8</td>
<td>0.8</td>
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<tr>
<td>Fecundity, age-3 fish</td>
<td>5607</td>
<td>3257</td>
<td>3257</td>
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<tr>
<td>Fecundity, age-4 fish</td>
<td>5607</td>
<td>4095</td>
<td>4095</td>
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<tr>
<td>Fecundity, age-5 fish</td>
<td>5607</td>
<td>5149</td>
<td>5149</td>
</tr>
<tr>
<td>Fraction female by age, used in &quot;propensity to breed&quot;</td>
<td>Varies by population</td>
<td>Varies by population</td>
<td>Varies by population</td>
</tr>
<tr>
<td>Fraction female, used in the NMFS Leslie matrix</td>
<td>0.5</td>
<td>Varies by population</td>
<td>Varies by population</td>
</tr>
<tr>
<td>Pre-spawning survival</td>
<td>0.9</td>
<td>0.9</td>
<td>0.9</td>
</tr>
<tr>
<td>SAR and $\lambda$</td>
<td>n/a</td>
<td>Free to vary</td>
<td>Free to vary</td>
</tr>
<tr>
<td>$\mu = $ total adult passage mortality average (MAR, JOH, IMN)</td>
<td>0.458</td>
<td>0.462</td>
<td>0.462</td>
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</table>

4.4 Results of STUFA deterministic model

The results for the “Maximize transport” and the “Dam breach/delayed mortality reduced” scenarios were influenced by choice of passage/transport model. Values of $S_2$ for the Baseline scenario (for CRiSP and FLUSH models) are identical because the $S_{em}$ values are estimated from PATH $m$-values (sum of instantaneous direct passage mortality and instantaneous extra mortality) from retrospective R/S data, using the respective passage/transport model and $D$ parameters (see Appendix D for details). Since the same R/S data must be fit using both passage/transport models, $S_2$ values are constrained to satisfy the condition $S_2 = \exp(-m)$ for the
Baseline years. On average, $S_2$ increased from 11.8% in the Baseline to 16.3% under “Maximize transport”, and to 35.9% under dam breach scenarios (Figure 4.2, Table 4.2). $S_2$ values for “Dam breach/delayed mortality reduced” scenario are identical under CriSP and FLUSH, because under this scenario the overall mortality must equal that estimated from the R/S data from the four-dam period (see Appendix D). Mean $S_2$ values for the “Dam breach/delayed mortality remains” scenario are much higher than “Maximize transport” $S_2$ values for FLUSH, and slightly lower than “Maximize transport” values for CriSP.

SARs improved an average of 32.3% with FLUSH under “Maximize transport”, and 46.2% with CriSP under “Maximize transport” (Figure 4.3). SARs increased by 205% with both passage/transport models under “Dam breach/delayed mortality reduced” bringing SARs from 0.0096 for Baseline, to 0.029 for “Dam breach/delayed mortality reduced”. That SAR under “Dam breach/delayed mortality reduced” is close to 1960s levels, which NMFS says should be achieved under the “Dam breach/delayed mortality reduced” extra mortality hypothesis (NMFS 1999a). The improvement in SARs under the dam breach scenario and the delayed mortality remains hypothesis is nearly identical to improvement in $S_2$.

The resulting increase in $S_2$ also affected λ's (Figure 4.4). On average across the three populations, for the FLUSH passage/transport model, λ improved by 6.2% under “Maximize transport”, and 28.6% under dam breach (Table 4.2). For the CRiSP passage/transport model, λ improved by 8.5% under “Maximize transport.” λ's were not appreciably different between the passage/transport models under dam breach, because with the delayed mortality reduced hypothesis, $S_2$ values for dam breach are fixed by the spawner-recruit data. Thus, regardless of passage/transport model, λ's increased over the Baseline model by 28.6% under dam breach. For both passage/transport models, the “Dam breach/delayed mortality reduced” scenario changes population growth rates from average declines of 6.6% per year, to average increases of 20% per year. For the delayed mortality remains hypothesis, the improvement in λ under dam breach for FLUSH was even greater than for the delayed mortality reduced hypothesis. For the “Dam breach/delayed mortality remains” scenario with CRiSP, the improvement in λ was much less than under the “Dam breach/delayed mortality reduced,” but it was still slightly greater than the improvement in CriSP’s λ under “Maximize transport.”
Figure 4.2. Juvenile passage survival (including extra mortality, $s_2$) estimates from FLUSH (F) and CRiSP (C) deterministic models (STUFA matrices) under various management scenarios: Baseline, Maximize transport, and Dam breach (remains = delayed mortality remains hypothesis, reduced = delayed mortality reduced hypothesis). Results from FLUSH and CRiSP are combined for Baseline scenario. CRI Leslie matrix estimate is included for comparison.
Table 4.2. Estimated average annual population growth rates ($\lambda$) from three different models under various management scenarios for three spring/summer chinook populations (MAR=Marsh Creek, POV=Poverty Flat, and IMN=Imnaha River). Median $\lambda$ values are presented for the STUFA stochastic model for reasons explained in text.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Stock</th>
<th>STUFA Deterministic</th>
<th>STUFA Stochastic</th>
<th>CRI Leslie matrix $\lambda$</th>
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<td>$\lambda$</td>
<td>Improvement over Baseline</td>
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<td><strong>Maximize transport (FLUSH)</strong></td>
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<td><strong>Dam breach/ delayed mortality reduced (both models)</strong></td>
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Figure 4.3. Average smolt-to-adult return rates (SAR) estimated from FLUSH (F) and CRiSP (C) deterministic models (STUFA matrices) for three spring/summer chinook populations (Marsh Creek, Poverty Flat, and Imnaha River) under various management scenarios: Baseline, Maximize transport, and Dam breach (remains = delayed mortality remains hypothesis, reduced = delayed mortality reduced hypothesis). CRI Leslie matrix estimate is included for comparison.
Figure 4.4. Average annual population growth rates ($\lambda$) estimated from FLUSH (F) and CRiSP (C) deterministic models (STUFA matrices) for three spring/summer chinook populations (Marsh Creek, Poverty Flat, and Imnaha River) under various management scenarios: Baseline, Maximize transport, and Dam breach (described in previous figures). CRI Leslie matrix estimate is included for comparison.

4.5 Development of the STUFA stochastic matrix

We developed a stochastic version of the STUFA matrix in order to examine how the uncertainties around the different variables affect the results of our deterministic Leslie matrices. To do this, we used Burgman et al.’s (1993) method for iteratively finding $\lambda$ using the Leslie matrix and an initial guess at the stable age distribution. This method assumes a stable age distribution has been achieved when the change in distribution between one iteration and the next is small (i.e., 0.0001). When that stable state has been achieved, $\lambda$ is assumed to be the quotient...
of the current population size divided by the previous iteration's population size. The age
distributions calculated for the different populations in the deterministic version were used as the
starting age distributions, but the method works just as well using an arbitrary distribution (it just
takes more iterations).

We used the same data sets that were used for the deterministic STUFA model analyses to derive
probability distributions to represent the parameters for each of three populations—one each for
spring, summer, and spring/summer chinook (Marsh Creek, Poverty Flats, and Imnaha;
respectively). We used the risk assessment add-in, @Risk (Palisade Corporation 1990-1997), to
set up Monte Carlo simulations in the STUFA matrices. We used the Latin hypercube sampling
technique rather than the traditional Monte Carlo sampling technique because this method
converges faster.

It is important to keep in mind that the precision of these stochastic analyses is limited by the
short time series of data on which the probability distributions can be based, and by a response
variable that cannot represent all pertinent aspects of the behavior of the actual populations.
Although temporal stationarity does not appear to be justified for these populations, the CRI
analyses focus on $\lambda$, the average annual population growth rate (represented by the dominant
eigenvalue of the Leslie matrices). It is clear that the population growth rates have been
decreasing since the mid-1970s, and that $\lambda$ is thus a non-representative response variable
(Burgman et al. 1993).

From a risk assessment perspective, the issue of non-stationarity is not the only issue, however.
The other issue is the fact that the Leslie matrices being used by the CRI are deterministic.
There is a great deal of uncertainty around all the variables in these models, and one way to get
at least a start on understanding the potential impacts of uncertainty is to modify the model to
incorporate uncertainty into the analyses.

Recognizing the limitations of applying the model to the populations at hand, we nonetheless
wanted to examine how uncertainty and variance (representing environmental variations) in the
matrix parameters could impact the potential range of $\lambda$'s and probability distributions. We also
used @Risk's sensitivity analysis tools to conduct multivariate sensitivity analysis in order to
develop a better understanding of the relative impacts of uncertainties on which the matrices are
built. This method of doing sensitivity analysis is not analogous to the CRI method, because this
method calculates the relative contribution of the uncertainty in each variable to the uncertainty
in the model output, whereas the CRI argues that their sensitivity analysis method shows where
management efforts should be applied. Further, we wanted to address the fact that different
management actions have differential effects on variance in vital rates, not just means.

We conducted these analyses for:
1) Deterministic and stochastic simulations.
2) Two juvenile transport models: FLUSH and CriSP (which we called CRiSP/NMFS in order to emphasize that the CRiSP model was modified to reflect current NMFS assumptions about the effectiveness of transportation, as incorporated in the ‘D’ parameter).

3) Three of the seven index populations: Marsh Creek (spring chinook), Poverty Flat (summer chinook), and Imnaha (spring/summer chinook).

4) The six management scenarios mentioned earlier: 1) Baseline, 2) Maximize transport (similar to A2 in PATH), 3) Dam breach/delayed mortality reduced, (similar to A3/Hydro in PATH), 4) Dam breach/delayed mortality remains (similar to A3/BKD in PATH), 5) Everything but dam breach, and 6) Everything including dam breach.

With the exception of juvenile passage variables, we assumed that the stochastic parameters all vary independently of one another, not because this is likely to be the case, but rather because of time limitations and the difficulty of determining exactly how they might co-vary. These Leslie matrices are quite simple representations of chinook life histories (Burgman et al. 1993). Also, Burgman et al. (1993) point out that the impact of ignoring correlations between variables can be examined in a rough way by assuming perfect correlation among all the elements in the matrix and comparing the results to the performance of the completely uncorrelated matrix. Burgman et al. (1993) further stated that the estimated risk of extinction will be higher for a perfectly correlated matrix than for less-correlated matrices. We assumed that the simplification we have chosen thus errs on the side of optimism (Burgman et al. 1993).

Another difficulty arises because there is such an obviously accelerating decline in these populations (i.e., the trend of the trends is increasingly negative), suggesting there is likely some level of autocorrelation in vital rates. When there is age structure in the population, as there is for salmon, results can be very sensitive to autocorrelated vital rates. But again, given uncertainty about the vital rates that are driving these observed declines, and that the scope of the data set may not be of sufficient length due to the relatively short period of time since the dams were finished, we did not attempt to include autocorrelation functions. If these trends are as negative as they seem to have been since 1980, the effect of ignoring autocorrelation in this case will be to produce results that are relatively optimistic. But if unknown trends such as improving ocean survival come into play, then perhaps the results will be relatively pessimistic. The future is of course speculative, and decision makers will have to rely on the evidence at hand and hope circumstances will prove more encouraging than the evidence since 1980 suggests. Either way, there does not seem to be an easy way of building such trends into a model as simple as this.

It seems clear that the results discussed here would be significantly impacted by ignoring declining trends as well as autocorrelation in the matrix variables. However, it also seems reasonable to hypothesize that if the trend continues to decline, then these results are overly optimistic, and incorporating the autocorrelation associated with this trend into the retrospective models would also tend to produce results more pessimistic than these.
4.5.1 Distributions

For any of the Leslie matrix parameters for which we had data (or modeled estimates) by brood year, we derived probability distributions using BestFit (Palisade Corporation 1993-2000). When identified, theoretically reasonable, continuous distributions with a confidence of greater than 80% were used. For most variables, however, the available data consisted of eleven to fifteen samples. Although trends were clear, distributions were not. Following accepted practice, for most of the survival and transport variables we used a lognormal distribution based on the mean and variance of the natural logarithm of the data series. In this manner, results could be compared to the deterministic versions that used the geometric mean. For some variables we did not have yearly data, therefore we made assumptions about what shapes and ranges the uncertainty might take (see summary of these probability distributions in Appendix E).

Because the parameters in $S_2$ are so closely linked to one another and to brood year in the data set, it did not seem appropriate to allow them to vary independently of one another. For most of the simulations, we calculated $S_2$ in a spreadsheet. For all FLUSH runs, we then used BestFit to fit a log-normal distribution to the set of $S_2$ values that were derived from FLUSH output and from the ‘$m$’ estimates from PATH (Appendix D). We used the same method for the CRiSP Baseline and “Dam breach” runs, as well.

For the CRiSP/NMFS “Maximize transport” scenario, we instead calculated $S_2$ values for each year by sampling from distributions for the independent variables, and then used BestFit to fit a lognormal distribution created from the NMFS 1994 to 1996 $D$ value estimates. These 500 $D$ values were used to calculate 500 $S_2$ values for each of the eleven migration years (corresponding to brood years 1980 to 1990). BestFit was then used to fit a distribution to about 2000 of these $S_2$ values (based on the CRiSP/NMFS passage/transport model). We also used 1980-1990 brood year passage/transport model estimates for FLUSH (see Appendix D).

4.6 Results of the STUFA stochastic model

Stochastic models in general can be expected to produce less optimistic results than their equivalent deterministic versions (Burgman et al. 1993). For one thing, stochastic models produce output in terms of probability distributions, which helps decision makers evaluate the uncertainty of available choices. Because deterministic models focus attention on a single number (e.g., average population growth rate or expected time to extinction), they do not emphasize the chance that the realized population growth rate could be something less than the average, or that a population with an expected finite rate of growth greater than one can have a high probability of extinction in a short time frame.

In addition to helping emphasize the uncertainty of model results, stochastic models often produce results that are quantitatively less optimistic than their deterministic counterparts. The primary reason for this is due to the fact that when stochasticity is simulated in a model, the...
output variable's probability distribution will tend to be skewed to the right (i.e., "bunched up" towards the left, with a long tail out to the right). The points that cause the tail of the distribution to trail out to the right represent relatively rare events, or outliers. A deterministic model must be based on estimates of central tendency and thus ignores the impacts of outliers. Only in a stochastic simulation can there be years when lots of things happen to go badly for populations\(^6\). It is these outliers that often cause populations to go extinct (Burgman et al. 1993).

In theory, in a stochastic simulation there can also be years when factors affecting survival tend to be optimistic (beneficial). If all the input distributions (i.e., survival probabilities and demographic variables) are normally distributed, and the model is linear, there should be as many outliers to the right as to the left, and the mean of a stochastic model would then be close to the mean of its deterministic counterpart. But in ecological systems (as stated above), demographic parameters are often lognormally distributed. A few outliers will reach extremely large abundances, but most of the trajectories will have considerably lower abundances. The larger the variances in the elements, the more strongly skewed the resulting distributions will be. (Burgman et al. 1993). As a result, the probability of drawing a low survival value, for example, is higher than drawing a high survival value. This tends to result in a more pessimistic model of population growth.

In short, in linear, additive stochastic models such as these, because many of the demographic and survival variable functions are skewed, there are more ways for the joint effect of sampling from all these distributions to be closer to zero than to be very large. Hence, more \(\lambda\)'s will be below the mean than above it (the mode will be less than the mean), and the probability distribution for the resulting \(\lambda\) will be less than the mean \(\lambda\) produced by a deterministic simulation (Burgman et al. 1993).

4.6.1 Baseline

The STUFA stochastic matrices produced less optimistic results in just the way Burgman et al. (1993) described. Compared to the deterministic counterparts, the mean\(^7\) \(\lambda\) for the Baseline model was almost 16% less than the mean \(\lambda\) from the deterministic STUFA Baseline matrix (Figure 4.5). In all management scenarios, median \(\lambda\)'s were lower for the STUFA stochastic model than for the STUFA deterministic model (Figure 4.6). In the stochastic matrix, the probability of \(\lambda\) being less than the nominally sustainable 1.0 was 85% for Marsh Creek, 90% for Poverty Flat, and 85% for Imnaha (Table 4.2). Over 1000 replications, \(\lambda\) ranged from 0.087 to 1.41 (averaged across the three populations). Results from the FLUSH and CRiSP/NMFS passage/transport models for the Baseline scenarios were not different from each other because

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\(^6\) All of these models ignored autocorrelation (correlation between years) as well as correlation among variables. When such correlations are taken into account, it tends to be easier for many things to go bad at once, which is why Burgman et al. (1993) said that ignoring correlations tends to underestimate risks.

\(^7\) To be consistent with CRI analyses, results of the deterministic models were given as mean \(\lambda\)'s. For the stochastic results, means and medians were both produced, and when a summary statistic was needed across the three populations, the average of the three median \(\lambda\)'s was used.
the Baseline scenario’s \( S_2 \) values are fit to the same spawner-recruit data (see Appendix D).

Figure 4.5. Estimated average annual population growth rates (mean \( \lambda \) values) from three matrix models under the Baseline management scenario averaged across three spring/summer chinook populations (Marsh Creek, Poverty Flat, and Imnaha River). Dotted reference line represents \( \lambda = 1 \).
Figure 4.6. Estimated average annual population growth rates from STUFA deterministic (FLUSH [F] and CRiSP[C]; dark gray bars) and stochastic models (median \( \lambda \) values; light gray bars) under various management scenarios (Baseline, Maximize transport, and Dam breach) averaged for three chinook populations (Marsh Creek, Poverty Flat, and Imnaha River). Dotted reference line is \( \lambda = 1 \). FLUSH and CRiSP model results are the same for the reduced hypothesis under Dam breach scenario.

