

A STANDARDIZED QUANTITATIVE ANALYSIS OF RISKS FACED BY SALMONIDS IN THE COLUMBIA RIVER BASIN

Cumulative Risk Initiative
Northwest Fisheries Science Center
NMFS-NOAA

17 July 2000

Table of Contents

- I. Executive Summary (p. 3)
 - II. Scope of the Problem (p. 9)
 - III. Goals and General Considerations (p.13)
 - IV. Dennis Extinction Risk Analysis –Tests and Refinements (p.18)
 - V. Standardized Comparison of Risks Across ESUs (p. 44)
 - VI. Detailed Analyses for Selected ESUs (p.86)
 - VII. Summary of Key Findings: The Ten Most Important Points (p.116)
 - VIII. References and Acknowledgements (p. 118)
-
- APPENDIX A. ESU Descriptions
 - APPENDIX B. Results Summary
 - APPENDIX C. Data Summary

I. Executive Summary

Last December, the National Marine Fisheries Service released a draft paper, known familiarly as the “All-H Study,” that examined the four Snake River population groups (or ESUs) of salmon and steelhead, with particular emphasis on how, together and separately, the so-called four H’s of habitat, hydropower, hatcheries and harvest, affected these stocks. At that time, the agency promised a more thorough analysis of the remaining eight Columbia Basin stocks. The result of that further analysis is this draft study, summarized below. Its is straightforward: all the Columbia River Basin salmon stocks are in a state of perilous decline, especially Upper Columbia Spring Chinook and Steelhead throughout its range. Put in starker terms: without substantial intervention, there is a greater than 50:50 chance that most of these ESUs will be extinct by the next century, some much sooner.

Thus, this draft report is a crucial management tool, quantifying for the first time the rates of declines for the Columbia River Basin salmonid stocks and articulating the management options available to arrest and reverse those declines.

A Standardized Quantitative Analysis of the Risks Faced by Salmonids in the Columbia River Basin

Since 1991, twelve salmonid Evolutionary Significant Units (ESUs) in the Columbia River Basin have been listed as threatened or endangered under the Endangered Species Act. Because these dozen ESUs share overlapping ranges, common waterways and common threats, it is neither practical nor wise to treat each ESU as a separate management problem. Instead, we need to broadly examine the entire Columbia River Basin and its salmonids. Until now, we have lacked reports presenting even the most basic population size and trend data for Columbia River Basin salmonids in a common format. Hence, standardized data synthesis and analysis is a key feature of this document. In addition, we present a standardized assessment of extinction risks and the magnitude of improvements required to mitigate these risks. Finally, to varying degrees, depending on what data is available, we begin to evaluate the potential effects of management actions aimed at different life stages or sources of mortality. The lessons learned from this synthesis of data and analyses are broadly sketched for the entire region.

A. Standard descriptions of data and summary metrics

Standardization requires the adoption of a consistent methodology. A lack of uniformity in the time periods for reporting or analyzing data, as well as methods of analysis, has made it impossible to compare different ESUs or different populations within the same ESU. Too often discussions regarding salmon become muddled because the parties involved discuss varying time intervals, or report data in different ways. In our approach to quantifying the risks faced by Columbia River Basin salmonids, we have chosen the following standards.

Time period: All analyses in this report use spawner counts or other population data from 1980 until current (or as current as is available). We have selected 1980 as a starting point because prior to that year the hydropower operations in the Columbia River Basin were not firmly established. Secondly, the farther back in time one goes, the less likely the data are to represent current biological and environmental conditions, and it is the current situation that needs to be clearly described and addressed. One factor not included in these analyses is the influence of different scenarios for altered ocean conditions relative to the baseline time period of 1980 to current. The possibility that ocean conditions may improve relative to our current period, or deteriorate even further, may need to be considered when examining the policy options for certain ESUs.

Population counts and running sums: At annual intervals we report the raw number of spawners counted, taking care to document where these counts were made, and the running sum of spawners tabulated in a way that measures the total spawner population, including the “unseen fish” in the ocean as well as those counted on the spawning ground. In addition to aggregated counts for eleven ESUs (sockeye salmon are not examined), we report and analyze time series of counts for 57 different index stocks.

Annual rate of population change: For both ESUs and individual index stocks we estimate average annual rate of population change or “lambda.” Lambda, which incorporates year-to-year variability, is the best summary statistic of how rapidly a population is growing or shrinking. A lambda less than 1.0 means the population is declining; a lambda greater than 1.0 means the population is increasing.

Risk of extinction: By combining lambda with estimates of environmental variability it is possible to calculate “extinction risk metrics.” All extinction metrics are calculated on a 24- and 100-year timeframe. For index stocks, where our data represent entire population counts, we estimate extinction risks in terms of the probability of an adult population falling to only one spawner. For ESUs we calculate extinction metrics as the probability of a 90% decline after 24 years and after 100 years, because it is unlikely that entire ESUs have been accurately counted.

Key diagnostics: Our estimates of annual rates of decline and extinction risks depend on several assumptions about the structure of these data. The most important assumptions concern whether or not there is evidence of density-dependence in the time series and whether there are trends in the temporal pattern of recruits per spawner. We test for density-dependence in a formal statistical manner, but rely on simple graphs to portray trends in recruits per spawner. We are developing methods for estimating the significance of trends. If graphs indicate striking declining trends in recruits per spawner, then the standardized extinction-risk metrics will be underestimates, assuming that the trends continue into the future.

B. Results of Analyses

Overview of Annual Rates of Population Change and Risks of extinction

At the ESU level, the annual rates of population change were less than 1.0 for ten of the eleven ESUs and less than 0.9 for Upper Columbia Spring Chinook salmon, Middle Columbia Steelhead, Upper Columbia Steelhead, and Upper Willamette Steelhead. The four ESUs showing lambdas less than 0.9 are decreasing at such a rapid rate, at least 10% per year, that we can expect to see only tiny fractions of their already depressed populations surviving out to 24 years. It is worth noting that at the ESU level the salmonids showing the most dire risks of perilous declines were *not* Snake River Spring/Summer Chinook.

At the index stock level, the range of risks is broader, but the same overall picture is evident. For example, over four-fifths of the stocks exhibited lambdas less than 1.0, and one third had lambdas less than 0.9, with the average lambda across 54 stocks at 0.93. Similarly, the extinction risks, in this case calculated as the probability of dropping to only one fish within 24 or 100 years, were also high, averaging 14% at 24 years and 59% at 100 years. These are minimum estimates of risk, as they are calculated assuming that hatchery fish contribute nothing to future generations.

Overview of Improvements Needed to Mitigate Risks

Generally, ESUs or stocks with the most rapid rates of decline – the lowest lambdas -- require the most improvement to mitigate extinction risks. However, this generality is complicated by the fact that low populations and high environmental variability can exacerbate extinction risks beyond what might be expected from lambda alone. The magnitude of improvements required in lambda ranged from less than 1% to as much as 112%, with most values falling between 5% and 20%. However, the needed improvements are much greater if hatchery fish are assumed to reproduce successfully.

The more difficult task is exploring opportunities for improving lambda, *i.e.*, increasing the number of recruits per spawner. The well-known “four H’s” (hydropower, habitat, hatcheries and harvest) represent the human-influenced arenas in which management can be altered in hopes of recovering ESUs. But because these four H’s vary enormously in the areas occupied by different ESUs, it is unlikely that a simple prescription can be drawn up that fits all ESUs. For example, the number of dams per kilometer varies from 0.4 to 2.8 depending on the region associated with each ESU. Land use characterization also varies widely across regions occupied by ESUs, with some regions characterized by a high percentage of rangeland (Upper Columbia and Snake Rivers), urbanization (lower Columbia, and upper Willamette Rivers), or cropland

(upper Willamette River). At the finer scale of index stocks, preliminary analyses indicate that three habitat variables at the subwatershed scale explain 60% of the variation in recruits per spawner: (1) percent of land classified as urban, (2) proportion of stream length failing to meet EPA water-quality standards, and (3) the ability of streams to recover from sediment flow events. Lastly, although nearly 100 hatchery facilities in the Columbia Basin release approximately 150 million smolts annually, the magnitude of this hatchery production varies by an order of magnitude among ESUs. The impact of this hatchery production is difficult to analyze because of the lack of large-scale controlled experiments. Some preliminary analyses suggest that in “poor ocean years” hatchery fish compete with wild fish and lower survival rates of wild fish.

In summary, there are no clear-cut analyses that allow confident predictions about likely improvements in lambda if actions are taken in hydropower, habitat or hatcheries. Generating such predictions is clearly a research priority. But right now, science cannot provide hard numbers on questions about how any ESU will respond to any particular management option, although the direction of effects and what would qualitatively represent an “improvement” are usually known. The one exception, of course, is harvest, because harvest is essentially a scheduled mortality, and analyzing changes in that mortality is straightforward. Harvest reductions, some of which already have been initiated, are clearly capable of achieving large increases in lambda (20% to 30%) for Lower Columbia Chinook, Upper Willamette Chinook, and Snake River Fall Chinook ESUs. For the remaining ESUs in the Columbia River Basin the opportunities for improvements due to harvest reduction are much less substantial. It is important to make clear that this analysis most emphatically does *not* mean that harvest reductions are the thing to do, but only that it is easiest to predict the consequences of a harvest reduction as compared to actions in habitat, hydropower, or hatchery operations.

C. The Next Scientific Steps

Critical Sampling Uncertainties

One of the greatest uncertainties does not involve the biology of salmonids; it is a simple counting problem. Hatchery fish spawn with wild fish to varying degrees throughout the Columbia River Basin. In some cases we have virtually no rigorously collected samples to indicate what percentage of the wild spawners are from a hatchery. In virtually all cases, even if we knew what fraction of spawners were hatchery fish, we do not know to what extent those hatchery fish are successful at spawning, or even if they were successful at all. The foundation of the most basic population analysis for any fish stock involves counts of spawners and recruits per spawner. When dealing with wild fish that mix with hatchery fish on the spawning ground, ignorance about the number of hatchery fish and their reproductive success means that all estimates of recruits per spawner are compromised. Without widespread quantitative estimates of hatchery spawning contributions and more selective estimates of relative reproductive fitness of hatchery fish, our analyses (and for that matter anyone’s quantitative analyses of salmonid populations) are highly uncertain. For instance, all of the numbers reported thus far assume that there is no reproduction from the hatchery fish. If instead one assumes that a hatchery derived spawner’s reproduction is equal to that of wild fish, an extreme assumption for illustrative purposes only, then the average lambdas for the 41 true wild fish from the index stocks where some information is available on the numbers of hatchery fish drops from 0.93 to 0.83 and the magnitude of improvements in lambda needed for recovery increases to over 20% in a large proportion of these cases.

A second sampling uncertainty is the magnitude of sampling error in all fish counts. All scientific measurements include some “observation error.” Since many of the run reconstructions for salmonids entail counts of redds (nests) per kilometer of stream that are then converted into estimates of female spawners per kilometer of stream (by some multiplier fraction) and then extrapolated to an entire spawning population, there is clearly great opportunity for an accumulation of observation error. From a scientific point of view, this is acceptable. However, what is *not* acceptable is the fact we have no systematic estimates of how large the observation error in this process is. It was the recognition of this fact that motivated us to design an extinction and population trend analysis that is relatively immune to sampling error. However, as the region moves towards actually attempting management actions and assessing their effectiveness it will be necessary to pay much closer attention to quantifying sampling error for each ESU – which will vary depending on the life history, ESU, lifestage, and watershed. This report produces an analysis of what is called “detectability,” the likelihood of detecting an increase in lambda of some fixed percentage within ten years given the observed variability in the past record of spawner counts. This detectability analysis could be very useful in designing management experiments, but only if it were better informed by estimates of sampling error.

The Need for Management Experiments

A summary of the available data suggests that in the short term, there is little hope of obtaining reliable indicators of the likely efficacy of any of the management options being considered. For example, even for the best studied ESU, the Snake River Spring/Summer Chinook salmon, there is good evidence that dam breaching would increase lambda, but not enough evidence to say by how much. Similarly, there is some evidence that habitat improvements might increase lambda for this ESU, but not enough evidence to calculate a likely percent increase. In order to offer more focused guidance, additional research is needed on quantitative relationships between habitat improvements, dam breaching, and hatchery changes and recruits per spawner.

The data clearly indicate the risks if things stay the same. In addition, we can monitor and see how well lambdas improve following management. However, decision-makers will not be able to turn to existing data to receive a prescription of exactly what actions will reap particular benefits. Instead, the way to interpret the results of this report is to realize that for low lambdas and high extinction risks there is little “wiggle room,” and the situation is close to “one must do everything.” If lambda does not reflect such a severe decline and only small improvements are needed, then there may be the potential to choose among different options. Importantly, even the smallest rate of decline means something must be done, and it can be extremely difficult to improve lambda by as little as 1%. The point is that the “worse” (or lower) lambda gets, the less opportunity there is for trying to choose among options and the more discussion should revolve around doing everything. Where exactly the switch between “choices and options” versus “do everything” occurs is a policy decision.

D. Synthesis of Findings and Recommendations

Rates of population decline and extinction risks vary widely across the Columbia River Basin, suggesting that management needs vary in accord with these different levels of risk. Most imperiled are Upper Columbia Spring Chinook, Middle Columbia Steelhead, Upper Columbia

Steelhead, and Upper Willamette Steelhead ESUs.

The amount of improvement in recruits per spawner that is required to mitigate risks can be modest (less than 1%) or quite large (as high as 65%). When needed improvements are modest there are probably management options, but when needed improvements are large there is little room to be selective about what actions are taken. We must do everything possible to increase recruits per spawners before it is too late. A lambda of 0.9 means that in less than 7 years a population is likely to be reduced to half its current level.

Reductions of harvest represent an easily identified mechanism for improving recruits per spawner in a few ESUs (Lower Columbia Chinook, Upper Willamette Chinook, and Snake River Fall Chinook). In other ESUs we lack data for making confident quantitative predictions about the likely effects of any particular management action. This is even the case for the much-studied Snake River Spring/Summer Chinook salmon where risks are substantial and the need for action is striking (particularly if one factors in the recent declining trend in recruits per spawner). Although there is some evidence that dam breaching is necessary for mitigating the extinction risk faced by Snake River Spring/Summer Chinook salmon (especially given the lack of evidence that needed improvements can be made by non-breaching management actions), it is highly unlikely that dam breaching alone will recover these populations. Hence, even in this most-studied of all cases, actions will be predicated on uncertainty. But what is not uncertain is the substantial rates of decline for Snake River Spring/Summer Chinook salmon and even worse rates of decline for several other ESUs.

In summary, the scientific uncertainty surrounding the likely outcome of everything but harvest reductions is not an argument for inaction, especially given the high risks faced by several ESUs. Quite the contrary. This level of uncertainty is, however, an observation that the public and policy makers should be aware of. From a scientific viewpoint the ideal action is rapid, targeted management action with effective monitoring programs. Secondly, establishment of quantitative links between management actions and salmon productivity are obviously a priority area for research. The region has suffered from an inattention to standardized reporting of data and analyses at a large scale and as a result currently lacks the scientific information required to make quantitative assessments of management scenarios. It is imperative that this last point be emphasized to the public and policy makers: collectively we have failed to manage Columbia River Basin salmonid populations and are now forced to undertake management actions as experiments, accepting that some will fail, but if they are properly designed, we can learn from our mistakes.

II. Scope of the Problem

Since 1991 twelve salmonid Evolutionarily Significant Units (ESUs) in the Columbia River Basin have been listed as threatened or endangered under the Endangered Species Act. Human impacts on the river basin and the species inhabiting it have led to dramatic declines in numbers of anadromous fishes and in the quality and quantity of habitat available to them. It is widely recognized that large sacrifices need to be made in many areas if these salmon are to be recovered (NRC 1996), but there is a lack of quantitative analysis for guiding what sacrifices might be most effective, or which ESUs and populations are at the greatest risk. This document presents the sorts of analyses needed to conduct basin-wide planning, but in no way is this document the final word; indeed some of the key findings pertain to subsequent analyses and data syntheses that need to be initiated as soon as possible.

II.A. Physical Setting and Historical Impacts

The Columbia River Basin covers about 250,000 square miles (an area nearly the size of Texas), in seven U.S. states and British Columbia, stretching from the Pacific Ocean to the Continental Divide. Within its boundaries are found wet and dry temperate coniferous forests, arid shrubland and grasslands, true desert, and alpine areas.

Returns of salmon and steelhead to the Columbia River basin before Euro-American influence have been estimated to range from 7-8 million (Chapman 1986) to 10-16 million (NPPC 1986) per year. Population declines appear to have begun in the late 1800s due to harvest pressures. Habitat degradation and loss, as well as blockage or impediments to fish passage from the construction of dams throughout the basin exacerbated these declines. Current returns of adult salmonids to the entire basin are about 1 million fish per year; approximately 80 percent of these fish are of hatchery origin.

Significant non-tribal harvest pressures began with the establishment, in 1866, of the first of forty commercial canneries on the Columbia. Peak in-river harvest may have been as high as 3-4 million fish (Chapman 1986), and the catch of spring chinook salmon began a steady decline after the 1870s, triggering switches in harvest to other species and runs. By the 1940s, the total catch of salmonids from the Columbia River was about half of that in the late 1800s (WDFW, ODFW 1994, cited in NRC 1996). Both harvest methods and rates have been regulated in this century, and several ESUs are currently subjected to only ceremonial and subsistence treaty harvest. Other stocks are more heavily impacted by both ocean and in-river fisheries.

The first salmonid artificial propagation program in the region was established in 1877 on the Clackamas River. Today, there are more than 80 hatcheries in the Columbia River Basin, releasing over 100 million juveniles annually (CBFWA 1990, NRC 1996). Although hatchery fish have played a role in sustaining run sizes, artificial propagation programs have a variety of potentially detrimental impacts on natural populations. Most directly, the presence of hatchery fish in mixed fisheries has led to harvest rates that cause overfishing of wild populations. In addition, the formerly widespread practice of using non-local stocks has contributed to a loss of natural patterns of genetic variation both within and between populations (NRC 1996). Other potential effects of hatchery releases on wild populations include a reduction in the average fitness of wild populations due to interbreeding between wild and hatchery fish, increased

competition due to the increased numbers of fish in the system, and predation on juvenile wild fish by the hatchery released fish.

Habitat degradation has been a long-term problem across the Columbia River Basin, and stems from many human activities. Grazing, logging, agriculture, mining and urbanization have had a wide variety of negative effects on riparian and riverine systems including increased runoff and erosion, higher sedimentation, increased channelization of rivers and streams, higher water temperatures, fewer pools and less cover in stream systems, and extensive alteration of native plant communities. These habitat impacts began early in the history of Euro-American settlement of the region, with livestock in the basin reaching their highest numbers before 1900, and the first sawmill constructed in 1827. While grazing has been reduced on public lands in recent years, riparian habitat conditions on public rangeland remain generally poor (GAO 1988). Logging continues to be a leading industry throughout the Pacific Northwest, with over 10 billion board feet harvested annually in Oregon and Washington through 1990. (Timber harvests on public lands have decreased in recent years). Habitat degradation and alteration does not stop at the river mouth, either. An estimated 65% of tidal swamps and marshes in the Columbia estuary have been lost due to diking and filling (Thomas 1983).

Construction of dams was the final insult to a system already taxed by human alteration. A total of 27 large dams were built between 1930 and 1975 on the Columbia and Snake Rivers within the historic range of anadromous salmonids. In addition, over one thousand smaller dams, some without fish passage facilities, are currently maintained on tributaries to the Columbia and Snake Rivers. In total, about 55% of the area and 31% of the stream miles formerly available to anadromous fishes have been blocked by dam construction (NRC 1996). Dams have also inundated important mainstem spawning habitat. Currently the healthiest (fall) chinook salmon population in the basin spawns in the Hanford Reach, the only accessible unimpounded stretch left on the mainstem of the Columbia River. Out-migrating juvenile fish must negotiate the reservoirs (and the non-native predators found there) and the dams on their way to the ocean. Juvenile fish pass the Snake and Columbia River dams through bypass systems, over the spillways and through turbines. Most effort in the past decades has focused on increasing juvenile survival through the hydropower corridor with improved collectors, bypass systems and transportation.

Finally, salmon populations also appear to be affected by variation in ocean conditions associated with short and long-term climatic fluctuations. In particular, salmon production appears linked to decadal-scale shifts in average sea surface temperatures (the Pacific Decadal Oscillation; Francis and Hare 1994, Hare et al. 1999). These temperature changes affect phytoplankton production, which in turn affects zooplankton abundance (Broder and Ware 1992), Sugimoto and Tadokoro 1997). Phytoplankton production appears to be very important for juvenile salmonid survival in the ocean. The variation in survival linked to these climatic conditions will contribute significantly to recruitment variation, although the exact extent of marine mortality varies among salmonid species (Bradford 1997).

II.B. Evolutionary Significant Units

Nearly as complex as the myriad factors affecting salmonid population trends is determining the appropriate unit for conservation. Amendments to the Endangered Species Act in 1978 defined a

species as "any subspecies of fish or wildlife or plants, and *any distinct population segment of any species* of vertebrate fish or wildlife which interbreeds when mature" (emphasis added).

NMFS considers a population or group of populations "distinct" and hence a "species" for purposes of the ESA if it represents an evolutionarily significant unit (ESU) of the biological species. A population must satisfy two criteria to be considered an ESU: first, it must be reproductively isolated from other conspecific population units, and second, it must represent an important component in the evolutionary legacy of the species. In defining ESU boundaries, genetic, demographic, life history, morphological and geographic information was considered (e.g., NMFS 1991 a, b, c, d, 1996, 1998). The twelve ESUs in the Columbia Basin listed under the Endangered Species Act that we consider here are listed in Table II-1.

Management of these listed ESUs is made particularly challenging not only by the wide array of habitats that they use, but also by the extreme variation in life history characteristics shown. Salmonids in the Columbia River basin spawn in the main river channel of the Columbia and Snake Rivers, in small streams and tributaries and in lakeshore gravels. Not only are both ocean and stream-type fish represented, but at least two ESUs include individuals that are not anadromous at all. As a result, juveniles or adults are migrating to or from some part of the basin in all months of the year. Therefore, management actions aimed at improving the situation for one ESU must be evaluated for their effects on other ESUs as well.

Table II-1. Salmonid ESUs listed under the Endangered Species Act in the Columbia Basin.

Species	ESU	Status
Chinook	Lower Columbia River	Threatened
	Upper Willamette River	Threatened
	Upper Columbia Spring-run	Endangered
	Snake River Spring/Summer-run	Threatened
	Snake River Fall-run	Threatened
Steelhead	Lower Columbia River	Threatened
	Upper Willamette River	Threatened
	Middle Columbia River	Threatened
	Upper Columbia River	Endangered
	Snake River	Threatened
Sockeye *	Snake River Basin	Endangered
Chum	Columbia River	Threatened

* Because Snake River Sockeye are near-zero in abundance, the risk of extinction is clear. As a result, we did not include this ESU in any of the quantitative analyses presented in this document.

III. Goals and General Considerations

III.A. Goals

This paper presents the first standardized analysis of all Columbia River Basin ESUs and populations. It has four important goals:

- **Address technical aspects of the Dennis extinction risk analysis with respect to available salmon data.** In Section IV we present tests of the assumptions of the Dennis model (Dennis et al. 1991) for each of the ESUs investigated. In addition, we provide a refinement of the model that is robust to sampling error, and we outline an approach to address the issue of ongoing environmental degradation that appears to be present in some stocks.
- **Provide a standard assessment of extinction risk for all listed ESUs in the Columbia River Basin.** In Section V we present results from our extinction risk analysis of eleven ESUs to allow comparison of extinction risk faced by these groups. We examine both the likelihood of stocks within each ESU reaching absolute extinction, and the probability of the ESU as a whole, or stocks within an ESU, experiencing significant declines. We also provide bounds on these estimates, given known hatchery fish presence on the spawning grounds. This is the first time that analyses for all ESUs within the Columbia Basin have been conducted in a standardized fashion. Note that because the current abundance of Snake River sockeye is extremely low, we were unable to conduct risk assessment for this ESU.
- **Estimate necessary improvements in population growth rate (or recruits per spawner) to mitigate extinction risk.** Also in Section V, we present relative estimates of changes in population trajectories that would be necessary to reduce the risk of extinction or significant decline to 5% in 100 years.
- **Provide more detailed analyses for those ESUs with sufficient data to support such an analysis.** Section VI includes revised analyses for the Snake River Spring/Summer Chinook. These analyses are based on the most recent spawner data, provided to us within the last two months. We also include previously developed analyses of Snake River Fall Chinook.

III.B. General Considerations

We have applied a standardized analysis to the ESUs in the Columbia River Basin. Each ESU obviously has its own suite of characteristics and considerations. However, there are several general factors that should be considered while interpreting or applying these analyses.

III B.1. Simple analyses

This paper presents a chain of simple analyses, addressing questions pertaining to salmon risk and risk management. The analyses we conduct are supported by the available data, which in

many, if not most, cases is restricted to counts of spawners or redds. Overparameterizing models or analyses, by including factors about which there is little information, can degrade the performance of more complicated analyses (Burnham and Anderson, 1998). In fact, due to the difficulties associated with estimating parameters, simple models may perform better than more elaborate or detailed analyses (e.g. Ludwig and Walters, 1985). For these reasons we use available data in a sequence of straightforward analyses as a chain of arguments in order to simplify the complexity of nature (Caswell, 2000). As technical teams develop recovery goals and apply VSP standards to particular ESUs, the Cumulative Risk Initiative (CRI) will tailor its analyses to these more specific venues. For instance, future analyses will assess carrying capacity and long-run population levels as well as population growth rates. Reliably estimating carrying capacity requires map-based assessments of habitat amount and quality, as well as quantitative links between habitat attributes and some measure of salmon population productivity. Therefore, these future estimates will necessarily involve additional kinds of data and experiments.

III.B.2. Stocks and Populations

Populations within ESUs in the Columbia River will eventually be identified using a combination of genetic, life history, demographic and other characteristics (VSP paper, McElhany et al. 1999). This process is complete for Upper Columbia River Spring Chinook and Steelhead, but has not begun for any other Columbia River ESUs. Since populations have not been delineated using biological criteria, we have used data for geographically defined stocks. In some cases, these stocks will correspond to biological populations. However, in others, a single stock may consist of more than one population, or several stocks may all belong to a single population. In these cases the risk metrics we provide may be inaccurate. For instance, analyzing a small stream as an independent population when it is actually part of a much larger population, receiving migrants from other streams or rivers in the population, will overestimate extinction risk. Similarly, lumping several streams together as a population, when they are in fact independent, will cause the extinction risk for some of the smaller independent units to be underestimated. Therefore, when populations are formally delineated estimates of extinction risk may change.

III.B.3. Time period analyzed

We used data from brood year 1980 to the present for both extinction analyses and Leslie matrices. Although in some cases data are available before 1980, we selected a 1980 starting date for several reasons. First, the four lower Snake River dams were completed in 1975, and the full complement of turbines installed by 1979. Additional engineering changes to these and other mainstem Columbia River dams were completed by the early 1980s. Thus, prior to 1980 the hydropower system was in a state of flux, whereas current operations have more or less been in place since 1980. In addition, a major shift in oceanographic conditions, accompanied by substantial decreases in marine primary production (Mantua et al. 1997), coincided with the completion of the Federal Columbia River Power System in 1975 (corresponding to outmigration year 1977). Also in 1975, completion of the Libby and Mica Dams in the upper reaches of the Columbia basin nearly doubled storage capacity in the river at the same time that climate shifts decreased annual average run-off. Finally, in some cases the quality of early data is not uniform across ESUs (Zabel and Williams in press). Thus, by using more recent data we eliminate some, though certainly not all, problems with differences in data quality among ESUs. By restricting

our analysis to the time period after 1980, we are, in effect, asking the question: **if trends continue as they have for the last twenty years, what is the likely status of the ESU (or stock) at some future date, relative to other ESUs (or stocks)?**

Since we ask this specific question, at least two issues should be considered when examining policy options for certain ESUs. First, the possibility that ocean conditions may improve relative to our current period, or deteriorate even further, may change the relative extinction risk for some ESUs. In addition, since the data were generally only available until brood year 1994, some of the most recent management actions (such as recent harvest reductions) have not had time to be expressed in the data.