4.6.2 Maximize transport

Results for the “Maximize transport” scenario followed a similar pattern, though the results from the CRiSP/NMFS passage/transport model version were, on average, less optimistic than FLUSH (Figure 4.7). The probability of \( \lambda \) being less than one was 75% for all three populations for FLUSH and 75% for CRiSP/NMFS (Table 4.2). The median \( \lambda \) (0.87 for FLUSH, 0.85 for CRiSP/NMFS, averaged across the three populations) was still much less than one.
Figure 4.7. Average annual population growth rates (median $\lambda$ values) estimated from FLUSH (F) and CRiSP (C) stochastic models (STUFA matrices) for three spring/summer chinook populations (Marsh Creek, Poverty Flat, and Imnaha River) under various management scenarios: *Baseline*, *Maximize transport*, and *Dam breach* (remains and reduced = delayed mortality hypotheses; *Ev Incl* = Everything including dam breach). CRI Leslie matrix estimate (mean $\lambda$ value) is included for comparison.
4.6.3 Dam breach/delayed mortality reduced

Results for the “Dam breach/delayed mortality reduced” scenario were more optimistic (Figure 4.7). There was still a significant probability that \( \lambda \) would be less than 1.0 (35% or 25%, depending on stock; Table 4.2). The median ranged from 1.06 to 1.109 for the three populations. Results were identical for the “Dam breach/delayed mortality reduced” scenario under both FLUSH and CRiSP/NMFS, because \( S_2 \)‘s were identical (Appendix D).

4.6.4 Dam breach/delayed mortality remains

The fourth scenario analyzed was the “Dam breach/delayed mortality remains” scenario (Figure 4.7). Whereas FLUSH produced its most optimistic result for “Dam breach/delayed mortality remains,” a median \( \lambda \) of 1.125, which is a 37% increase over Baseline—CRiSP/NMFS produced “Dam breach/delayed mortality remains” results that were less optimistic than for the “Dam breach/delayed mortality reduced” scenario (i.e., only about 10% improvement over Baseline; Table 4.2). The “delayed mortality remains” hypothesis could be expected to produce less optimistic results than the “delayed mortality is reduced” hypothesis because the “delayed mortality is reduced” hypothesis posits that breaching the dams would decrease extra mortality of non-transported fish, whereas the “delayed mortality remains” hypothesis posits no decrease in extra mortality of non-transported fish. This expected ranking of improvement in \( \lambda \) between the two hypotheses is reflected in the CRiSP/NMFS results but not in the FLUSH results. Reasons are explained in detail in Appendix D.

4.6.5 Everything but dam breach

The next-to-last scenario analyzed was the "Everything but dam breach" scenario. This scenario was approximately analogous to what the CRI did (NMFS 1999b), but was adjusted to reflect a rough estimate of feasibility. "Everything but dam breach" is similar to “Maximize transport” with these exceptions:

1. Harvest: like the CRI, this scenario assumed no harvest (or cessation of harvest)
2. The CRI decreased egg-to-smolt mortality by 10%. The STUFA Baseline stochastic \( S_I \) is based on an estimated range of egg-to-smolt survival probabilities for 1980-1993 for the index populations with a geometric mean of 4.8% and a range of 2.6% to 8.7% (Appendix C). This range was then converted to a histogram for the stochastic simulations. The "Everything but dam breach" scenario used the estimated potential improvements in \( S_I \) for these populations (Appendix C; 2% for the Imnaha, 6% for Marsh Creek, and 11% for Poverty Flat).
3. The CRI decreased estuary mortality by 10%, and reduced predation on smolts by 22%. According to the CRI, this produced a net survival increase in the estuary of 26.3%. In addition, the calculations were based on 1980-1990 data, and Caspian terns did not start having a significant impact until the late 1980's. Thus, the potential improvement indicated
by CRI likely overestimates the amount of benefit over the chosen Baseline period that tern removal may provide. We used recent analyses and reports on tern predation (and potential relocation) to estimate a practicable reduction in estuary mortality due to tern predation (6%; Appendix F). Because no feasible mechanism has been suggested for other ways to decrease estuary mortality by the 10% posited in the CRI, we did not include that extra increment. Because the STUFA model assigns only passage-related and “extra” mortality to $S_2$, that means mortality due to the terns is incorporated into $S_3$, not $S_2$; hence, the "Everything but dam breach" scenario reduces the early ocean mortality ($1-S_3$) by 6%.

This option did not perform nearly as well as the “Dam breach/delayed mortality reduced” or the “Dam breach/delayed mortality remains” scenarios, for either passage/transportation model (Figure 4.7). The "Everything but dam breach" scenario produced $\lambda$’s that were 15% less than the “Dam breach/delayed mortality reduced” scenario with FLUSH, and 18% less than the “Dam breach/delayed mortality reduced” scenario with CRiSP/NMFS. The "Everything but dam breach" scenario produced $\lambda$’s which were 1.3% less than the “Dam breach/delayed mortality remains” with CRiSP/NMFS, and 19% less than “Dam breach/delayed mortality remains” with FLUSH. Median $\lambda$'s were less than one for both passage/transport models, and the probability of $\lambda$ being less than one was 65% to 70%, in the "Everything but dam breach" scenario (Table 4.2).

4.6.6 Everything but dam breach

The last scenario was “Everything including dam breach” which included the increased $S_1$, cessation of harvest, and decrease in Caspian tern predation (as in the "Everything but dam breach" scenario). Both the “Dam breach/delayed mortality reduced” and the "Everything but dam breach" scenarios were the same for FLUSH and CRiSP/NMFS passage/transport models, and the result was a 36.6% increase in median $\lambda$ (averaged over the three populations; Figure 4.7) compared to the Baseline scenario (Table 4.2). It also reduced the probability of $\lambda$ being less than one by 5% (absolute; Table 4.2).

4.7 Sensitivity analysis

The standard elasticity method for doing sensitivity analysis, and the constant percent method preferred by the CRI are problematic in that the results tend to be fore-ordained by the method. For example, the elasticity method will tend to show that results are most sensitive to high-survival rate variables such as adult harvest, while the constant percent method will show that results are most sensitive to low-survival rate variables such as $S_1$ (Mode and Jacobson 1987, Caswell 1989, Crooks et al. 1998, Doak et al. 1994, Ludwig 1999, Mills et al. 1999). The CRI argument that a particular sensitivity analysis method applied to such a simple model can tell us what we should do to save these populations may be questionable. We did not try to replicate that method, because the sensitivity analysis would show either that $S_1$ or $S_2$ is the most important (using the constant percent method) or that $S_4$, $S_5$, and adult migration are the most

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important (using the elasticity method).

Instead, we used a multivariate sensitivity analysis approach, which we applied only to the stochastic model. @Risk has a convenient routine built in to perform both regression and rank correlation analyses on the variance, so that the variance of the output can be partitioned into its component parts, and their relative contributions ranked. It is important to emphasize that the goal of this sensitivity analysis was only to investigate the relative impacts on the results of our best estimates of uncertainty associated with each of the variables. This analysis of the relative impacts of model uncertainty does not determine what the best approach is for saving Snake River salmon. That would require a formal decision and feasibility analysis. However, if the question is about reducing risk, it is very much about reducing uncertainty. That is the kind of question this sort of analysis can help illuminate.

In every scenario simulated in this section, this sensitivity analysis showed that the two variables that contributed by far the most to the uncertainty in \(\lambda\) were \(S_2\) (juvenile passage and extra mortality) and \(S_3\) (first year ocean survival). \(S_2\) accounted for around 75% of the variance "explained" by the regression, and \(S_3\) typically accounted for around 20% or less. The simulations converged with fewer than 1000 replications (1000 replications were run), and the sensitivity analysis regressions typically produced \(R^2\) values greater than 0.75.

5. Fitting CRI Matrix Directly to Historical Spawner-Recruit Data

The analyses presented in Chapters 2 through 4 use the STUFA matrix and results from PATH analyses to explore the effects of “extra mortality” on CRI’s findings and conclusions. The PATH results used come from decomposing the Snake River spring/summer chinook spawner-recruit data, using both historical and recent recruits per spawner data (R/S data) for these stocks, and also by using R/S data from downstream stocks of the same species and life-history type as controls. CRI has expressed doubt about the validity of using downstream stocks as controls. In PATH, we believed the downstream stocks provided useful information on how broad-scale climate patterns affect Columbia Basin stream-type chinook salmon. In fact, goodness-of-fit tests of the MLE (Maximum Likelihood Estimation) model used to fit R/S data from the Snake River and downstream stocks indicated that a common effect (“year effect”) of climate on all the stocks resulted in a better model than models where completely independent climatic variation was assumed (and when number of parameters used in fitting the models was taken into account).

However, a key point to be made is that extra mortality of Snake River stocks is not simply an artifact of PATH, and its existence is not even dependent upon using downstream stocks as controls. Only the magnitude of extra mortality used in these analyses is unique to PATH’s method of estimating it. Extra mortality is defined in Marmorek and Peters (1998b, page 67) as “any mortality occurring outside of the juvenile migration corridor that is not accounted for by either: 1) productivity parameters in spawner-recruit relationships; 2) estimates of direct
mortality within the migration corridor (from passage models); or 3) for the delta model only, common year effects affecting both Snake River and Lower Columbia River stocks” (italics added). In addition to the ‘delta’ model (which assumed common year effects), an ‘alpha’ model was used to estimate mortality in different life stages from the R/S data. The alpha model assumed upriver and downriver stocks varied independently, and actually found more extra mortality of upriver stocks (Appendix D).

Using the historical R/S data of the Snake River stocks alone to test for extra mortality can serve as a kind of validation, or check, of the model parameterization. We can apply the CRI deterministic matrix method to historical Snake River R/S data, taking into account differences in life stage vital rates that are known to have been different in the past. If there is no extra mortality in the present, compared to the historical period, the difference between historical and current \( S_I \) and SAR values estimated from the matrix should mirror the difference between historical and current values estimated empirically. If the resultant \( S_I \) and SAR estimates do not seem plausible, this will suggest that extra mortality is apparent even without using PATH analyses or downstream indicator stocks, and we can estimate the magnitude of extra mortality that needs to be accounted for. This would support the PATH conclusions about the presence of extra mortality, providing insight into the relative likelihood of different hypotheses about the causes of extra mortality. It would therefore have implications for the CRI analysis of the expected efficacy of future management actions in helping to avert extinction and achieve recovery of Snake River spring/summer chinook.

We can use historical R/S data independently of any PATH analyses, and without using any data from downstream stocks, to test for the existence and magnitude of extra mortality. Under the CRI default parameterization of the deterministic Leslie matrix, the only parameters that would be expected to vary between the present and the 4-dam period would be: 1) the component of \( S_2 \) describing direct mortality through the hydrosystem (since mass transportation hadn’t begun, the parameter \( S_d \) would completely specify survival through direct juvenile passage mortality); 2) \( \mu \) (the mortality of adults as they swim upstream), since harvest rates and conversion rates (survival rates of adults passing dams) were different; 3) the propensity to breed and generation time, since these are affected by the age structure in the data used; and 4) egg-to-smolt survival rate (\( S_1 \)), since this is the vital rate parameter varied to fit a series of R/S data, after other vital rates are estimated. The parameters \( S_e \) (part of \( S_2 \)), \( S_3 \), \( S_4 \), and \( S_5 \) would not be expected to change, given the rationale for the CRI parameterization noted earlier in this paper.

By applying a Leslie matrix to information from a period prior to completion of the Snake and lower Columbia River hydrosystem, we can see what effect using the appropriate NMFS and CRI estimates for historical period vital rates has on the estimate of \( S_I \). We can compare the relative magnitude of these ‘historical’ \( S_I \) estimates with matrix estimates for current values, and compare the change in magnitude between historical and recent periods to independent, empirically-based estimates of the trend in spawning and rearing survival rates between the two periods. The historical configuration of the matrix will also result in an average SAR value (Lower Granite Dam as juveniles to Columbia River mouth as adults—see earlier calculations) different from the recent period, since the parameters comprising \( S_I \) (except for \( S_e \)) change. As
with \( S_I \) estimates, we can compare these “before” and “after” SAR estimates with empirically derived estimates.

We used R/S data from a period when Snake River spring/summer chinook passed through only four dams and before mass transportation of smolts was instituted. The period from brood year (BY) 1957 to 1967 represents a period with R/S data for all of the index stocks, and hydrosystem configurations that resulted in Snake River spring juvenile migrants having to pass from three to five dams (three for BY 1957-1959, four for BY 1960-1965, and five for BY 1966-1967). This length of this period is also the same as the period of time initially used by CRI to parameterize the Leslie matrix (BY 1980-1990). The hydrosystem configuration of that era was also similar to the new configuration being proposed for the future under the Snake River dam breach option (\textit{Dam breach} or \textit{A3}).

We adjusted for suspected differences in vital rates in a manner intended to be consistent with NMFS and CRI hypotheses. We used NMFS estimates of four- to five-dam and current juvenile passage direct mortality, and adjusted for harvest and adult passage mortality differences. We were then able to use the CRI method to estimate \( S_I \) values for the historical period, and calculate what other resulting parameters were, one of which (SAR) could then be compared to empirically-based estimates of this rate during the period where Snake River fish passed four or five dams.

We performed this comparative analysis using the same three index stocks used for the analyses presented in Chapters 2, 3, and 4. Parameter estimates used for each of the life stages, for both the original CRI parameterization of the matrix for 1980-1990 (or 1994) brood years, and for the 1957-1967 brood year data are shown in Table 5.1.

The resulting \( S_I \) and SAR values for each of the three stocks is shown in Table 5.2. Figure 5.1 shows the comparison between historical SARs derived from the matrix and recent SARs derived from the matrix. Figure 5.2 shows the values of \( S_I \) derived from the matrix from the historical period, along with the values obtained for two different recent periods (one including R/S data through 1995, the other through 1999).
Table 5.1. Parameter values used in Recent and Historical Period CRI-type Leslie matrix.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value used for Recent Period (1980-1995)</th>
<th>Value used for Historical Period (1957-1972)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>$S_1$</td>
<td>Stock specific</td>
<td>Stock specific (See Table 5.2)</td>
<td>Estimated from Euler equation</td>
</tr>
<tr>
<td>$S_2$</td>
<td>0.058</td>
<td>0.029</td>
<td>(1)</td>
</tr>
<tr>
<td>$S_3, S_4, S_5$</td>
<td>0.8</td>
<td>0.8</td>
<td>CRI</td>
</tr>
<tr>
<td>Fecundity</td>
<td>Stock specific</td>
<td>Stock specific</td>
<td>CRI, see Table 2.1</td>
</tr>
<tr>
<td>Fraction Female</td>
<td>0.5</td>
<td>0.5</td>
<td>CRI</td>
</tr>
<tr>
<td>$P_s$</td>
<td>0.9</td>
<td>0.9</td>
<td>See Table 2.1</td>
</tr>
<tr>
<td>$\mu$</td>
<td>Stock specific</td>
<td>Stock specific</td>
<td>(2)</td>
</tr>
<tr>
<td>$b_3$</td>
<td>Stock specific</td>
<td>Stock specific</td>
<td>See Table 3.2 (3)</td>
</tr>
<tr>
<td>$b_4$</td>
<td>Stock specific</td>
<td>Stock specific</td>
<td>See Table 3.2 (3)</td>
</tr>
<tr>
<td>$b_5$</td>
<td>1</td>
<td>1</td>
<td>See Table 3.2</td>
</tr>
</tbody>
</table>

(1) Uses CRI $S_x$ of 0.07. Recent values use CRI estimates for $p_t$, $s_d$, and $s_b$ (See Table 1.1). Historical $s_d$ value (0.42) is average of NMFS estimates of four- or five-dam $s_d$ for 1966-68 (NMFS 1999a, Appendix A, Annex B).

(2) Recent values of $\mu$ from CRI (see Table 1.1): MAR = 0.496; IMN = 0.458; POV = 0.420. Historic values used: MAR = 0.721; IMN = 0.651; POV = 0.579.

(3) In order to save time, we used the “propensity to breed” values estimated from the recent data in the historical period matrix. Had we used the historical data to estimate them, the propensities would have been different, but likely not so different to substantially change the results.

Table 5.2. SAR and $S_I$ values for historical period resulting from CRI-type matrix.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>MARSH</th>
<th>POVERTY FLAT</th>
<th>IMNAHA</th>
</tr>
</thead>
<tbody>
<tr>
<td>SAR</td>
<td>0.016</td>
<td>0.016</td>
<td>0.016</td>
</tr>
<tr>
<td>$S_I$</td>
<td>0.083</td>
<td>0.037</td>
<td>0.067</td>
</tr>
</tbody>
</table>
Figure 5.1. Average SARs obtained from ‘Historical’ (1957-1972) and ‘Recent’ (1980-1995; original CRI), and latest ‘Recent’ CRI (dated 3-21-00) configurations of CRI Leslie matrix.

Recent SARs derived from the original CRI matrix parameterization are much higher than those measured recently from PIT-tagged smolts (Chapter 1). In PATH, and other previous analyses, it was generally agreed that SARs prior to 1970 were higher than those from 1980 on; what was disputed was the reason for this. The lower empirically-estimated recent SARs track the lower recent R/S values, as would be expected (Figure 5.3; reproduced from Appendix B, Figure B.1). Historical SARs derived from the CRI matrix, however, are much lower than estimates from the late 1960s. This counter-intuitive results suggests that applying the CRI matrix method (i.e., ignoring extra mortality) to historical data predicts, incorrectly, that recent SARs have been higher than those in the historical period. This also requires survival rates early in the life cycle to have been dramatically higher in the historical period than they have been recently.
In fact, for two of the stocks, a dramatic (nearly 8-fold for Marsh Creek) decline in egg-to-smolt survival rate has to have occurred to explain the decline in R/S values from the historical period to the recent period (Figure 5.2). However, these two stocks (Marsh Creek and Imnaha River) are in drainages where the habitat quality is currently considered ‘good’ (Beamesderfer et al. 1997). The Poverty Flat stock, in the South Fork Salmon River (Idaho) drainage, is in more degraded habitat. There were major human-induced and naturally produced sedimentation episodes in the 1960s which likely depressed production in that period (Beamesderfer et al. 1997). Since that time, conditions have improved somewhat. In contrast, the $S_I$ estimated from the CRI method for Poverty Flat shows a slight decrease from the earlier period. This exercise can be run for the other index stocks; results for those would likely be more similar to Marsh Creek and Imnaha River results than Poverty Flat (except perhaps for Johnson Creek, which is also in the South Fork Salmon River drainage). Some of these other index stocks are in wilderness areas, so it would be even harder to explain an estimated decrease in egg-to-smolt survival rates of an amount similar to the results for Marsh Creek or Imnaha River.

We can compare the difference in $S_I$ estimates between historical and recent periods with the

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trend in smolt-per-spawner estimates for the entire ESU (Figure 5.3). There is no apparent trend in the values, confirming that the dramatic decline in $S_1$ implied by the CRI matrix parameterization is suspect.

Figure 5.3. Patterns of SAR and smolts/spawner (natural log scale) for Snake River wild spring/summer chinook, smolt years 1962-1994. See Appendix B for details.

The analysis here strongly suggests that mortality in some other life stage, most probably the stages after juveniles have migrated to below the hydrosystem, is much higher now than it was in the 1960s. If, as this analysis suggests, the magnitude of the drop in spawning and rearing survival needed to fit the data isn’t credible, it raises questions about what was responsible for the decline in survival rates, questions which were addressed in PATH. It is incumbent upon CRI to delineate the hypothesized magnitude of changes in the other life stages, and what mechanisms have caused these changes. We have presented analysis and evidence suggesting delayed effects of the presence and operation of the hydrosystem and transportation program are the most likely culprits. Other causes are possible, but empirical and mechanistic evidence should be advanced if these are to be considered plausible. These questions have substantial implications for the prospects of different hydrosystem management actions for recovering Snake River spring/summer chinook salmon. The analysis here and in previous chapters suggests that without putting forth credible explanations for the substantially higher spawner to recruit survival in the four-dam period, statements such as “drawdown alone will not recover” Snake River spring/summer chinook salmon are premature.
6. Implications for draft EIS (A-Fish Appendix) conclusions

The DEIS (NMFS 1999a) and other products based on the CRI, place emphasis on results based on varying the Leslie matrix parameters to simulate the relative benefits that could be achieved by focusing on different life stages (or model parameters) in the matrices. They conclude that:

1) "...improvements in first year survival (S₁) and in survival upon entering the estuary and ocean would have the greatest impact on annual rates of population growth" (NMFS 1999a, p. A ES-6). The CRI finds that reducing egg-to-smolt mortality by 10% (increasing S₁) will increase average population growth rate by 20%-30% (average of 28.5%), whereas a 10% reduction in estuary and first year in the ocean (increasing Sₑ) would increase λ by an average of 19.8%.

We wanted to understand how the model structure and parameter values affect this conclusion. We ran the Baseline scenario (using the stochastic STUFA matrix) in combination with the estimates for potentially feasible habitat improvements (i.e., increase S₁, egg-to-smolt survival) described in Appendix C (namely 6% for Marsh, 11% for Poverty Flat, and 2% for the Minam River). This “status quo and habitat improvement scenario” produced an increase in median λ of 1.7% to 2.9%—far less than the 28.5% demonstrated by the CRI. In addition, the probability of λ being less than one ranged from 75% to 80%.

We again ran the Baseline scenario, this time improving Sₑ instead of S₁. Our model did not have an estuary survival variable Sₑ, but rather an extra mortality Sₑm parameter which was not directly comparable. In our model, estuary mortality is included in S₃ rather than S₂ (in the CRI Leslie matrix Sₑ is included in S₂). In order to simulate this improvement in estuary survival, we thus decreased mortality in the stage that included estuary mortality, i.e., we reduced estuary mortality (1-Sₑ) by 10%. This produced an average increase of 10.3% in the median λ's, much less than the CRI Leslie matrix results (19.8%). In addition, this 10% increase only increased the expected λ up to 0.90 to 0.93 for the three populations, with probabilities of λ being less than one of 65% to 75%. It is worth noting that because S₁ is much less than Sₑ, if we repeated the CRI's “constant percent” sensitivity analysis for S₁, it would show that a 10% percent decrease in egg-to-smolt mortality would produce a larger change in λ than a 10% decrease in early ocean mortality. This relative increase is similar to the results from CRI's constant percent sensitivity analysis indicated that increasing S₁ would have a bigger effect than increasing Sₑ. However, as the CRI noted, it is adult mortality that plays the biggest role in sensitivity analysis when using the more common elasticity sensitivity analysis method. Thus, sensitivity analysis conducted with either of these two methods produces a pre-determined result that depends on the method chosen.

2) "...further management actions aimed at harvest and downstream survival...(excluding dam breaching) are not likely to be that helpful" (NMFS 1999a, p. A8-20), and "...perfect downstream survival by itself would not be enough given the mortality suffered during other life stages of spring/summer chinook salmon" (NMFS 1999a, p. A8-20).
"Perfect downstream survival" could mean either that all mortality due to the hydrosystem (direct and delayed) is eliminated, or that only direct mortality due to the hydrosystem is eliminated. The CRI did not include extra mortality in their analyses. To simulate the scenario most similar to the CRI assumption, which assumes that only direct mortality is eliminated, we set $S_b$ and $S_d$ to one, and reran the Baseline scenario. This had the effect of leaving extra mortality in the STUFA model but eliminating direct downstream mortality. $S_2$ is represented by lognormal distributions in the stochastic simulations, and this assumption increased the expected value of $S_2$ from 0.17 to 0.26 (53% increase in expected value of $S_2$). This produced an increase in median $\lambda$ from 0.82 to 0.88, an increase of only of 7.67% (averaged across the three populations). It also reduced the probability of $\lambda$ being less than one from 87% to 75% (averaged across the three populations: Marsh, Poverty Flat, and Imnaha). The CRI predicted only a 3.6% increase in $\lambda$ with perfect system survival, and although the STUFA matrix yielded almost twice this increase, we agree that perfect downstream survival by itself would not be enough.

Another way to look at system survival is to include the possibility that perfect downstream survival implies that extra mortality is somehow reduced or eliminated. To simulate that, we increased $S_2$ to 1.0 in the Baseline scenario (100% survival from Lower Granite Dam to below Bonneville Dam). This change had a relatively large effect, producing an increase in the median $\lambda$ (averaged over the three populations) of over 70%, bringing $\lambda$ up to around 1.4 (from 0.82) with less than a 15% probability of $\lambda$ being less than one.

3) In the CRI-version of our "Everything but dam breach" scenario, they analyzed a combination of: (1) no harvest or cessation of harvest, (2) a 22% reduction in predation on smolts, (3) 100% transport, (4) a 10% decrease in estuary mortality ($1-S_e$), and (5) a 10% decrease in mortality in the $S_1$ stage. CRI concluded that "...a 14% increase in annual population growth rates... could be expected, which is likely to recover the populations of spring/summer chinook salmon" (NMFS 1999a, A8-21).

In our "Everything but dam breach" scenario, we took feasibility into account when we modified the parameters. We assumed that the improvement in $\lambda$ would happen immediately, as did the CRI. With the FLUSH passage/transport model assumptions, this scenario produced an average 11.6% improvement in $\lambda$ over Baseline, but the probability of $\lambda$ being less than one was 70%, and the median $\lambda$ averaged an unsustainable 0.92 for the three populations. Under CRiSP/NMFS, the improvement over Baseline was a more modest 8.1% and increased the median $\lambda$’s up to a similar median of 0.89 (averaged across the three populations). If this modeled 8% to 12% improvement represented what would happen in the real world with harvest moratoriums and improvements in downstream survival, then they may be large enough to significantly increase $\lambda$, but will still fall far below the increase in $\lambda$ needed for survival.

4) Dam breaching alone and habitat and harvest actions "...are roughly equivalent in their effect on population growth, and neither by themselves is likely to recover Snake River chinook salmon" (NMFS 1999a, p. A8-22).
Comparing the "Everything but dam breach" and the dam breach scenarios, the only way that these scenarios are equivalent is if the delayed mortality remains hypothesis is assumed with the CRiSP/NMFS passage/transport model. In that case, λ's do not reach sustainable levels either way, but they are very similar to each other in magnitude (0.887 for breaching, and 0.899 for "Everything but dam breach"). With CRiSP/NMFS, "Everything but dam breach" produces λ's that are 18% less than the “Dam breach/delayed mortality reduced” scenario. Thus, with the CRiSP/NMFS passage/transport model, whether or not breaching is indeed equivalent to "Everything but dam breach" depends on whether the delayed mortality hypothesis is assumed to be true. In other words, the relative benefit of dam breach versus “Everything but dam breach” depends on to what degree delayed mortality is related to hydrosystem experience. Under FLUSH, the "Everything but dam breach" scenario produced λ's that are 15% to 19% less than the dam breach scenarios. Instead, as indicated in PATH, the original CRI, and our current analysis, the most risk averse (most robust) option appears to include aggressive action in all H’s including dam breach.

7. Conclusions

We concluded that:

1) The CRI model assumes values for life stages for which estimates are relatively weak, while allowing the model to fit values for parameters for which relatively robust, independent estimates are available. The CRI matrix parameterization produces SARs that are more than threefold greater than the USACE and NMFS have reported elsewhere, including the DEIS (BPA 1999, NMFS 1999a). It also produced egg-to-smolt survival rates that were less than half those estimated in PATH and agency reports for these and other similar Snake and Columbia River spring and summer chinook populations.

2) Because the CRI sensitivity analyses and numerical experiments play such an important role in the DEIS, the answer to the question "what should we do?" depends on how mortality is allocated. If the lowest survival rate is in the egg-to-smolt stage, as it is in the CRI analyses, then the emphasis will be on freshwater survival. If the lowest survival rate is in the estuary/early ocean phase, which it is when survival rates are based on empirical data, then the emphasis will be on the estuary/early ocean life stage survival—a finding more consistent with PATH.

3) For the deterministic analyses of the key options being considered in the DEIS, we found that although juvenile passage/transport survival probabilities produced by the FLUSH and CRiSP/NMFS passage/transport models differed from each other for some of the scenarios, the rank-ordering of the alternatives is consistent with PATH. Deterministically modeled SARs and λ's that resulted from dam breaching scenarios were higher than those that resulted from the Baseline (status quo) or “Maximize transport” scenarios—with one exception: with the CRiSP/NMFS passage/transport model, when the delayed mortality remains was assumed, then dam breaching actually produced a lower SAR and thus λ than “Maximize transport” (i.e., without dam breach), though the average λ was still a significant (38.5%) improvement over the status quo.
4) The stochastic analyses produced less optimistic results and provided more insight into the relative impacts of different sources of uncertainty than did the deterministic analyses. The stochastic version of the Baseline matrix model produced lower average λ's and higher probability of λ's being less than one ⁸ than the CRI or the STUFA deterministic version for both the FLUSH and the CRiSP/NMFS passage/transport models.

For the Baseline scenario, 85% to 90% ⁹ of the 1000 replications produced average λ's less than one, the nominal replacement rate, and the average of the λ's for the three populations (0.785) was significantly lower than the average CRI λ’s (0.852).

5) Comparing the effectiveness of different management actions with a deterministic matrix is misleading, because only mean vital rates change. This ignores the effect of changing variance in vital rates on the median growth rate and on the probability of growth rates being less than one. The ranking of the “Maximize transport” scenario between the two passage models, in terms of percent improvement over Baseline, switches from deterministic analysis to stochastic analysis (under the “Maximize transport” scenario, CRiSP estimate is higher than FLUSH for deterministic; opposite is true for stochastic). The ranking of effectiveness of actions as measured by improvement in λ is sensitive to use of stochastic versus deterministic matrix. With the deterministic matrix, “Everything but dam breach” would be better than the “Dam breach/delayed mortality remains” scenario with CRiSP. In stochastic analysis, dam breach scenarios are always the best option, regardless of passage model or delayed (or extra) mortality hypothesis.

6) Only with the dam breach scenarios (delayed mortality remains or is reduced) does the stochastic version produce median λ's greater than one. Depending on passage/transport model (FLUSH or CRiSP/NMFS) and whether delayed mortality (remains or reduced hypotheses) was assumed, the most optimistic results indicated that 25% to 35% of the replications produced λ's less than one, and the most pessimistic results were that 65% to 70% of the replications produced λ's less than one.

7) The "Everything but dam breach" scenario, which roughly modeled feasible improvements in survival without dam breaching and assumed they were implemented immediately, produced at most about one third the improvement in survival that dam breaching scenarios did. The dam breaching alone scenarios (even with the NMFS assumption of D = 0.825) produced median λ's greater than one. There were no feasible non-breach scenarios that provided benefits adequate to move median λ above one. The "Everything but dam breach" scenario produced lower λ's than the breaching scenarios: 0.915 under FLUSH and 0.887 under CRiSP, with 65% to 70% of the replications producing λ's less than one.

8) The "Everything including dam breach" scenario produced a 36.6% increase in median λ over Baseline (with both passage/transportation models). It also reduced the probability of λ

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⁸ These were not extinction analyses, but when λ’s are less than one, if λ is assumed to represent a temporally stable population, then the population growth rate is less than what is required for sustainability. If λ is 0.9, for example, that represents a decline of 10% per year.

⁹ The stochastic models were only run for Marsh Creek, Poverty Flat, and the Imnaha populations.
being less than one by 5% (down to 20% to 30%). To put it in context, however, adding the improvements in survival probabilities represented only a 3.7% increase over the “Dam breach/delayed mortality reduced” scenario.

9) Rather than conducting single-variable sensitivity analysis with the stochastic model as we did with the deterministic version, we used a multivariate sensitivity analysis approach, which allows the variance of the output to be partitioned into its component parts, so that their relative contributions can be ranked. This analysis illuminates the importance of reducing uncertainty, given that we are attempting to identify actions that will reduce risk. In every scenario simulated with the stochastic matrix, this kind of sensitivity analysis showed that the two variables that contributed the most to the uncertainty in \( \lambda \) were \( S_2 \) (juvenile passage survival including extra mortality) and \( S_3 \) (first year ocean survival). \( S_2 \) typically accounted for around 60% to 75% of the variance "explained" by the analysis, and \( S_3 \) typically accounted for around 20% or less. This analysis does not necessarily indicate that the best option for saving these populations is to improve \( S_2 \)—instead it indicates that variation in juvenile passage and early ocean survival has a large influence on the effectiveness of management actions.

10) The existence of “extra mortality” is not dependent on PATH analyses or the use of downstream stocks as controls for the Snake River stocks. Fitting the Leslie matrix using the CRI method to historical Snake River R/S data, from a period where hydrosystem configuration was similar to the dam breach option, provides a kind of validation of method, by comparing resulting survival rates to empirical estimates. This PATH-independent method confirms PATH results: there is substantial extra mortality in recent years, not accounted for in the CRI approach. It suggests that until a weight of evidence process on hypotheses of extra mortality is done, statements such as “drawdown alone will not recover” Snake River spring/summer chinook salmon are premature.

It is important to keep in mind that these conclusions are based on the responses of a simple model to changes in a few variables, and that the response variable is also single and simple. However, comparative analyses of management actions focusing on relative improvements in \( \lambda \) may be useful. Overall, these model results are generally consistent with PATH: the scenarios that included dam breaching had the highest probability of increasing population growth rates. The degree of improvement depends on assumptions about delayed mortality and the passage/transport model used.

8. Discussion

In general, the goals of our analysis were to evaluate the parameterization and structure of the original NMFS matrix model, to compare the results from this modeling approach to the results from the PATH approach, and to evaluate how the conclusions of the NMFS matrix model are affected by model structure, uncertainties, and data limitations. Our approach involved several steps. We first evaluated the distribution of mortality in the NMFS matrix model and how model estimates of survival in some life stages compared to empirically-based data estimates from outside of the model structure. Then we re-parameterized the original deterministic (not affected
by variability) NMFS matrix model based on these empirically-based data estimates using what we believe was a more data-driven approach that corroborated with smolt-to-adult survival rates (SARs). We used this model to evaluate specific management actions (with feasibility incorporated) in terms of their relative increase in the population growth rate. And finally, we stochasticized our STUFA matrix model such that it incorporated environmental variability and measurement error where possible.