III.B.4. Risk metrics

We consider two “extinction” metrics: probability of absolute extinction and probability of a 90% decline in abundance. Measures based on % decline are critical for two reasons. First, it is often difficult to obtain an estimate of the number of fish in the entire population. For example, many of the count data are index counts that do not encompass the entire population or ESU. In these cases, it is impossible to calculate an accurate estimate of the probability of reaching an abundance threshold (i.e., extinction). (This is particularly true for ESU-level data, since often only sub-samples are available. We did not consider any abundance threshold metrics (extinction) at the ESU-level for this reason). Second, in some cases, population numbers are currently relatively high, but the overall trend is declining. Probability of reaching a threshold in these cases is relatively low, even though the population is clearly at risk. A measure of decline, therefore, offers a measure of risk that is independent of absolute abundance.

We have not considered the probability of reaching an abundance threshold greater than absolute extinction in this document for two reasons. First, as discussed above, data are often not available at the ESU level to determine the risk of reaching a particular population size, making estimates of achieving *any* threshold impossible. Second, a primary goal of this work was to provide a standardized and comparable assessment of risk across the stocks in the Columbia River Basin. At the stock level, the geographic or stock units for which we had data were often not comparable. For instance, comparing the probability of chinook populations of small streams in the lower Columbia River reaching 250 individuals with populations in the Yakima River compares two systems of very different potential capacities. Put another way, an extinction threshold of 1-fish is the only extinction threshold that has the same biological meaning regardless of which index stock or population is being examined.

This presentation of the risk of absolute extinction alone does not reflect a policy decision about acceptable population levels, nor does it indicate that CRI scientists are ignoring the possibility that depensation occurs in these populations. Instead, it is the only level that we can be certain is biologically meaningful across all systems. As populations are delineated according to biological criteria, and depensation thresholds are better defined, we will be in a better position to apply other abundance thresholds. Obviously, the threshold we have used – absolute extinction – is dire, and estimates of risk must be considered in this light. ***In general, if “extinction peril” is a quantity to be estimated, because of the poor quality of existing data the CRI feels that the probability of a 90% decline is the best measure of risk.*** No one would argue that a 90% population decline from current levels is tolerable. Most importantly, even if total populations are poorly estimated, probabilities of percentage decline can be well estimated.

A final critical metric is “lambda”, or the median annual rate of population change. Lambda, more than any other parameter, summarizes the likely fate of a population. In general, “managing for lambda” is a reliable way of managing for a species viability and productivity (Caswell 2000), since a positive trend (i.e. a lambda value greater than one) will result in more individuals and a lower extinction risk. A second value of lambda as a metric is that one can estimate 95% confidence intervals of lambda from previous data, and hence ask whether future population trends indicate significant improvements or deteriorations in the situation. Some scientists favor focusing on absolute population numbers or on probabilities of extinction as key metrics. The CRI agrees that both of these metrics convey useful information. But the CRI believes lambda, or annual population growth, is the best measure of how a population is faring – one can estimate lambda unambiguously, provide confidence intervals, and using lambda estimate how big a population might be in the future, or whether a population is likely to even persist into the future. Moreover, annual population change is something that is both easily monitored and easily related to stage-specific survival improvements. When a population is operating without density-dependence, then a 10% increase in survival during any lifestage corresponds to a 10% increase in recruits per spawner, which is equivalent to a 10% increase in lambda. Lastly, because salmonid populations are a valuable resource for harvest, the lambda measure also is conveniently related to surplus production and how much of the production might be harvested, yet still provide for annual population growth (e.g., a lambda of 1.5 could be reduced by harvest to a lambda of 1.1, and still provide for 10% annual growth).

III.B.5. "Acceptable" risk and magic numbers?

We have calculated the change in annual population growth rate necessary to reduce the risk of absolute extinction for individual stocks to less than 5% in 100 years. This value was chosen based on IUCN standards (1994) for inclusion of species in its Red Lists. (A species with a ten percent or greater risk of absolute extinction in 100 years is considered to be *vulnerable*, the lowest category of concern). Again, this level is not a policy statement about jeopardy or recovery standards. Rather, it is a convenient and internationally accepted standard against which to gauge necessary improvements. As mentioned above, when estimates of total population size are uncertain, the probability of a 90% decline in 100 years is the more reliable measure of risk.

Regulators and policy makers gravitate to measures relating to extinction probabilities or risk. There needs to be a better understanding of the limitations of ANY metric that involves a probability of extinction. One has to build a model to produce a “probability of extinction”. Any such model will include numerous simplifications and guesses regarding parameter values, and **no model will be the correct model**. Moreover, it will be impossible to test a model of extinction probability (unless the model predicts a 100% or 0% probability, and subsequent observations contradict those “certain” predictions). Often, arguments are made that a risk estimate is “too high” or “too low”. But rarely is it so black-and-white. For example, one could argue that the risk models developed by CRI exaggerate risks because estimates of environmental variation are inflated, because populations are treated as isolated (or closed) when strays can in fact exert a “rescue effect”, because Ricker dynamics are NOT used and Ricker “unc” away from low levels due to reduced competition, and because the possibility of improved ocean conditions is not considered in any fashion. Conversely, one could argue the CRI models under-estimate risks because the critical thresholds

are too low, because catastrophes are not included, because genetic deterioration is not considered, and because density-dependence is not factored into the calculations. Both arguments are correct. The CRI accepts the uncertainty of any extinction calculation, and prefers to emphasize the importance of STANDARDIZATION, so that the calculations can be used in a relative sense (are things getting better or worse? is stock A at greater or less risk than stock B? and so forth). More importantly, by minimizing model complexity, it is a simple matter to update risk calculations as each year of data are added. More generally, the limitation of “probability of extinction” calculations is one reason that CRI emphasizes lambda (annual population growth) as a descriptive metric and as a metric on which to focus recovery goals and targets for management actions.

III.B.6. Change in annual population growth rate vs. change in recruits-per-spawner ratios.

In general, we have presented results in terms of annual population growth rates (lambda, λ). This quantity (the average rate of change in the population size per year) is not equivalent to the commonly used recruits-per-spawner ratio (rate of change in the population size per generation). To translate between changes in lambda and changes in recruits per spawner requires detailed re-estimation of lambda given altered recruit-per-spawner data. However, if we are interested in making calculations to assess needed management improvements, and if we assume that management actions alter mean recruits per spawner but NOT variability in recruits per spawner, it is possible to write an explicit equation that approximately converts between lambda and recruits per spawner:

$$\ln(\lambda) \sim \ln(R/S)/(G) \times \text{constant}$$

where G is the mean generation time, and the constant is determined by environmental variability in recruits per spawner (which, we assume is not altered by management). This approximation is usually accurate within 10% (Stearns 1992); to be totally accurate one needs to solve the Euler equation (equation 5.4, page 90). Given the above equation we can see that:

$$\lambda^G \propto (R/S)$$

Using that proportionality, it is simple to convert any required % increase in lambda into a % increase in recruits per spawner. For example, a 5% increase in lambda, with a mean generation time of three years would be a 16% increase in recruits per spawner (1.05 raised to the third power = 1.16, hence a 16% increase).

IV. Dennis Extinction Risk Analysis – Tests and Refinements

IV.A. Are extinction analyses useful?

Estimates of extinction risk are standard “tools of the trade” in conservation biology, yet these very same estimates have been criticized for a variety of reasons. Recently, several mathematical biologists have cautioned that point estimates of extinction risk typically have such huge confidence intervals that the estimates become “meaningless” (e.g., Ludwig 1999; Frieberg and Ellner 2000). In some cases where confidence intervals are large, risk estimates can be unduly pessimistic because they are calculated for long time horizons, using very sparse data sets, and using less-than-the-best analytical methods. Beyond these cases, however, large confidence intervals are common in risk estimates. But as Caswell points out, to say that uncertainty makes the results “meaningless” creates an erroneous distinction between results and uncertainty, “*uncertainty does not make the results meaningless, the uncertainty is part of the results*” (Caswell 2000). First, we need to stop and ask how estimates of extinction risk are used. The simplest uses are to compare stocks, to compare ESUs, to compare management options, and to evaluate relative risks. For these uses the confidence interval is less of a problem, because one is assessing relative risk and not absolute risk. Secondly, we need to consider the alternative to calculating an extinction risk metric. The alternative is either randomly ranking populations with respect to risk, or using “expert guesses” (which are very hard to standardize). The value of standardization is so extensive that we have adopted a modified Dennis approach as the minimum standard for analyses across all ESUs, well aware that there is uncertainty surrounding each estimate. At a minimum, this assessment of risk is explicit, repeatable, and responsive to the addition of new data. Simultaneously, we have undertaken several theoretical studies to understand in what direction its biases might be, and under what circumstances those biases could be large. Other scientists are pursuing similar analyses; results thus far suggest that many simple viability models, which are clearly over-simplifications, still perform surprisingly well (Meir and Fagan 2000, Fagan et al. 1999, Caswell 2000, Brook et al. 2000). Of course, to properly apply these methods, key assumptions underlying this approach should be tested and the data analyzed such that sources of error are clearly exposed.

IV.B. A simple extinction model with minimal data requirements – the Dennis approach

In 1991, Dennis et al. published an extremely important and influential paper that outlined an approach to quantifying extinction risk with census data as opposed to detailed demographic studies. Dennis et al. has found wide application, and has been extended and compared to more complex models in several different research publications (Gerber et al. 1999; Morris et al. 1999; Nicholls et al. 1996). The Dennis model approach reflects the strategy of estimating statistical properties from a time series and then projecting the population forward using those statistical properties. Suppose that one had population counts for a particular species (see Figure IV-1). One could then analyze the distribution of N_{t+1}/N_t and project the population into the future by a stochastic simulation such as:

$$N_{t+1} = N_t * \mathbf{q}(t, N) \quad [4.1]$$

where $\mathbf{q}(t, N)$ is the distribution of N_{t+1}/N_t and might be a function of time and population size. The projected population trajectory would be one of many possible trajectories since this is a stochastic simulation. By running the simulation a large number of times, one could determine probabilities of the population going extinct in certain time frames. Notice that with this particular method of viability analysis, no specific population dynamics model is fit to the data, but rather the statistical properties of N_{t+1}/N_t are determined and these are used to parameterize a stochastic simulation, which is then used to explore possible trajectories to extinction.

For a wide variety of species, including species with strong age structuring such as salmon, it has been observed that the trajectories of the total population size often have particular statistical properties (Dennis et al. 1991). Namely, the ratio of $N_{t+\tau}/N_t$ is lognormally distributed with variance $\mathbf{s}^2 \mathbf{t}$ and mean $\mathbf{m} \mathbf{t}$, where N_t is the total population size at time t , and \mathbf{m} and \mathbf{s}^2 are parameters that characterize the rate of population decline and its variability, and tau (\mathbf{t}) is the time increment over which the parameters are calculated. The statistical properties of $N_{t+\tau}/N_t$ have a strong theoretical foundation (Tuljapurkar and Orzack 1980, Heyde and Cohen 1985), allowing one to conveniently describe population change as:

$$N_{t+\tau} = N_t \exp(\mathbf{m} \mathbf{t} + \mathbf{e} \mathbf{t}) \quad \text{where} \quad \mathbf{e} \sim N(0, \mathbf{s}^2) \quad [4.2]$$

and thus $\frac{N_{t+\tau}}{N_t} \sim \Lambda(\mathbf{m} \mathbf{t}, \mathbf{s}^2 \mathbf{t})$, is lognormally distributed (Dennis et al. 1991). Note that the stochastic model, [4.2], is based on the assumption that $\mathbf{q}(t, N) = \mathbf{q}$, that is that the distribution of $N_{t+\tau}/N_t$ is neither a function of time nor population size. In salmon terms, this is equivalent to assuming that the R/S ratios are not changing in time and are not density-dependent.

The parameter, $\hat{\mathbf{m}}$, is the maximum likelihood estimate from the observed time series data for the instantaneous rate of decrease (or increase) of the underlying stochastic process. The estimate of the median rate of long-term decline is (eqn. 77 from Dennis et al. 1991):

$$\hat{\mathbf{I}} = \exp(\hat{\mathbf{m}}) \quad [4.3A]$$

The confidence intervals on $\hat{\mathbf{I}}$, due to the fact that one uses a finite rather than infinite time series for estimation are (eqn. 31 in Dennis et al. 1991):

$$(\hat{\mathbf{m}} - t_{\alpha/2, tq-2} \sqrt{\hat{\mathbf{s}}^2 / tq}, \hat{\mathbf{m}} + t_{\alpha/2, tq-2} \sqrt{\hat{\mathbf{s}}^2 / tq}) \quad [4.3B]$$

where $t_{\alpha q}$ is the quantile of a student's-t distribution at probability α and degrees of freedom q , and tq is the length of the running sum time series.

λ is the standard reported parameter for deterministic matrix models. For stochastic population models (as ours is), one can present either the mean or median long-term rate of decline. We

use the median, which we will refer to throughout this document as $\hat{\mathbf{I}}$. Note that this is a different convention than that in Dennis et al. 1991 in which λ is used for the mean and α for the median.

IV.C. Are the assumptions of the Dennis model met?

The Dennis approach to estimating extinction risk entails several critical assumptions and restrictions:

- I. Population counts must be an exhaustive survey of the population or a fraction thereof so that the timeseries (N_t N_{t+1} N_{t+2} ...) is indeed a Markov process where N_{t+1} is directly related to N_t .
- II. The variability estimated by Dennis approach is a measure of environmental variability and not sampling error.
- III. The variance in N_{t+t}/N_t increases with tau (\mathbf{t}) the time increment over which the change is calculated.
- IV. The yearly rates of population growth (i.e., N_{t+1}/N_t) are lognormally distributed.
- V. Although the populations themselves may be increasing or decreasing (i.e., show a trend), there should be no trend in the rates of decline or increase (such that the rate of decline is getting progressively worse or better).
- VI. Over the range of population sizes examined, the rates of population change are assumed to be independent of the density of fish.

Assumption 1: Are population counts an exhaustive survey of the population, such that the time series is a Markov process?

Spawner counts are not an exhaustive survey of the population, or a fraction thereof. In addition, spawner counts at time $t+1$ do not bear a direct relation to spawner counts at time t . Therefore, applying the Dennis model in the standard fashion to spawner counts will grossly overestimate the variance, and therefore overestimate extinction risk. We present a refinement of the Dennis model in Section IV.D. to deal with this violation.

Assumption 2: The variability estimated by the Dennis approach is a measure of environmental variability and not sampling error

Although recent numerical work has indicated that extinction risks estimated by the Dennis et al. approach are robust to modest amounts of observation error (on the order of 25%, see Meir and Fagan 2000), the observation error in run-reconstruction data is likely to be extremely large, probably larger than 25%. This is especially evident when one realizes that often there are less than ten spawners (maybe even as few as one or two spawners) as the denominator of recruit per spawner ratios; a miscount of only one or two fish at such low population sizes can easily yield errors of 50 to 100%. Fortunately, however, \mathbf{s}^2 can still be estimated from stage-specific data (such as spawner counts) by using a modified estimation procedure (Holmes 2000) that reduces

the problem of inflated estimates of environmental variation due to sampling error. We present this refinement in Section IV.D.

Assumption 3: Linear increase through time in variance of $N_{t+\delta}/N_t$

One of the inherent properties of the Dennis model is that the variance in the difference between the log of two population counts ($\ln(N_{t+\tau}) - \ln(N_t)$) increases linearly with the time between the counts, τ . Our estimate of \mathbf{s}^2 is based on this property. For each ESU and population analyzed, we plot the variance of $\ln(N_{t+\tau}/N_t)$ versus τ , the time between the counts (Figure IV-2). The variance is markedly linear for 8 of the 11 ESUs; the variance for two of these ESUs is near zero. These latter two situations correspond to cases where there is virtually no variance in the rate of population change (e.g., straight declines at a constant rate). Only the Columbia River Chum data set strongly violates the non-linearity assumption. The reason the Columbia River chum violates the linearity assumption is evident from inspecting its population behavior (see Figure IV-3) – its population shows strikingly periodic behavior during the interval sampled.

In general, the linear increase in variance indicates that the estimation procedure and diffusion approximation are likely to succeed. For those situations that markedly violate this linear assumption, there is typically evidence of a cyclical or periodic population behavior such that instead of steadily increasing through time, the variance levels off or drops due to a return to previous conditions.

Assumption 4: Lognormal rates of yearly population growth N_{t+1}/N_t

Frequency distributions of N_{t+1}/N_t generally satisfied the assumption of a lognormal distribution. Normal quartile plots of these distributions for several ESUs and individual stocks are illustrated in Figure IV-4. This assumption is likely to be satisfied for most time series of population growth rates because these growth increments will generally be the product of many independent factors operating on reproduction and survival (i.e., central limit theorem).

Assumption 5: A population's rate of change may fluctuate, but it is not getting progressively better or worse in a predictable fashion.

A key technical challenge is appropriately addressing the possibility that trends in environmental degradation are linked to increasing declines in annual rates of population growth through time. Such declines would be far more serious than simply declining populations because they would imply that not only are populations declining, but also that the rate of decline is increasing. We address this issue in three ways. First, we graphically display the time series used in our analyses so that any bias inherent in the extinction analyses resulting from a trend is apparent. Second, we test for a temporal trend in the population growth trajectory using a likelihood ratio method modified from Dennis and Taper (1994). Third, we are developing new analytical tools that can incorporate trends using formal statistical models (Burnham and Anderson 1998).

Simple plots of spawner population abundance (Figure IV-5) and annual growth rates (Figure IV-6) at the ESU-level suggest that while there are trends for some of the ESUs or stocks examined, trends are not apparent in the majority of cases. In particular, plots of the temporal pattern in $\ln(N_{t+\tau}/N_t)$ indicate no consistent upward or downward trends from 1980 onward for all but Lower Columbia River Chinook, Upper Columbia River Spring Chinook and Snake River

Spring/Summer Chinook (Figure IV-6). However, time scale can affect the appearance of a trend. If one includes data prior to 1980 (Figure IV-7), the Snake River Chinook do not show as unambiguous a trend as the post-1980 data might indicate. To be conservative, however, it is best to conclude that the extinction risks estimated by the Dennis approach are underestimates for Lower Columbia River Chinook, Upper Columbia River Spring Chinook and Snake River Spring/Summer Chinook. This under-estimation arises because the data suggests that the decline is becoming progressively steeper with time.

Since trends are not evident across all ESUs, and the impression of a trend varies with the time scale examined, a formal means of identifying trends in recruits per spawner is needed. One approach is the Dennis and Taper (1994) likelihood ratio approach in conjunction with bootstrap simulations that we use to test for density-dependence (see results presented in Assumption 6 below). Another approach might be to formally propose a new diffusion approximation that includes a trend in the drift parameter. We are currently working on such an approach; unfortunately this is not a straightforward problem. Until we or other scientists in the region perfect an approach to trend modeling that is clear and unambiguous, we advocate inspecting plots such as those shown in Figures IV-6 and 7, and using that examination to color the interpretation of the simple extinction results. To repeat the example from above, there may indeed be a declining trend in recruits per spawner for Spring/Summer Chinook salmon in the Snake River, and as a result, extinction analyses may be underestimates and thus too optimistic.

Assumption 6: Density-independence

If population growth or decline is density-dependent, then describing annual increments in total population size as a simple lognormal markov process is inadequate. All ecologists know that populations cannot grow in a density-independent manner forever. Eventually populations that are growing must become so large that the organisms are crowded and each individual's prospects for survival or reproduction decline. In fact the density regulated Ricker function and its many modifications have a long history as the population growth models employed in fisheries biology; the Ricker model assumes that the log of the rate of recruitment per spawner decreases linearly as spawner density increases. Alternatively, shrinking populations could become so small that a female has a low probability of locating a mate, and density-dependence sets in, producing a decline in recruits per spawner as densities plummet. Although density-dependence is sure to ultimately exert itself, it is possible for populations to behave for extended periods of time in a generally density-independent manner (when numbers are neither too low nor too high). As long as the data provide no evidence of density-dependence, then it is appropriate to approximate population behavior with a Dennis-like model. When there is density-dependence, a more complex description of population behavior is necessary.

Distinguishing between density dependence and temporal trends in population growth rate.

Density dependence can be compensatory (as in the Ricker function) or depensatory.

Depensation in salmonids is thought to occur in populations with small numbers of reproducing individuals for any of several reasons (e.g., because mates fail to locate one another, because genetic deterioration accumulates, or because declining numbers of spawners implies depressed nutrient inputs into the fresh-water spawning grounds). Unfortunately, for declining stocks, depensation-like effects can also be attributed to a downward trend in λ . For example, if environmental conditions are deteriorating steadily such that population growth rates are declining, then decreasing population sizes will be observed concomitant with decreased population growth rates. The problem then becomes one of distinguishing between a trend in λ

caused by a degrading environment versus a trend cause by density-dependence. This is not just an arcane technical point, especially when we consider the implications of density-dependence for harvest policy. If a population has fallen to abundances at which depensation plays a role (see results in Table IV-1), then the harvest of an adult fish not only reduces the population, it actually accelerates population decline more than expected because recruits per spawner decline with declining spawner numbers.

To assess assumptions regarding density-dependence, as well as temporal trends in productivity, the time series of spawner and recruit counts were fit to a series of models. Results of these models were evaluated using a likelihood ratio test (Dennis and Taper 1994). This test, which is far more robust than regression methods, compares the likelihood of the data if the underlying model is a stochastic logistic model (density-dependent, allowing for either compensation or depensation) to the likelihood of the data if the underlying process is a stochastic exponential model (density-independent null model). We modified the method to also compare the density independent model to a stochastic population process that allows for a temporal trend in the growth rate. Below we present both scenarios as applied to the same data, and a simplistic method for assessing the situations where both density dependent and time dependent population processes are indicated by the data. In this approach we test the relative fit of the following three models to the data:

Model 1, stochastic exponential growth (density independent null):

$$\ln\left(\frac{N_{t+1}}{N_t}\right) = a_1 + \mathbf{s}_1^2 Z_t$$

Model 2, stochastic logistic growth (density dependence):

$$\ln\left(\frac{N_{t+1}}{N_t}\right) = a_2 + b_2 N_t + \mathbf{s}_2^2 Z_t$$

Model 3, stochastic exponential growth (time trend):

$$\ln\left(\frac{N_{t+1}}{N_t}\right) = a_3 + b_3 t + \mathbf{s}_3^2 Z_t$$

Where Z_t is a normally distributed random variate with mean 0 and variance 1.

In this technique, the distribution of the test-statistic (T_{12} , for the ratio of models 1 and 2, and T_{13} , for the ratio of models 1 and 3, Table IV-1) is generated by parametric bootstrapping of the estimated regression parameters (stochastic population growth: $a1$; density dependent population growth: $a2$, $b2$; temporal trend in population growth rate: $a3$, $b3$). If the calculated test statistic is greater than 95% of the randomly generated values, the null hypotheses of density-independent growth or lack of temporal trend in productivity are rejected. For example, the test statistic (T_{13}) for the Lower Columbia Chinook fell well above the 95th percentile of simulated T-statistics, indicating that the temporal trend model was a better fit to the population time series. In this case, the underlying process was an increasing productivity ($a3 > 0$), but the temporal trend coefficient was negative ($b3 < 0$), implying that as time passes the population growth rate becomes progressively smaller. In the cases where both independent null hypotheses were rejected (the data supports both the density dependent and temporally varying productivity hypotheses, independently), we present the ratio of the test-statistics (T_{13}/T_{12} , Table IV-1). The

ratio of the likelihood ratio test-statistics is an indication of the relative explanatory power of the two independent hypotheses provided that they are each compared to the same null model (stochastic exponential population growth) and that the alternative hypotheses are of similar power (number of terms used in the predictive equation). The tests for density-dependence and temporal trends are provided for each ESU and stock within an ESU for which long time series were available.

Approximately 30% of the time series analyzed indicated either density dependence and/or temporal trends in productivity (21 of 69 time series). It is worth recalling that these trends are exhibited after 1980, which is well after any major additions to the hydropower system. In only two cases was density dependence (compensatory) alone indicated, Kalama River Spring Chinook and Summer Steelhead. In 13 cases a temporal trend in productivity, decreasing in all but two cases (Washougal Summer and Green River Winter Steelhead), was indicated. In the remaining six cases both a temporal trend and density dependent models were better fits to the data than exponential growth alone. However, in all cases the temporal trend model was a better fit to the data than the density dependent model alone.

At the ESU level, three of eleven ESUs violated the simplest exponential model, with the violation always including environmental degradation as a plausible alternative. Notably, Snake River Spring/Summer Chinook salmon population analyses suggest an environmental trend (degrading though time), but no density-dependence. It is for this reason that in the detailed matrix analyses of Snake River spring/summer chinook salmon (see Section VI), we break out the most recent five brood years (the “worst” brood years) for a separate analysis. Population data from the Lower Columbia River chinook ESU also suggest a degrading environmental trend (but no density dependence), which means subsequent analyses of extinction risks for this ESU are under-estimates. For the Upper Columbia River Chinook Salmon there is evidence supporting both density-dependence and a degrading environment, with minimal power to distinguish between the two explanations. The remaining eight ESUs conform well to the simplest model – the density-independent, constant environment null model (Model 1 above).

Our statistical approach needs further development. The biggest constraint is that we cannot explore the possibility that both density-dependence and a trend in λ are important population processes. Secondly, we cannot assert with any measure of confidence that one “violation” of the null model (e.g., density versus trend effects) is more credible than another. We are developing an information content approach to address these issues (Burnham and Anderson 1998) and hope in the future to be able to relax the requirement of comparing only models of similar structure or sets of nested models.

Table IV-1. Test for density dependence and a temporal trend in population growth rate in Columbia River Basin stocks. Bold values indicate cases in which the null hypothesis was rejected.