While the effect of these changes in the analysis were revealing and highlight some important points discussed below and throughout the paper, we note that we still have considerable concerns with the type of modeling approach adopted by NMFS. And while our re-parameterized and stochasticized model does address some of these concerns, there are limitations of this type of deterministic, single-hypothesis modeling approach that cannot be overcome without moving toward a biological decision approach like the one used in PATH. In particular:

1) Neither the original CRI matrix model nor our re-parameterized and stochasticized model addresses the limitations of using the population growth rate as a response variable;

2) The original CRI matrix model as well as our re-parameterized and stochasticized model assume that demographic and environmental characteristics of these populations have been and will continue to remain homogeneous;

3) The original CRI matrix model as well as our re-parameterized and stochasticized model ignore the effects of non-stationary changes in stock/recruitment patterns, such as the declining trend observed over the last 40 years for the Snake River stocks; and

4) The original CRI matrix model as well as our re-parameterized and stochasticized model ignore potential effects of density dependence.

Perhaps most important, because neither of these matrix model analyses explicitly takes a multiple hypothesis/biological decision analysis approach, they do not address the risk of taking one management action over another, given critical remaining uncertainties. Given the high extinction risk faced by these stocks in the near future, choosing a management action (or combination of actions) with the least amount of risk is crucial.

In our analysis, we demonstrate the importance of corroborating model-based vital rates with empirically-based estimates where possible. In the original NMFS CRI model, estuary survival rate was based on data for a different species (from a different geographical region) over a different time period (1.5 years as compared to a few days in their life cycles). The smolt-to-adult survival rates (SARs) that result from this estuary survival rate and from ocean survival rates do not compare to those observed for these indicator stocks. The allocation of mortality should be corroborated, wherever possible, with empirically-based estimates of survival for each life stage, from outside the model. Otherwise, model predictions, and therefore management decisions, may be artificially influenced by the way the model was parameterized. For example, NMFS concludes, from their original matrix model, that the greatest potential for improving survival overall is in the egg-to-smolt survival stage. In terms of management actions, survival
in this life stage is expected to be affected most by habitat quality and quantity. However, in our re-analysis of the original NMFS matrix model, we demonstrate that egg-to-smolt survival rates from empirically-based data (not generated by the model itself) are much higher than those resulting from the NMFS matrix model. Thus the potential for increasing survival rate in this life stage, due to habitat improvement, may be much lower than NMFS suggests.

Similarly, we demonstrate that when the matrix model is calibrated with SARs (smolt-to-adult survival rates), the results from the NMFS analysis switch such that the greatest potential for improvement in survival now comes from changes to estuary or early ocean survival (where delayed hydrosystem mortality is likely to occur) instead of from changes in egg-to-smolt survival. The CRI distribution of mortality is influenced by values used for estuary and ocean survival. A review of the cited literature revealed that there are many values that could have been inferred from these references. More important, many of the literature values were not specific to spring/summer chinook of the Columbia River Basin. In fact, literature values for the estuary were based on either coastal coho or Alaska pink salmon over a year and half in the estuary and early ocean. Inputs for ocean survival, estimated for sockeye salmon, were described in a reference of a reference. This reversal in rank of the life stage estimated to have the greatest potential for improvement demonstrates how influential the assumed distribution of mortality is on model results and therefore how important it is to corroborate model derivations of survival with empirically-based estimates wherever possible. The allocation of mortality (or survival) used in this type of matrix model will ultimately determine which life stages have the greatest potential for improvement in survival from management actions in all H’s (hydro, harvest, habitat, and hatcheries).

In addition, we demonstrate the importance of considering the feasibility of a management action, in terms of improving survival in certain life stages. In the example above, NMFS investigated the potential increase in population growth rate that the CRI matrix model would produce given a reduction in egg-to-smolt mortality of 10%. Since this 10% decrease in mortality nets a large increase in survival overall (i.e., across the whole life cycle), NMFS concluded that the greatest potential for improving survival will come from improving survival in this early egg-to-smolt life stage. However, we point out that there are at least two aspects of feasibility that are being ignored using the NMFS approach, a biological aspect and a practical aspect. First, a 10% decrease in mortality may not be biologically possible. Survival in the egg-to-smolt stage is constrained by inherent stock productivity and habitat quantity, in addition to habitat quality. Therefore, assuming that improving habitat quality will decrease mortality by 10% may not be realistic.

Second, it is possible that we may not be able to improve habitat quality beyond its current state, as many stocks modeled by NMFS and by PATH are currently in good, even pristine habitat (i.e., in wilderness areas). It is inappropriate (or perhaps unrealistic) to assume that the ESU as a whole has some potential for improvement in survival from a management action that may have no or little effect on survival for a substantial number of the individual spawning stocks that comprise the ESU. The modeling exercises also assume that all habitat improvements happen immediately, yet in reality, these improvements may take decades before they are effective. And
finally, we may not be able to improve habitat quality for purely practical reasons, such as private land ownership. We are concerned that the NMFS approach may overestimate the potential survival improvements in some life stages because they do not explicitly model management scenarios. In addition to the problems highlighted above, this approach leaves decision makers with no context to deal with, or even understand the importance of, remaining uncertainties, and with no concrete actions to consider. We believe it is more appropriate to explicitly model different management scenarios including the effect of remaining uncertainties, instead of leaving it up to a decision maker to try and guess how to get a 10% reduction in mortality in a certain life stage, or across several life stages. Finally, NMFS fails to distinguish between “natural” and “human-induced” mortality and, therefore, cannot conclude that life stages with high levels of mortality have the greatest potential for improvement.

In our re-analysis of the original NMFS matrix model, we explicitly model management scenarios and consider the biological constraints of survival in each life stage as well as a preliminary attempt to address the practical aspects of feasibility. When these considerations are incorporated into the analysis, dam breach demonstrates a greater increase in the population growth rate, as compared to other actions or combinations of other actions. In terms of the expected improvement under a status quo or improved existing hydrosystem scenario, our results agree with the NMFS matrix results and indicate that little further improvement in population growth rate can be expected under either status quo hydrosystem management (Baseline) or by maximizing transportation (Maximize transport). However, our results demonstrate that even when the NMFS assumptions of a high ‘D’ (little delayed mortality of transported fish relative to in-river fish) were incorporated, when feasibility was incorporated into our analysis, it was not possible to increase the population growth rate significantly without dam breach. Our results indicate that implementing “Everything but dam breach” is insufficient, and that the best strategy for minimizing extinction risk includes improvements in the other H’s identified in “Everything but dam breach” and dam breach management scenarios.

We believe that there are several lines of evidence that link hydrosystem experience of both transported and non-transported (in-river) fish with delayed mortality in the estuary and early ocean. Evidence for extra mortality comes in several forms. There is indirect evidence from retrospective analyses of stock and recruitment data, which indicates that stocks which migrate through fewer dams have higher survival than their upriver counterparts. Similarly, historical data from Snake River stocks (i.e., when they passed through three to five dams and were not subject to transportation) indicate much higher adult return rates than in recent years, even though direct passage mortality is estimated to be less than in that historical period. These differences could not be explained by direct mortality related to hydrosystem passage. There is also empirical evidence of extra mortality, and the relationship between hydrosystem experience and this extra mortality, from recent NMFS PIT tag data documenting individual hydrosystem passage and survival histories. When the differential delayed mortality of transported fish is greater than zero (i.e., when $D < 1$), this is evidence of hydrosystem-based delayed mortality of transported fish.

From a biological perspective, hydrosystem delayed mortality is expected due to the cumulative
stresses of hydrosystem passage, including the collection/bypass systems (see discussions of the hydro extra mortality hypothesis in Marmorek and Peters 1998a, b). Consider, for instance, that when surface-oriented smolts approach a dam, they are delayed (Rondorf et al. 1995, Adams et al. 1996). As the water current pulls smolts downward toward the turbine intakes, radio tag studies show that smolts fight the current. From the intake screens, the guided smolts are returned in 3 seconds back to the surface (about 70 feet) into a turbulent gatewell. Smolts go from 1, to 3, and back to 1 atmospheric pressures in about 10 seconds. At Lower Granite Dam they are then piped from the gallery nearly a quarter mile to below the dam at high velocity (30 ft/second) and pressure through two 90-degree turns, experiencing high turbulence and rapid deceleration at the end. Smolts are then de-watered and passed through a separator (USACE 1981). Typically for transport evaluations, smolts are then held in raceways up to 48 hours, dip-netted and transferred to the sample room, anesthetized and marked, returned to the raceways for recovery, then barged, trucked, or flushed through an 8-inch pipe for release to the river. In addition, there is a plethora of literature discussing the cumulative affects of stress on fish and mechanisms that may cause delayed mortality in the saltwater stage. More detailed discussions of these topics and of ‘D’, can be found in several references (Marmorek et al. 1998; Marmorek and Peters 1998a, b; Bouwes et al. 1999; NMFS A-Fish Appendix 1999a).

Our analysis also highlights the importance of including variability in survival rates and model parameters when comparing alternative management scenarios. At low population sizes, it may be as important to reduce the variability in survival rates as it is to increase the mean survival rate. Management scenarios that result in widely fluctuating survival patterns, or do not take into account fluctuating environmental patterns, may push the population to low abundance levels where depensatory processes (i.e., negative effects on population size that occur at very low population sizes) are influential. These processes may act to increase the rate of decline of the population. None of these simple matrix models take these concerns into account.

In addition, due to mathematical properties that affect model predictions, deterministic models (no variability) tend to produce more optimistic results compared to stochastic models, which include variability. When we incorporated stochasticity into the STUFA matrix model, the most likely population growth rates were substantially lower than those observed from the deterministic model. This result is expected because deterministic models are based on measures of central tendency and thus ignore the impacts of outliers (Burgman et al. 1993). Only in a stochastic simulation do such risks have an opportunity to exhibit their potential impacts. Our findings agree with the Independent Scientific Advisory Board’s review of CRI (ISAB 1999) that variance in the finite growth rate must be incorporated in any exercise designed to gauge the potential of different management options to help avoid extinction. Further, given the high risk of extinction faced by these stocks, given that we know things are not constant but are continuously changing, and understanding that effective actions aimed at improving survival rates will likely change not only the mean survival rates, but the variability around the mean, it is more appropriate to explicitly include variability in the modeling.

In order to emphasize the robustness of PATH’s findings on the importance of extra mortality, we also performed an analysis designed to investigate the presence and importance of extra
mortality, without resorting to PATH analyses or using lower Columbia River stocks in any way. The exercise served as a kind of validation, or check of the CRI model parameterization by fitting it to R/S data from before the completion of the last several dams on the lower Snake River/lower Columbia River system. We applied the CRI deterministic matrix method using NMFS estimates of 4-dam and current juvenile passage direct mortality, and adjusting for harvest and adult passage mortality differences. We compared the resulting parameters to empirical estimates of life stage survival rates from the historical and recent periods, and showed that there is much extra mortality to be explained even if PATH analyses and downstream stocks are not considered. The lack of an analysis by CRI of the causes and magnitude of extra mortality call into question conclusions such as “dam breaching alone will not recover Snake River spring/summer chinook salmon.”

The PATH modeling approach, the original NMFS CRI analysis, our re-parameterized and stochasticized version of the NMFS Leslie matrix model, and fitting the CRI matrix directly to historical spawner-recruit data all highlight delayed hydrosystem mortality as the key remaining uncertainty for decisions regarding the removal of the four lower Snake River dams. PATH analyses demonstrated that dam breach has the greatest probability of survival and recovery unless the delayed differential mortality of transported fish is very low (i.e., ‘D’ is close to one) and the extra mortality of in-river fish is unrelated to their experience through the hydrosystem. NMFS CRI analyses concluded that dam breach alone is unlikely to be sufficient for survival unless a substantial portion of mortality that is modeled to occur in the estuary and ocean is related to hydrosystem experience. The PATH approach is a biological decision analysis that incorporates conflicting hypotheses and models a range of values describing this extra mortality (differential for transported fish and extra mortality of in-river fish) such that results show not only the option with the best chance of survival, but also the option with the least amount of risk to the stocks, given these key remaining uncertainties. In contrast, the CRI approach does not explicitly incorporate conflicting hypotheses and modeling results reflect only the NMFS favored hypothesis regarding delayed differential mortality of transported fish and the extra mortality of in-river migrating fish. In this paper, we show that incorporating hydrosystem delayed mortality into a NMFS Leslie matrix type model results in model outcomes that mirror those observed in PATH. Management actions that include dam breach produce the highest population growth rates and demonstrate the greatest probability of survival, especially when some portion of delayed mortality that occurs in the estuary and early ocean is assumed to be linked to hydrosystem experience. Therefore, regardless of the tool used, hypotheses about the link between delayed mortality, transportation, and hydrosystem experience will determine the predicted outcome of dam breach management actions, relative to no-breach actions.

Given this unresolved difference and the importance of extra mortality in determining the outcomes from both approaches, we are concerned that decision makers are being left with a enormous responsibility--determining the degree of evidence for and against hydrosystem based delayed mortality. We believe this responsibility is better suited to the scientific community and should be addressed with a formal weight of evidence of delayed hydrosystem mortality. Using this approach, the scientific community familiar with the question and available data would assemble and present all the available information regarding delayed hydrosystem mortality. The compilation of all the available information would then be presented to an independent
scientific review panel agreed upon by all interested parties. We recommend some combination of the Independent Scientific Advisory Board and the PATH Scientific Review Panel. This panel would then evaluate the evidence for and against hydrosystem-based delayed mortality and provide weights and recommendations. Their weights and recommendations could then be used in modeling to demonstrate the likely effect of a management action and in evaluation of existing analysis given the evidence for and against delayed hydrosystem mortality. Although a similar weight of evidence was already completed by PATH, NMFS ignores this part of PATH based on what they believe is more recent and relevant information. This weight of evidence would now give NMFS the opportunity to provide this recent information for decision makers benefit.

We believe a weight of evidence approach for hydrosystem delayed mortality would allow decisions makers to more fully evaluate the options for survival and recovery of Snake River salmon and steelhead with the best available information. This approach would allow the evidence for and against the critical remaining uncertainty, delayed hydrosystem mortality, to be explicitly incorporated and evaluated, such that a decision could be made soon. Delaying action while we study this key remaining uncertainty is risky given the long period of time it may take to measure and/or reasonably estimate the components of delayed mortality. The high probability of extinction faced by these stocks demonstrates the need to take action immediately.
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APPENDIX A

Evaluation of CRI age-specific survival estimates

With the exception of $S_1$, and the $S_d$ and $S_b$ components of $S_2$, survival estimates used in the CRI Leslie matrices were based on literature values. Because it was not clear from the CRI documentation how these survival estimates were determined, we tried to reconstruct the same survival estimates using the same references.

**Literature estimate of $S_e$**

In the CRI Leslie matrices, second year (age-2) survival ($s_2$) covered the period of juvenile migration from Lower Granite Dam (LGR) to the early ocean life-phase. The CRI $s_2$ included the products of LGR to Bonneville Dam survival ($s_b$ and $s_d$) and $s_e$ (Figure A.1). We tried to determine the rationale for CRI’s estuary survival estimate ($S_e = 0.07$) by investigating the three sources referenced in CRI documentation (i.e., Nickelson 1986, Pearcy 1992, and Ratner et al.1997)

1) Nickelson (1986) estimated early ocean survival for coho smolts for years of weak and strong upwelling. Mean survival (age-invariant smolt-to-adult) ranged from 3.4% to 8% (for MYs 1961-1980; Table A1). The ultimate range was 2.2% to 12.7%.

2) Pearcy (1992) included survival estimates from Parker (1968). Parker estimated that mortality for the first 40 days of ocean life (for pink salmon) ranged from 2% to 4% per day (Table A1). Daily mortality rates for the next 410 days were 0.4% to 0.8% per day. Based on these estimates, first year ocean survival was calculated as follows:

- **Low estimate:** $(0.96)^{40} \times (0.992)^{325} = 0.014$
- **High estimate:** $(0.98)^{40} \times (0.996)^{325} = 0.12$

This equates to roughly 1 - 12% survival in the first year (365 days) of ocean residence.

From Parker’s mortality rates, an estimate of estuary survival ($Parker S_e$), depending on what is estimated for estuary residence time, can be calculated as follows:

If smolts spend:

- 20 days in estuary, $Parker S_e = (0.96)^{20} = 0.44$ to $(0.98)^{20} = 0.67$, geometric mean (geomean) = 0.54
- 40 days in estuary, $Parker S_e = (0.96)^{40} = 0.20$ to $(0.98)^{40} = 0.45$, geomean = 0.3
- 60 days in estuary, $Parker S_e = (0.96)^{40} \times (0.992)^{20} = 0.17$ to $(0.98)^{40} \times (0.996)^{20} = 0.4$, geomean = 0.26
- 80 days in estuary, $Parker S_e = (0.96)^{40} \times (0.992)^{40} = 0.14$ to $(0.98)^{40} \times (0.996)^{40} = 0.3$, geomean = 0.23
Pearcy’s own survival estimates for coho salmon showed that mortality is high (2 to 8% per day) for the first 30-40 days at sea, while later-ocean-life (out to 450 days) survival ranges from 0.2% to 1.0% per day. Based on these estimates, first year ocean survival was calculated as follows:

Low estimate: \((0.92)^{40} \times (0.99)^{325} = 0.0014\)  
High estimate: \((0.98)^{40} \times (0.998)^{325} = 0.23\)

This equates to roughly 0 - 23% survival in the first year (365 days) of ocean residence.