		<i>a1</i>	<i>a2</i>	<i>b2</i>	<i>T</i> ₁₂	95%tile	<i>a3</i>	<i>b3</i>	<i>T</i> ₁₃	95%tile	<i>T</i> ₁₃ / <i>T</i> ₁₂
LCR Chinook	Total ESU	0.01240	1.00735	-0.00001	2.269	17.349	0.33895	-0.21770	169.37	19.429	
	Bear Creek	-0.13774	0.04966	-0.00021	0.192	9.042	-0.53698	0.08872	0.582	5.297	
	Big Creek	-0.02303	0.08959	-0.00001	0.466	5.112	0.02120	-0.00737	0.367	4.385	
	Clatskanie	-0.06857	0.16700	-0.00268	0.914	8.278	-0.19029	0.02029	0.245	4.794	
	Cowlitz Tule	-0.02794	0.03071	0.00000	0.178	5.462	0.09213	-0.02001	2.828	4.739	
	Elochoman	0.04095	0.30802	-0.00013	1.410	9.706	-0.06028	0.01687	0.207	4.427	
	Germany	-0.02140	0.50024	-0.00046	2.648	9.961	0.00908	-0.00554	0.020	5.139	
	Gnat	-0.01547	0.13586	-0.00035	0.653	9.679	0.16798	-0.03058	0.760	5.110	
	Grays Tule	-0.10841	-0.09940	-0.00001	0.002	7.339	-0.00028	-0.01802	0.173	4.731	
	Kalama Spring	-0.09631	0.41986	-0.00045	8.153	7.295	-0.34188	0.04465	1.506	4.981	
	Kalama R	0.05318	0.29354	-0.00001	1.589	9.430	0.24711	-0.03526	0.807	5.307	
	Klaskanine	-0.06654	0.39248	-0.00808	0.498	8.347	-0.49140	0.07725	0.415	5.052	
	Lewis R. Bright	-0.00927	0.23348	-0.00001	1.526	8.945	-0.00748	-0.00030	0.001	4.561	
	Lewis Spring	-0.08213	-0.10057	0.00000	0.016	6.389	0.32993	-0.06339	14.846	5.087	
	Lewis, EF Tule	-0.00772	0.18234	-0.00016	0.965	7.937	0.05863	-0.01106	1.401	5.039	
	Mill Fall	-0.16367	-0.07266	-0.00005	0.183	6.546	-0.14958	-0.00352	0.003	5.754	
	Plympton	-0.00222	0.46790	-0.00008	2.685	9.648	-0.01534	0.00219	0.005	4.612	
Sandy Late	-0.01577	0.30617	-0.00007	1.535	8.354	-0.05496	0.00980	0.173	5.302		
Skamokawa	-0.14638	-0.14659	0.00000	0.000	4.714	-0.02108	-0.02088	0.735	4.578		
Youngs	-0.01124	0.19774	-0.00142	0.727	9.573	0.35388	-0.07302	0.836	5.209		
UCR Chinook	Total ESU	-0.16296	-0.52677	0.00003	14.827	4.614	0.15396	-0.04876	39.884	5.018	2.69
	Entiat	-0.13635	-0.74853	0.00016	8.922	4.745	0.32287	-0.07065	44.167	4.532	4.95
	Methow	-0.14417	-0.38251	0.00029	5.587	4.779	0.03700	-0.02787	8.591	4.916	1.54
	Wenatchee	-0.23379	-0.34960	0.00002	5.711	4.684	-0.08542	-0.02698	10.196	4.494	1.79
SR S/S Chinook	Total ESU	-0.01033	0.10676	-0.00001	0.397	8.616	0.21530	-0.03471	28.043	4.991	
	Bear Creek	-0.00569	0.13436	-0.00011	0.833	9.843	0.18681	-0.02962	5.597	4.718	
	Imnaha River	-0.05294	0.02673	-0.00004	0.087	5.435	0.04998	-0.01583	1.481	5.049	
	Johnson Creek	-0.00585	0.17477	-0.00028	0.978	8.758	0.11607	-0.01876	4.875	4.822	
	Marsh Creek	-0.03966	-0.02594	-0.00002	0.014	4.790	0.11049	-0.02310	4.668	4.914	
	Minam River	0.03111	0.24199	-0.00021	1.703	9.741	0.28932	-0.03689	4.292	4.987	
	Poverty Creek	0.00588	0.15716	-0.00009	1.250	9.359	0.18487	-0.02557	10.639	5.017	
	Sulphur Creek	0.02020	0.23269	-0.00035	1.168	9.959	0.45779	-0.06732	9.571	4.448	
SR Fall Chinook	Snake R. LGD	-0.04131	0.06133	-0.00004	0.358	4.929	-0.02637	-0.00299	0.049	4.997	
UWill Chinook	Total ESU	-0.05819	-0.08873	0.00000	0.058	4.995	0.03882	-0.01617	1.914	4.904	
	Leaburg Dam	0.00895	0.15550	-0.00001	0.938	9.523	0.30797	-0.04984	18.336	4.890	
CR Chum	Total ESU	0.00860	0.43383	-0.00008	2.230	9.866	0.10283	-0.01713	0.300	5.222	
	Grays R. WF	0.18123	0.70832	-0.00159	3.159	9.714	0.40535	-0.04075	0.497	5.116	
	Grays R. WF	-0.00885	0.49911	-0.00012	2.414	9.694	0.10468	-0.02064	0.387	5.270	
	Hardy Ck.	0.03121	0.28230	-0.00022	1.327	9.163	0.05684	-0.00466	0.023	4.877	
LCR Steelhead	Total ESU	-0.01960	0.78330	-0.00001	0.750	6.171	0.00649	-0.01739	0.355	19.499	
	Clackamas (S)	-0.11174	-0.35212	0.00001	4.851	5.159	0.03520	-0.02939	11.517	5.110	
	Clackamas (W)	-0.04010	-0.23218	0.00004	0.299	4.631	0.04533	-0.01553	3.517	4.876	
	Green River (W)	-0.10185	0.35558	-0.00071	4.279	8.066	-0.50982	0.16319	40.684	8.040	
	Kalama (S)	-0.02985	0.56194	-0.00003	11.651	5.091	-0.16232	0.02649	4.627	5.397	
	Kalama (W)	-0.00052	0.41113	-0.00006	2.318	10.016	0.04158	-0.00842	0.712	4.896	
	Lewis River (W)	-0.16479	0.06684	-0.00050	10.950	7.545	-0.24472	0.05329	28.655	18.622	2.62
	Sandy (W)	-0.05835	-0.30735	0.00002	3.646	4.928	0.06504	-0.02243	17.517	4.843	
	Toutle (W)	-0.13324	-0.23834	0.00002	1.066	6.295	-0.08701	-0.01541	1.822	6.879	
Washougal (S)	-0.14415	0.07468	-0.00053	4.910	7.981	-0.24294	0.04940	10.982	11.650		
MC Steelhead	Total ESU	-0.09079	-0.23733	0.00000	0.974	5.838	-0.01732	-0.02449	3.635	6.622	
	Beaver Creek (S)	-0.13714	-0.19411	0.00081	0.097	6.637	-0.11583	-0.01421	0.342	14.256	
	Deschutes (S)	0.00272	0.14768	0.00000	0.821	9.287	0.03708	-0.00573	0.236	4.618	
	Eightmile Ck (W)	-0.10525	0.36190	-0.00615	0.847	10.891	-1.05487	0.31654	2.765	6.696	
	Fifteen Mile Ck (W)	-0.09704	0.10008	-0.00155	2.450	5.886	-0.23932	0.04065	4.531	6.262	
	Mill Ck (S)	-0.00695	0.28075	-0.00349	1.009	10.117	0.14745	-0.03860	3.442	5.040	
	Ramsey Ck (W)	0.00145	0.45660	-0.00751	1.083	12.209	-0.53844	0.17996	5.578	6.648	
	Shitike Ck (S)	-0.08229	-0.02950	-0.00028	0.386	4.743	-0.08242	0.00002	0.000	4.569	
	Umatilla River (S)	-0.04570	0.34643	-0.00004	7.959	5.832	-0.12845	0.02758	7.956	6.745	1.00
	Warm Spr NFH (S)	-0.06358	-0.37795	0.00015	1.648	4.995	0.16179	-0.05008	58.653	5.036	
Yakima River (S)	0.02391	0.79728	-0.00013	6.283	6.246	0.15628	-0.03782	3.205	5.924		
UC Steelhead	Upper Columbia	-0.10220	-0.07745	0.00000	0.060	5.246	-0.10143	-0.00015	0.000	5.175	
SR Steelhead	Total ESU	-0.02265	0.02896	0.00000	0.099	4.856	-0.00203	-0.00375	0.575	4.916	
	SR A-Run	-0.01314	0.40740	0.00000	1.401	5.154	0.06448	-0.01294	3.277	4.788	
	SR B-Run	-0.04879	-0.27917	0.00000	2.073	5.024	0.07220	-0.02420	19.381	5.238	
UWill Steelhead	Total ESU	-0.07424	-0.12048	0.00000	0.165	4.986	0.05409	-0.02139	3.038	4.839	
	Calapoia	-0.07508	-0.03395	-0.00004	0.054	6.226	0.01576	-0.01514	0.288	4.326	
	Mollala	-0.08001	-0.11986	0.00001	0.101	4.871	0.06906	-0.02484	3.129	4.872	
	N. Santiam	-0.07528	-0.12806	0.00000	0.240	4.925	0.04343	-0.01979	2.867	5.154	
	S. Santiam	-0.06809	-0.10098	0.00000	0.077	4.786	0.05931	-0.02123	3.021	4.998	

IV.D. Refinements of the Dennis model

We have made some refinements to the Dennis model in order to deal with violations of two of the assumptions presented above: population counts do not represent a Markov process, and sampling error is likely to be significant. As mentioned above, we are exploring some formal methods to assess and incorporate trends in R/S into the risk assessment.

IV.D.1. Estimating total spawner population size

In order to ensure that the time series of population counts used in our analyses did indeed represent a Markov process, we needed to use a count in which N_{t+1} comes from the individuals in the count N_t (which is not the case for spawner counts). While a total population count would satisfy this assumption, the data we have are in terms of spawner counts, not counts of total populations. There are ways of estimating total spawner populations (or spawners per generation) using age-structured data. For example, if every year one recorded the age distribution of spawners, one could use that information to obtain:

- (i) spawner to spawner ratios, denoted by SS_{t-j} for each year class of spawners, S_t , and
- (ii) the fraction of spawner recruits from parents S_t that are still alive (either have yet to spawn or are spawning this year) at age j , denoted by $A_{j,t}$

The total living current and future spawners would then be:

$$N_t = \sum_{age=1}^{\max age} A_{j,t-j} S_{t-j} SS_{t-j} \quad [4.4A]$$

This algorithm is shown pictorially in Figure IV-8. Unfortunately, we typically do not have spawner to spawner ratios for each time t , nor do we have age of return for all spawners. As an alternative that works with the data typically available, we approximate the total population by using estimates of the mean age structure of spawners and the mean spawner to spawner ratio:

$$\begin{aligned} \hat{N}_t &= \overline{SS} \sum_{age=1}^{\max age} \overline{A}_j S_{t-j+2} \\ &= N_t + \mathbf{e} \end{aligned} \quad [4.4B]$$

where \overline{SS} is the mean spawner to spawner ratio and \overline{A}_j is the average fraction of fish of age j that have yet to spawn or are spawning this year. The +2 in the S subscript attributes the year of the running sum to one year prior to the most recent spawner count in the running sum.

To illustrate, here is a concrete example. The average frequency distribution of return times for Marsh Creek Spr/Sum Chinook is (Table C-II) is Year 1 = 0.0, year 2 = 0.0, year 3 = 0.03, year 4 = 0.254 and year 5 = 0.716. This means that 0% of recruits return at age 1-2, 3% return at age 3, 25.4% return at age 4 and the rest, 71.6%, return at age 5. From this distribution we can calculate the fraction of recruits that either have yet to return or are returning this year at age j :

$$A_1 = 1, A_2 = 1 - (0), A_3 = 1 - (0 + 0), A_4 = 1 - (0 + 0 + .03), A_5 = 1 - (0 + 0 + .03 + .254)$$

The following spawner counts were made (Table C-I)

$$S_{1980} = 16, S_{1981} = 115, S_{1982} = 71, S_{1983} = 60, S_{1984} = 100, S_{1985} = 196, S_{1986} = 171, S_{1987} = 268$$

Then using [4.4B] in conjunction with the average age structure, we find that

$$\begin{aligned} \hat{N}_{1984} &= \overline{SS} * (A_1 * S_{1985} + A_2 * S_{1984} + A_3 * S_{1983} + A_4 * S_{1982} + A_5 * S_{1981}) \\ &= \overline{SS} * (1 * 196 + 1 * 100 + 1 * 60 + .97 * 71 + .716 * 115) = \overline{SS} * 507.2 \end{aligned}$$

[4.4B] allows us to estimate N_t using only a timeseries of spawner counts and an estimate of the age structure of spawners. Simulations indicate that when the above approximation is used, estimates of lambda or probability of 90% declines are not sensitive to the age structure estimate as long as gross errors are not made (i.e., assuming that 90% of spawners return by age 3 when actually only 10% return by age 3). \hat{N}_t is the number graphed in Figure IV-5. The running sums that we calculated are shown in Appendix C (Table C-IV). The raw spawner counts and age structures used are in Tables C-I and C-II. \overline{SS} was set to 1.0.

IV.D.2. Estimating variance and mu accurately

Sampling error is likely to be large in spawner data, resulting in an overestimation of the variance and therefore, of extinction risk. In addition, the estimation of N_t [4.4A] via [4.4B] adds another error term. Fortunately, the variance (\mathbf{s}^2) can still be estimated from stage-specific data (such as spawner counts) by using a modified estimation procedure (Holmes, 2000). Briefly, \mathbf{s}^2 can be estimated from the slope of y versus t in:

$$\text{var} \left[\log \left(\frac{\hat{N}_{t+t}}{\hat{N}_t} \right) \right] \text{ versus } t \quad [4.5]$$

where \hat{N}_t is the estimated living current and future spawners at time t . This is possible because the variance of log-transformed weighted sums of stage or age counts (e.g., \hat{N}_t) is approximately $(\mathbf{s}^2 + C_1)t + C_2$ where C_1 and C_2 are unknown constants and C_1 is small if the weighting function, \overline{A}_j , is approximately correct (Holmes 2000). This is shown graphically in Figure IV-9. One of the advantages of estimating variance from the slope of this relationship is that the slope is robust to lognormal observation error (a standard assumed distribution for sampling error). The effect of lognormal sampling error is to shift the variance vs tau line (Figure IV-9) up or down without appreciably changing its slope. There is of course a limit to the robustness of the method; it will break down under severe sampling error and short time series. However,

simulations indicate robustness under 20 year time series with an average of 100% sampling error (lognormal with mean 0 and variance 0.5; see Holmes 2000).

Using a similar method, we can minimize the influence of observation error on the estimation of μ , the instantaneous rate of population growth, by using the slope of

$$\text{mean} \left[\log \left(\frac{\hat{N}_{t+\tau}}{\hat{N}_t} \right) \right] \text{ versus } \tau \quad [4.6]$$

See Figure IV-9. In implementing this method, one must choose the maximum τ over which to calculate the slope. In our analyses, the following algorithm was used: if the length of the running sum = 6, use 3 lags, if it is > 6 then use 4 lags. Simulations indicate that this gives unbiased parameter estimates that remain unbiased with relatively low variance even in the face of severe sampling error (Holmes 2000). This is not the case for the standard method of estimation, which is simply the mean of $\log(N_{t+1}/N_t)$; the regression method of Dennis et al. 1991 for census data collected every year. Because of the modifications we have adopted for estimating instantaneous rates of change and environmental variance, our modified Dennis approach is not likely to founder on the assumption of no sampling error.

IV.E. Extinction Risk Metrics and Data

IV.E.I. Extinction Risk Metrics

If we know the rate of population change and the magnitude of environmental variation in that rate of population change, it is straightforward to estimate extinction risks by running a stochastic simulation that has been appropriately parameterized. The observed probability of extinction over a large number of simulations gives an extinction risk metric (also called the probability of extinction). However, if $N_{t+\tau}/N_t$ is lognormally distributed and the other assumptions discussed in IV-C are met, one can determine the probability of the stochastic simulation going extinct without actually having to run simulations. This is possible by using a diffusion approximation for the stochastic process [4.2] (see Dennis et al. 1991 for a discussion). The behavior of such diffusion processes is well established and in particular the probabilities and times to reaching thresholds, such as extinction, can be easily calculated. The probability of reaching a particular threshold N_e from the current population size N_0 within time t_e is (eqn. 16 x eqn. 84 in Dennis et al. 1991):

$$G * \mathbf{p}' = \mathbf{p}' * \Phi \left(\frac{-\ln(N_0/N_e) + |\hat{\mathbf{m}}| t_e}{\mathbf{s}_e} \right) + \exp(2 \ln(N_0/N_e)) |\hat{\mathbf{m}}| / \mathbf{s}^2 \Phi \left(\frac{-\ln(N_0/N_e) - |\hat{\mathbf{m}}| t_e}{\mathbf{s}_e} \right) \quad t_e > 0 \quad [4.7]$$

$$\text{where } \mathbf{p}' = \left\{ \begin{array}{l} 1, \mathbf{m} \leq 0 \\ \exp(-2 \mathbf{m} \ln(N_0/N_e)) / \mathbf{s}^2, \mathbf{m} > 0 \end{array} \right\}$$

Another quantity that we use is the probability that the population is 90% lower than its current population size at time t_e . This is (eqn. 6 in Dennis et al. 1991):

$$\Pr \left(\frac{N_{t+t}}{N_t} < \frac{x}{1} \right) = \Phi \left(\frac{-\ln(x/1) + \hat{\mathbf{m}} t_e}{\sqrt{\hat{\mathbf{s}}^2 t_e}} \right) \quad [4.8]$$

where $x=10$ for a 90% decline. We use the probability of a 90% decline to measure risks in those cases where we may not know what the total population is, but still want to quantify the risks of perilous declines. For example, at the level of an entire ESU, it usually is impossible to know total ESU population (since only a subset of stocks in the ESU are sampled), but the sampled portions of the ESU could nonetheless give a representative portrait of the risks of severe declines. In some cases we examine the probability of a 50% decline (in which case $x=2$ in [4.8]). Clearly many healthy populations regularly suffer 50% declines; we use the “50% decline metric” simply to compare the behavior of populations as indicated by their recent history of population changes not as a measure of extinction likelihood.

IV.E.1.a. Accounting for population structure at the ESU level

At the ESU-level, we must deal with the amount of environmental and dispersal-mediated correlation between populations within the same ESU. Populations that are composed of completely independent stocks have lower probabilities of decline than populations that are correlated either via dispersal or environment. We are currently working on methods for teasing apart environmental versus dispersal-mediated correlation. However, for the analyses in this report we make no assumptions about levels of dispersal between stocks. Instead, we consider that there are two possible extremes:

All stocks are completely connected with 100% dispersal. In this case, each stock i is merely a random weighted sample (weighted in the sense that some samples are larger than others) of the total ESU population. For the ESU level population, $\hat{\mathbf{m}}$ and $\hat{\mathbf{s}}^2$ are calculated using the same procedures as indicated in section IV.D.2 in [4.5] and [4.6], with $\sum_i N_{i,t}$ in place of N_y :

$$\hat{m} = \text{slope of mean} \left[\log \left(\frac{\sum_i \hat{N}_{i,t+t}}{\sum_i \hat{N}_t} \right) \right] \text{ versus } t$$

$$\hat{s}^2 = \text{slope of var} \left[\log \left(\frac{\sum_i \hat{N}_{i,t+t}}{\sum_i \hat{N}_t} \right) \right] \text{ versus } t$$
[4.9]

The probabilities that the ESU level population is 90% declined at time t_e is calculated using \hat{m} and \hat{s} from [4.9]. This will overestimate extinction risk in general, since all stocks are assumed to have the same underlying population dynamics (i.e., rate of decline and variance).

All stocks are completely independent. In this case, the number of current and future spawners in each stock i , N_i , fluctuates independently of the other stocks. The probability that the total ESU level population is 90% lower at time $t + t$ than at time t can be calculated as the probability that

$$\sum_i N_i(t+t) < 0.1 * \sum_i N_i(t) \text{ where } N_i \sim N(\hat{m}t, \hat{s}_i t)$$
[4.10]

This will in general underestimate the risk of declines because index stocks with a higher m will not be affected by declines in stocks with a lower m .

Neither of the above assumptions is correct, but they represent the extremes between which the true value must lie. Results using the first assumption only (that all stocks are completely connected) are presented, and thus the risk estimates will tend to be higher than the true values.

IV.E.2. Data Used for Stock and ESU Level Analyses

Data used in these analyses, and their source, are listed in Appendix C. All stock data included in the analyses met the following criteria.

1) Index or total live counts of adult spawners were available. When possible, total live counts were used. In many cases, these total counts included both hatchery born and wild born fish, although the amount of information regarding the hatchery component of the total count was widely variable (see criteria 2 below). In all cases, we attempted to use counts that indicated the number of spawners on the spawning grounds. For example if we used a dam count, we did not count fish removed for brood stock and pre-spawning harvest when this information was available. Counts generally include males and females. Note that our basic risk analyses were conducted using counts that included both hatchery-born and wild-born spawners.

2) To evaluate how the inclusion of hatchery fish in spawner counts influence risk estimates, we needed either time series of the number/fraction of hatchery spawners or a point estimate of

percent hatchery fish. When available, these data were used to estimate μ and σ for wild fish only (as opposed to wild + hatchery fish). Note that these data are typically very poor. The hatchery fractions are often not based on direct data (such as counts of fin-clipped fish) but instead are derived from estimates of hatchery stray rates.

3) Each stock time series must include data through at least 1995, so that we have some representation of “current conditions”.

4) The length of the time series must be at least (*maximum age of return* + 6).

For each ESU, we summed together stock data that met the above criteria plus one additional criterion:

1) Only stocks with total live counts of adult spawners were used (with the exception of Lower Columbia River Chum for which peak counts were added together). This restriction was added because index counts (such as redds per mile) do not indicate the total size of the spawner population and the count would not be weighted properly when added to other counts from other stocks.

In some ESUs, such as Upper Willamette Chinook, we used dam counts recorded at the lower end of the ESU as our ESU level data, whereas stock level data were stream counts for individual stocks in the ESU. Appendix C, Table C-I shows the raw spawner count data. If an ESU count is shown, it indicates that an independent ESU level count was available.

IV.F. Accounting for the Masking Effects of Hatchery Fish in Spawner Counts

In many of the stocks, there are significant numbers of hatchery fish that may be reproducing, and the population process is approximately

$$\mathbf{W}_{t+1} = \mathbf{A}_t \times (\mathbf{W}_t + \mathbf{I}_t) \tag{4.11}$$

where \mathbf{A}_t is the underlying stochastic matrix for which we are trying to estimate μ and σ^2 . \mathbf{W}_t is the vector of wild born fish at time t and \mathbf{I}_t is the input of spawners of hatchery origin and takes the form:

$$\begin{bmatrix} 0 \\ 0 \\ 0 \\ \dots \\ R_{hw} S_{h,t} \end{bmatrix} \tag{4.12}$$

where $S_{h,t}$ the number of hatchery spawners at time t , and R_{hw} is the reproductive effectiveness of those spawners relative to the wild born spawners. We can define \mathbf{I}_t in terms of \mathbf{W}_t by defining

the fraction of reproductive hatchery origin spawners relative to total spawners: $h_t = (R_{hw} \text{ *hatchery origin spawners}) / (\text{wild born spawners} + R_{hw} \text{ *hatchery origin spawners})$. Then

$$\mathbf{I}_t = \begin{bmatrix} 0 & 0 & 0 & \dots & 0 \\ 0 & 0 & 0 & \dots & 0 \\ 0 & 0 & 0 & \dots & 0 \\ 0 & 0 & 0 & \dots & 0 \\ 0 & 0 & 0 & \dots & h_t / (1 - h_t) \end{bmatrix} \times \mathbf{W}_t \quad [4.13]$$

$$= \mathbf{B}_t \times \mathbf{W}_t$$

Combining Equation **Error! Bookmark not defined.** and **Error! Bookmark not defined.**, we have

$$\mathbf{W}_{t+1} = \mathbf{A}_t \times (\mathbf{W}_t + \mathbf{B}_t \times \mathbf{W}_t) = \mathbf{A}_t \times (\mathbf{I} + \mathbf{B}_t) \times \mathbf{W}_t \quad [4.14]$$

the ratio of $\mathbf{W}_{t+1} / \mathbf{W}_t$ could be used now to estimate the μ and σ^2 of the matrix $\mathbf{A}_t \times (\mathbf{I} + \mathbf{B}_t)$, but the question is what is the relationship between these parameters and the μ and σ^2 of the matrix \mathbf{A}_t – which is what we are trying to estimate? This is straight-forward to derive by noting the following:

$$\mathbf{A}_t \times (\mathbf{I} + \mathbf{B}_t) = \mathbf{A}_t \times \begin{bmatrix} 1 & 0 & 0 & \dots & 0 \\ 0 & 1 & 0 & \dots & 0 \\ 0 & 0 & 1 & \dots & 0 \\ \dots & \dots & \dots & \dots & 0 \\ 0 & 0 & 0 & \dots & 1 + h_t / (1 - h_t) \end{bmatrix} \quad [4.15]$$

$$= \mathbf{A}_t + \begin{bmatrix} 0 & 0 & 0 & \dots & F * h_t / (1 - h_t) \\ 0 & 0 & 0 & \dots & 0 \\ 0 & 0 & 0 & \dots & 0 \\ \dots & \dots & \dots & \dots & 0 \\ 0 & 0 & 0 & \dots & 0 \end{bmatrix} = \mathbf{C}_t$$

where F is the mean fecundity rate of spawners and appears in the upper right corner of matrix \mathbf{A}_t . Since \mathbf{A}_t and \mathbf{C}_t differ only in the fecundity term, the net reproductive value, $R_{0,C}$ of \mathbf{C}_t is related to the net reproductive value, $R_{0,A}$ of \mathbf{A}_t , as

$$R_{0,C_t} = R_{0,A_t} \times F \times (1 + h_t / (1 - h_t)) / F = R_{0,A_t} \times 1 / (1 - h_t) \quad [4.16]$$

The relationship between the net reproductive rate and μ is (Caswell 1989)

$$\lambda^T = R_0 \text{ or}$$

$$T * \ln(\lambda) = T * \mu = \ln(R_0) \quad [4.17]$$

where T is the mean generation time. Since salmon spawn and die, this is the mean return time for the salmon species of concern. Using this relationship, we can solve for the relationship between the observed μ , μ_C , and the μ we wish to estimate, μ_A :

$$\begin{aligned} \mathbf{m}_{C_t} &= \frac{1}{T} \ln(R_{0,C_t}) \text{ and } \mathbf{m}_{A_t} = \frac{1}{T} \ln(R_{0,A_t}) \\ \mathbf{m}_{A_t} &= \frac{1}{T} \ln(1 - h_t) + \mathbf{m}_{C_t} \end{aligned} \quad [4.18]$$

Since μ_{C_t} is $\ln(N_{t+1}/N_t)$, the estimates of the mean and variance of μ_{A_t} , which is the μ and σ^2 we are trying to estimate, could be calculated using the running sums of spawners counts as a estimate of the current living and future wild born spawners, $N_t = \sum_i S_{t-i}$. For h_t , we used the fraction of reproductive hatchery spawners in the running sum count, rather than the spawner count at time t as defined above.

$$\begin{aligned} \hat{\mathbf{m}} &= \text{mean} \left[\frac{1}{T} \ln(1 - h_t) + \ln \left(\frac{N_{t+1}}{N_t} \right) \right] \\ \hat{\mathbf{S}}^2 &= \text{var} \left[\frac{1}{T} \ln(1 - h_t) + \ln \left(\frac{N_{t+1}}{N_t} \right) \right], \end{aligned} \quad [4.19]$$

The slope method can derived in this case as follows:

$$\begin{aligned} A &: \frac{1}{T} \ln(1 - h_{t+1}) + \ln(N_{t+1}/N_t) \sim N(\mathbf{m}, \mathbf{S}^2) \rightarrow \\ B &: \frac{1}{T} \ln(1 - h_{t+2}) + \ln(N_{t+2}/N_{t+1}) \sim N(\mathbf{m}, \mathbf{S}^2) \\ A + B &: \ln(N_{t+2}/N_t) + \frac{1}{T} \ln((1 - h_{t+2})(1 - h_{t+1})) \sim N(2\mathbf{m}, 2\mathbf{S}^2) \end{aligned} \quad [4.20]$$

repeat the above operations to arrive at

$$\ln(N_{t+t}/N_t) + \frac{1}{T} \ln \left(\prod_{i=1}^t (1 - h_{t+i}) \right) \sim N(\mathbf{m}t, \mathbf{S}^2 t)$$

Thus an estimate for μ and σ^2 using the slope method that are robust to sampling error is:

$$\begin{aligned} \hat{\mathbf{m}} &= \text{slope of mean} \left[\ln \left(\frac{N_{t+t}}{N_t} \right) + \frac{1}{T} \ln \left[\prod_{i=1}^t (1 - h_{t+i}) \right] \right] \text{ versus } \mathbf{t} \\ \hat{\mathbf{S}}^2 &= \text{slope of var} \left[\ln \left(\frac{N_{t+t}}{N_t} \right) + \frac{1}{T} \ln \left[\prod_{i=1}^t (1 - h_{t+i}) \right] \right] \text{ versus } \mathbf{t} \end{aligned} \quad [4.21]$$

Unfortunately, a critical uncertainty when estimating the parameters describing population change in wild stocks is the fraction and effectiveness of hatchery fish on the spawning grounds. Often the data do not make it clear to what extent hatchery fish were excluded from spawner counts, nor is there information specifying the fraction of spawners that are hatchery fish. A priority for the region should be to develop better population databases that include rigorous estimates of hatchery numbers on spawning grounds. Secondly, we need direct empirical measures of the reproductive contribution of hatchery-born fish compared to wild fish, denoted R_{hw} . In the absence of such data, we have proceeded with a suite of analyses as described below.