From Pearcy’s mortality rates, an estimate of estuary survival (\(P_{\text{pearcy}e}\)), depending on what is estimated for estuary residence time, can be calculated as follows:

If smolts spend:

- 20 days in estuary, \(P_{\text{pearcy}e} = (0.92)^{20} = 0.19\) to \((0.98)^{20} = 0.67\), geomean = 0.36
- 40 days in estuary, \(P_{\text{pearcy}e} = (0.92)^{40} = 0.036\) to \((0.98)^{40} = 0.45\), geomean = 0.12
- 60 days in estuary, \(P_{\text{pearcy}e} = (0.92)^{40} \times (0.99)^{20} = 0.030\) to \((0.98)^{40} \times (0.998)^{20} = 0.43\), geomean = 0.11
- 80 days in estuary, \(P_{\text{pearcy}e} = (0.92)^{40} \times (0.99)^{40} = 0.024\) to \((0.98)^{40} \times (0.998)^{40} = 0.41\), geomean = 0.10

CRI’s Leslie matrices appeared to only utilize Pearcy’s survival estimate for \(\frac{1}{2}\) year of the early ocean phase (part of \(CRI_{S2}\)), although Pearcy’s estimate extended into \(CRI_{S3}\) (Figure 1). Therefore, age-3 survival (\(CRI_{S3}\)) in the CRI Leslie matrices should have incorporated portions of ocean phase survival estimates from Pearcy (and Nickelson), since \(P_{\text{pearcy}ocean}\) seems to encompass aspects of \(CRI_{S3}\), \(CRI_{S2}\), and \(CRI_{S3}\).

Figure A.1. Schematic depicting life-phase spanned by survival rate estimates used in CRI analysis and by Pearcy (1992). Grey area designates period spent in the estuary. LGR is Lower Granite Dam.
3) The Ratner et al. (1997) analysis of spring chinook salmon in the South Umpqua River estimated egg-to-fry survival $= 0.00227$, while subsequent yearly survival estimates $= 0.8$ (Table A.1). Ratner et al. further set $s_2 = 0.8$ (age-invariant estimate from Ricker 1976 in Healey 1991 for sockeye salmon) while their estimate of $s_1 = 0.00267$ (annual variance $= 3.045 \times 10^{-6}$, egg-to-fry survival). Combining $\text{CRI}_e$ with through-hydrosystem survival (both barged, $\text{CRI}_{sb}$, and in-river, $\text{CRI}_{sd}$), the CRI then estimated $s_2 = 0.05$. The fact that Umpqua River spring chinook salmon exhibit an ocean type life history instead of the stream type life history of Snake River spring/summer chinook may provide the rationale for differences in the survival rates used by Ratner et al. and those used in CRI. Different delineations for life history may also explain the survival rate differences. It appears that Ratner et al.’s $s_2$ included only ocean-phase survival. In contrast, CRI’s $s_2$ encompassed components of smolt survival through the hydrosystem, estuary, and approximately $\frac{1}{2}$ year of ocean life.

**Literature estimates of $S_3$, $S_4$, $S_5$**

Ocean survival rates in the CRI Leslie matrices were set to $s_3 = s_4 = s_5 = 0.8$ as per Ratner et al. (1997, from Ricker 1976). Ratner et al. used Ricker’s estimates of survival (adult mortality rates in the ocean are thought to be about 20% per year) which were estimated for sockeye salmon.

To use the survival estimates described above for spring/summer chinook is somewhat arbitrary because the range of values is extremely large, are borrowed from other species from different systems, and occur over incomparable portions of the life history.
Literature cited


Table A.1. Life-stage variations in survival for various salmon stocks.

<table>
<thead>
<tr>
<th>Species</th>
<th>Life stage</th>
<th>Survival or mortality estimate</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>sockeye</td>
<td>egg-to-smolt</td>
<td>survival is about 1%</td>
<td>Foerster (1968) as in Pearcy (1992)</td>
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<td>ocean</td>
<td>survival is about 10%</td>
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<td>sockeye</td>
<td>egg-to-fry</td>
<td>survival is about 40%</td>
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<td>egg-to-smolt</td>
<td>average survival is about 10-12%</td>
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<td>smolt-to-adult</td>
<td>survival is 4.5%</td>
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<td>sockeye</td>
<td>ocean, first 4 months</td>
<td>90% of ocean mortality occurs</td>
<td>Furnell and Brett (1986) as in Pearcy (1992)</td>
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<td>sockeye, Fraser</td>
<td>ocean, first 200 days</td>
<td>total survival rate = 0.45</td>
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<td>ocean, first 200 days</td>
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<td>sockeye</td>
<td>age variant</td>
<td>survival rate = 0.8</td>
<td>Ricker 1976 as in Ratner et al. (1997)</td>
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<tr>
<td>pink</td>
<td>fry-to-adult</td>
<td>survival ranged 0.2-23%</td>
<td>Vallion et al. (1981) as in Pearcy (1992)</td>
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<td>egg-to-fry</td>
<td>survival ranged 0.06-21.75%</td>
<td>Heard (1978) as in Pearcy (1992)</td>
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<td>ocean, first 40 days</td>
<td>daily loss rate = 2.4%</td>
<td>Parker (1969) as in Pearcy (1992)</td>
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<td>ocean, day 40-410</td>
<td>loss rate = 0.4-0.8%</td>
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<td>total survival rate = 0.3-0.1</td>
<td>Walters et al. (1978)</td>
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<td>ocean, first 200 days</td>
<td>total survival rate = 0.16-0.19</td>
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<tr>
<td>chum</td>
<td>ocean, first 4 days</td>
<td>loss of 31-46% per day</td>
<td>Bax (1983)</td>
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<td>ocean, first 200 days</td>
<td>total survival rate = 0.6-0.11</td>
<td>Walters et al. (1978)</td>
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<td>chum, Cent. coast</td>
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<tr>
<td>coho</td>
<td>ocean, first 40 days</td>
<td>mortality 2% per day</td>
<td>Mathews and Buckley (1976) as in Pearcy (1992)</td>
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<td>ocean, day 40 - 1.4 yrs.</td>
<td>mortality 0.3% per day</td>
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<td>ocean, first few weeks</td>
<td>mortality 2-8% per day</td>
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<td></td>
<td>later ocean life</td>
<td>mortality 0.2-1.0% per day</td>
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<td>coho, hatchery</td>
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<td>average survival ranged 3.4-8%</td>
<td>Nickelson (1986)</td>
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<td>average survival ranged 7.0-7.4%</td>
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<td>survival ranged from 1-6%</td>
<td>Ryding and Skalski (1999)</td>
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<td>Chinook, CRI</td>
<td>s&lt;sub&gt;1&lt;/sub&gt;, egg-to-fry</td>
<td>annual survival probability = 0.002267</td>
<td>from Ratner et al. 1997</td>
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<td>s&lt;sub&gt;2&lt;/sub&gt;</td>
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<td>s&lt;sub&gt;3&lt;/sub&gt;</td>
<td>annual survival probability = 0.8</td>
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<td></td>
<td>s&lt;sub&gt;4&lt;/sub&gt;</td>
<td>annual survival probability = 0.8</td>
<td>Ratner et al (1997) from Ricker (1976) in Healey (1991)</td>
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<td>annual survival probability = 0.8</td>
<td></td>
</tr>
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<td></td>
<td>adult</td>
<td>mortality rates about 20% per year</td>
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<td>In-stream spawners</td>
<td>mortality set to 0.1</td>
<td>used in Ratner et al. (1996)</td>
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<td>chinook, Fraser</td>
<td>ocean, first 200 days</td>
<td>total survival rate = 0.06-1.0</td>
<td>Walters et al. (1978)</td>
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<td>chinook, Skeena</td>
<td>ocean, first 200 days</td>
<td>total survival rate = 0.32-0.33</td>
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<td>Chinook, wild</td>
<td>Fry-to-adult</td>
<td>0.013-1.17%, Mean survival = 0.079</td>
<td>Umwin (1997)</td>
</tr>
<tr>
<td>Chinook, hatchery</td>
<td>Fry to adult</td>
<td>0.008-3.28%, mean = 0.34%</td>
<td></td>
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</table>
APPENDIX B

Alternative approach to estimating egg-to-smolt survival based on SAR

Sensitivity analyses performed in CRI, and reported in NMFS’ Anadromous Fish Appendix to the DEIS (USACE 1999), suggested that the improvements in egg-to-smolt survival represented the major opportunity for recovery of listed Snake River spring/summer chinook populations. The CRI analysis appeared to contradict conclusions of the PATH retrospective analysis (Marmorek and Peters 1996), which indicated that any declines in survival rates through the freshwater spawning and rearing life-stage since the 1970s were not of a magnitude to explain the dramatic declines in life-cycle survival. PATH analyses indicated that the major declines in life-stage survival, following completion of the Federal Columbia River Power System, occurred in the smolt-to-adult return rates (SAR; Figure B.1). Our preliminary review of the CRI results also suggested that the CRI analysis might have underestimated survival in the egg-to-smolt stage and overestimated SARs for spring/summer chinook compared to the empirically derived information from PATH.

We investigated an alternative approach to estimating egg-to-smolt survival ($S_1$), which is fitted as a last step in the CRI matrices. This alternative approach was based on PATH estimates for smolt and adult numbers of wild, aggregate Snake River spring/summer chinook from the 1960s through the 1990s.

Objectives of this analysis were to: (1) estimate egg-to-smolt survival and smolt-to-adult return rates for naturally spawning Snake River aggregate spring/summer chinook for brood years 1980-1994; (2) incorporate these empirically derived values into our evaluation of the CRI analysis.

Methods

**Egg-to-Smolt Survival (S1)**

Annual egg-to-smolt survival rates ($S_1$) were estimated for the aggregate Snake River spring/summer chinook, brood years 1980-1993, using annual estimates of smolts and spawners, pre-spawning survival rate, fraction female, weighted average fecundity, and smolt survival rate through Lower Granite pool. Two spawner indices were used in the analysis, excluding and including hatchery fish spawning in the wild. Two wild smolt indices were also used based on alternative estimates of FGE in recent years.

Total annual egg deposition was estimated by adjusting spawner indices for pre-spawning survival rate, annual fraction female, and weighted average fecundity:

\[
\text{EggDep} = \text{SP} \times \text{PreSpawn} \times \text{FracFem} \times \text{Fecund}
\]

- **EggDep** = egg deposition
- **SP** = spawner index (SP1 or SP2)
- **PreSpawn** = pre-spawning survival rate (constant 0.9)
- **FracFem** = fraction female
- **Fecund** = eggs per female

Values for spawner indices SP1 (excluding hatchery spawners) and SP2 (including hatchery spawners) were from Petrosky and Schaller 1996; Table 2). SP1 and SP2 represented escapement to the uppermost Snake River Dam (Lower Granite). Pre-spawning survival rate was a constant 0.9, used in both PATH and CRI estimates of R/S (note that this assumption is merely a scalar for both S1 and R/S estimates). Fraction female represented the average frequency (proportion) of females out of total spawners, averaged across the seven index stocks that were used in the CRI matrices (12-13-99matrix.xls). Fecundity was estimated from annual average frequency (proportion) females by age (CRI matrices), and age-specific fecundity obtained from Subbasin Planning data (S. Kiefer, personal communication, June 1991). Fecundity values for aggregate Snake River spring/summer chinook were 4095 eggs/female for age-4 and 5149 eggs/female for age-5. Age-3 females represented a very small percentage (0.3%) of total spawners; their fecundity was assumed to be 3257 eggs/female (4095*[4,095/5149]). Average annual fecundity for aggregate spring/summer chinook was 4874 (SD=129).

We used Petrosky and Schaller (1996) wild smolt estimates for brood years 1980-1982 and 1990-1993, and estimated wild smolt yields for the missing brood years, 1983-1989. Wild smolt yields for the missing brood years were predicted values based on SP1 and SP2 spawner
numbers and the relationship of ln(smolts/spawner) vs. spawner (Petrosky and Schaller 1996; Table 13 coefficients for 1975-1993). Four annual values of wild smolt yield (indexed at Lower Granite Dam) were obtained from the two spawner indices (SP1 and SP2) and two smolt indices (FGE=0.56; FGE=0.40).

We calculated annual estimates of $S_I$ by dividing the annual wild smolt yield by the annual egg deposition, and adjusting for smolt survival rate through Lower Granite Pool. This adjustment (dividing by a constant 0.95) was needed to index $S_I$ to smolts arriving at the upper end of the hydrosystem, consistent with the life-stage partitioning in the CRI analysis.

**Smolt-to-Adult Return (SAR)**

Smolt-to-adult return rate (SAR) was estimated for the aggregate Snake River spring/summer chinook, brood years 1980-1992. Smolts were estimated at Lower Granite Dam (LGR) for the four combinations of spawner index and FGE. We estimated two measures of SAR. The first represented total returns of age-3 to age-5 fish (jacks plus adults) to the upper dam plus prior in-river harvest. This measure was consistent with the approach used historically by Raymond (1988), and the SAR2 measure reported in Petrosky and Schaller (1998). The second measure of SAR represented total returns of age-3 to age-5 fish to the Columbia River mouth by also accounting for adult passage mortality (i.e., conversion loss). This SAR measure (SAR\textsubscript{LGR-River Mouth}) was used in the matrix analysis.

Adult returns to the upper dam were based on expansions of the age-structured wild spawner index SP1 from Petrosky and Schaller (1998) for run years 1980-1997. Because SP1 represented age 4-5 adults only, we expanded SP1 for the proportion of jacks in the total run-year return (Petrosky and Schaller 1998; Table 3). Total wild returns (including jacks; SP1J) to LGR by run year were partitioned by age using Table 3 of Petrosky and Schaller (1998), and expanded for the in-river harvest rate and (for SAR\textsubscript{LGR-River Mouth}) by the conversion rate. Expansion methods, and estimated in-river harvest and conversion rate estimates were from Beamesderfer et al. (1997) and updated PATH run reconstructions (svr99_I_12_2000.xls). Age-structured returns were then summed by brood year to estimate SAR.

---

1 We also investigated and rejected another method to estimate wild smolts. This method estimated: (1) the expected numbers of hatchery smolts based on release numbers; (2) the total smolt numbers using different FGE assumptions; and (3) the wild smolt numbers as the difference between total and hatchery smolt estimates. Although there was a good relationship over all years between release numbers and hatchery smolt yields, this method was overly sensitive to FGE assumptions for the total smolt yield. Since hatchery smolts dominated the total yield in these years, the residual (wild smolt estimate) could be negative for some plausible FGE estimates.
Results and Discussion

**Egg-to-Smolt Survival ($S_1$)**

Wild spawner and smolt estimates for the aggregate wild Snake River spring/summer chinook, brood years 1962-1995 are presented in Table B.1. Smolts/spawner did not show a pattern of decline from the 1960s through 1993 (Figure B.1). Declines in survival rates (if any) through the freshwater spawning and rearing life-stage since the 1970s were not of a magnitude to explain the dramatic declines in life-cycle survival (Marmorek and Peters 1996, Petrosky and Schaller 1996). Estimates of smolt numbers for brood years 1983-89 and 1994-95 (shaded values) were the predicted values from smolt/spawner relationships in Petrosky and Schaller (1996). Therefore, annual variability in $S_1$ is likely underestimated by this method.

Empirically derived $S_1$ estimates were nearly three times those used in CRI for brood years 1980-93. Our $S_1$ estimates had an overall geometric mean of 4.8%, with annual estimates for different assumptions ranging from 2.6% to 8.7% (Table B.2). In contrast, CRI matrices estimated $S_1$ to range from 1.5% to 3% for the different index populations. Note that our approach used aggregate stock information, and that empirical $S_1$ estimates are not available for individual populations.

Little of the difference between the empirically derived $S_1$ estimates and those of CRI can be explained by choices in parameter values. Parameter values were similar (fecundity) or identical (pre-spawning survival and fraction female by age) between the two methods. The annual estimated fraction female (from CRI matrices) ranged from 0.46 to 0.58 for these brood years (Table B.2). Average annual fecundity for aggregate spring/summer chinook was 4874 (Table B.2). Our aggregate fecundity estimate was virtually identical to the CRI fecundity average for the seven stocks (4862; range 4086 to 5607).

**Smolt-to-Adult Return (SAR)**

We generated two sets of SAR estimates for brood years 1980-1992. The first indexed adult and jack returns to Lower Granite Dam plus prior river-harvest (Zones 1-6). This accounting method is useful for historical comparison (e.g., Figure B.1), and consistent with Raymond’s (1988) method (referred to as SAR2 in Petrosky and Schaller 1998). For use in the CRI evaluation, we indexed adult and jack returns to the Columbia River mouth, brood years 1980-1992.

The geometric mean for “SAR2” was 0.71% for brood years 1980-1992 (Table B.3). Our SAR2 estimates for brood years 1980-1982 (based on spawner index SP1) were lower than those of Raymond (1988). Raymond’s SARs ranged from 1.8% to 2.8% compared to 1.0% to 1.5% using the SP1 index. The difference may be due to different methods of accounting hatchery/wild
adults at Lower Granite Dam; our method is more consistent with that used by the US v. Oregon Technical Advisory Committee.

Empirically derived estimates of SAR (to the river mouth) were about one-fourth those derived from the CRI analysis. SARs to the Columbia River mouth for brood years 1980-1992 had a geometric mean of 0.96%, with annual estimates ranging from 0.21% to 2.23% (Table B.4). In contrast, CRI estimates were approximately 4%.

**Literature Cited**


Figure B.1. Patterns of SAR and smolts/spawner (natural log scale) for Snake River wild spring/summer chinook, smolt years 1962-1994. Smolt/spawner estimates represented by SP1 and FGE = 0.56 assumptions. (Sources: Petrosky and Schaller 1996, 1998; Raymond 1988).
Table B1. Smolt and spawner estimates used in S1 calculations from Petrosky and Schaller (1996), and predicted numbers of wild smolts for combinations of spawner and smolt indices, brood years 1962-95.

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<thead>
<tr>
<th>Brood Year</th>
<th>Smolt Year</th>
<th>SP1</th>
<th>SP2</th>
<th>Upper dam smolt # wild .56fg</th>
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Table B2. Egg-to-smolt survival estimates (S1), and parameter values used, brood years 1980-93. Shaded values represent S1 estimates using predicted smolts/spawner (brood years 1983-89).

<table>
<thead>
<tr>
<th>Brood Year</th>
<th>Smolt Year</th>
<th>Prespawn Survival</th>
<th>Fraction Female</th>
<th>Weighted Average Fecundity</th>
<th>Egg-Smolt SP1 0.56FGE</th>
<th>Egg-Smolt SP1 0.40FGE</th>
<th>Egg-Smolt SP2 0.56FGE</th>
<th>Egg-Smolt SP2 0.40FGE</th>
<th>Egg-Smolt Geomean</th>
</tr>
</thead>
<tbody>
<tr>
<td>80</td>
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<td>0.90</td>
<td>0.4731</td>
<td>4786</td>
<td>5.0%</td>
<td>5.0%</td>
<td>5.0%</td>
<td>5.0%</td>
<td>5.0%</td>
</tr>
<tr>
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<td>83</td>
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<td>0.4758</td>
<td>4704</td>
<td>5.6%</td>
<td>5.6%</td>
<td>5.2%</td>
<td>5.2%</td>
<td>5.4%</td>
</tr>
<tr>
<td>82</td>
<td>84</td>
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<td>0.5028</td>
<td>4893</td>
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<td>5.4%</td>
<td>5.2%</td>
<td>5.2%</td>
<td>5.3%</td>
</tr>
<tr>
<td>83</td>
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<td>0.5691</td>
<td>5039</td>
<td>4.0%</td>
<td>4.6%</td>
<td>3.7%</td>
<td>4.2%</td>
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<td>5.5%</td>
</tr>
<tr>
<td>85</td>
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<td>4850</td>
<td>4.9%</td>
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<td>4.3%</td>
<td>4.8%</td>
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</tr>
<tr>
<td>86</td>
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<td>0.5024</td>
<td>4898</td>
<td>4.5%</td>
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<td>3.7%</td>
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</tr>
<tr>
<td>87</td>
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<td>3.9%</td>
<td>4.3%</td>
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<tr>
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</tr>
<tr>
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<td>4838</td>
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<td>6.2%</td>
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<td>5.5%</td>
<td>5.5%</td>
</tr>
<tr>
<td>90</td>
<td>92</td>
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<td>4.7%</td>
<td>4.5%</td>
</tr>
<tr>
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<td>7.3%</td>
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</tr>
<tr>
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<td>94</td>
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<td>0.4552</td>
<td>4679</td>
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<td>3.7%</td>
<td>2.1%</td>
<td>2.9%</td>
<td>2.8%</td>
</tr>
<tr>
<td>93</td>
<td>95</td>
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<td>6.2%</td>
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<td>6.1%</td>
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<tr>
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</tr>
</tbody>
</table>

Geomean 4.8% 5.6% 4.1% 4.8% 4.8%
Table B3. Smolt-to-adult return rate (SAR2) estimates for combinations of spawner and smolt indices, and returns to upper dam and harvest (harvest + SP1J escapement), brood years 1980-92. The SAR2 accounts for returns consistent with Raymond (1988) definitions.

<table>
<thead>
<tr>
<th>Run or Brood Year</th>
<th>Smolt Year</th>
<th>Harvest + SP1J Esc.</th>
<th>SAR2 SP1/.56</th>
<th>SAR2 SP1/.40</th>
<th>SAR2 SP2/.56</th>
<th>SAR2 SP2/.40</th>
<th>Geomean</th>
</tr>
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<td>1.48%</td>
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<tr>
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<td>83</td>
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<td>0.96%</td>
</tr>
<tr>
<td>82</td>
<td>84</td>
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<td>0.99%</td>
<td>0.99%</td>
<td>0.99%</td>
<td>0.99%</td>
</tr>
<tr>
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<td>1.45%</td>
<td>1.63%</td>
<td>1.44%</td>
<td>1.54%</td>
</tr>
<tr>
<td>84</td>
<td>86</td>
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<td>0.54%</td>
<td>0.61%</td>
<td>0.53%</td>
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</tr>
<tr>
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<tr>
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</tr>
<tr>
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<tr>
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<tr>
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<td>0.76%</td>
<td>1.06%</td>
<td>0.76%</td>
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</tr>
</tbody>
</table>

Geomean 0.79% 0.69% 0.73% 0.64% 0.71%

Table B4. Smolt-to-adult return rate estimates for combinations of spawner and smolt indices, and total returns to river mouth (conversion + harvest + SP1J escapement), brood years 1980-92. These SARs were used in Leslie matrix evaluations.

<table>
<thead>
<tr>
<th>Run or Brood Year</th>
<th>Smolt Year</th>
<th>Conversion + Harvest + SP1J Esc.</th>
<th>SAR SP1/.56</th>
<th>SAR SP1/.40</th>
<th>SAR SP2/.56</th>
<th>SAR SP2/.40</th>
<th>Geomean</th>
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<td>1.87%</td>
<td>1.87%</td>
<td>1.87%</td>
<td>1.87%</td>
</tr>
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<td>1.15%</td>
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</tr>
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<td>15199</td>
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<td>1.27%</td>
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</tr>
<tr>
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<td>0.79%</td>
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</tr>
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<td>0.90%</td>
</tr>
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</tr>
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</tr>
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<tr>
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<td>1.13%</td>
<td>1.58%</td>
<td>1.13%</td>
<td>1.34%</td>
</tr>
</tbody>
</table>

Geomean 1.07% 0.92% 0.99% 0.86% 0.96%
APPENDIX C

PATH Habitat Feasibility Assessment

PATH Habitat Scenarios A and B

In 1997, a subgroup of PATH evaluated the likelihood of improving survival for index populations of Snake River spring/summer chinook under two general land management options. Subgroup participants familiar with the specific habitats and populations judged the probability that estimated productivity would increase, decrease, or stay the same within 48-years (i.e., time frame for NMFS recovery standard). Baseline productivity, ln(R/S) at low density or Ricker a, was defined by maximum likelihood estimates for brood years 1957 (for most stocks) through 1990. Habitat options evaluated were status quo and active restoration/protection. Rationale, criteria and methods were described in the PATH Preliminary Decision Analysis (Marmorek and Peters 1998), which are excerpted with minor edits below.

Rationale

Habitat conditions and natural disturbances or management actions, which affect habitat have been widely observed to affect salmonid survival during freshwater rearing (Jones et al. 1997 Retrospective Report revised chapter 10 PATH FY96 Conclusions Document). In addition, egg-to-smolt mortality rates, which typically exceed 90% suggest that a significant scope exists for habitat-related changes in freshwater rearing survival. However, relationships between population productivity and habitat conditions or actions that affect habitat condition are difficult to quantify. Comparisons of stock-recruitment data for spring chinook salmon generally failed to identify significant correlations between landscape or land use variables and index stock productivity (Paulsen 1997 Retrospective analysis). Confounding problems included a lack of adequate measures of habitat quality, incomplete data sets on land use, difficulties in defining appropriate spatial scales, and uncertainties in defining lag times for effects. Thus, while few would disagree that habitat can be a critical limiting factor in freshwater rearing or that changes in land use can affect habitat quality and survival, the effects of any given set of habitat improvement activities on stock productivity cannot be predicted. Prospective analyses of the potential effects of habitat changes on future salmon stock performance were therefore based on plausible changes in stock productivity described by the observed range of variability in stock-recruitment parameters among index populations from habitats of varying condition.

We have focused our attention on the Ricker a parameter. Our rationale for this choice is that the stocks of interest are generally accepted to be at levels far below their carrying capacities,

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based on historical estimates of abundance. This implies that habitat changes, while they may in fact affect both $a$ and $b$ values, are far more likely to affect the probability of stock survival or recovery through their influence on $a$, which directly affects productivity at low stock sizes. The $a$ parameter can be thought of as reflecting the quality of the habitat in the area utilized by the stock for spawning and pre-smolt juvenile rearing. The challenge is thus to judge how changes to habitat might affect average egg-to-smolt survival for the stock, translated into a change in the Ricker $a$ parameter.

How much of a change in the Ricker $a$ parameter is appropriate to consider for each stock? There is no “right” answer to this question. We have chosen to define a range of no greater than a unit increase or decrease in the $a$ value from its current value, whatever that might be. A unit change in $a$ is equivalent to an approximately three-fold change in stock productivity (or, in other words, in egg-to-smolt survival), since productivity $(R/S)$ is approximately equal to $e^a$ at low stock sizes, and $e^1 = 2.7$. We offer three reasons for considering this range in $a$ to be plausible:

1. For the Snake River basin stocks, the range in current estimated Ricker $a$ values is approximately one;

2. A preliminary analysis of PIT-tag recoveries showed an approximately three-fold variation in average recovery rates between releases in wilderness areas and releases in managed areas; and

3. Smolt production models developed during the sub-basin planning exercise assumed a three-fold range of smolt density capacities between sites classified as having “fair” habitat, and those having “excellent” habitat.

We are not arguing that this evidence provides a convincing reason for believing that habitat management actions will necessarily increase (or mis-management will decrease) productivity three-fold from the current stock condition. We suspect that making such an absolute judgement would be exceedingly difficult, if not impossible. Instead we use this evidence to suggest that three-fold changes in productivity are plausible. Just how plausible such a change is for a given stock and management action will affect the assignment of a probability to such a change, as described below.

Before discussing the assignment of probabilities, however, there is a further caveat. We suspect an upper limit exists on the Ricker $a$ value for the stocks in a particular region, defined by the intrinsic productivity of the area as determined by physiography and climate. We have thus constrained the plausible increases in the Ricker $a$ value to not exceed the maximum $a$ value observed for the up-river stocks. In contrast, we do not believe there is a similar constraint on the downside; stock productivity can reasonably decline by a factor of three, even if it is relatively low to begin with, provided habitat conditions worsen considerably.

We originally chose to examine two contrasting options for future habitat management. The first option (A) can be described as continued management according to existing habitat management plans in the regions of interest (status quo option). In the ICBEMP reports (Quigley et al. 1996)
three options are presented - our Option A is equivalent to Option 1 in their report. The second option (B) is more akin to Option 2 in the ICBEMP report (active restoration of ecological integrity), although we stress the aquatic component more heavily. We characterize this option by the words, “Make every practical effort to restore and protect anadromous fish habitat”. These two options provide contrast in the degree to which habitat protection and restoration will be emphasized - we do not believe that an option that reduces emphasis on habitat relative to the status quo is likely for the endangered stocks. The prospective model results presented in the PATH Preliminary Decision Analysis Report (Marmorek and Peters 1998) consider only Option B, and examine the contrast between this option and the scenario in which no future changes in Ricker $a$ values are expected to occur due to habitat management options.

**Implementation of Habitat Uncertainty in the Prospective Model**

For each stock and habitat option, we judged the probability that the Ricker $a$ value would either: (1) increase by up to one unit, but to a value no higher than the observed maximum; (2) remain the same; or (3) decrease by one unit, over the next 48 years (the proposed NMFS recovery standard time frame). We also needed to judge how rapidly the changes would occur, should a change occur at all. This is summarized by specifying the probability that $a$ will have changed to a new value by year 12 (or 24), given that it is expected to change by year 48. If the change is likely to occur very slowly (i.e., a gradual reduction of fines in stream substrates, following sediment control, or a slow phase-in of a riparian management option) then the probability of change occurring in twelve years, even if it does occur in 48 years, is very low. On the other hand, if the change is likely to result from a sudden event (more likely for a negative change due to a catastrophic event) that is equally likely to occur anytime during the next 48 years, the probability of a change by year 12 is 0.25 and by year 24 is 0.5, again given that the event has occurred by year 48. These values (0.25, 0.5) could also reflect a gradual but steady progression over time towards the 48-year value.

Our judgements of each of these probabilities for each of the index stocks included in the prospective modeling are summarized in Marmorek and Peters (1998; Table A.3.5.1). In the prospective model, these probabilities were used to determine whether, for a given run, the Ricker $a$ value for the stock being simulated should be modified to reflect a habitat management effect in Year 12, 24 or 48 of the simulation. Again, only Option B was included in the results presented in Marmorek and Peters (1998).

Using Bear Valley Creek as an example, under Option A, we assumed equal probabilities (0.15) of an increase or a decrease in Ricker “a” at 48 years, with the highest probability (0.7) being for “no change” (Marmorek and Peters 1998; Table A.3.5.1). If a change were to occur, we judged that an increase in Ricker “a” might occur more slowly than a decrease (see 12 and 24-year probabilities). Under Option B, we judged that an improvement was more likely (0.6) than no change (0.4) or a decrease (0.0).
PATH Habitat Scenario C

An alternative formulation of the “full protection” option (Option B, described above) was evaluated in the PATH FY1998 Final Report (Marmorek et al. 1998). Concern had been raised that because the estimated Ricker $a$ actually decreased for some stocks under Option B assessments (e.g., Poverty Flat)$^2$, that productivity comparisons between “full protection” and baseline (scenario 0) would mask the intended, simulated effects of habitat improvement options. The alternative formulation, habitat scenario C, is analogous to the implementation in scenario 0, so these two scenarios are directly comparable. Similarly habitat scenarios A and B are directly comparable. This formulation simply takes the difference between Ricker $a$ in scenario B and scenario A, and adds it to the baseline Ricker $a$. Scenario C is somewhat optimistic because it explicitly assumes that productivity will not decrease under status quo habitat management. In disturbed drainages such as the South Fork Salmon River (Poverty Flat population), it may be unrealistic to assume no risk of a declining productivity even under an active restoration effort.

We used scenario C in the Leslie matrix simulations for all stocks with one exception. Productivity increases for the Marsh Creek stock had been judged identical under Options A and B, since the primary restoration action (removing cattle from part of the drainage) had already occurred in the early 1990s. (i.e., the calculated difference in Ricker $a$ was zero according to criteria of scenario C, even though an improvement was expected). To correct for this discrepancy in the simulations, we used baseline and Option B estimated productivities to define the survival improvement for Marsh Creek.

The estimated survival change due to habitat was implemented in the Leslie matrix simulations as a scalar on egg-to-smolt survival rate ($S_1$). Survival change was defined as:

$$\text{Survival Change} = \frac{(e^a \text{ for Option C})}{(e^a \text{ for Baseline})}$$

For simplicity, survival improvements were implemented immediately in the Leslie matrix simulations, rather than phased-in over a 48-year period.

Results

PATH maximum likelihood estimates of Ricker $a$ ranged from 2.67 to 3.91 for the 17 Snake River stocks included in the habitat assessment (Table C.1). The Ricker $a$ estimates for the seven PATH index stocks had a narrower range (3.43 to 3.70), and fewer low values than the total population data set. The difference between the maximum estimated productivity (3.91), and those of the PATH index stocks ranged from 0.20 to 0.48.

$^2$ The Option B decrease in estimated productivity under maximum habitat protection was due to two factors: an estimated high risk of continued watershed degradation from previous disturbance; and the baseline Ricker $a$ being relatively close to the cap.
Table C.1. Maximum likelihood estimates of productivity (Ricker $a$) and slope (Ricker $b$) for 17 populations of Snake River spring/summer chinook populations, 1950s brood years through 1990. The seven PATH index stocks and coefficients are bolded. (Source: Rick Deriso e-mail to PATH, 8/25/97, MLE Model 1).

<table>
<thead>
<tr>
<th>Stock (Subbasin)</th>
<th>Ricker $a$</th>
<th>Ricker $b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lostine River (Grand Ronde)</td>
<td>3.908</td>
<td>0.003853</td>
</tr>
<tr>
<td><strong>Sulphur Creek (Middle Fork Salmon)</strong></td>
<td>3.704</td>
<td>0.002547</td>
</tr>
<tr>
<td>Upper Big Creek (Middle Fork Salmon)</td>
<td>3.688</td>
<td>0.004608</td>
</tr>
<tr>
<td><strong>Bear Valley Creek (Middle Fork Salmon)</strong></td>
<td>3.583</td>
<td>0.000886</td>
</tr>
<tr>
<td>Upper Valley Creek (Salmon)</td>
<td>3.559</td>
<td>0.003658</td>
</tr>
<tr>
<td><strong>Johnson Creek (South Fork Salmon)</strong></td>
<td>3.556</td>
<td>0.002811</td>
</tr>
<tr>
<td>Imnaha River (Imnaha)</td>
<td>3.542</td>
<td>0.000910</td>
</tr>
<tr>
<td>Secesh River (South Fork Salmon)</td>
<td>3.535</td>
<td>0.003549</td>
</tr>
<tr>
<td><strong>Minam River (Grand Ronde)</strong></td>
<td>3.526</td>
<td>0.001417</td>
</tr>
<tr>
<td><strong>Marsh Creek (Middle Fork Salmon)</strong></td>
<td>3.521</td>
<td>0.001609</td>
</tr>
<tr>
<td>Catherine Creek (Grand Ronde)</td>
<td>3.478</td>
<td>0.001214</td>
</tr>
<tr>
<td><strong>Poverty Flat (South Fork Salmon)</strong></td>
<td>3.432</td>
<td>0.000906</td>
</tr>
<tr>
<td>Upper Grand Ronde River (Grand Ronde)</td>
<td>3.410</td>
<td>0.001597</td>
</tr>
<tr>
<td>Wenaha River (Grand Ronde)</td>
<td>3.287</td>
<td>0.000730</td>
</tr>
<tr>
<td>Lemhi River (Salmon)</td>
<td>3.260</td>
<td>0.000630</td>
</tr>
<tr>
<td>Lookingglass Creek (Grand Ronde)</td>
<td>2.947</td>
<td>0.001723</td>
</tr>
<tr>
<td>Big Sheep Creek (Imnaha)</td>
<td>2.671</td>
<td>0.001851</td>
</tr>
</tbody>
</table>

Productivity estimates for the index stocks under baseline, habitat scenarios A, B, and C are shown in Table C.2. For the Leslie matrix habitat sensitivity, we focused on the contrast between Scenario C and the baseline. The geometric mean survival improvement for the seven index stocks was 9% (i.e., survival changes by a factor of 1.09), with a range from 0% to 34%. In PATH simulations of Option C, there was no survival change for Marsh Creek, whereas we have assumed a 6% improvement in the matrix simulations.
Table C.2. Estimated productivity (Ricker \( a \)) for baseline habitat, and habitat scenarios A, B, and C, and improvement in survival expected with active restoration, seven PATH index stocks.