In the face of these critical uncertainties, we estimated population parameters in three ways:

- 1) Use the counts of total spawners (wild-born + hatchery-born). Parameter estimates are from [4.5] and [4.6] with $\hat{N}_t = \hat{N}_{t, total}$. The estimates of \hat{m} and \hat{S}^2 will reflect the parameters for in-stream breeding wild-born fish if the hatchery fraction is relatively constant (even if high) and hatchery-born fish do not produce future spawners ($R_{hw} = 0$).
- 2) Use an estimate of the fraction of spawners at time t that were hatchery fish and assuming that these hatchery-born fish do not produce offspring, $R_{hw} = 0$. Parameter estimates are from [4.5] and [4.6] with $\hat{N}_t = (1 - h_t) * \hat{N}_{t, total}$ where h_t is the fraction of hatchery fish in the spawner count. The estimates of \hat{m} and \hat{S}^2 are not appreciably different than 1) unless the fraction of hatchery fish is changing.
- 3) Use an estimate of fraction of spawners at time t that were hatchery fish, assuming that these hatchery-born fish reproduce with the same success as wild-born fish, i.e., $R_{hw} = 1$. Parameter estimates are from [4.21]. If the hatchery fraction is high, the estimate of \hat{m} will be significantly lower.

Why does method 3, with relative fitness of hatchery fish equal to wild fish ($R_{hw} = 1$), produce lower estimates of \hat{m} ? \hat{m} is our estimate of instantaneous per capita population growth due to reproduction in-stream which is qualitatively similar to the wild-born spawner recruits divided by the number of "parents". If the "parents" are only the wild born fish, then the per capita in-stream reproduction must be high to account for the number of wild born recruits (as in method 1). If the "parents" include all hatchery-born spawners reproducing similarly to wild-born spawners, the per capita in-stream reproduction of wild fish must be much lower since the parent pool is much larger. Note that the lower \hat{m} is not due to any negative ecological or genetic effect of hatchery fish, but arises as an "accounting effect" simply because the "parent" pool is much larger and thus the number of offspring produced per parent is reduced.

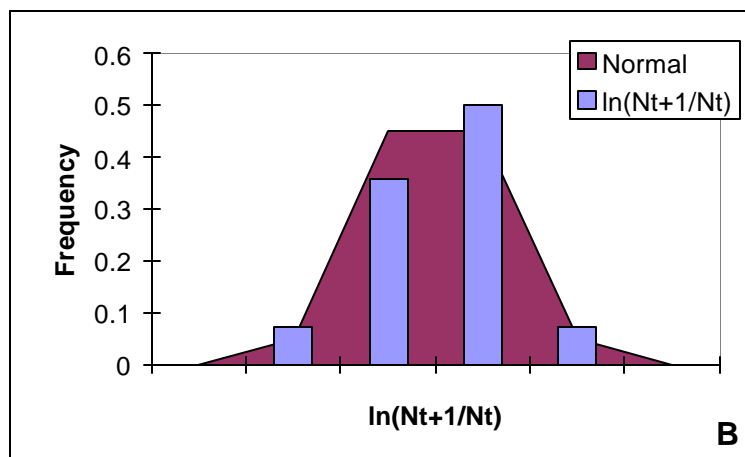
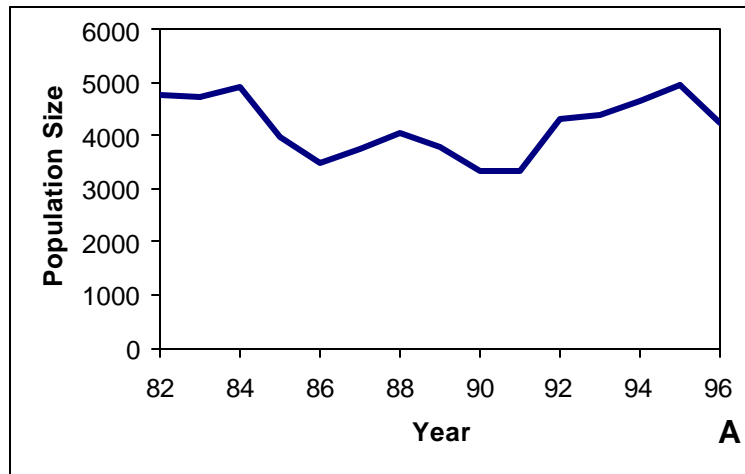


Figure IV-1. Population trajectory and histogram of the natural log of population counts at time $t+1$ and t . These are data from Kalama River winter run steelhead. The population size is an estimate derived from a weighted sum of spawner counts as described above.

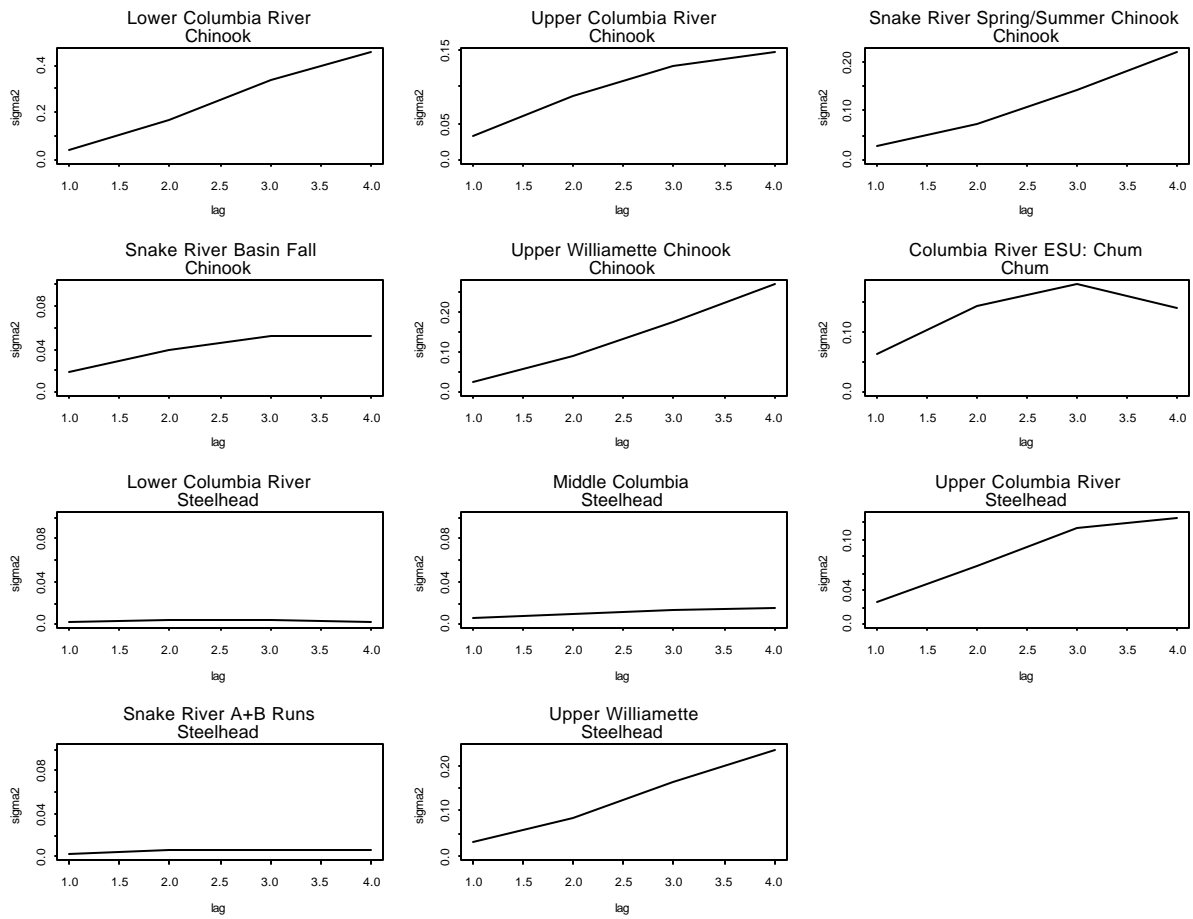


Figure IV-2. The variance in $\ln(N_{t+1}/N_t)$ where N_t is the weighted sum of spawner counts as described in the text. A basic assumption of the analysis is that this relationship is linear. The slope of this relationship is used to estimate the variance of the total living fish that are current or future spawners (i.e., the population size at time t that we cannot observe). Plots that are flat indicate ESUs for which the variance was 0 or close to 0.

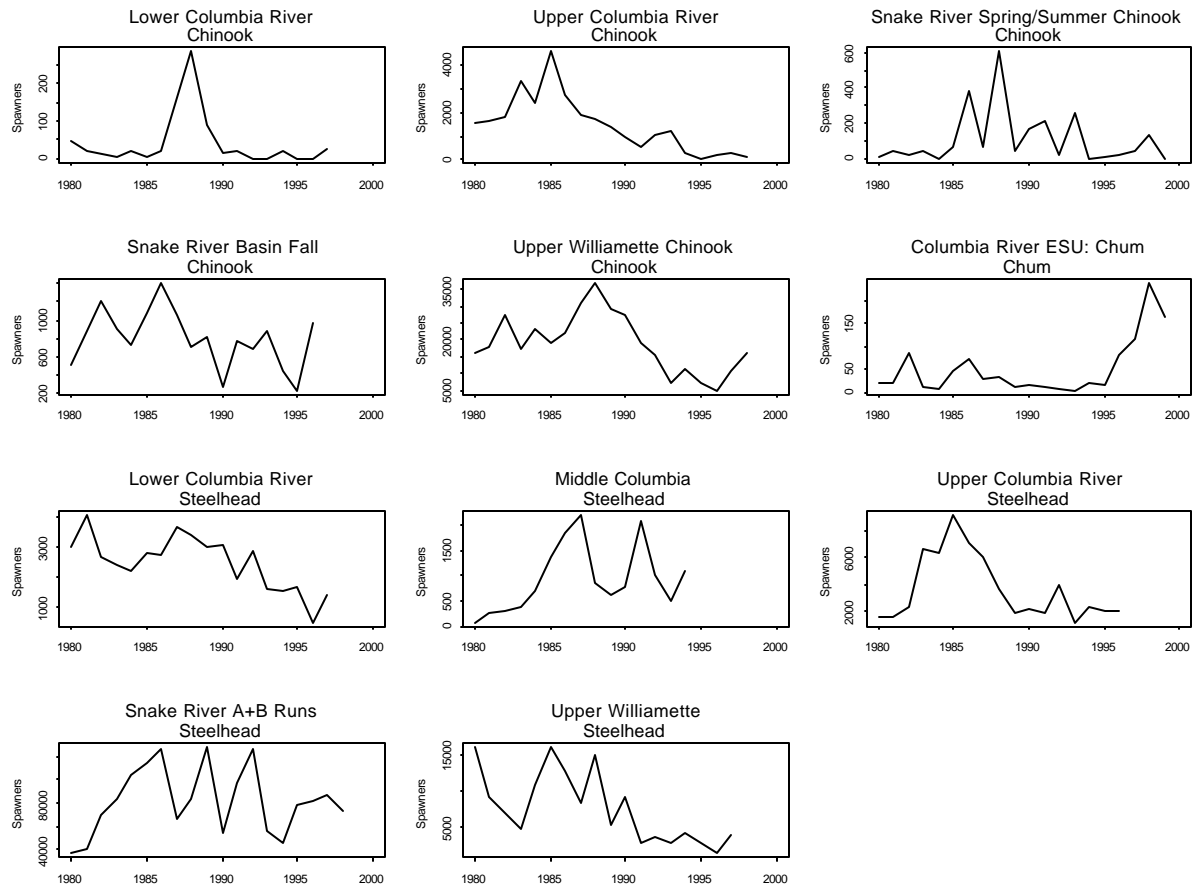


Figure IV-3. Raw spawner counts used for the analyses. Counts include hatchery fish that spawn in the wild. The raw data are shown in the Appendix C.

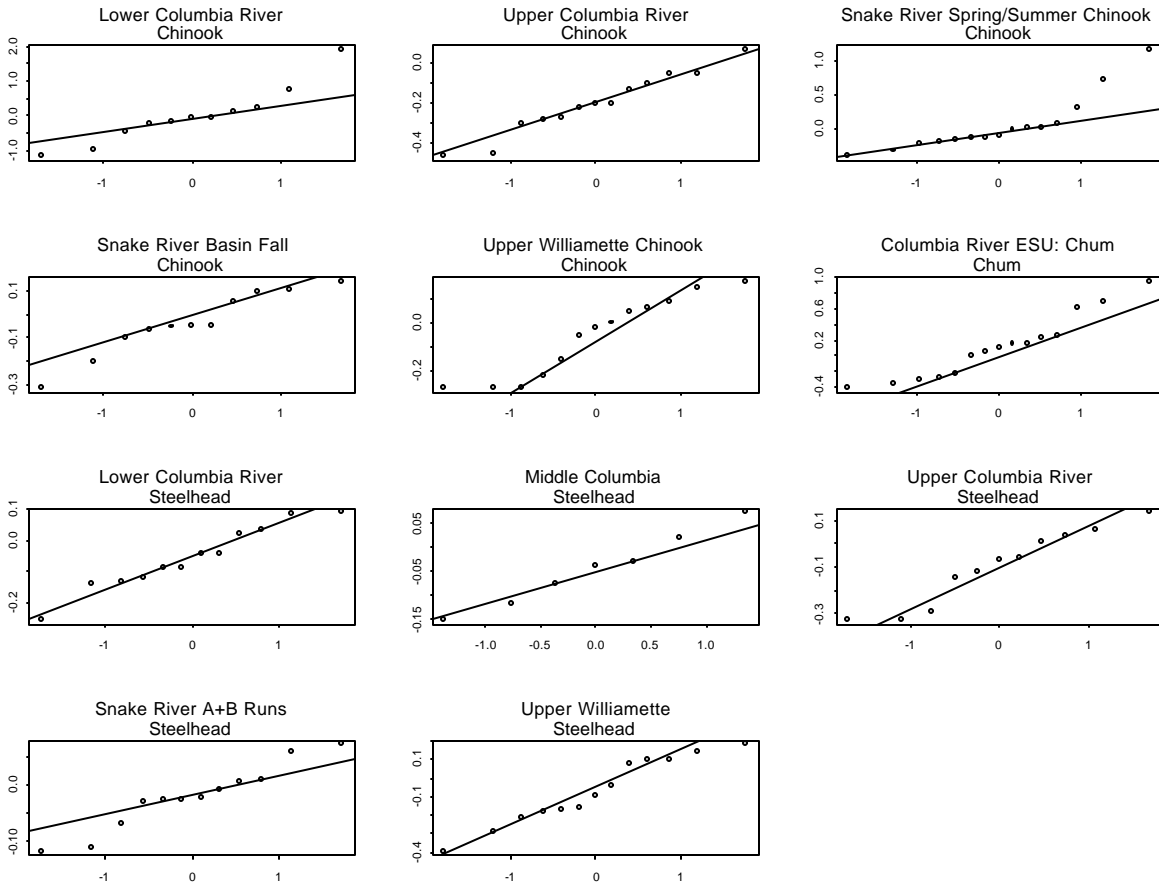


Figure IV-4. Test of the normal distribution of $\ln(N_{t+1}/N_t)$ where N_t is the weighted running sum of spawners at time t . The line shows the expected values from a normal distribution. The data points should fall approximately on this line. The x-axis is the quartiles of a standard normal and the y-axis is the $\ln(N_{t+1}/N_t)$ values.

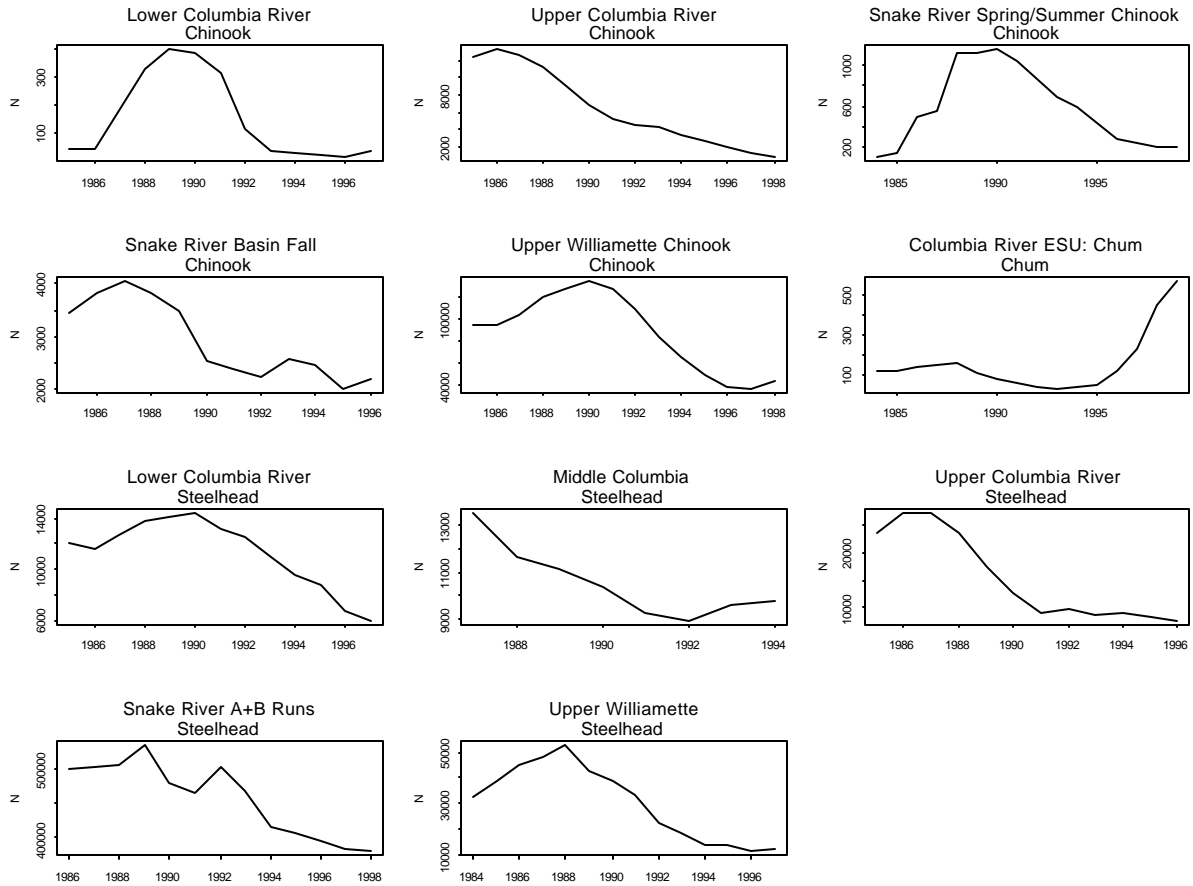


Figure IV-5. Weighted running sums of spawner counts used in the analyses. As described in the text, this is an estimate of the living fish that are current spawners or that will survive to be future spawners (i.e., the total population size at time t which we cannot observe). The running sum numbers are given in Appendix C.

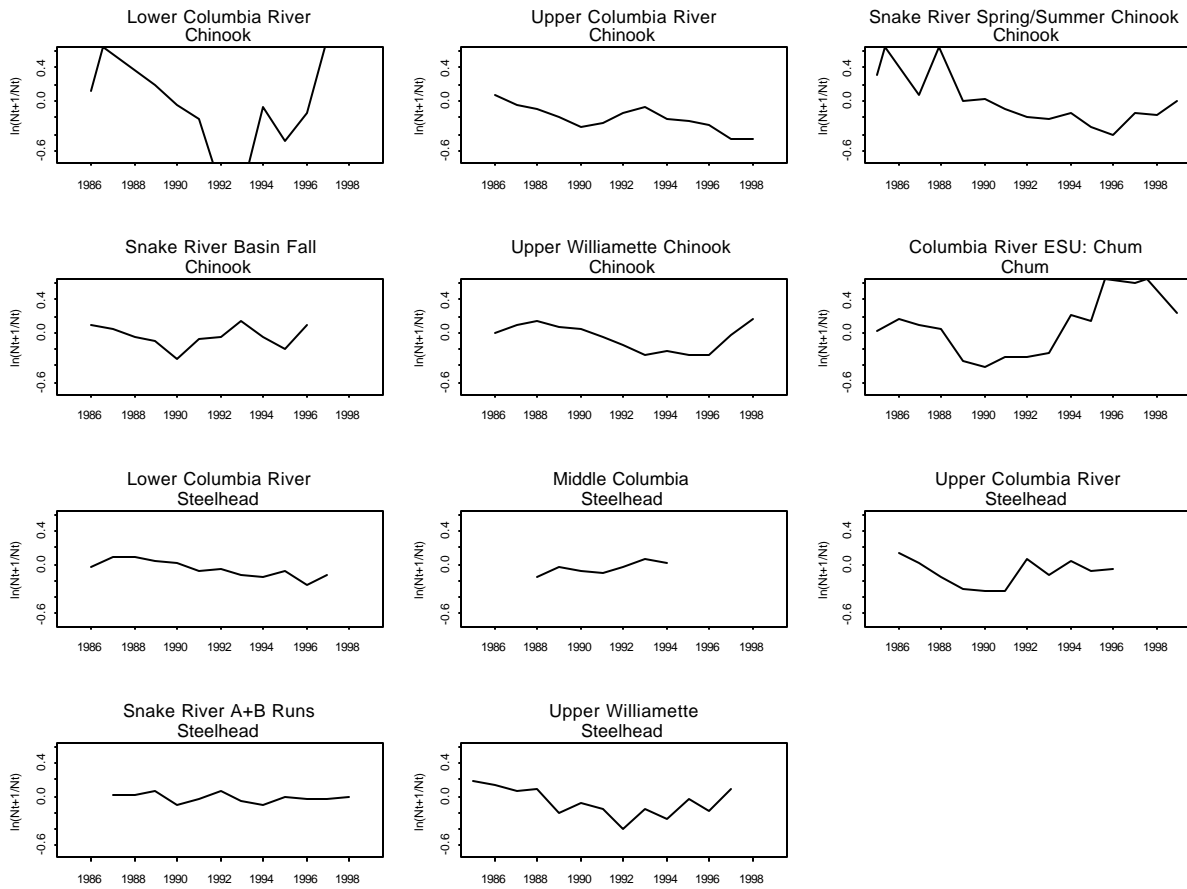


Figure IV-6. $\ln(N_{t+1}/N_t)$ data which can be thought of as the $\ln(R/S)$ relationship. The analyses assume that there is no trend in this relationship. Two stocks show apparent trends in the 1980-present data used in these analyses: Upper Columbia River Chinook and Snake River Spring/Summer Chinook; however, an examination of longer time series (1970 to present) suggest that only the Upper Columbia River Chinook shows a downward trend (Figure IV-7).

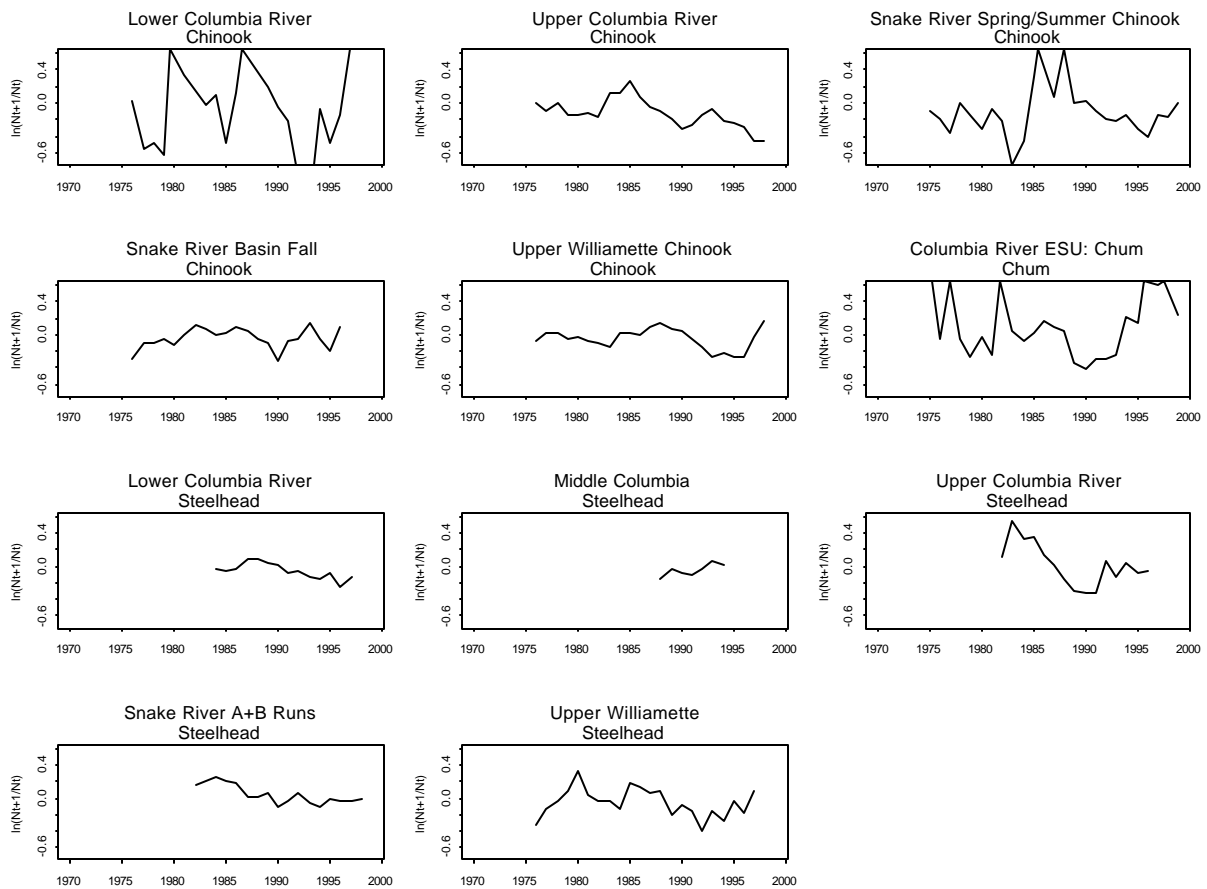


Figure IV-7. $\ln(N_{t+1}/N_t)$ for 1970 to present where data are available.

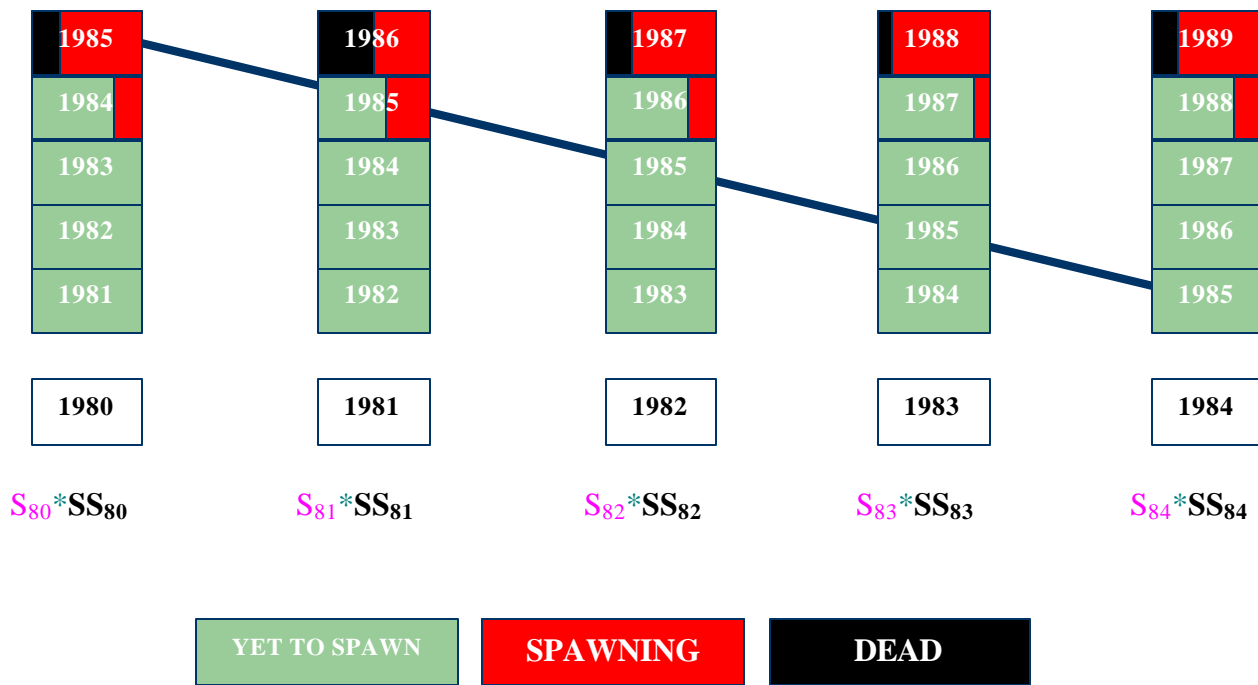


Figure IV-8. Graphical demonstration of the total current and future spawners at time t . At each year in the white squares, S_t , spawners spawn. These give rise to SS_t recruits to the spawning grounds. The status of these recruits (ocean, spawning this year, previously spawned and now dead) in years $t+i$ is indicated in the shaded boxes. To determine the total number of current and future spawners in year 1985, say, we add up all the spawners that are yet to spawn or spawning this year in the boxes connected by the black line. This is the algorithm indicated by [4.4A, B].

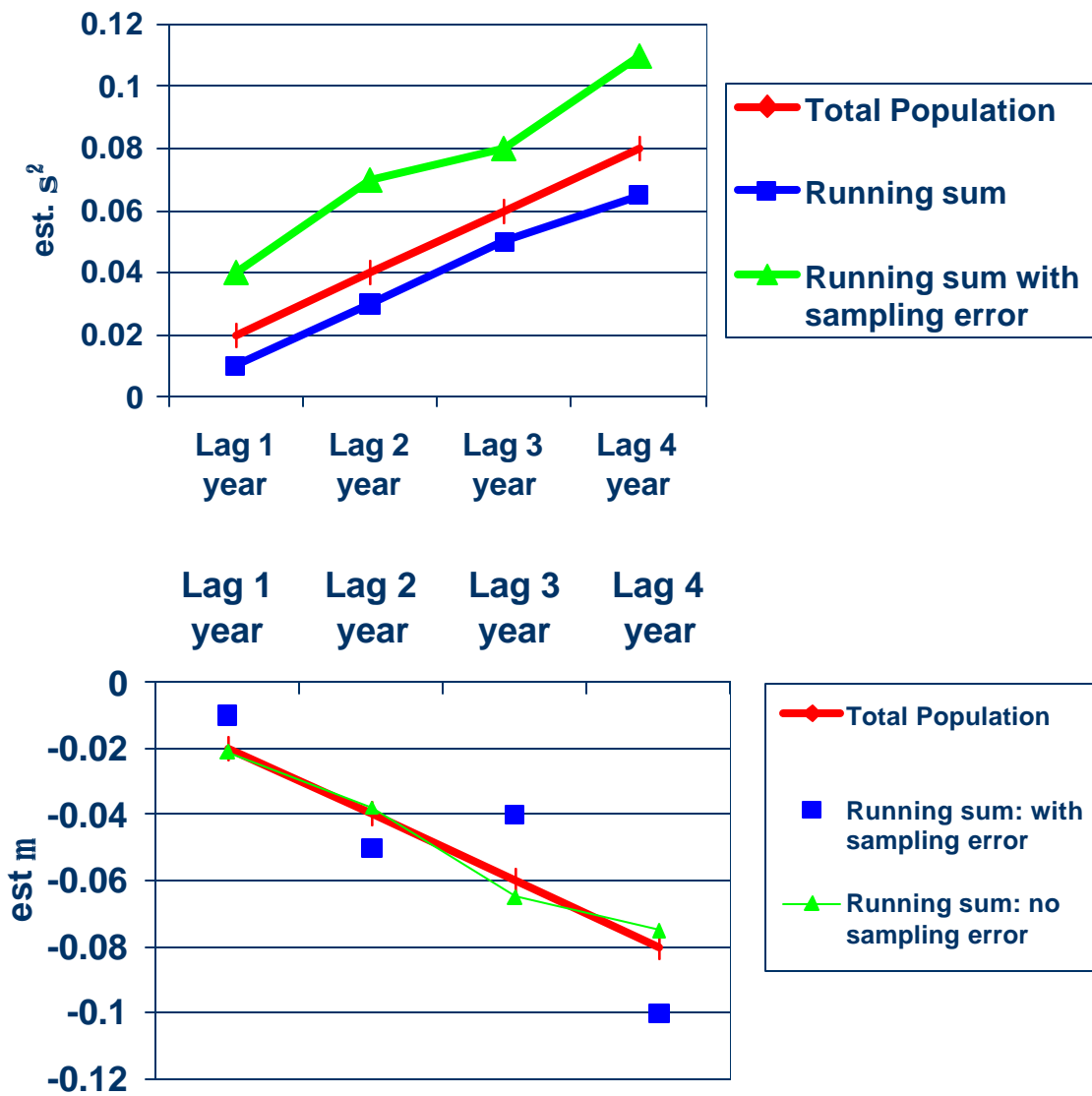


Figure IV-9. Graphical representation of the method for estimating σ^2 , the true variance of $\ln(N_{t+1}/N_t)$ and μ , the mean from $\hat{S}^2 t$ and $\hat{m} t$ which are the estimated values from $\ln(\hat{N}_{t+t} / \hat{N}_t)$. The slope of the $\hat{S}^2 t$ (denoted est. σ^2 on the y-axis) versus tau, the lag, is an estimate of σ^2 . The slope of $\hat{m} t$ (denoted est. μ on the y-axis) versus tau is an estimate of μ . The effect of sampling error on the $\hat{S}^2 t$ versus τ line is to raise the line while keeping the slope (used to estimate σ^2) approximately the same (top panel). The effect of sampling error on the $\hat{m} t$ versus τ line is to increase the variance of the data around the line without changing the slope.

V. Standardized Comparisons of Risks across ESUs

In this section we present the results of our standardized analyses. We first report the trend and rate of population change for individual stocks and ESUs. We then report several standardized measures of risk. At the ESU level, we present the risk of experiencing significant declines, and the most likely time to reach those declines as long and short-term measures of risk, respectively. At the stock level, we present both the risk of experiencing significant declines and the risk of reaching absolute extinction. We then present the necessary change in the rate of population change to reduce these measures of risk. Finally, we briefly discuss the types of analyses we are undertaking as first steps in assessing the feasibility of achieving these improvements.

V.A. What are current trends and rates of population change for ESUs and individual stocks?

Current trends in the number of spawners and the weighted running sum of spawner counts for ESUs are shown in Figures V-1 and V-2. Several ESUs, including Lower Columbia Chinook, Upper Willamette Chinook and Columbia River chum, exhibited peaks in spawner abundance in the late 1980s or early 1990's. Even though these numbers include hatchery fish that spawn in-stream, the trends are strongly declining in most ESUs over the time period analyzed. Analyses of these data indicate that most ESUs and individual stocks within ESUs have an annual population growth rate less than one, even when hatchery fish are assumed to contribute nothing to future generations (see below). The following summary refers to these analyses of raw data, with no distinction between hatchery-origin and wild spawners.

Individual Stocks. In 83% of the individual stocks analyzed, lambda was less than one (Figure V-3). One third of the stocks analyzed had rates of decline less than 0.9, indicating these stocks are in severe decline. A lambda of 0.9 means that a population will be cut in half in less than seven years. Population growth rates were increasing for the remaining 17% of individual stocks; all positive lambda values were less than 1.2.

ESUs. Among ESUs, lambda was less than 1.0 for 10 of the 11 ESUs analyzed. Rate of population decline was less than 0.9 for four of these ESUs (Figure V-4). It is worth noting that although Columbia River chum has a population growth rate greater than 1 (which implies growing populations), this result should not be a source of great comfort. This ESU has confidence intervals that extend well below 1. (In contrast, the four ESUs with lambda less than 0.9, have confidence intervals that never exceed 1.) In addition, the positive (though very uncertain) estimate of rate of population change for Columbia River chum is consistent with the reasons for its listing under the ESA. (Threats to its habitat rather than population dynamics were the primary concern for this species.) Because of its large numbers, poor data, and "high lambda", the Columbia River chum is a consistent outlier in all of the subsequent analyses. For that reason, our ensuing discussion of "general results" typically does not apply to this ESU. Finally, it is important to remember that all these estimates of population growth rate are a maximum – any reproduction by hatchery-origin spawners will reduce these estimates.

Range of values for lambda, given the presence of hatchery fish.

All our measures of population trends are hampered (as any assessment of population dynamics will be) by the inclusion of hatchery-origin fish in spawner counts. In effect, inclusion of these fish, which are not derived from wild spawners, complicate the "accounting," by appearing to be recruits from the wild population. If the proportion of fish that are hatchery-born increases through time, or if those hatchery fish are successfully reproducing, rates of population change will be overestimated, and measures of risk will be underestimated (see Section IV. F. for a complete discussion.) Although the proportion of hatchery fish present in the population has been estimated for 55 of the populations we have analyzed (half of these are point estimates rather than time series), the reproductive success of those fish is virtually universally unknown. Therefore, we have made two corrections to bound the possible range of rates of population change when estimates of the fraction of hatchery fish in the population were available:

- 1) Assuming these hatchery-born fish do not produce offspring. The estimates of \hat{m} and \hat{S}^2 will not be appreciably different from the estimates when no correction is applied, unless the fraction of hatchery fish is changing.
- 2) Assuming these hatchery-born fish reproduce with the same success as wild-born fish. If the hatchery fraction is even moderately high, the estimate of \hat{m} will be significantly lower.

In the 54 stocks for which hatchery proportion estimates were available, the average rate of population decline worsened from 0.93 to 0.83 (average lambdas across 54 stocks) when hatchery-born fish were assumed to reproduce at the same rate as wild-born fish (Appendix B). Among ESUs, the rate of population decline also worsened when hatchery fish were assumed to reproduce in-stream (Figure V-5). The average rate of population decline across ESUs, assuming that hatchery fish and wild fish contribute to the next generation at the same rate is 0.79. The proportion of hatchery fish present in the Snake River Steelhead population increases with time, so the estimate of lambda, even with no reproduction from hatchery fish decreases (Figure V-5, Appendix B).

The implications of these results are tremendous for all estimates of risk assessment, since all of these metrics depend on the value of lambda. In cases where available spawner counts include an unknown proportion of reproducing hatchery fish (i.e., we falsely assume all reproduction is by wild-born fish), estimates of risk are optimistic. Similarly, in those situations where the proportion of hatchery fish in the population increases over time (such as Snake River Steelhead), even if they are not reproducing, the estimates of risk are optimistic. Because information on the rate of reproduction of hatchery-origin spawners is extremely limited, the risk estimates we present should be viewed as being bounded by the two estimates we present. (For reference, reproductive success of Lower Columbia Steelhead of hatchery origin (non-indigenous stock) is thought to be around 15% of that of wild fish. Most indigenous stocks are thought to have substantially greater reproductive success than these fish.) Note also that for stocks in which the proportion of hatchery fish increases over time, (again, most notably Snake River Steelhead), the most appropriate minimum estimate of risk is that with a hatchery correction, but reproductive success set to zero.

V.C. Risk estimates for individual stocks and ESUs

We completed a risk evaluation that addressed the following questions for stocks and/or ESUs:

(i) What is the risk of individual stocks reaching 1 fish/1 generation within the next 24/48/100 years (Eqn. 4.7)? For the current population size (N_0), we use the most current running sum (N_t) estimate (Appendix C-4).

(ii) What is the probability of observing a 50% or 90% decline from current abundances within the next 24/48/100 years (Eqn. 4.8)? (for stocks we show 90% and for ESUs we show 50% and 90%)

(iii) What is the most likely time for ESUs to reach their first decline to either 50% or 90% of current abundances? Here we present the mode of the time to reach 50 and 90% declines. This represents the most likely time to hit these percent declines. It should be kept in mind that this will over-estimate the median time to reach these declines. The maximum likelihood estimate of the mode is (eqn. 98 in Dennis et al. 1991),

$$\log(x/1) / \mathbf{m} \left\{ \left[1 + \frac{9\mathbf{s}^4}{4(\ln(x/1) | \mathbf{m})^2} \right] - \frac{3\mathbf{s}^2}{2\ln(x/1) | \mathbf{m}} \right\} \quad [5.1]$$

where $x=2$ for a 50% decline and 10 for a 90% decline.

When looking at the results below, note that the most likely time to reach a threshold measures short-term risk while the probability that the stock is 50 or 90% lower than current levels in 100 years measures long-term risk. This is because the latter probability indicates where the stock will be in 24 or 100 years, but not what happened along the way. For example, a stock with $\mathbf{I} > 1$ and high variance will increase and have a low probability that it is 50 or 90% below current levels in year 24 or 100, but may reach 50 or 90% declines (relative to current levels) in year 2 or 5, due to the high variability, but then increase well above these levels in subsequent years. The most likely (ML) time to first reach 50 or 90% declines (relative to current levels) captures this short-term risk. Because ML time captures short-term risk (i.e., is most strongly influenced by the variance \mathbf{s}^2) and the 24 and 100-year probabilities capture long-term risk (i.e. is most strongly influenced by \mathbf{m}), these metrics can be very different. For example, chinook generally have higher variance than Steelhead but lower \mathbf{m} . Thus they tend to have higher short-term risk (lower ML time), but lower long-term risk (24 and 100 year probabilities of 50 or 90% decline). (This difference in variance is due in part to the fact that data for chinook stocks were generally available for smaller geographic and demographic units.)

Generally, all analyses were conducted for both ESU and stock-level data when possible. In some cases, however, data were not conducive to specific analyses. For example, estimating the risk of reaching 1 fish/1 generation was not feasible for ESUs because this analysis requires an

estimate of total abundance for the ESU. In most ESUs, data were available for only a subset of stocks. Thus, an estimate of total population size was not feasible.

Because of the sheer number of analyses and subsequent results, we show figures only for the results for stocks and ESUs with no correction for hatchery fish (except for the risk of absolute extinction). The results below are therefore a lower limit to the risk metrics for each of these stocks/ESUs. (Again, note that the most appropriate lower limit for the wild component of Snake River Steelhead is the hatchery correction, with no reproductive success.) As a lower limit for the risk of absolute extinction at the stock level, we show the results of the analysis with hatchery fish removed from the count, but contributing nothing to subsequent generations. Results of all combinations of stock/ESU, 24/48/100 years, 1 fish in one generation/50% decline/90% decline, with/without hatchery fish are presented in Appendix B.

(i) What is the risk of individual stocks reaching 1 fish/1 generation within the next 24/48/100 years? (note that this analysis is not possible for ESUs)

On average, the risk of the wild component of individual stocks reaching 1 fish/1 generation is 16% (24 years) and 60% (100 years; Appendix B, Table B-4). Short-term risks of 16% are high; some chinook stocks have substantially greater risks. Overall, the risks were slightly higher for Chinook compared to Steelhead, resulting from higher variances and smaller population sizes in Chinook stocks. (Note that in some cases the larger Steelhead "population" sizes are an artifact of sampling, rather than the true demographic unit.)

(ii) What is the probability of stocks/ESUs being at a 50% or 90% of current abundances at 24/100 years? The probability at 48 years is presented in tables in Appendix B.

Stocks. The probability of individual stocks being at 90% of current abundances in 24 or 100 years is high (Figures V-6 and V-7). Among the 60 stocks analyzed, the average probabilities were 40% (24 years; median = 0.31) and 69% (100 years; median = 0.94). Results were comparable between chinook and steelhead stocks.

ESUs. The probability that ESUs will have fallen to 90% of their current abundances in 24 or 100 years is extremely high (average = 0.86, median = 1.00) (Figures V-8 and V-9). Even in the short term, five of the ESUs have a greater than 50 percent chance of being at abundances only 10% of their current levels. The risk of a 50% decline in numbers, if current conditions continue, is even greater.

(iii) What is the most likely time for ESUs to decline to either 50% or 90% of current abundances?

The estimates for each ESU are shown in Figure V-10. The most likely (ML) time until ESUs first decline to 50% of current abundance is extremely short, averaging 8 years across all ESUs. The ML time to decline was extremely short for chinook ESUs (average = 3 years) and slightly longer for steelhead ESUs (average = 9 years). These differences between chinook and steelhead are due to greater variance in chinook ESUs. The average time for ESUs to first decline 90%

from current abundance was 33 years, with differences between chinook and steelhead ESUs similar to those observed at 50% declines.

V.D. How much improvement in lambda is needed to reduce risk?

One way that we can model the impacts that changes in habitat, hatcheries, harvest or hydropower have on salmon stocks is through modifying λ , the rate of population decrease or increase. Here, we evaluate how much improvement in λ is needed to reduce estimates of risk, recognizing that opportunities to affect λ will obviously vary from ESU to ESU.

We evaluated the degree of improvement necessary to reduce risk in two ways. First, we calculated the percent increase in λ necessary to reduce the risk of extinction to less than 5% in 100 years. This is a metric commonly used in risk assessment, and is consistent with IUCN standards (1994), making our analyses comparable with many others in the conservation literature. We also calculated the percent change in λ necessary to reduce the probability of 90% decline in 100 years to less than 5%. These two analyses differ in the threshold to be avoided. In the first case, the threshold is absolute extinction (1 fish/1 generation); in the second case, the threshold to be avoided is a 90% decline from current abundances. The second threshold is much less sensitive to errors in our estimate of total stock size or to the presence of non-reproducing hatchery fish in the counts. Both of these analyses were done at the stock level because this is the scale at which most management actions are likely to occur. Estimates of necessary improvements in lambda were made using parameters generated from all three methods (see section IV.F): 1) no hatchery correction, 2) assume hatchery fish do not reproduce and 3) assume hatchery fish reproduce at rates equal to wild fish. Results for this analysis incorporating both hatchery corrections are presented in Appendix B.

For all analyses, the percent increase in λ needed to avoid extinction was, not surprisingly, variable among stocks (Figures V-11, Appendix B). If hatchery fish are assumed to have no reproductive success, a 13.2% increase in lambda is necessary on average to reduce extinction risk to less than 5% in 100 years, however the range of necessary increases spans 0-112%,. Incorporating the proportion of hatchery fish on the spawning grounds increased the estimates of needed increases in λ . Under the extreme assumption that hatchery fish reproduce at rates equal to those of wild fish, an average required increase in lambda of 27% is required. In general, the needed improvement to reduce the risk of a 90% decline was greater than that required to reduce the risk of extinction (average 17.6% improvement needed across stocks to achieve a less than 5% chance of this decline in 100 years when hatchery fish are assumed not to reproduce.)

The percent increase in λ necessary to prevent extinction or 90% decline depends on both m (the instantaneous rate of decline) and s^2 (the variability in that rate) – in a counterintuitive way. A stock can have a high probability of reaching a 90% decline in 100 years, but need a low percent increase in λ if the variability in m is small. The individual chinook stocks that we analyze are small (individual creeks) with high variability whereas the individual steelhead stocks tend to be much larger (sometimes entire basins) with lower variability. For this reason, the percent increase in λ required to prevent extinction or 90% decline is lower for steelhead

than for chinook while the probabilities of reaching thresholds with no improvements is higher for steelhead than for chinook.

V.E. How likely are we to detect increases in lambda in 10 years?

The ESA mandates that threatened and endangered populations require recovery actions to mitigate the anthropogenic sources of risk. Recovery goals often involve increases in population size and reversing downward trends in population trajectories. In either case, to achieve recovery, population growth rates must be changed. Due to our poor understanding of the determinants of salmon population dynamics we may be forced to undertake management actions without a clear knowledge of their efficacy. Unfortunately, recovery actions may take tens of generations to reach their goal, and as such, futile or even harmful actions may be in place for many years. Alternatively, successful actions that could be applied elsewhere may not exhibit their benefits rapidly, thus delaying their adoption into the salmon conservation repertoire. Can we use the population projection approach of the Dennis model to predict when a change in population growth rate is detectable? That is, given that a management action changes only the population growth rate, λ , can we use our standard population projection technique to examine the deviation of population trajectories with and without an altered growth rate?

In the following analyses we increase and decrease λ by 1% and 10% and ask with what certainty can we detect a change in the population sizes resulting from the altered and unaltered trajectories in 10 years. To do this we project the populations forward using the standard Dennis approach,

$$\ln\left(\frac{N_{t+t}}{N_t}\right) = \ln(\mathbf{m}t, \mathbf{s}^2 t) \quad [5.2]$$

Where N_t is the population size at time t , t is the time interval over which the projection is made and $N(\mathbf{m}t, \mathbf{s}^2 t)$ is a normally distributed random variable of mean $\mathbf{m}t$ and variance $\mathbf{s}^2 t$. To assess the likelihood of detecting a difference between the two stochastic population trajectories with and without an increase in λ , we calculate the separation of the resulting population size distributions assuming no sampling error. The natural logpopulation sizes are normally distributed random variables $N(\mathbf{m}t, \mathbf{s}^2 t)$ and $N(\mathbf{m}^+t, \mathbf{s}^2 t)$, where $\mathbf{m}^+ = \mathbf{m} + \ln(1.01)$. Thus, the probability of detecting a change in natural logpopulation size ($p < 0.05$, one-sided test) in 10 years due to a change in λ is the cumulative probability of the second distribution that lies to the right of $(\mathbf{m}t + 1.645\mathbf{s}t^{1/2})$.

For all Columbia River Basin stocks for which we have estimated \mathbf{m} and \mathbf{s}^2 we increased and decreased λ by 1% and 10% and assessed the probability of detecting this change in 10 years (Figure V-13, V-14). It is sobering to note that given a 1% increase in λ in only one of the stocks would we have a > 50% chance of seeing the effect of an action in only 10 years (Figure V-13). However, a 10% change λ is much more likely to be detected and 28/53 stocks had a > 50% of showing an effect (Figure V-14). In general, it would be easier to detect an effect in

steelhead populations than in chinook populations due to their more rapid rate of decline and lower variability in population size through time.

This projection of management actions hinges on several key assumptions, the consequences of which we are only beginning to address. For example, the hypothetical recovery action only influenced the population's growth rate, λ , and did so instantaneously. More likely, the effects of actions such as habitat restoration will manifest themselves as gradual changes in productivity. Since our metric of detectability integrates the change in λ over time, a gradually changing population trajectory would require more time to reach a given detectability threshold than an instantaneously effective one. Additionally, our ability to assess the efficacy of management actions is strictly dependent on the collection of unbiased estimates of population size. Counts of spawning salmonids are notoriously noisy, especially for steelhead and Spring/Summer Chinook that breed in small remote tributaries (Korman and Higgins 1997).

To explore the consequences of sampling error we ran a similar detectability analysis for all Columbia River Basin stocks (1% and 10% change in λ , assessed at $p < 0.05$ in 10 years), but in the presence of 10% measurement error. To simulate multiplicative non-systematic measurement error we augmented the variance of the "treatment" population but not that of the "control" population. The additional variance due to sampling error is equivalent to a lognormally distributed random multiplier with unit mean and variance such that the average sample residual is increased by 10%. Figures V-15, 16 show the probability of detecting a 1% and 10% change in λ , respectively, given 10% sampling error. Notice that there is a general decrease in the detection probability for those stocks with $P_{det} > 50\%$. While the loss of accuracy is small, it is not at all clear how a 10% increase in the variance of $\ln(N_{t+1}/N_t)$ relates to sampling errors in counts of spawners and spawner age distributions.

V.F. Achieving needed improvements in lambda

One great challenge for salmon science is to link specific actions to hypothesized changes in lambda. Management changes in the arenas of harvest, habitat, hatcheries, and hydropower as well as changes to ocean conditions associated with climatic events all have the potential to affect population growth rate. Unfortunately, few studies have specifically addressed the link between management actions and population growth rates at appropriate scales. Below (and in Section VI), we present a first step toward assessing the potential to achieve needed changes in population growth rates through management actions. Much more thorough work is clearly needed not only in regards to the effect of management actions and the distribution of characteristics across the landscape, but also with respect to ocean conditions, climate cycles and salmon productivity.

V.F.1. Hydropower corridor

Modifications to the hydropower corridor that have the potential to affect population growth rate for Snake River Chinook ESUs are discussed thoroughly in Section VI. Discussion of hydropower modifications relevant to Upper Columbia ESUs will be provided in an update of this document. In addition, we identify the number of dams present on the BPA GIS data-layer in each ESU in Table V-1 (methods in Section V.F.2.).

On average, there are about 27 dams present within ESU boundaries. To state the obvious, however, the potential to achieve improvements in population growth rate through modifications to dams and hydropower facilities vary tremendously from ESU to ESU, since the actual number of dams varies widely. In addition, dams not included within the ESU boundaries may still pose an obstacle during migration (both upstream and downstream) for some ESUs.

Table V-1. Total area, and total number and density of dams in each of the 12 ESU's.

<i>ESU Name</i>	<i>Area (km²)</i>	<i>Dams</i>	<i>Dams/1000 km²</i>
<i>Lower Columbia River Chinook</i>	16,264.91	38	2.34
<i>Snake River Fall Chinook</i>	35,531.93	14	0.39
<i>Snake River Spring/Summer Chinook</i>	58,158.62	30	0.52
<i>Upper Columbia River Spring Chinook</i>	18,146.36	14	0.77
<i>Upper Willamette River Chinook</i>	22,269.02	37	1.66
<i>Columbia River Chum</i>	10,988.11	17	1.55
<i>Snake River Sockeye</i>	1,322.81	0	0.00
<i>Lower Columbia River Steelhead</i>	13,128.37	37	2.82
<i>Middle Columbia River Steelhead</i>	69,452.20	43	0.62
<i>Snake River Basin Steelhead</i>	76,060.28	34	0.45
<i>Upper Columbia River Steelhead</i>	24,748.43	43	1.74
<i>Upper Willamette River Steelhead</i>	12,654.84	19	1.50
Mean -->	29,893.82	27.17	1.20
Maximum -->	76,060.28	43.00	2.82
Minimum -->	1,322.81	0.00	0.00

V.F.2. Habitats – Landscape level characteristics

V.F.2.a. Land use characterization

Land use and land cover differ widely across the 12 ESUs. To examine these characteristics broadly, we characterized the general landscape within each of the 12 Columbia River Basin ESU's on the basis of dam and anadromous fish production facility density, and land use and land cover (LULC, Tables V-1 - 5). We overlaid the boundaries for each ESU (NMFS 1999) with the three landscape geospatial datalayers using ESRI ARC/INFO. The geographic boundaries of individual ESU's only include freshwater areas where spawning and rearing occur. We characterized both the number and density of dams and production facilities (dams/production facilities/1000 km²) that occur within each ESU distribution. To examine the types of habitat within each ESU at a broad scale, we also quantified the percent of the total area in a range of land use and land cover habitat categories (34 categories total). We grouped the 34 second-level categories into broader land use or land cover units (Table V-3).

Table V-2. Summary table of geospatial data-layers used for landscape characterization for the 12 ESU's.

<i>Datalayer</i>	<i>Source</i>	<i>Type</i>	<i>Scale</i>	<i>Comments</i>
<i>Land Use and Land Cover (LULC)</i>	United States Geological Survey (USGS)	Polygon	1:250K	Land use and land cover generated using Anderson et al. (1976) protocols. Four or 16 ha minimum mapping unit (MMU). Late 1970's
<i>Dams</i>	Bonneville Power Administration (BPA)	Point	N/A	July, 1995
<i>Anadromous Fish Production Facilities</i>	Bonneville Power Administration (BPA)	Point	N/A	October, 1994

Table V-3. Second level categories used in each general land use or land cover category.

	Category	Second Level Categories	
L A N D U S E	Rangeland	Herbaceous Rangeland; Mixed Rangeland; Shrub and Brush Rangeland	
	Cropland	Cropland and Pasture; Orchard, Grove, Vineyard, Nursery; Other Agricultural Land	
	Urban	Mixed Urban or Built; Commercial and Services; Other Urban or Built-Up; Residential	
	Industrial	Industrial; Industrial and Commercial Complexes; Transportation, Communications, Utilities	
	Reservoirs	Reservoirs	
	Strip Mines	Strip Mines	
	Confined Feeding Operations	Confined Feeding Operations	
		Category	Second Level Categories
	L A N D C O V E R	Forest Land	Deciduous Forest Land; Evergreen Forest Land; Mixed Forest Land
	Alpine	Herbaceous Tundra; Shrub and Brush Tundra; Wet Tundra; Mixed Tundra; Glaciers; Perennial Snowfields	
Wetland	Forested Wetland; Non-Forested Wetland		
Bare	Bare Exposed Rock; Bare Ground; Beaches; Sandy Area (Non-Beach)		
Water Bodies	Lakes; Canals and Streams		
Transitional	Transitional Areas		

Table V-4. Land use characterization in each of the 12 ESU's.