<table>
<thead>
<tr>
<th>Stock</th>
<th>Ricker ( a ) Baseline</th>
<th>Ricker ( a ) Option A</th>
<th>Ricker ( a ) Option B</th>
<th>Difference (B – A)</th>
<th>Ricker ( a ) Option C</th>
<th>Survival Change</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sulphur Cr.</td>
<td>3.70</td>
<td>3.70</td>
<td>3.70</td>
<td>0.00</td>
<td>3.70</td>
<td>1.00</td>
</tr>
<tr>
<td>Bear Valley Cr.</td>
<td>3.58</td>
<td>3.48</td>
<td>3.78</td>
<td>0.30</td>
<td>3.88</td>
<td>1.34</td>
</tr>
<tr>
<td>Johnson Cr.</td>
<td>3.56</td>
<td>3.41</td>
<td>3.50</td>
<td>0.09</td>
<td>3.65</td>
<td>1.10</td>
</tr>
<tr>
<td>Imnaha R.</td>
<td>3.54</td>
<td>3.51</td>
<td>3.53</td>
<td>0.02</td>
<td>3.56</td>
<td>1.02</td>
</tr>
<tr>
<td>Minam R.</td>
<td>3.53</td>
<td>3.49</td>
<td>3.51</td>
<td>0.02</td>
<td>3.54</td>
<td>1.02</td>
</tr>
<tr>
<td>Marsh Cr.</td>
<td>3.52</td>
<td>3.58</td>
<td>3.58</td>
<td>0.00</td>
<td>3.58(^a)</td>
<td>1.06(^a)</td>
</tr>
<tr>
<td>Poverty Flat</td>
<td>3.43</td>
<td>3.01</td>
<td>3.11</td>
<td>0.10</td>
<td>3.53</td>
<td>1.11</td>
</tr>
</tbody>
</table>

\(^a\) Option C for Marsh Creek assumed Ricker \( a \) from Option B.

**Literature Cited**


APPENDIX D

Extra Mortality

Description of Extra Mortality

During the PATH process Deriso et al. (1996) compared the survival of six Snake River spring/summer chinook stocks with that of six control or comparison stocks from farther downstream. The resulting differential survival was greater than that explained by mainstem passage survival models, and the unexplained portion came to be known as delayed mortality (Deriso et al. 1996). Later, in acknowledgment that this portion of mortality may not necessarily be delayed mortality from the hydrosystem, the term “extra” mortality was employed. The subject was dealt with extensively in PATH weight of evidence process (Marmorek and Peters 1998a, 1998b, 1998c). Because the level of extra mortality is substantial, model results vary considerably depending on assumptions about the disposition of extra mortality. For example, the efficacy of breaching depends to some extent on whether the extra mortality is hydro-induced and will be reduced by breaching dams, or is due to BKD or other mechanisms unrelated to the mainstem migration and is “here to stay”. A detailed discussion about extra mortality hypotheses and their effects on simulations appears in Marmorek and Peters (1998a).

In PATH analyses, life-cycle mortality was separated into two components, direct and extra mortality. For some life stages, we have data that allowed us to estimate the direct mortality that occurred in that life stage (e.g., freshwater harvest). This is mortality that occurs immediately and as a result of some cause in that life stage. A portion of direct mortality occurs while juvenile and adult salmon and steelhead pass by dams and travel through reservoirs that comprise the hydrosystem. Direct mortality can be further compartmentalized into juvenile fish that were transported and those that migrated in-river. All direct mortality is incorporated into life-cycle models, which are used to describe this mortality over the complete life cycle. We use the overall life-cycle mortality (from spawner and recruit data) and direct mortality to define a second component of mortality, extra mortality.

PATH analyses put the expression of extra mortality common to transported and non-transported fish in the period of the life cycle after passing Bonneville Dam on the outward migration. Its cause could occur before fish encounter the hydrosystem, in the hydrosystem, or after they encounter the hydrosystem. The range of hypotheses about extra mortality acknowledged the possibility that a fish’s experience in one life stage may affect its survival in a later life stage. Under a hypothesis that extra mortality at one stage is caused by experience in an earlier a stage, this mortality can be thought of as delayed or latent mortality and is analogous to the case where someone who smokes cigarettes when young, later dies of lung cancer. The person does not die at the moment he smokes his first cigarette, but he may die prematurely as a result of the interaction between this earlier experience and other factors affecting long-term health and fitness.
One approach used for estimating this extra mortality is comparison of survival rate patterns for Snake River stocks to the patterns of their counterparts downstream (which migrate through fewer dams). These downstream counterparts migrate at the same time and size, go to similar areas in the ocean, return as adults at a similar time, age, and size, and are exposed to similar ocean conditions and estuary predators. The completion of the Federal Columbia River Power System (FCRPS) in the late 1960s through the mid-1970s, was immediately followed by considerably sharper declines in survival rates of Snake River stocks (over the same time period), than of down-stream stocks (Schaller et al. 1999).

These sharper declines observed for the Snake River stocks were probably due to the increasing level of direct and extra hydrosystem mortality. The declines continued despite drastic reductions in freshwater harvest. In addition, spring/summer chinook stocks experience little ocean harvest. Most Snake River spawning and rearing habitat degradation had occurred prior to the stock declines, and populations in degraded and good habitat responded similarly. A climatic index could not be found which could explain why Snake River stocks declines were greater than their lower River counter parts. Although there was some correspondence between overall hatchery production levels and declines in Snake River spring chinook, there was little to no correspondence between hatchery production and declines in individual sub-basins. In addition, there was little to no correspondence between overall hatchery production and declines in the down-stream counter parts (spring chinook in lower Columbia index areas). These analyses are discussed in detail in Marmorek et al. (1996) and Marmorek and Peters (1998a, 1998b, 1998c).

These sharper declines in survival rates, for Snake River stocks, could not be explained entirely by the patterns of direct mortality estimated for juvenile fish that are transported around or migrate through the hydrosystem. Therefore, after accounting for the difference in direct mortality between the upper and lower stocks and a common year effect among stock groups, there is still an unexplained portion of mortality between the two stock groups, which accounts for the differences in overall survival patterns (see Marmorek et al. 1998c). This quantity is an estimate of the extra mortality. Extra mortality can be further apportioned between the fish that are transported around the hydrosystem and those which migrated in river. The quantity which describes the difference between the extra mortality (or delayed mortality) of transported fish and fish that migrate in-river, is called ‘D’. As modeled in PATH, extra mortality is tied to hypotheses about the potential causes and thus accounts for the fact that a fish’s experience in one life stage may affect its survival in a later life stage.

**Calculations of extra mortality**

In PATH, extra mortality for Snake River stocks is any mortality occurring outside the juvenile migration corridor that is not accounted for by either: 1) productivity parameters in spawner-recruit relationships; 2) estimates of direct mortality within the migration corridor; or 3) for the ‘Delta’ model, common year effects affecting both Snake River and Lower Columbia River stocks (Marmorek and Peters 1998b). In addition to the Delta model, an ‘Alpha’ model was also
used to estimate mortality in different life stages from the R/S data. The Alpha model assumed upriver and downriver stocks varied independently, and actually found more extra mortality of upriver stocks. This is because some of the greater mortality of Snake River stocks in recent years is explained by lower recent year effects in the Delta model; while there is no common year effect explaining part of the difference between the historical and recent period in the Alpha model. Extra mortality estimates used in this analysis were estimated with the Delta model.

Extra mortality is assumed to occur in the estuary and ocean, from the time the fish pass Bonneville dam as juveniles to the time they return as adults. The causes may occur in the hydrosystem, above the hydrosystem during spawning, rearing, or migration to the beginning of the hydrosystem, or in the estuary or ocean. In practice, within PATH and in the STUFA matrix analysis, extra mortality is applied to a parameter representing a scalar of the post-Bonneville Dam survival rate of non-transported fish. Extra mortality expressed on an annual basis is here denoted by ‘EM’.

We first attempted to isolate extra mortality from the other sources of mortality in the Delta model. The Delta model partitions mortality according to:

\[ \ln(R_{t,i}) = (1 + p) \ln(S_{t,i}) + a_i - b_i S_{t,i} - m_{t,i} + \delta_t + \epsilon_{t,i} \]

where

- \( R_{t,i} \) = Columbia River returns (recruitment) originating from spawning in year \( t \) and sub-basin \( i \)
- \( S_{t,i} \) = spawners in year \( t \) and sub-basin \( i \)
- \( a_i \) = Ricker \( a \) parameter, which depends on sub-basin \( i \)
- \( b_i \) = Ricker \( b \) parameter, which depends on sub-basin \( i \)
- \( p \) = depensation parameter
- \( m_{t,i} \) = Snake River spring/summer chinook specific instantaneous mortality (passage + extra)
- \( \delta_t \) = common year effect
- \( \epsilon_{t,i} \) = normally distributed mixed process and recruitment measurement error, which depends on year \( t \) and sub-basin \( i \)

The parameter \( m_t \) can be estimated from the spawner recruit data by using the maximum likelihood estimates for two parameters, \( \mu_t \) and \( X \) according to

\[ m_t = n_t X + \mu_t \quad \text{(1)} \]

where
\( \mu_t \) = Incremental total mortality between the Snake River Basin and the John Day project in year \( t \):

\( n_t \) = Number of first level (lower Columbia) dams Snake River stocks must pass in year \( t \)

\( X \) = estimated total mortality per first level dam (does not vary with year).

We can solve for the instantaneous extra mortality (\( \Delta m_t \)), by subtracting \( M_t \) (defined as direct downstream instantaneous mortality from a passage model, for year and region) from \( m_t \). Extra mortality is then specific to a particular passage (and transportation effectiveness) model. There is a tradeoff between direct and extra mortality, since the extra mortality is fit to \( m_t \) values from the spawner-recruit data. The lower the direct mortality predicted by a passage model for a given year, the higher the extra mortality estimate for that year.

We estimated this quantity using PATH model MLE retrospective model estimates for BY 1980-1990 (only years available). The complement of annual extra mortality (1-EM) can be expressed as the post-Bonneville Dam survival factor \( S_{em} \):

\[
S_{em} = \exp(-\Delta m)
\]  

(2)

In our STUFA Leslie matrix, we explicitly modeled total extra mortality by incorporating \( D \) into this parameter (\( S_{em} \)).

**Compartmentalizing \( S_{em} \) for different management scenarios**

In order to evaluate different management scenarios using different hypotheses related to extra mortality (e.g., hydrosystem related = delayed mortality reduced, BKD/Stock Viability related = delayed mortality remains) and different hypotheses about differential delayed mortality for transported fish, we segregated the post-Bonneville Dam survival factors as follows.

(Note: Equations below are used to calculate the parameters for each brood year. The year \([t]\) subscripts are henceforth omitted to avoid confusion with parameters applying to transportation)

\( S_{em} = 1 - EM. \)

This can be expressed in terms of the post-Bonneville Dam survival factors of each component
of the migration, namely, transported and non-transported smolts.

\[ S_{em} = P_{bt} \chi_t + (1 - P_{bt}) \chi_n \]  

(3)

where

\[ P_{bt} = \text{Proportion of smolts surviving to immediately below Bonneville Dam which were transported} \]

\[ \chi_t = \text{‘delayed survival factor’ of transported smolts (the parameter known in PATH as } \lambda_t [\text{no relation to finite rate of population growth from matrix}]) \]

\[ \chi_n = \text{‘delayed survival factor’ of non-transported smolts (the parameter known in PATH as } \lambda_n [\text{no relation to finite rate of population growth from matrix}]) \]

Further, we can define EM(n)—the extra mortality experienced by non-transported smolts—as 1 - \( \chi_n \).

Since \( D = \frac{\chi_t}{\chi_n} \) (e.g., Marmorek and Peters 1998b), \( S_{em} \) can be written as

\[ S_{em} = \chi_n (DP_{bt} + 1 - P_{bt}) \]  

(4)

\( S_{em} \) is estimated using output from passage models and from PATH MLE (Maximum Likelihood Estimation) models. As described above, the quantity \( m \) represents the MLE estimate of direct and delayed passage (or otherwise extra) instantaneous mortality. The direct passage instantaneous mortality \( (M) \) estimate is output from the passage models. Again, the instantaneous extra mortality is found from

\[ \Delta m = m - M \]  

(5)

then \( (2) S_{em} = \exp(-\Delta m) \).

So from (4),

\[ \chi_n = \frac{S_{em}}{DP_{bt} + 1 - P_{bt}} \]  

(6)
Rather than using $D$ explicitly in the STUFA matrix, we wanted to incorporate total extra mortality into the model as part of $S_2$. Extra mortality is incorporated as the “survival through extra mortality” stage (remember that $S_{em} = 1 - EM$). We reformulated the CRI expression for direct downstream passage survival rate in order to more easily accommodate the output of the passage models and allow for explicit incorporation of variance estimates in all relevant parameters. The direct total downstream passage survival equals $\exp(-M)$ in PATH (where $M$ is as defined above), and is the expression on the right hand side of equation 7 (except for $S_{em}$):

$$S_2 = ((1-p_t) * S_d + p_t * V_t * S_b) * S_{em}$$ (7)

Where:

$p_t$ = fraction of population encountering the hydrosystem that is barged
$S_d$ = survival of non-barged fish to below Bonneville Dam
$V_t$ = survival of transported fish up to the point of transport
$S_b$ = survival of barged fish from collection to below Bonneville Dam = 0.98

In this formulation, $S_2$ is equal to $\exp(-m)$, where $m$ is the $m_t$ defined above.

Table D.1 shows the annual $m$ values from a PATH MLE model run, for the brood years 1980-1990. Also shown are baseline $M$ and resultant baseline $S_{em}$ and $\chi$ values for CRiSP/NMFS and FLUSH passage/transportation models.

D. 6
Table D.1. Baseline direct and extra mortality parameters for ‘CRiSP’ and FLUSH passage model with D values applied to PATH Snake River spring/summer chinook m’s. CRiSP estimates were done using CRiSP passage model output, combined with approximate ‘D’ estimated by NMFS from recent PIT-tag data (0.8). FLUSH used annual ‘D’ estimates from ‘Turb 5’ runs (average ~ 0.3).

<table>
<thead>
<tr>
<th>Brood Year</th>
<th>m from MLE</th>
<th>CRiSP M</th>
<th>CRiSP $S_{em}$</th>
<th>CRiSP $\chi_n$</th>
<th>FLUSH M</th>
<th>FLUSH $S_{em}$</th>
<th>FLUSH $\chi_n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1980</td>
<td>1.01</td>
<td>0.87</td>
<td>0.87</td>
<td>0.98</td>
<td>0.36</td>
<td>0.52</td>
<td>1.03</td>
</tr>
<tr>
<td>1981</td>
<td>0.99</td>
<td>0.95</td>
<td>0.97</td>
<td>1.09</td>
<td>0.52</td>
<td>0.63</td>
<td>1.29</td>
</tr>
<tr>
<td>1982</td>
<td>1.44</td>
<td>0.59</td>
<td>0.43</td>
<td>0.50</td>
<td>0.50</td>
<td>0.39</td>
<td>0.66</td>
</tr>
<tr>
<td>1983</td>
<td>1.30</td>
<td>0.54</td>
<td>0.47</td>
<td>0.57</td>
<td>0.39</td>
<td>0.40</td>
<td>1.34</td>
</tr>
<tr>
<td>1984</td>
<td>2.40</td>
<td>0.53</td>
<td>0.15</td>
<td>0.18</td>
<td>0.36</td>
<td>0.13</td>
<td>0.34</td>
</tr>
<tr>
<td>1985</td>
<td>2.90</td>
<td>0.54</td>
<td>0.10</td>
<td>0.12</td>
<td>0.44</td>
<td>0.09</td>
<td>0.41</td>
</tr>
<tr>
<td>1986</td>
<td>1.82</td>
<td>0.53</td>
<td>0.27</td>
<td>0.34</td>
<td>0.41</td>
<td>0.24</td>
<td>1.33</td>
</tr>
<tr>
<td>1987</td>
<td>2.67</td>
<td>0.56</td>
<td>0.12</td>
<td>0.15</td>
<td>0.43</td>
<td>0.11</td>
<td>0.33</td>
</tr>
<tr>
<td>1988</td>
<td>2.67</td>
<td>0.48</td>
<td>0.11</td>
<td>0.14</td>
<td>0.37</td>
<td>0.10</td>
<td>0.44</td>
</tr>
<tr>
<td>1989</td>
<td>2.51</td>
<td>0.37</td>
<td>0.12</td>
<td>0.14</td>
<td>0.31</td>
<td>0.11</td>
<td>0.41</td>
</tr>
<tr>
<td>1990</td>
<td>3.58</td>
<td>0.31</td>
<td>0.04</td>
<td>0.05</td>
<td>0.33</td>
<td>0.04</td>
<td>0.21</td>
</tr>
</tbody>
</table>

The columns of $S_{em}$ values in Table D.1 show that except for a couple of years, the amounts of EM estimated by CRiSP/NMFS model and FLUSH model are very close. Note also that both models agree that during the period, survival through extra mortality decreased with time (i.e., extra mortality increased with time). Comparison of the $\chi_n$ values resulting from the two models shows the effect that the different assumptions about D have on the allocation of EM. FLUSH $\chi_n$’s are higher, suggesting less EM of non-transported fish. This results from FLUSH D estimates effectively allocating more EM to transported fish than the NMFS D does. The trade-off between D and extra mortality of non-transported fish in fitting the R/S data is shown in Figure D.1.