<i>ESU Name</i>	<i>Rangeland</i>	<i>Cropland</i>	<i>Urban</i>	<i>Industrial</i>	<i>Reservoir</i>	<i>Strip Mines</i>	<i>Confined Feeding Ops</i>
<i>Lower Columbia River Chinook Snake River Fall Chinook</i>	0.9393	7.6030	6.6295	0.8379	0.3559	0.1057	0.0087
<i>Snake River Spring/Summer Chinook</i>	22.8950	20.3402	0.2567	0.0351	0.3390	0.0208	0.0001
<i>Upper Columbia River Spring Chinook</i>	26.9259	10.3894	0.1868	0.0547	0.2251	0.0397	0.0005
<i>Upper Willamette River Chinook</i>	21.2784	8.5429	0.5343	0.0686	0.4533	0.0403	0.0004
<i>Columbia River Chum</i>	0.4904	30.3431	4.5969	0.5025	0.2438	0.0920	0.0179
<i>Snake River Sockeye</i>	1.4172	8.7389	8.2674	1.2161	0.5990	0.1333	0.0125
<i>Lower Columbia River Steelhead</i>	15.9286	2.3542	0.2178	0.1009	0.0700	0.1084	0.0000
<i>Middle Columbia River Steelhead</i>	0.9280	7.6736	7.4844	0.9391	0.4345	0.1257	0.0052
<i>Snake River Basin Steelhead</i>	31.7046	25.9629	0.6706	0.2791	0.6612	0.0312	0.0042
<i>U. Columbia River Steelhead</i>	23.1428	11.9918	0.2015	0.0532	0.1755	0.0370	0.0004
<i>U. Willamette River Steelhead</i>	27.9963	18.8276	0.5191	0.2247	0.9527	0.0517	0.0035
<i>Mean --></i>	0.2012	39.8750	4.8634	0.4885	0.0688	0.0950	0.0283
<i>Maximum --></i>	14.4873	16.0535	2.8690	0.4000	0.3816	0.0734	0.0068
<i>Minimum --></i>	31.7046	39.8750	8.2674	1.2161	0.9527	0.1333	0.0283
	0.2012	2.3542	0.1868	0.0351	0.0688	0.0208	0.0000

Table V-5. Land cover characterization in each of the 12 ESU's.

<i>ESU Name</i>	<i>Forest Land</i>	<i>Alpine</i>	<i>Wetland</i>	<i>Bare</i>	<i>Water Bodies</i>	<i>Transitional</i>
<i>Lower Columbia River Chinook Snake River Fall Chinook Snake River Spring/Summer Chinook</i>	80.1254	0.1545	0.6786	0.2862	2.2357	0.0385
<i>Upper Columbia River Spring Chinook</i>	54.9592	0.0975	0.0157	0.8642	0.1353	0.0180
<i>Upper Willamette River Chinook</i>	59.7899	1.1615	0.0613	1.0262	0.0919	0.0184
<i>Columbia River Chum Snake River Sockeye</i>	65.6111	1.8928	0.3916	0.6525	0.5130	0.0204
<i>Lower Columbia River Steelhead</i>	62.9377	0.1063	0.3482	0.0299	0.2003	0.0800
<i>Middle Columbia River Steelhead</i>	75.0198	0.0434	0.9949	0.2521	3.2621	0.0421
<i>Snake River Basin Steelhead</i>	65.2998	8.6963	0.6905	5.2012	1.2797	0.0054
<i>U. Columbia River Steelhead</i>	80.0688	0.1914	0.4189	0.2965	1.3996	0.0332
<i>Upper Willamette River Steelhead</i>	40.3472	0.0570	0.1647	0.0098	0.0593	0.0411
<i>Mean --></i>	62.1189	0.9033	0.0513	1.1715	0.1139	0.0157
<i>Maximum --></i>	48.6822	1.3878	0.2986	0.4882	0.4163	0.1508
<i>Minimum --></i>	53.6682	0.0000	0.3728	0.0018	0.2127	0.1184
	62.3857	1.2243	0.3739	0.8567	0.8266	0.0485
	80.1254	8.6963	0.9949	5.2012	3.2621	0.1508
	40.3472	0.0000	0.0157	0.0018	0.0593	0.0054

Some ESUs had high percentages of rangeland (Upper Columbia and Snake), cropland (Upper Willamette), and urbanization (Lower Columbia, Upper Willamette; Tables V-4 & 5), all land uses that can substantially affect freshwater habitats. Although percentages of area attributable to industry, reservoirs, strip mines, feeding operations, bare cover and wetlands are small, these land uses/covers can also have notable impacts on freshwater habitats.

The landscape characterization is intended only as a qualitative reference. The characterization cannot be used for quantitative spatial analyses because: the spatial scale of the geospatial datalayers is too coarse; the characterization is based on static data; and the LULC datalayer is too old. The scale over which Pacific salmon population dynamics and biology occurs, ranges from the reach (a few tens of meters) all the way up to the sub-basin (thousands of square

kilometers). In addition, habitat/fish interactions vary considerably with species, stock, and sub-basin biogeography. The complexity of these interactions is not captured in our characterization. Finally, some of the ESU's spatially overlap with each other, violating the assumption of independence required for doing statistically rigorous hypothesis testing.

V.F.2.b. Preliminary studies linking habitat characteristics and productivity

Two studies conducted at the Northwest Fisheries Science Center provide some evidence for opportunities to improve productivity through changes in freshwater habitat characteristics, although we emphasize strongly that until the journal peer review process tests these analyses, we consider these results to be tentative.

The first study by Regetz (in review), investigated correlations between recruits per spawner of 22 Columbia basin chinook stocks to the following 10 landscape-scale habitat variables: (1) urban/built land cover, (2) agriculture/rangeland land cover, (3) forested land cover, (4) distribution of grazing allotments, (5) the number of mining operations per square kilometer of total subwatershed area, (6) the summed length of EPA 303(d)-listed streams per total streamlength within the subwatersheds ("EPA 303(d)" refers to a section of the Federal Water Pollution Control Act requiring states to list all waterbodies for which current pollution controls are insufficient to meet water quality standards), (7) master watershed sensitivity index (MWSI), (8) riparian integrity, (9) disturbance recovery potential, and (10) erosion potential. Three of these environmental variables: percent of land classified as urban or "built-up," proportion of stream length failing to meet water quality standards, and an index of the ability of streams to recover from sediment flow events accounted for over 60% of the variation in mean salmon recruitment. Interestingly, within the areas corresponding to the 22 index stocks, the percent of urban/built land cover was quite small (<1%) even in the "worst" locations, which suggests that stocks are sensitive to even minor variations in urban development. The magnitude of the difference in productivity between the best and worst stocks in these cases is large enough to be relevant to managers. For example, the difference between the stocks found in the areas with the best water quality and those in the worst is nearly two-fold (using the median R/S since 1980 for each site).

Furthermore, it appears that these landscape attributes may limit the maximum recruitment rates of salmon. Plots of arithmetic mean and maximum R/S against numerous habitat attributes often share a similar "wedge" pattern, with most or all data points falling below a diagonal line from the upper left to the lower right (Figure V-17). Productivity can clearly be low even when habitat quality (measured at the landscape level) seems to be very high. However, in all cases the most productive populations occur only where landscape-level habitat conditions are good, whereas index areas characterized by low quality habitat are almost invariably associated with lowered stock productivity. This pattern suggests that some subwatershed scale habitat attributes might act as limiting factors. In other words, although good habitat conditions do not necessarily correspond to high salmon productivity (because myriad other factors can still depress populations), diminishing habitat quality leads to lower salmon productivity.

The second study, conducted by the Watershed Processes Program (WPP) at the Northwest Fisheries Science Center, consists of spatial analyses on the interaction between freshwater habitat and salmon production, as inferred from spawner prevalence. The goal of their research

is to identify key relationships between habitat type and condition and productivity. From these relationships, they hope to be able to predict which areas in a watershed have the best potential for restoration or protection.

The WPP first tested their methodology for chinook salmon (*O. tshawytscha*) in the Salmon River Basin, Idaho, which is in the Snake River Basin/High Desert Ecoregion. They are currently running similar analyses in the Snohomish River Basin, WA (coho, *O. kisutch*), and in the Willamette River Basin, OR (chinook and steelhead, *O. mykiss*). For the Salmon River Basin, they compared time series of Spring/Summer Chinook salmon redd counts (1960 to 1998) from 24 locations in the watershed to a suite of spatially-explicit habitat variables describing both landform and land use. Abundance was related to geology (granitic, sedimentary, surficial deposits, and carbonates and shale); hill and channel slope; climate (mean, minimum, and maximum annual temperature and mean cumulative annual precipitation); water quality (EPA 303(d)); land use type (rangeland, agriculture, water diversions); vegetation (forested, wetland); and bank erosion and sediment hazard potential. The area of influence (AOI) for these habitat variables was characterized at the watershed (total area flowing through and upslope of any given site) and reach (area within a 500 m buffer of any given site) scales. This dual scale approach facilitates a more accurate estimate of the relative influence of habitat variables. For example, the presence of wetlands within a given watershed AOI may have little significance to salmon abundance if they are not contiguous to the main channel. Data analysis techniques included a combination of classification and regression tree (CART) analysis and hierarchical linear models (HLM). The CART analysis was completed first as a “data mining” technique. Statistical significance of relationships between redd density and habitat attributes was tested using a randomization test based on the HLM approach. The HLM was also used to generate a multivariate salmon abundance model for the entire basin.

Classification tree analysis examines all variables (predictors) one at a time (similar to forward selection regression), creates a split in the tree that divides dependent variable classes into two groups (nodes), each of which is more pure than the original, based on the Gini index (Breiman et al. 1984). The technique is powerful in that it can accommodate categorical and ordinal predictors; is free from distribution requirements and assumptions; and facilitates statistical significance testing via cross validation of numerous variables.

The HLM approach facilitates detection of consistent relationships between fish productivity and habitat characteristics over time. The approach has two steps. In the first step, fish productivity across index reaches in one year is modeled as a function of a particular habitat characteristic or set of habitat characteristics. In the second step, regression parameters from the analyses for each year are tested for significant patterns over time. Final significance levels are assessed using randomization tests to correct for spatial and temporal correlation between observations. As an initial method for understanding the data, the Watershed Processes Program researchers conducted univariate analyses, examining the individual effect of each potential predictor variable on salmon productivity. The same technique was then used to develop a multivariate model with the goal of identifying suites of significant predictor variables.

There are consistent differences among spawning sites with respect to redd density over time. Certain locations consistently support greater densities of redds compared to other sites. Chinook salmon abundance is positively correlated with granitic geology, cumulative mean annual precipitation; ambient air temperature; total area of hill slope less than 1.5%; and total area of certain riparian vegetation (graminoid or forb; shrub dominated; mixed). In contrast, abundance

is negatively correlated with total area of rangeland, sediment hazard, and water diversions. As was the case with the Regetz research, the WPP research found “wedge” shaped patterns in plots of some habitat variables against salmon abundance.

Based on preliminary results, the WPP researchers expect that the methodology will be a useful tool for creating a coarse, first level assessment of the conservation or restoration potential of habitat areas within the basin. Using the multivariate productivity model, we should be able to predict potential salmon abundance in areas lacking fish data, based on the physical attributes and land use patterns of river reach and its watershed. This approach may also enable prediction of population response to future alterations in habitat quality.

It is important to emphasize that this coarse scale methodology identifies where restoration or conservation activities might be most effective. It does not identify exactly what needs to be done to restore or enhance salmon abundance at a given location. Detailed, on the ground, assessments of habitat conditions and landscape processes are critical. Traditional approaches to habitat management focus on repairing or augmenting specific habitat conditions, rather than on restoring landscape processes that form and sustain habitats. Habitat modifications such as placing log structures or protecting stream banks often fail to create expected habitat conditions because they are constructed without consideration of the physical causes of habitat degradation (Frissell and Nawa 1992, Kauffman et al. 1997). Additionally, neglecting the biological context of projects often results in conditions that do not address factors limiting production or that help one species but harm others (Reeves et al. 1991). Many authors have suggested that a more holistic approach to managing salmon habitats would help to avoid these problems (e.g., Doppelt et al. 1993, Reeves et al. 1995, Beechie and Bolton 1999).

In order to successfully restore salmon habitats we first need to identify the causes of habitat degradation (Cairns 1990, Frissell and Nawa 1992, Beechie et al. 1996). Causes of habitat degradation are related to habitat conditions by the processes that form and sustain habitats, such as the supply and movement of sediment from hillslopes, or woody debris recruitment and shading of the stream from the riparian forests (Figure V-18). That is, land use practices alter habitat-forming processes, which in turn degrade salmon habitats. We should also recognize that habitat-forming processes are dynamic, even in the natural environment. Many processes that create salmon habitat operate on time scales of decades or longer (e.g., channel migration and the formation of off-channel habitats). Interrupting these processes (e.g., through bank stabilization) can lead to loss of salmon habitat over the long term (Beechie and Bolton 1999). Successful restoration requires that we understand how different species of salmon utilize different parts of a stream network, and the time periods during which those habitats are occupied (e.g., Lichatowich et al. 1995). Moreover, individual stocks are adapted to local environmental conditions (Ricker 1972, Miller and Brannon 1982, Healey 1991), which means that generic habitat targets should be avoided. A final limitation of most habitat analyses is the fact that the “variables” recorded in our GIS databases may do a poor job capturing how the subwatersheds will respond to disturbances, especially major floods or landslides. Such disturbances have been a common feature of salmon evolutionary history, and the persistence of salmonid species clearly requires survival through and recovery from such events (Bisson et al 1997).

V.F.3. Hatcheries – Distribution and preliminary analyses

V.F.3.a. Distribution of Hatcheries within ESUs

In Table V-6 we summarize the number and density of anadromous fish production facilities within ESU boundaries. While the average ESU has approximately 15 production facilities within its boundaries, again there will be widely varying opportunities to affect population growth rate through hatchery actions. Potential ecological and genetic effects of hatchery fish on wild populations have been well described (NMFS 1999). However, the rates and occurrence of these effects has not been well quantified. Therefore, the potential to achieve changes will depend on several factors: where effects occur (e.g., freshwater habitat or estuary), the mechanisms by which they occur (e.g., predation, competition or genetic contamination), and the rates at which they occur (e.g., the rate at which hatchery and wild fish breed, and the reproductive success of hatchery fish).

In total, nearly 100 facilities in the Columbia River Basin release approximately 150 million smolts annually. Production by hatcheries is presently capped and hatchery operation goals and principles are undergoing a congressionally mandated review.

V.F.3.b. Preliminary analyses

The use of hatcheries to augment harvest is based on the assumptions that (1) the freshwater environment limits natural production; (2) carrying capacity of the ocean exceeds the production of natural populations; and most importantly, (3) hatchery production will not negatively impact natural populations. The degree to which production hatcheries impact population growth rates of natural fish is largely unknown. However, a preliminary, unpublished analysis of smolt to adult returns from 1975 to the present suggests that hatchery production can dramatically impact survival of wild fish (Figure V-19). During years of poor ocean conditions (defined here as positive values of the El Nino – Southern Oscillation Index) survival rates of wild fish varied inversely with the number of hatchery fish entering the ocean with a four-fold greater survival when hatchery releases were lowest compared to when they were highest. In contrast, this effect was absent when ocean conditions were better (negative El Nino – Southern Oscillation Index values). The interaction of ocean conditions with hatchery releases suggests that there may be benefits for wild stocks if management were to modify hatchery production during periods likely to induce higher ocean mortality. Clearly this hypothesis warrants further study.

Table V-6. Total area, and total number and density of anadromous fish production facilities, in each of the 12 ESU's.

<i>ESU Name</i>	<i>Area (km²)</i>	<i>Production Facilities</i>	<i>PF/1000 km²</i>
<i>Lower Columbia River Chinook</i>	16,264.91	35	2.15
<i>Snake River Fall Chinook</i>	35,531.93	12	0.34
<i>Snake River Spring/Summer Chinook</i>	58,158.62	15	0.26
<i>Upper Columbia River Spring Chinook</i>	18,146.36	11	0.61
<i>Upper Willamette River Chinook</i>	22,269.02	9	0.40
<i>Columbia River Chum</i>	10,988.11	33	3.00
<i>Snake River Sockeye</i>	1,322.81	1	0.76
<i>Lower Columbia River Steelhead</i>	13,128.37	23	1.75
<i>Middle Columbia River Steelhead</i>	69,452.20	9	0.13
<i>Snake River Basin Steelhead</i>	76,060.28	20	0.26
<i>Upper Columbia River Steelhead</i>	24,748.43	13	0.53
<i>Upper Willamette River Steelhead</i>	12,654.84	4	0.32
Mean -->	29,893.82	15.42	0.88
Maximum -->	76,060.28	35.00	3.00
Minimum -->	1,322.81	1.00	0.13

V.F.2. Sensitivity of Annual Population Growth Rate to Changes in Harvest

We determined total (ocean and in-river) exploitation rate for each ESU using estimates from the Pacific Salmon Commission, ODFW, WDFW, and IDFG, as well as PATH run-reconstructions for Snake River, and the QAR process for the Upper Columbia River. Because the bulk of the spawner counts we used were restricted to the 1980s and early 1990s, we used average harvest rates during this time period. However, in the mid to late 1990s, Endangered Species Act concerns resulted in the substantial reduction of harvest rates.

Harvest rates were expressed as fraction of recruits to the spawning grounds removed due to harvest. This puts all harvest, be it in the ocean or stream or on different age classes, in the same currency. The relationship between the observed lambda and the potential productivity (R/S) is then:

$$\mathbf{I} = \left((1-h) * \frac{R}{S} \right)^{\sqrt[\text{generationtime}]{} }$$

From this relationship, the lambda, \mathbf{I}_{new} , expected if harvest is reduced from level h to some new level (denoted d) is given by:

$$\mathbf{I}_{new} = \mathbf{I}_{prior} \left(\frac{1-d}{1-h} \right)^{\sqrt[\text{generationtime}]{} } \quad [5.3]$$

where \mathbf{I}_{prior} is the lambda estimate during the period of time subject to harvest rates, h .

Because both the prior harvest rates and generation time influence the effect of altered harvest rates, ESUs vary in their response to changes in those rates. Thus, harvest reductions or moratoria will have the greatest potential for increasing population growth rates in those ESUs with short generation times and high harvest rates (Figure V-20).

If harvest were eliminated entirely, increases from 20 to 30% in lambda would be expected in Lower Columbia Chinook, Upper Willamette Chinook, and Snake River Fall Chinook (Figure V-20, Table V-8). In these ESUs rates of population growth increase from 0.95 to 1.24, 1.01 to 1.28 and 0.93 to 1.15, respectively (Figure V-20, Table V-7, 8). Some steelhead ESUs appear likely to also potentially benefit substantially from harvest moratoria; however steelhead have such low lambdas that even a total cessation of harvest only increases the population growth rate of two of these ESUs above 1.0 (Figure V-20, Table V-7, 8). As mentioned before, harvest rates in some cases have already been reduced due to ESA concerns. It should also be kept in mind that this is a gross analysis, at the ESU level. In addition, the base lambdas used for this analysis assume that hatchery fish have a reproductive success of zero. If hatchery fish reproduce at all, the initial lambda will be lower than these presented here, making the lambda that can be achieved also lower.

Table V-7. Predicted median annual population growth rate with given harvest rates.

	λ	New lambda under different harvest rate scenarios													
		Harvest rate Mean 1980s to early 1990s	Return Time	55%	50%	45%	40%	35%	30%	25%	20%	15%	10%	5%	0%
Chinook															
L. Columbia	0.943	0.58	3.29	0.963	0.994	1.024	1.051	1.077	1.101	1.125	1.147	1.168	1.189	1.209	1.227
U. Columbia Spr	0.876	0.09	4.25	0.742	0.761	0.778	0.794	0.810	0.824	0.837	0.850	0.862	0.874	0.885	0.896
Snake R. Spr/Sum	0.967	0.06	4.73	0.828	0.846	0.863	0.879	0.894	0.909	0.922	0.935	0.947	0.958	0.969	0.980
Snake R. Fall	0.933	0.53	3.67	0.922	0.949	0.974	0.997	1.019	1.040	1.060	1.079	1.097	1.114	1.130	1.146
U. Willamette	0.906	0.65	4.47	0.958	0.981	1.002	1.022	1.040	1.058	1.074	1.090	1.105	1.119	1.132	1.145
Chum															
Columbia River	1.016	0.44	3.61	0.956	0.984	1.011	1.035	1.059	1.081	1.101	1.121	1.140	1.159	1.176	1.193
Steelhead															
L. Columbia	0.952	0.31	4.47	0.865	0.886	0.905	0.922	0.939	0.955	0.970	0.984	0.997	1.010	1.022	1.034
Mid Columbia	0.893	0.04	5.17	0.772	0.787	0.802	0.816	0.828	0.840	0.852	0.862	0.873	0.882	0.892	0.901
U. Columbia	0.860	0.28	5.17	0.785	0.801	0.816	0.830	0.843	0.855	0.866	0.877	0.888	0.898	0.907	0.916
Snake River	0.969	0.35	3.78	0.879	0.904	0.927	0.949	0.969	0.988	1.006	1.024	1.040	1.056	1.071	1.086
U. Willamette	0.879	0.2	5.17	0.786	0.803	0.818	0.831	0.844	0.857	0.868	0.879	0.889	0.899	0.909	0.918

Table V-8. Percent change in lambda with given harvest rates.

	λ	Harvest rate 1980s to early 1990s	Mean Return Time	Percent change in lambda under different harvest rate scenarios											
				55%	50%	45%	40%	35%	30%	25%	20%	15%	10%	5%	0%
Chinook															
L. Columbia Chinook	0.95	0.58	3.29	2.119	5.442	8.542	11.451	14.195	16.797	19.272	21.635	23.897	26.068	28.157	30.171
U. Columbia Spr Chinook	0.87	0.09	4.25	-15.269	-13.143	-11.173	-9.335	-7.612	-5.987	-4.448	-2.986	-1.592	-0.260	1.017	2.244
Snake R. Spr/Sum Chinook	0.94	0.06	4.73	-14.423	-12.495	-10.714	-9.056	-7.504	-6.043	-4.662	-3.352	-2.106	-0.915	0.224	1.317
Snake R. Fall Chinook	0.93	0.53	3.67	-1.179	1.702	4.382	6.889	9.249	11.480	13.598	15.616	17.544	19.392	21.166	22.873
U. Willamette Chinook	1.01	0.65	4.47	5.781	8.303	10.636	12.809	14.847	16.766	18.581	20.305	21.947	23.516	25.018	26.461
Steelhead															
L. Columbia Winter Steelhead	0.98	0.31	4.47	-9.121	-6.953	-4.948	-3.079	-1.327	0.322	1.883	3.365	4.777	6.126	7.418	8.658
Mid Columbia Steelhead	0.87	0.28	5.17	-8.692	-6.811	-5.077	-3.466	-1.959	-0.544	0.793	2.059	3.263	4.411	5.509	6.562
U. Columbia Steelhead	0.90	0.35	3.78	-9.261	-6.699	-4.319	-2.093	0.000	1.978	3.854	5.641	7.347	8.981	10.549	12.058
Snake R. Aggregate Steelhead	0.90	0.2	5.17	-10.536	-8.693	-6.994	-5.415	-3.938	-2.551	-1.241	0.000	1.180	2.305	3.381	4.412
U. Willamette Steelhead	0.91	0.21	4.08	-12.885	-10.606	-8.493	-6.520	-4.668	-2.921	-1.265	0.309	1.810	3.247	4.624	5.948

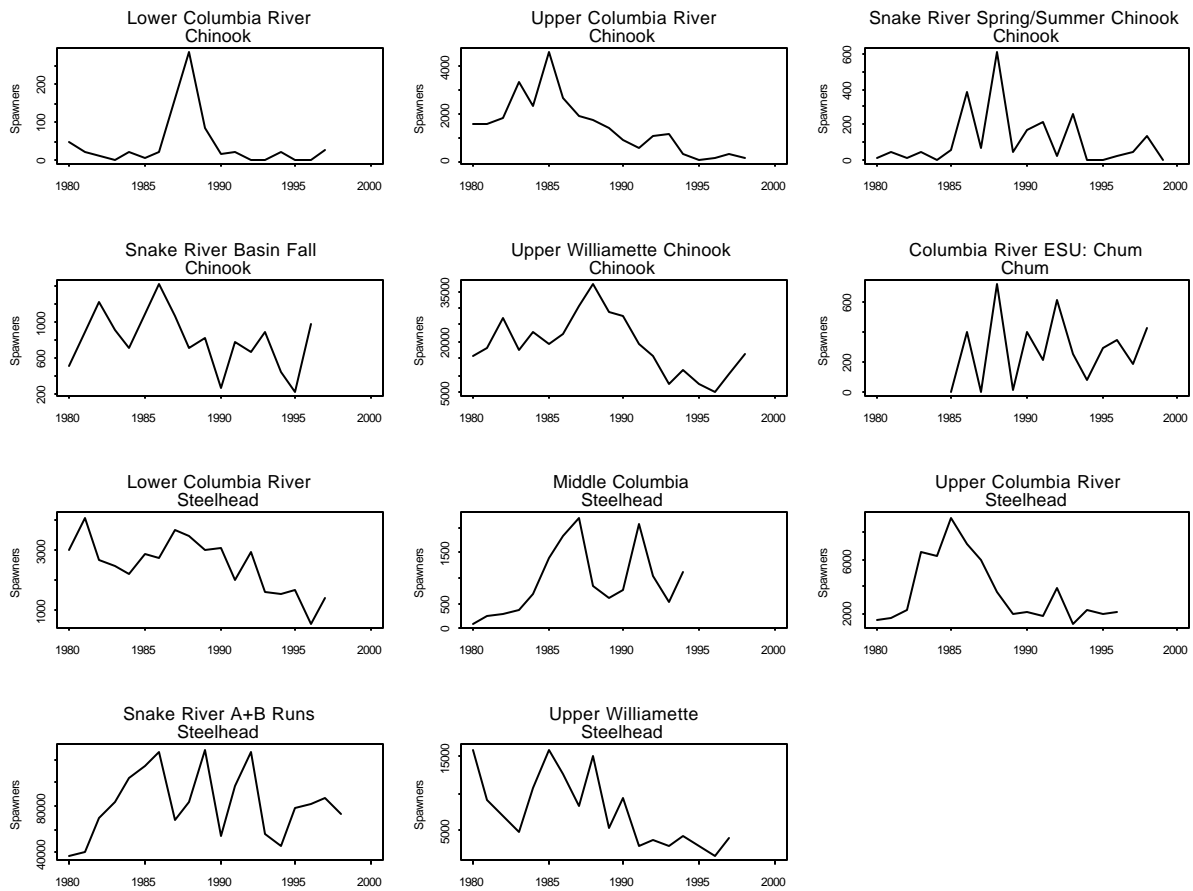


Figure V-1. Raw spawner counts used for the analyses. Counts include hatchery fish that spawn in the wild. See Appendix C for the numbers.

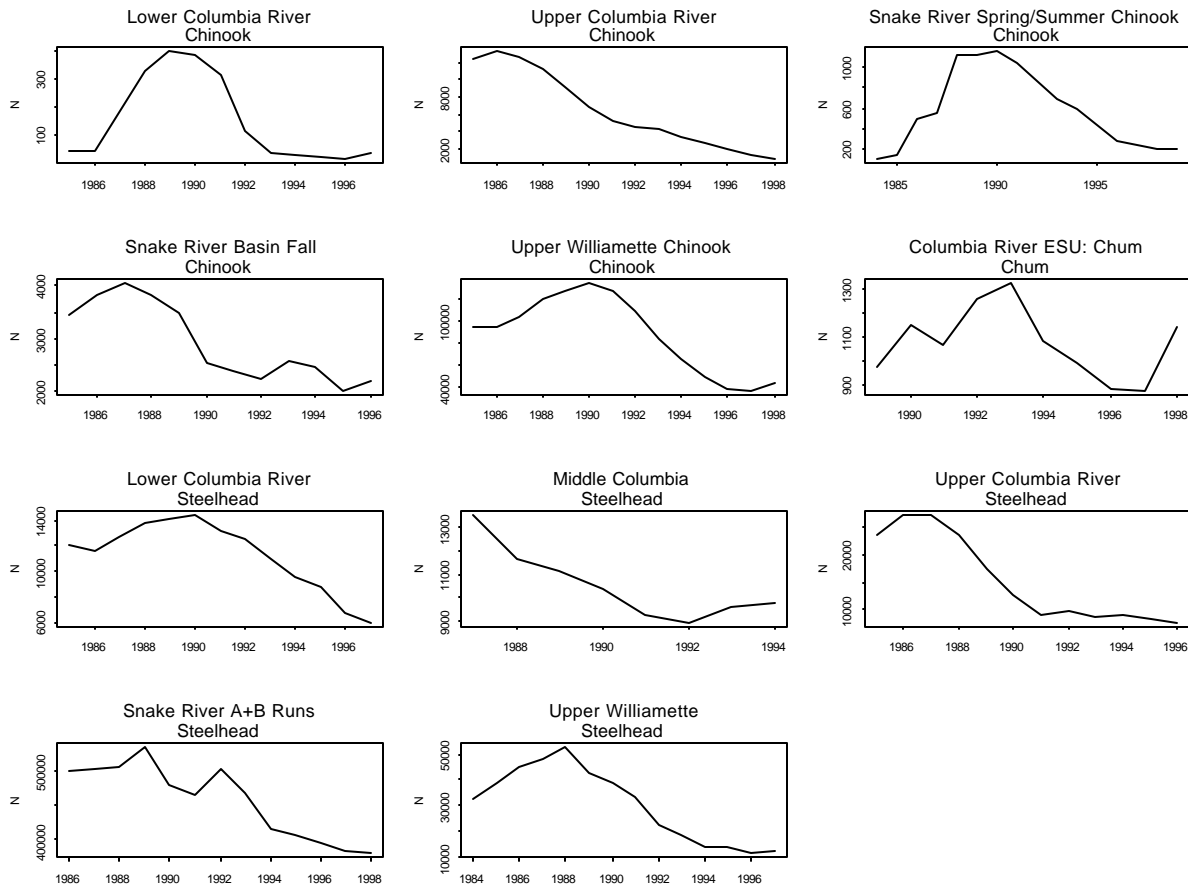


Figure V-2. Weighted running sums of spawner counts used in the analyses. As described in the text, this is an estimate of the living fish that are current spawners or that will survive to be future spawners (i.e., the total population size at time t which we cannot observe). See Appendix C for the numbers.

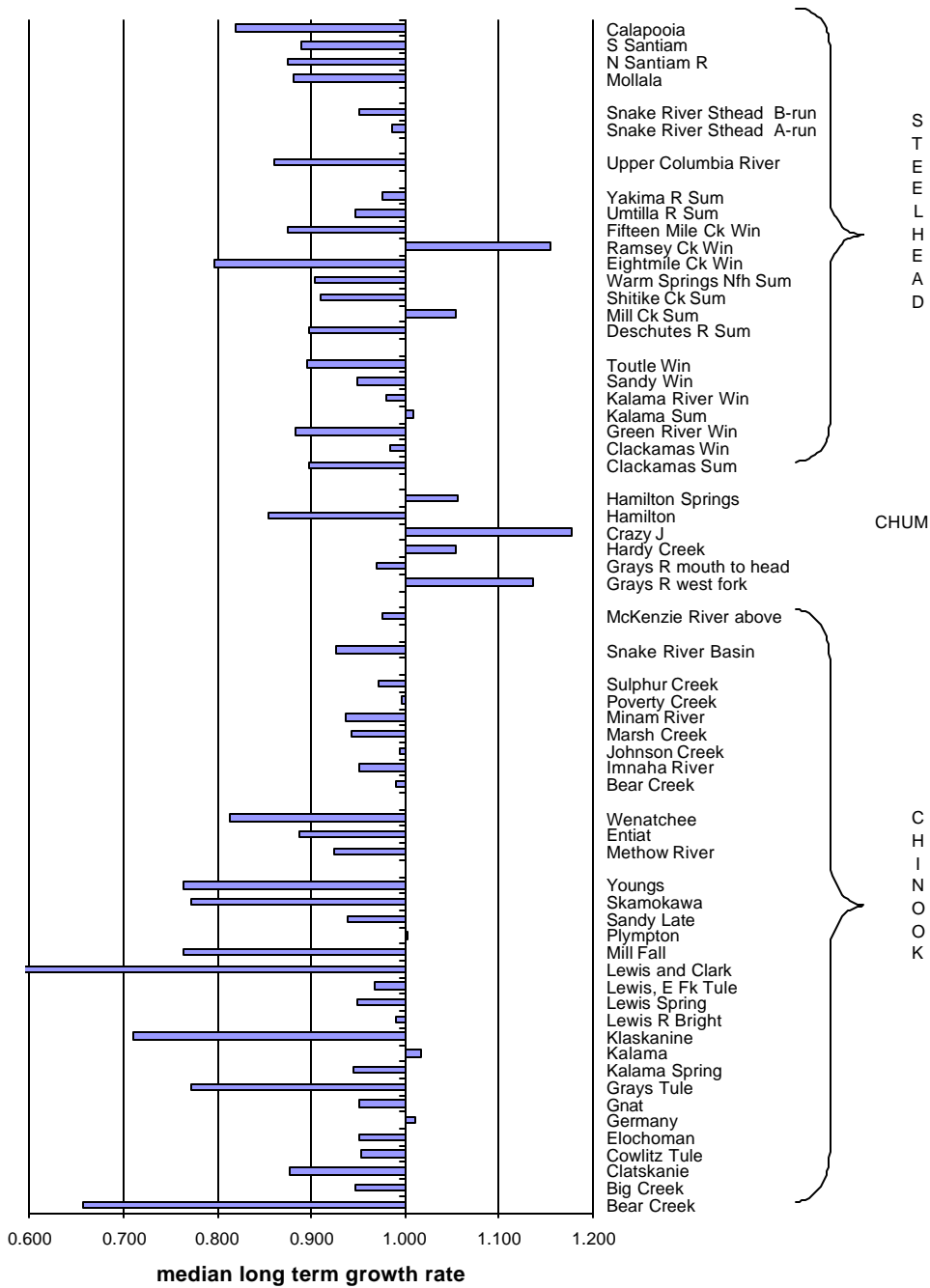


Figure V-3. Estimated lambda, median long-term growth rate, at the stock level. No correction for hatchery fish (this is approximately equal a no hatchery fish reproduction assumption).

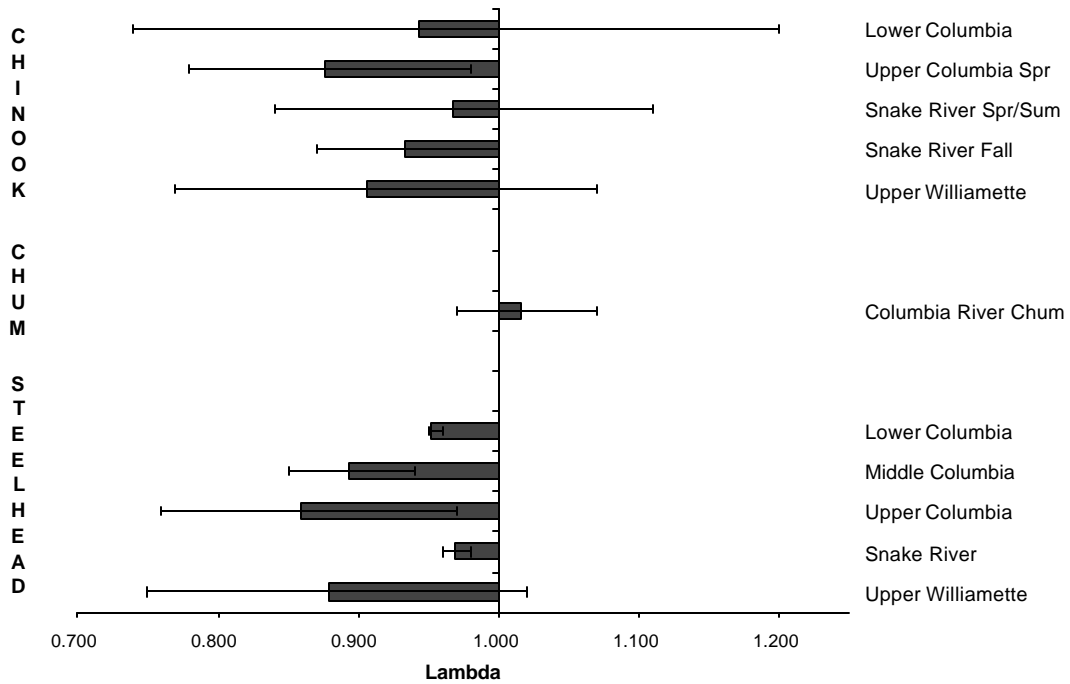


Figure V-4. Estimated lambda at the ESU level. The error bars indicated the confidence that the estimated lambda reflects the long-term rate of decline (or increase) rather than a short-term trend. ESUs with large error bars indicate ESUs with high variability and short data sets. Note that the error bars do not reflect uncertainty due to sampling error – and thus our estimate of the true short-term rate of decline.

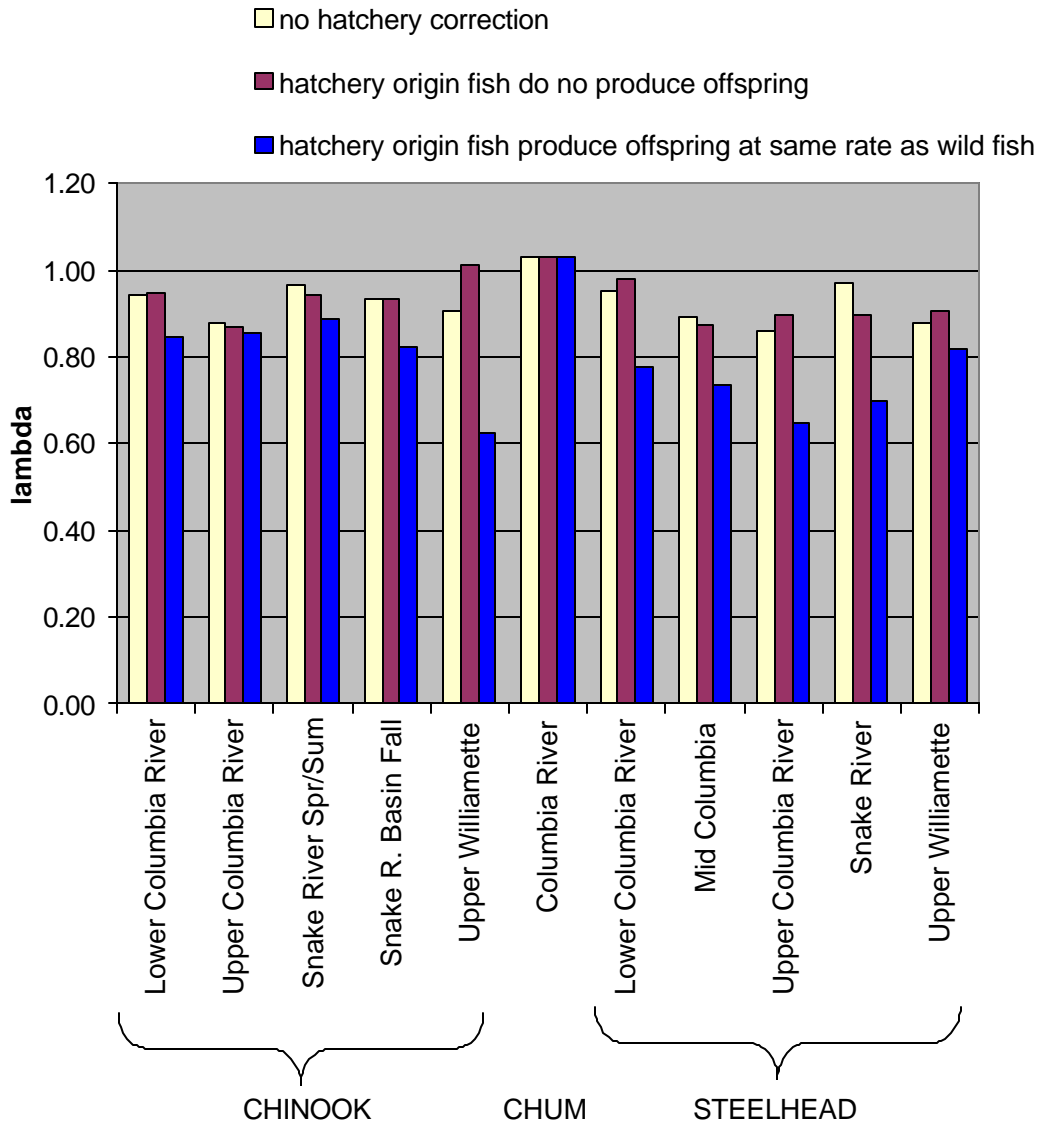


Figure V-5. Estimates of the rate of population decline/growth for wild fish that accounts for the presence of hatchery fish in spawner counts. The lambda estimates with no hatchery correction are shown in the light left bars for reference. This estimate will be close to the in-stream lambda (which we are trying to estimate) if hatchery fraction is not changing appreciably and hatchery fish do not reproduce. Compare the left light bars to the light gray middle bars which is the estimate with hatchery fish removed from the count and assuming that they did not produce offspring. If the hatchery fraction is decreasing (Upper Willamette chinook) or increasing (Snake River Steelhead) the estimate without removing the hatchery fish will be correspondingly low or high. The rightmost dark bars show the lambda estimates assuming that hatchery fish reproduce at the same rate as wild fish. Note that the potential influence of hatchery fish is greater for steelhead than for chinook ESUs due to generally higher fractions of hatchery fish in the spawner counts. See section IV.F for a description of methods.

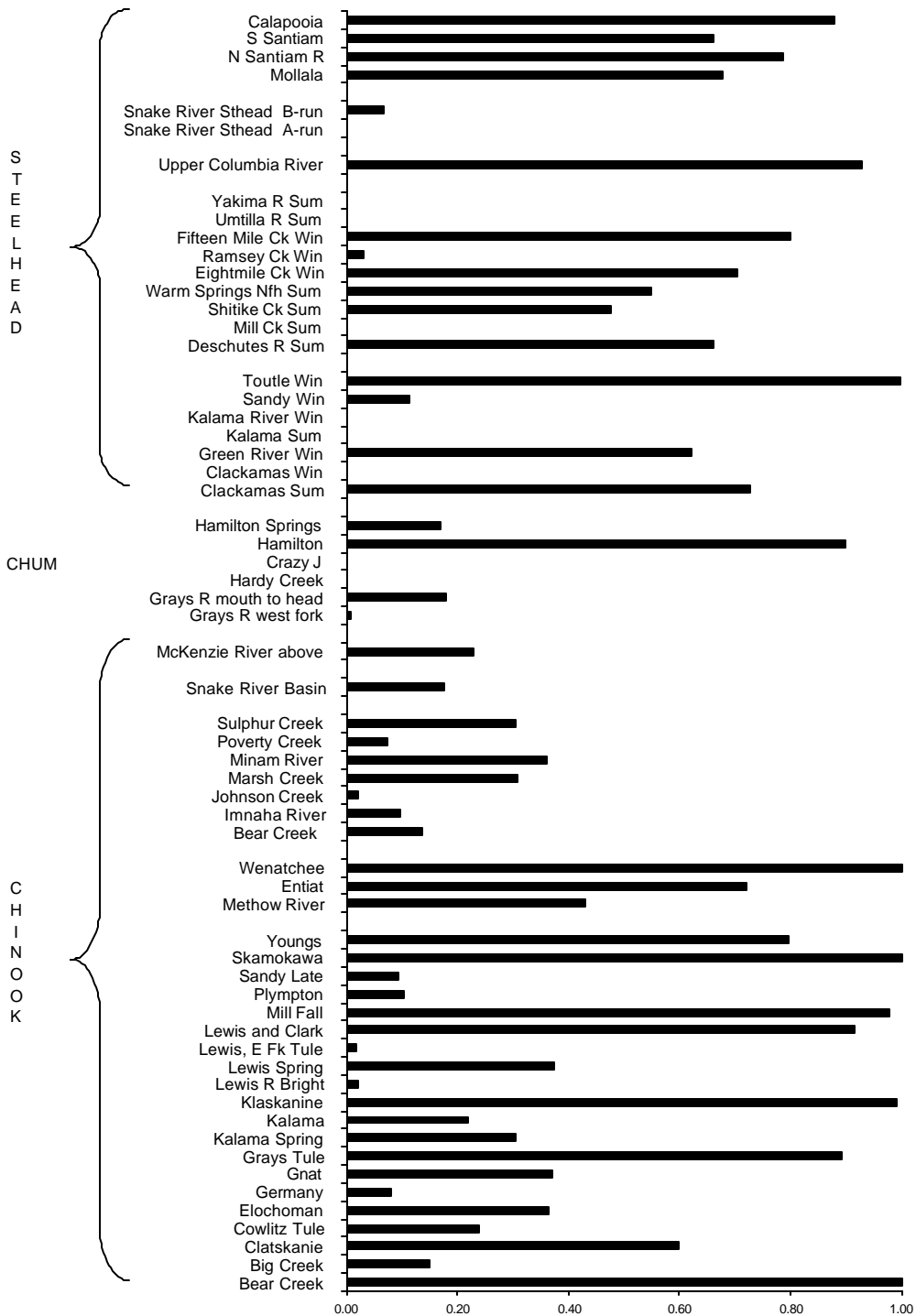


Figure V-6. Probability that stock-level is 90% below current levels in 24 years. Estimates of probability of extinction are shown in the appendices for the subset of stocks where an estimate of population size was possible with the available count data.

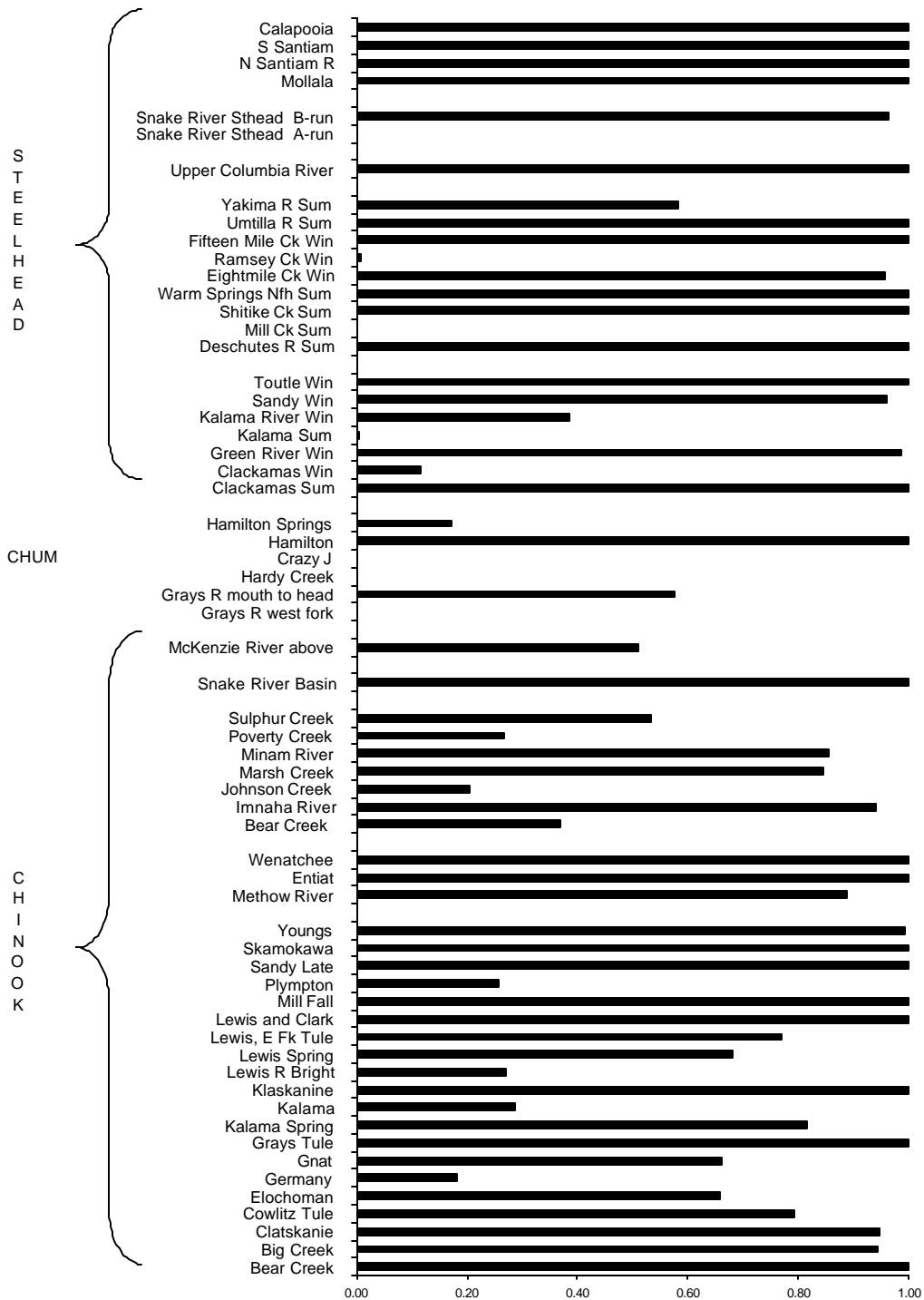


Figure V-7. Probability that stock-level is 90% below current levels in 100 years. Estimates of probability of extinction are shown in the appendices for the subset of stocks where an estimate of population size was possible with the available count data.

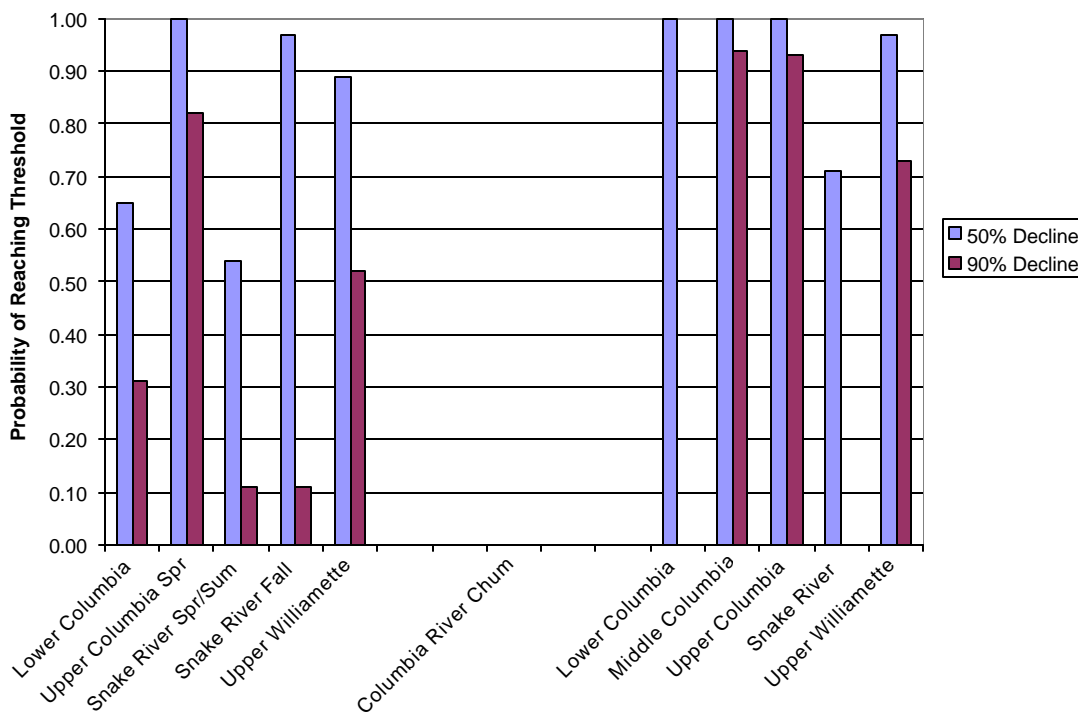


Figure V-8. Probability that ESU is 50 or 90% below current levels at 24 years in the future. Note that this is not the probability that the ESU has dipped 50% or 90% below current levels within 24 years. This probability is better reflected by the most likely time to first hit a 50 or 90% decline. Note that ESUs with a positive lambda may have a short most likely time to first hit a 50 or 90% decline but a small probability that the stock is 50 or 90% lower than current abundance at year 24.

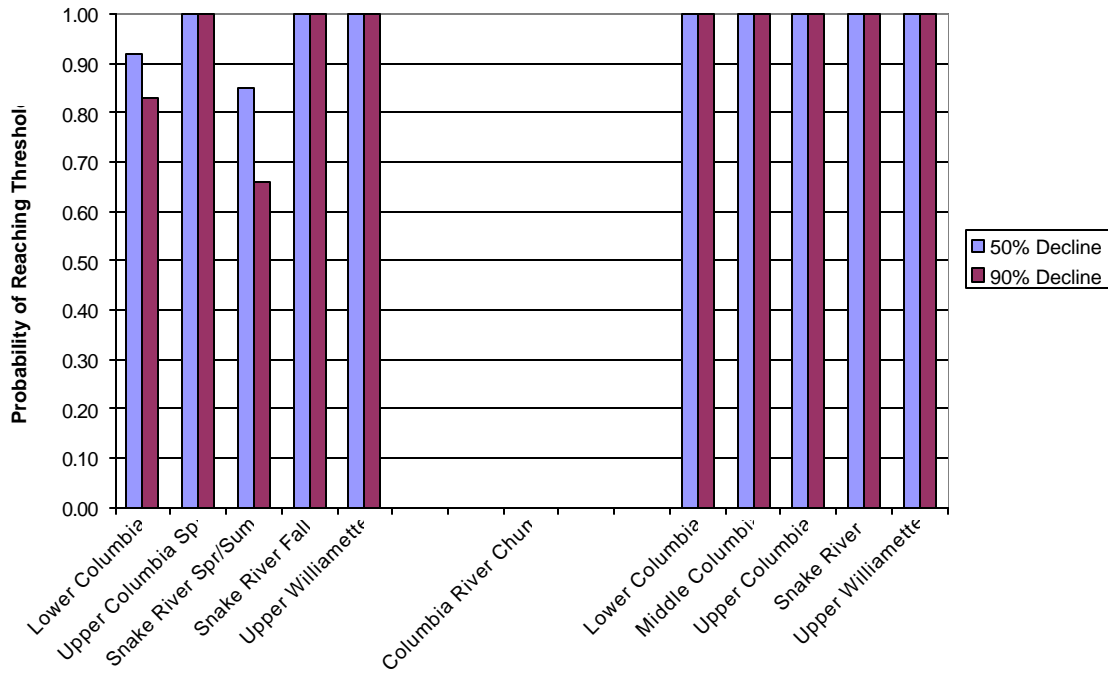


Figure V-9. Probability that ESU will be 50 or 90% below current levels 100 years in the future. Note that this is not the probability that the ESU has dipped 50% or 90% below current levels within 100 years (and recovered since then). This probability is better reflected by the most likely time to first hit a 50 or 90% decline. Note that ESUs with a positive lambda may have a short most likely time to first hit a 50 or 90% decline but a small probability that the stock is still 50 or 90% declined in 100 years.