From Figure D.1, it can be seen that although total EM is not very different between CRiSP/NMFS and FLUSH models, the allocation of EM between transported and non-transported components is very different. The high D assumed by NMFS requires a high EM(n) to fit the R/S data, whereas the low FLUSH D results in a correspondingly lower estimate of EM(n) to fit the same data.
Figure D.1. Mean total extra mortality (EM), extra mortality of non transported fish \[EM(n) = 1 - \chi_n\], and \(D\) for 1980-90 brood years, CRiSP/NMFS passage/transportation model and FLUSH passage/transportation model.

**Predicting \(S_{em}\) for different prospective scenarios and EM hypotheses**

Implementation of the prospective scenarios [as described in main text: Baseline, Maximize Transport (A2), Dam Breach (A3/BKD and A3/Hydro), and Everything But Dam Breach (EBB)] required estimating prospective \(S_{em}\) values to include in the \(S_2\) parameter. Under the Baseline scenario, the \(S_{em}\) values used are simply the ones estimated from the retrospective data, since this scenario represents the assumption that the survival rates don’t change from those estimated for 1980 to the present. Since the same \(m\) values are used to fit both CRiSP and FLUSH \(S_{em}\) values, the overall annual direct and extra mortality estimates are the same for either model for Baseline runs \([S_{em} = \exp(-m)]\).

Under the Maximize transport (A2) scenario, \(S_{em}\) changes from the baseline, and the amount of change depends on which passage/transportation model is used. In both models, changes in hydrosystem operations result in a different (on average, greater) portion of fish transported (the \(P_{bt}\) parameter) than under the baseline. This changes the overall \(S_{em}\), since transported fish experience a lower survival rate in the estuary and ocean than non-transported fish, according to
For the Dam Breach option (A3), two EM(n) hypotheses were modeled. Under either the delayed mortality remains (‘BKD’) hypothesis or the delayed mortality reduced (‘hydro’) hypotheses, the part of extra mortality that is a consequence of $D$ being less than 1 is removed, since transportation would be halted. Under the BKD hypothesis, the magnitude of the EM is equal to that estimated for the EM(n) of non-transported fish in the Baseline period. In other words, $EM = EM(n)$ for the Baseline. Under the ‘hydro’ hypothesis, EM is estimated by using PATH MLE $m$ and $M$ estimates as described earlier, on the assumption that under the A3/hydro scenario, total direct and delayed passage mortality would revert to the level estimated for the four-dam historical period. The years used for $m$ are brood years 1959-1965. The $m$ estimated for that period is a fixed value; it is the product of the fixed per dam mortality ($X$) and the number of dams ($n$; Equation 1). Using MLE estimate of $X = 0.2563$ and $n = 4$, $m$ for this period is equal to 1.025. The value of $S_{em}$ for a particular passage model is calculated using $m$, the passage model parameters under A3 (in this case, just $S_d$, since there is no transportation), and Equations (5) and (2). As in the Baseline scenario, fitting to the historical estimates in this manner [setting $S_2 = exp(-m)$] results in identical values of $S_2$ for the two passage models under scenario A3/hydro. Although the historical $m$ (and hence $S_2$) was fixed due to the method used to estimate it, in stochastic matrix simulations we used this $S_2$ as a point estimate of the mean, and applied a variance equal to that estimated for $S_2$ from the baseline period.

$S_{em}$ values used are shown in Table D.2. $S_2$ values are shown in Table D.3.
Table D.2. Annual $S_{em}$ values for different prospective scenarios for FLUSH and CRiSP/NMFS passage/transportation models. CRiSP $A2/EBB$ annual values are averages of 500 randomized estimates simulating variability around mean ‘$D$’.

<table>
<thead>
<tr>
<th>Brood Year</th>
<th>Baseline $S_{em}$</th>
<th>$A2/EBB$ $S_{em}$</th>
<th>$A3/Hydro$ $S_{em}$</th>
<th>$A3/BKD$ $S_{em}$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>FLUSH</td>
<td>CRiSP</td>
<td>FLUSH</td>
<td>CRiSP</td>
</tr>
<tr>
<td>1980</td>
<td>0.52</td>
<td>0.87</td>
<td>0.44</td>
<td>0.87</td>
</tr>
<tr>
<td>1981</td>
<td>0.63</td>
<td>0.97</td>
<td>0.51</td>
<td>0.97</td>
</tr>
<tr>
<td>1982</td>
<td>0.39</td>
<td>0.43</td>
<td>0.29</td>
<td>0.43</td>
</tr>
<tr>
<td>1983</td>
<td>0.40</td>
<td>0.47</td>
<td>0.47</td>
<td>0.47</td>
</tr>
<tr>
<td>1984</td>
<td>0.13</td>
<td>0.15</td>
<td>0.12</td>
<td>0.15</td>
</tr>
<tr>
<td>1985</td>
<td>0.09</td>
<td>0.10</td>
<td>0.11</td>
<td>0.10</td>
</tr>
<tr>
<td>1986</td>
<td>0.24</td>
<td>0.27</td>
<td>0.33</td>
<td>0.27</td>
</tr>
<tr>
<td>1987</td>
<td>0.11</td>
<td>0.12</td>
<td>0.11</td>
<td>0.12</td>
</tr>
<tr>
<td>1988</td>
<td>0.10</td>
<td>0.11</td>
<td>0.11</td>
<td>0.11</td>
</tr>
<tr>
<td>1989</td>
<td>0.11</td>
<td>0.12</td>
<td>0.10</td>
<td>0.12</td>
</tr>
<tr>
<td>1990</td>
<td>0.04</td>
<td>0.04</td>
<td>0.05</td>
<td>0.04</td>
</tr>
</tbody>
</table>
Table D.3. Annual $S_2$ values for different prospective scenarios, for FLUSH and CRiSP/NMFS passage/transportation models. CRiSP $A2/EBB$ annual values are medians of 500 randomized estimates simulating variability around ‘$D$’ point estimate. $A3/Hydro$ value is geometric mean estimate for all years; variance about this mean was included in stochastic simulations (see text).

<table>
<thead>
<tr>
<th>Brood Year</th>
<th>Baseline $S_2$</th>
<th>$A2/EBB$ $S_2$</th>
<th>$A3/Hydro$ $S_2$</th>
<th>$A3/BKD$ $S_2$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>FLUSH</td>
<td>CriSP</td>
<td>FLUSH</td>
<td>CriSP</td>
</tr>
<tr>
<td>1980</td>
<td>0.36</td>
<td>0.36</td>
<td>0.38</td>
<td>0.64</td>
</tr>
<tr>
<td>1981</td>
<td>0.37</td>
<td>0.37</td>
<td>0.44</td>
<td>0.71</td>
</tr>
<tr>
<td>1982</td>
<td>0.24</td>
<td>0.24</td>
<td>0.25</td>
<td>0.35</td>
</tr>
<tr>
<td>1983</td>
<td>0.27</td>
<td>0.27</td>
<td>0.40</td>
<td>0.39</td>
</tr>
<tr>
<td>1984</td>
<td>0.09</td>
<td>0.09</td>
<td>0.10</td>
<td>0.12</td>
</tr>
<tr>
<td>1985</td>
<td>0.06</td>
<td>0.06</td>
<td>0.09</td>
<td>0.08</td>
</tr>
<tr>
<td>1986</td>
<td>0.16</td>
<td>0.16</td>
<td>0.27</td>
<td>0.23</td>
</tr>
<tr>
<td>1987</td>
<td>0.07</td>
<td>0.07</td>
<td>0.10</td>
<td>0.10</td>
</tr>
<tr>
<td>1988</td>
<td>0.07</td>
<td>0.07</td>
<td>0.09</td>
<td>0.10</td>
</tr>
<tr>
<td>1989</td>
<td>0.08</td>
<td>0.08</td>
<td>0.09</td>
<td>0.10</td>
</tr>
<tr>
<td>1990</td>
<td>0.03</td>
<td>0.03</td>
<td>0.04</td>
<td>0.03</td>
</tr>
</tbody>
</table>

From Tables D.2 and d.3, it can be seen that, perhaps contrary to expectation, $S_{en}$ and $S_2$ for $A3/BKD$ on average is somewhat higher than for $A3/Hydro$ scenario for FLUSH. This is a result of the tradeoff between EM(n) and $D$ in apportioning total EM (Figure D.1). The magnitude of extra mortality of non-transported fish under $A3/BKD$ or $A3/Hydro$ is determined from ‘$m$’ estimates derived in PATH from the historical four-dam period, when there was no transportation, whereas current levels of extra mortality are estimated from brood years 1980-90 and include both transported and non-transported fish. Therefore, the assumed $D$ value affects how much extra mortality must be assigned to non-transported fish to fit the time series of $m$ values from the recent period. Passage/transport models with lower $D$ values have less extra mortality left over to attribute to non-transported fish. In the case of the FLUSH runs used, $D$ is low enough that extra mortality of non-transported fish from the recent period (about 42%) is slightly less than that of the four-dam period (about 47%). Therefore, assuming that recent levels of extra mortality of non-transported fish continue (i.e., delayed mortality remains hypothesis) results in a higher level of “dam breach” post-Bonneville Dam survival than assuming extra mortality levels go back to the estimated four-dam values (i.e., delayed mortality reduced hypothesis).
Literature Cited


This alphabetical listing of the stochastic parameters only shows some example distributions from Marsh Creek (FLUSH simulations).
Fraction of spawners of age-3
Histogram(0,0.083,{9,1,3,4,0,0,0,0,1,2}) 0.023
Best fit, fit to subbasin planning estimates for 1980-1995 brood years

Fraction of spawners of age-4
Histogram(0,0.7,{3,2,1,3,5,2,0,1,2,1}) 0.30
Best fit, fit to subbasin planning estimates for 1980-1995 brood years

Fraction of spawners of age-5
Histogram(0.267,1,{1,1,2,1,2,2,6,0,2,3}) 0.69
Best fit, fit to subbasin planning estimates for 1980-1995 brood years

Fecundity (age-3)
Normal(Ave, s.d.) 3257, s.d. = 930.9
WDFW data, analyzed by Olaf Langness.

Fecundity (age-4)
Normal(Ave, s.d.) 4095, s.d. = 830.8
WDFW data, analyzed by Olaf Langness.

Fecundity (age-5)
Normal(Ave, s.d.) 5149, s.d. = 1031
WDFW data, analyzed by Olaf Langness.

Fraction female (age-3)
Uniform(0, 0.1) 0.05
Nominal from CRI, arbitrary range (C.V. = 0.1)

Fraction female (age-4)
Normal(0.49, 0.05) 0.49
Nominal from CRI, arbitrary range (C.V. = 0.1)

Fraction female (age-5)
Normal(0.67, 0.067) 0.67
Nominal from CRI, arbitrary range (C.V. = 0.1)

Initial population
Used in Leslie matrix calculations

Prespawn survival
Truncated normal distribution with left cdf of 0.1 and right cdf of 0.9

Prespawn survival
Nominal from CRI 1980-1995 brood years

Prespawn survival
Nominal from CRI 1980-1995 brood years

Prespawn survival
Nominal from CRI 1980-1995 brood years

Prespawn survival
Nominal from CRI 1980-1995 brood years

Prespawn survival
Nominal from CRI 1980-1995 brood years

Prespawn survival
Nominal from CRI 1980-1995 brood years

Prespawn survival
Nominal from CRI 1980-1995 brood years

Prespawn survival
Nominal from CRI 1980-1995 brood years

Presawn survival
Nominal from CRI 1980-1995 brood years

Presawn survival
Nominal from CRI 1980-1995 brood years

Presawn survival
Nominal from CRI 1980-1995 brood years

Presawn survival
Nominal from CRI 1980-1995 brood years

Presawn survival
Nominal from CRI 1980-1995 brood years

Presawn survival
Nominal from CRI 1980-1995 brood years

Presawn survival
Nominal from CRI 1980-1995 brood years

Presawn survival
Nominal from CRI 1980-1995 brood years

Presawn survival
Nominal from CRI 1980-1995 brood years

Presawn survival
Nominal from CRI 1980-1995 brood years
Probability of surviving from egg to smolt: 0.02103, 0.08696, {2, 4, 6, 10, 18, 9, 4, 1, 0, 2} (histogram from hs_S1_8389.xls, 1980-1992 brood years, 4 methods).

Probability of surviving from emigration to below Bonneville: Lognormal distribution, varies by scenario.
- Geomeans: Baseline: FLUSH and CRiSP: 0.1205
- FLUSH: 0.1545, CRiSP: 0.1448
- A3: FLUSH 0.3938, CRiSP 0.1628
- A3/hydro: FLUSH and CRiSP: constant 0.359

Analyses by Paul Wilson, 1980-1990 brood year FLUSH and CRiSP/NMFS (D=.8).

Probability of surviving from 2nd to 3rd birthday: Uniform(.04993, .1669) 0.1084 Calculated best and worst case scenarios.

Probability of surviving from 3rd to 4th birthday: Uniform(0.8*0.9, 0.8*1.1) 0.8 Nominal from CRI, arbitrary range (±10%).

Probability of surviving from 4th to 5th birthday: Uniform(0.8*0.9, 0.8*1.1) 0.8 Nominal from CRI, arbitrary range (±10%).

Smolt-to-adult survival (Lower Granite to river mouth):
- Histogram(0.00206, 0.02232, {4, 8, 5, 6, 10, 7, 3, 1, 6, 2}) 0.01 BestFit, from hs_S1_8389.xls, 1980-1992 brood years, 4 methods.
APPENDIX F

Potential reduction in smolt predation from Caspian terns on Rice Island

Estimates of chinook predation by avian predators (Caspian terns, Sterna caspia) in the vicinity of Rice Island vary widely depending on estimation method and assumptions about survival from the point of release (for tagged fish) to arrival in the estuary (e.g., survival through the hydrosystem or survival of barged fish transported around the hydrosystem). For 1998, Schreck et al. (submitted March 2000) estimated avian predation rates (included both terns and cormorants around Rice and East Sand Island) on spring/summer chinook smolts to be 12 to 17% of the fish released at Bonneville Dam (run-of-river smolts) and from barges. However, these estimates are based on the number of radio-tagged fish that were released. Fish are not always “reheard” from after initial hearing (causing a conservative estimate of mortality). In addition, radio-tagged fish may be more susceptible to avian predation (Adams et al. 1998) causing an over-estimate of mortality. Numbers of PIT-tags (for hatchery spring chinook tagged in the Comparative Survival Study) detected on Rice Island from in-river and transport groups relative to the estimated population size below Bonneville Dam ranged approximately 2 to 10% for 1996-1998 migration years (FPC 1999). Estimates using a bird bioenergetics approach in combination with data on diet of Rice Island predatory birds indicated that avian predation rates on salmon smolts ranged from 6 to 25% (for all outmigrating smolts, USACE 2000). Collis et al. (1999), using population-based bioenergetics modeling, estimated that 11-30% (mean 18%) of all smolts reaching the estuary are preyed upon by avian predators. Of those avian predators, Caspian terns were estimated to consume an average of 11% (8 to 16%) of out-migrating smolts that reached the estuary in the 1998 migration year. PIT-tag estimates may be conservative as some portion of tags are likely lost during in-flight defecation over water while bioenergetic estimates may be biased high from maximum consumption, seasonal differences, and other related bioenergetic assumptions.

Recognizing that all estimation methods have notable limitations, we used the median of these various estimates for establishing an average reduction in smolt mortality due to tern relocation efforts. The median of the three different estimates was a below-Bonneville based predation rate of approximately 11% (2 to 25%). In 1999, relocation efforts attempting to move the tern population to a different island lower down in the estuary (East Sand Island) appeared to reduce predation on salmon smolts by 43% (from 77% of the diet to 44% of the diet, USACE 2000). If we apply that reduction potential to the 11% median smolt predation rate, we get 6%. In addition, both radio tags and PIT tags indicated there was no significant difference in smolt predation rates between smolts that were transported versus those that migrated in-river. Therefore, for the “Everything but dam breach” scenario, we reduced mortality in the estuary by 6% according to the logic explained above. The 6% reduction in mortality was applied to S2 since there was no apparent difference in avian predation rates on transported smolts relative to in-river smolts and in an attempt to keep extra mortality factors separate from avian predation.
Literature cited