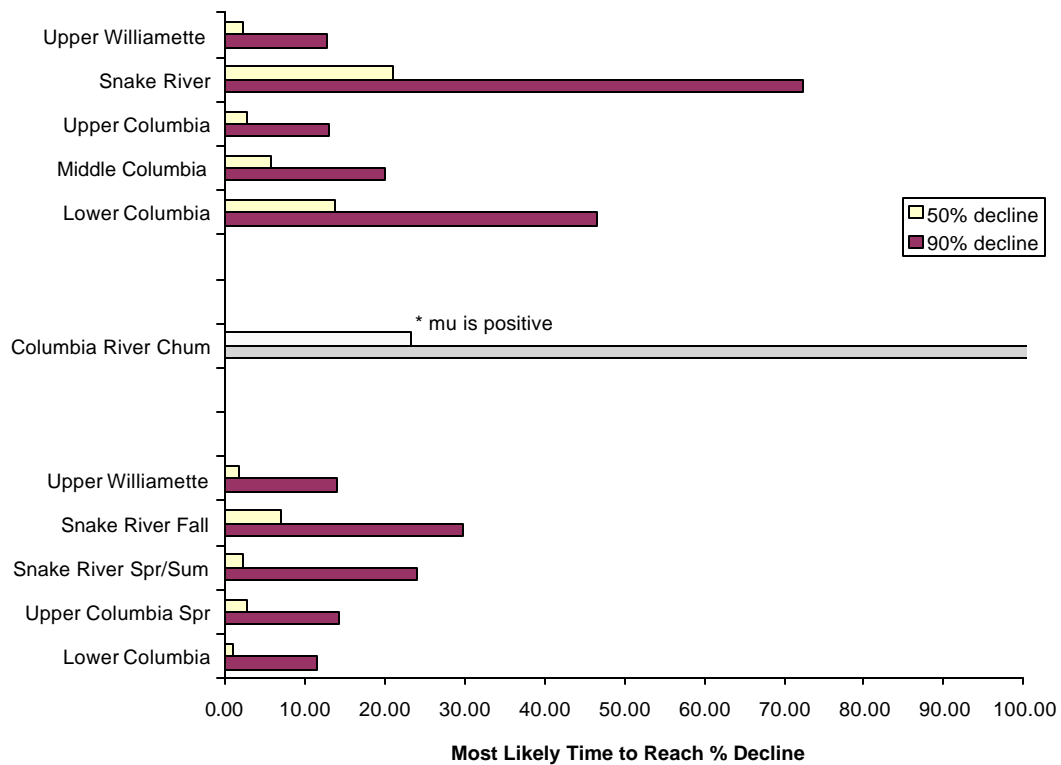


Figure V-10. Most likely time to reach a 50% or 90% decline in the total population. This is the mode of the distribution of times to reach these declines and thus will tend to be lower than the mean time or median time. Note that the most likely time to reach these levels and the probability that the stock is 50% or 90% declined at year 24 or 100 are very different statistics. The first is the mean time to FIRST reach a 50% or 90% declined level while the second is the probability that at year 24 or 100 the stock is 50% or 90% declined. Stocks with positive lambda and high variance may have a high probability of hitting 50% or 90% declines early (due to high variance), but have a very low probability of being 50% or 90% declined in the long-term (because the overall population growth rate is positive).

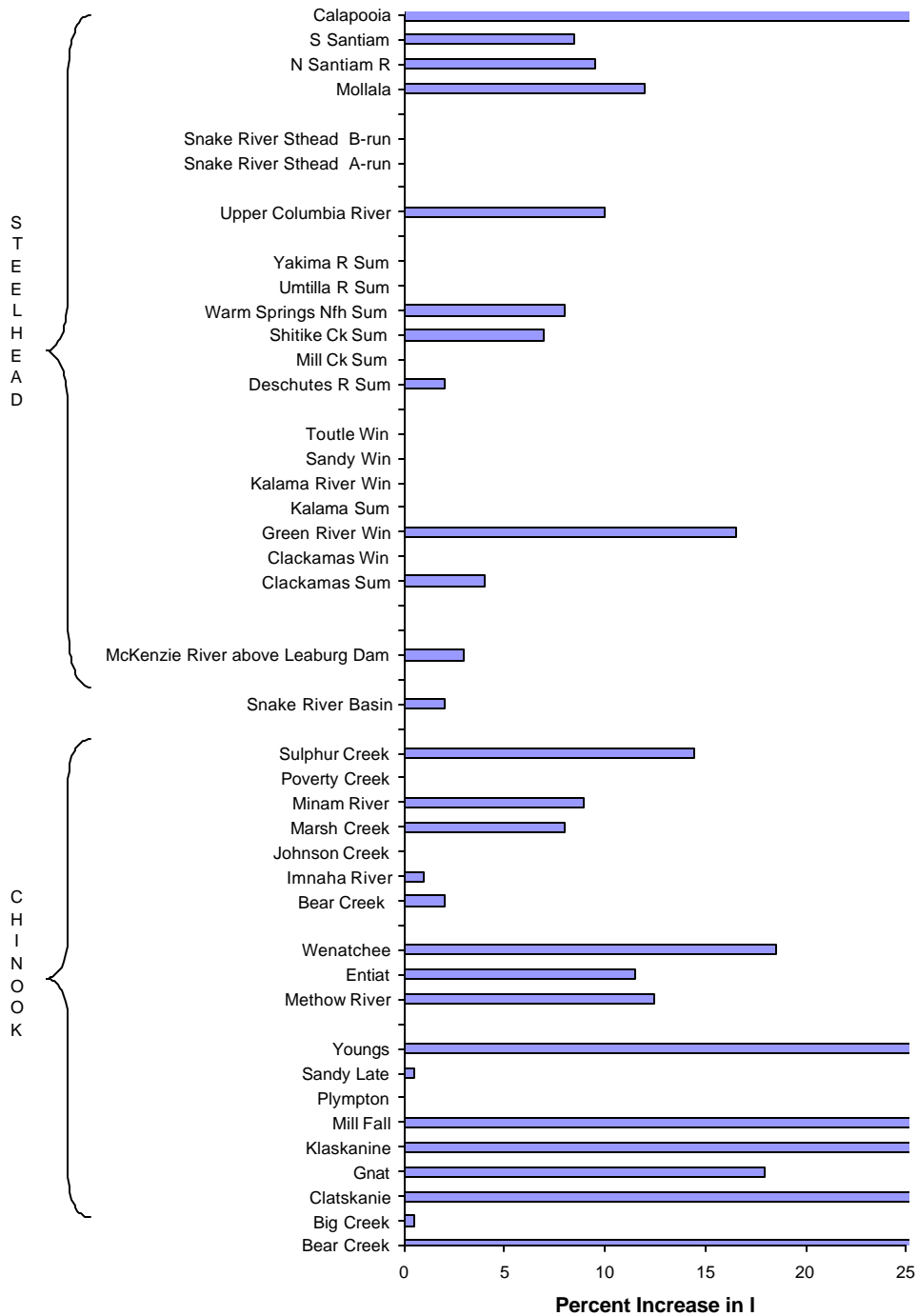


Figure V-11. Percent increase in lambda required to reduce the risk of extinction (one fish in one generation) in 100 years to less than 5%. Results shown for those stocks for which a population estimate was possible with the available data. No hatchery correction (this equals approximately a no hatchery fish reproduction assumption).

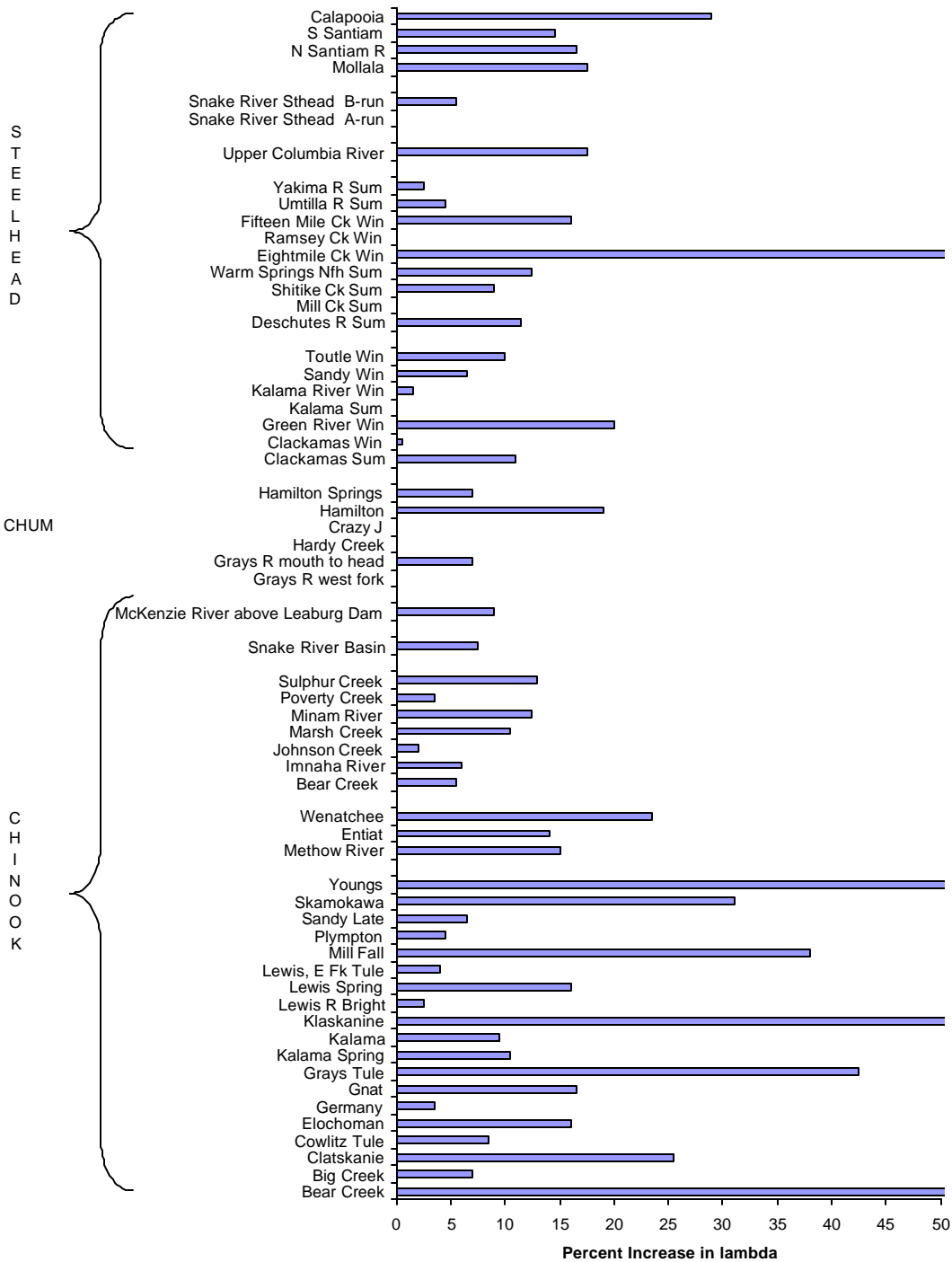


Figure V-12. Percent increase in lambda required to reduce the risk to less than 5% that the stock declines to 90% of current levels in 100 years. This extinction risk measure is much less sensitive to errors in our estimate of the total number of spawners in the stock. No hatchery correction (this equals approximately a no hatchery fish reproduction assumption).

Detectability of a 1% Increase in λ

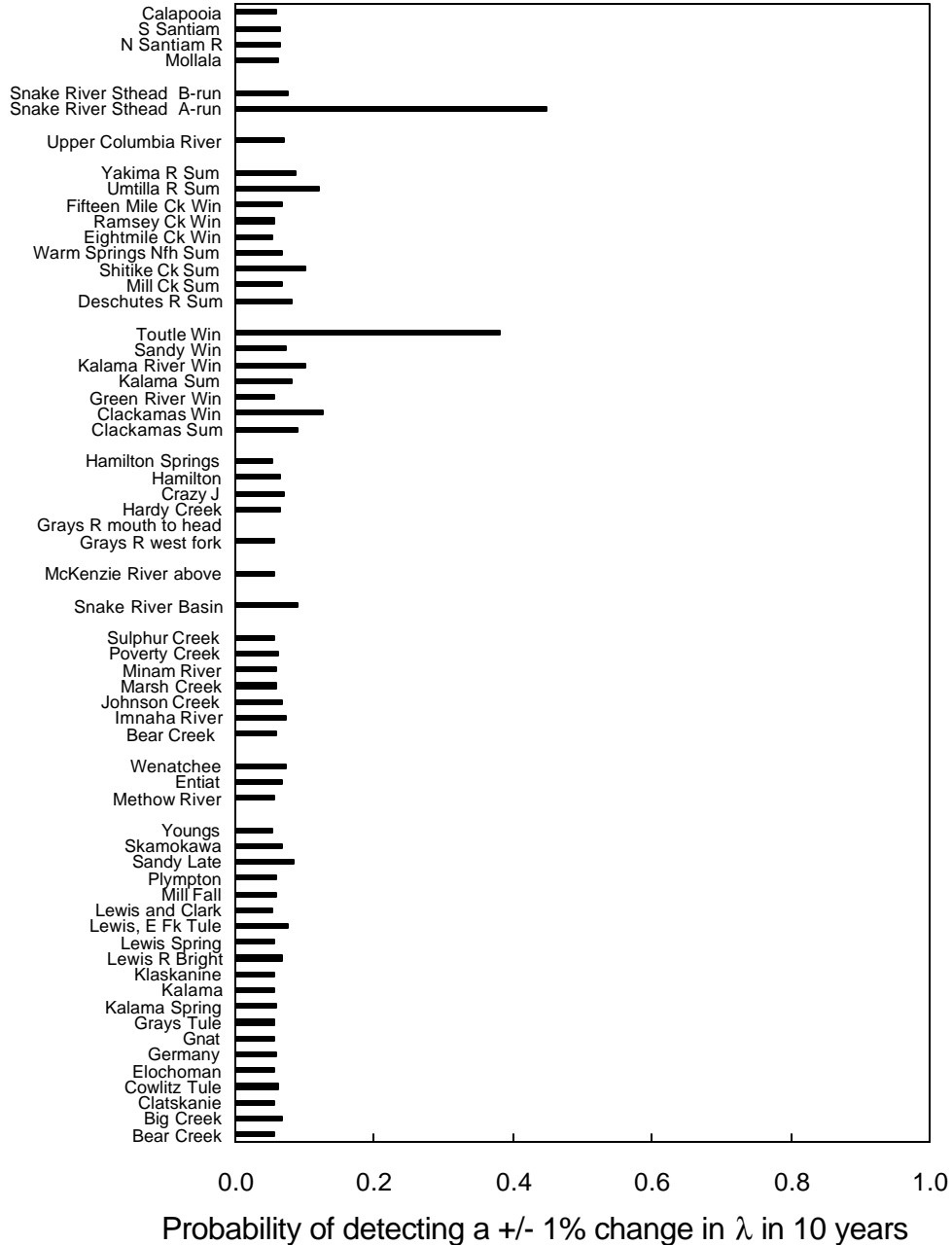


Figure V-13. Detectability of management actions on Columbia River stocks. With an imposed change in population growth rate (λ) of +/- 1%, what is the probability that in 10 years the projected population size differs from a population trajectory with λ unchanged at the $p < 0.05$ level?

Detectability of a 10% Increase in I

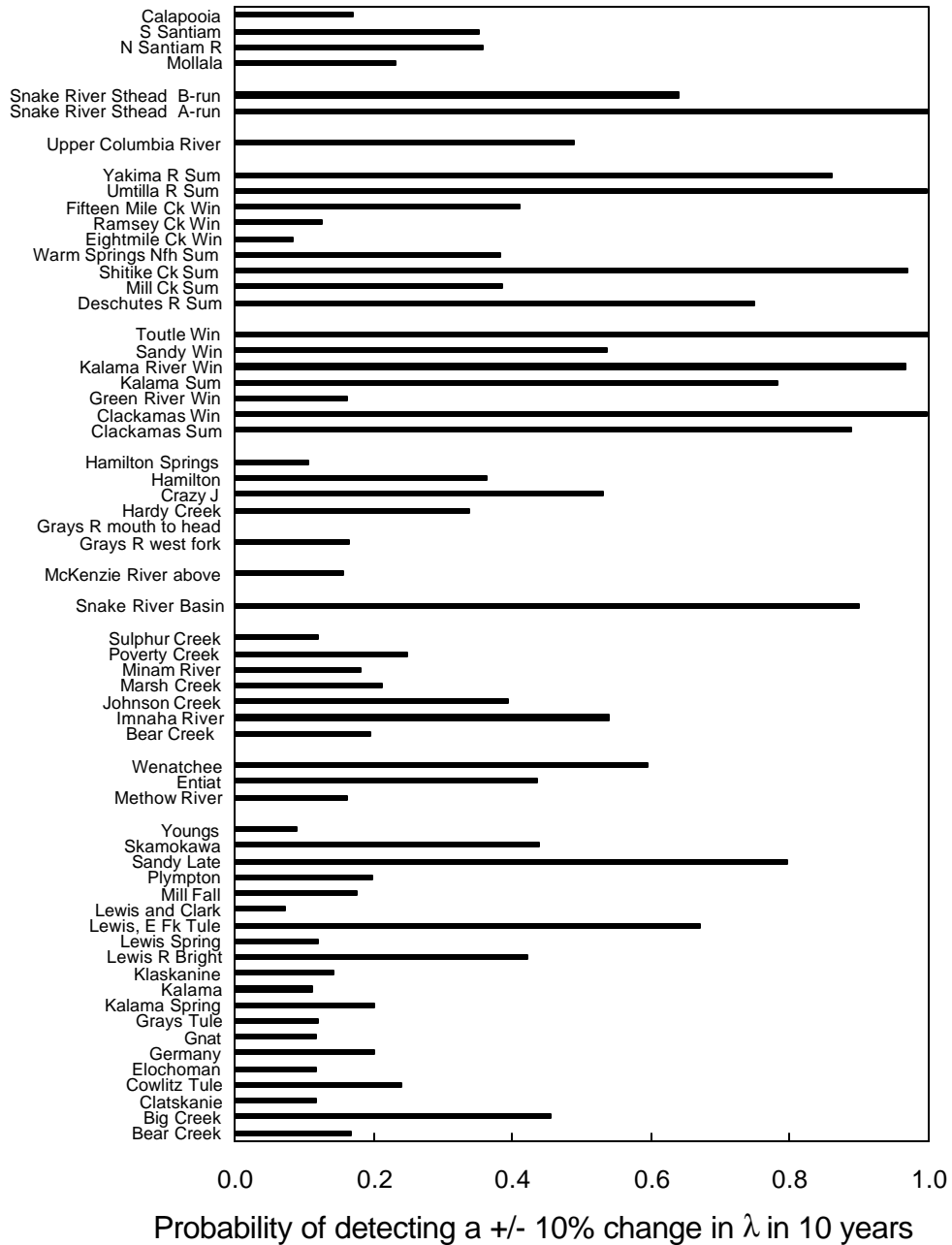


Figure V-14. Detectability of management actions on Columbia River stocks. With an imposed change in population growth rate (I) of +/- 10%, what is the probability that in 10 years the projected population size differs from a population trajectory with I unchanged at the $p < 0.05$ level?

Detectability of a 1% Increase in λ with 10% error

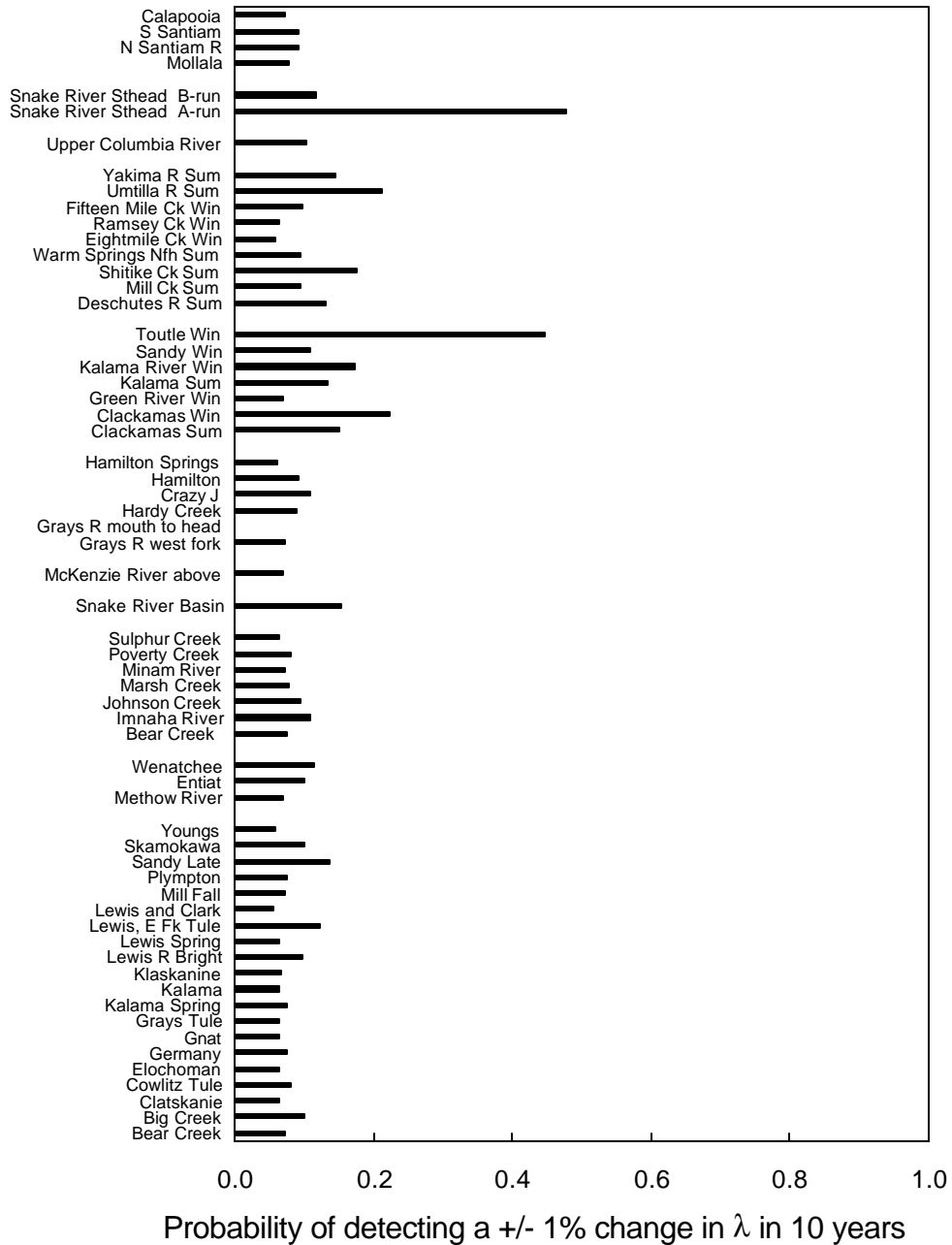


Figure V-15. Detectability of management actions on Columbia River stocks when sampling error is added. With an imposed change in population growth rate (λ) of +/- 1%, what is the probability that in 10 years the projected population size differs from a population trajectory with λ unchanged at the $p < 0.05$ level? Sampling error of mean standard deviation 10% was added to the observed population sizes at year 10.

Detectability of a 10% Increase in λ with 10% error

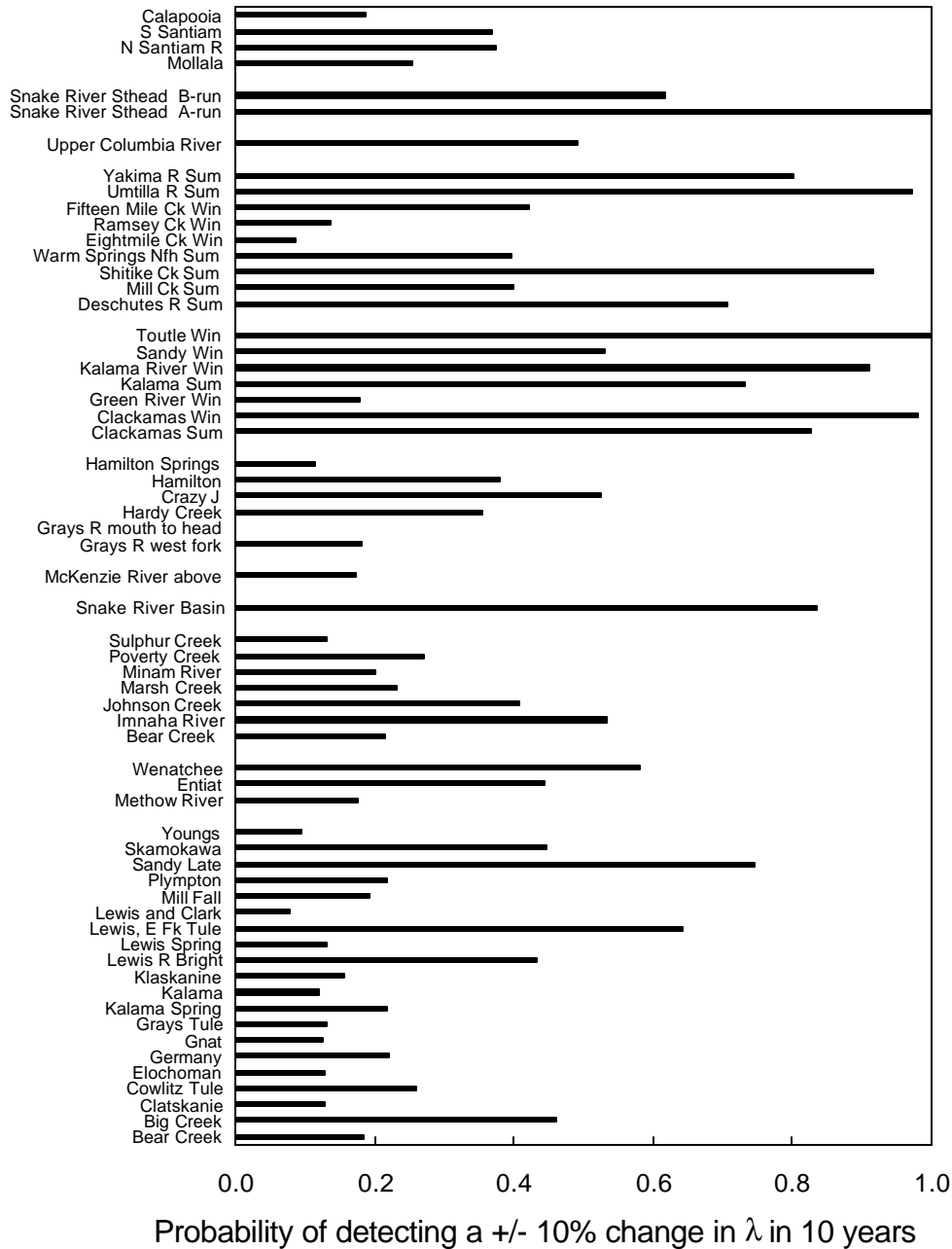


Figure V-16. Detectability of management actions on Columbia River stocks when sampling error is added. With an imposed change in population growth rate (λ) of +/- 10%, what is the probability that in 10 years the projected population size differs from a population trajectory with λ unchanged at the $p < 0.05$ level? Sampling error of mean standard deviation 10% was added to the observed population sizes at year 10.

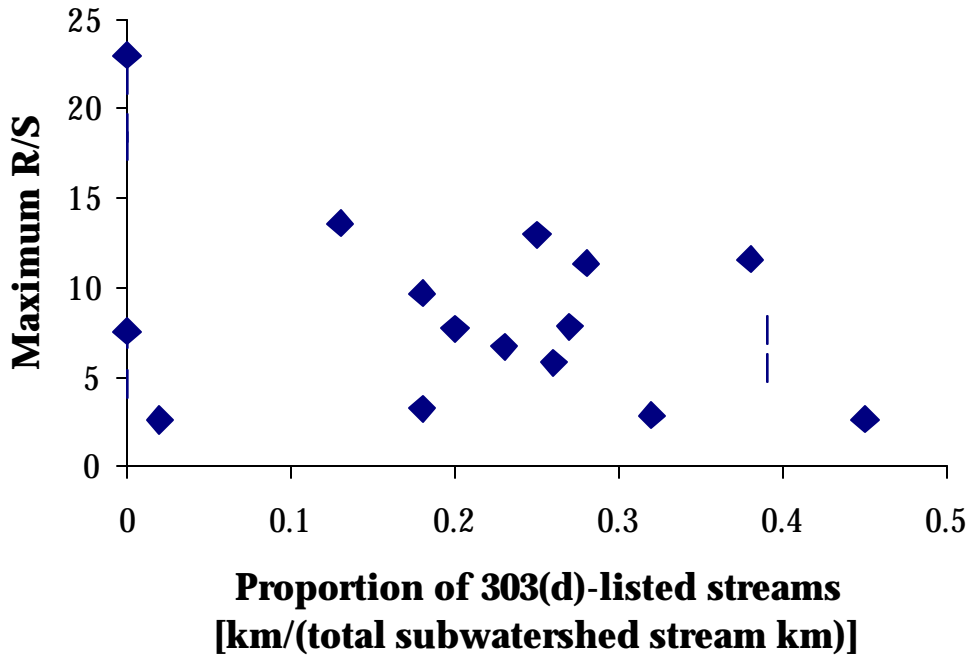
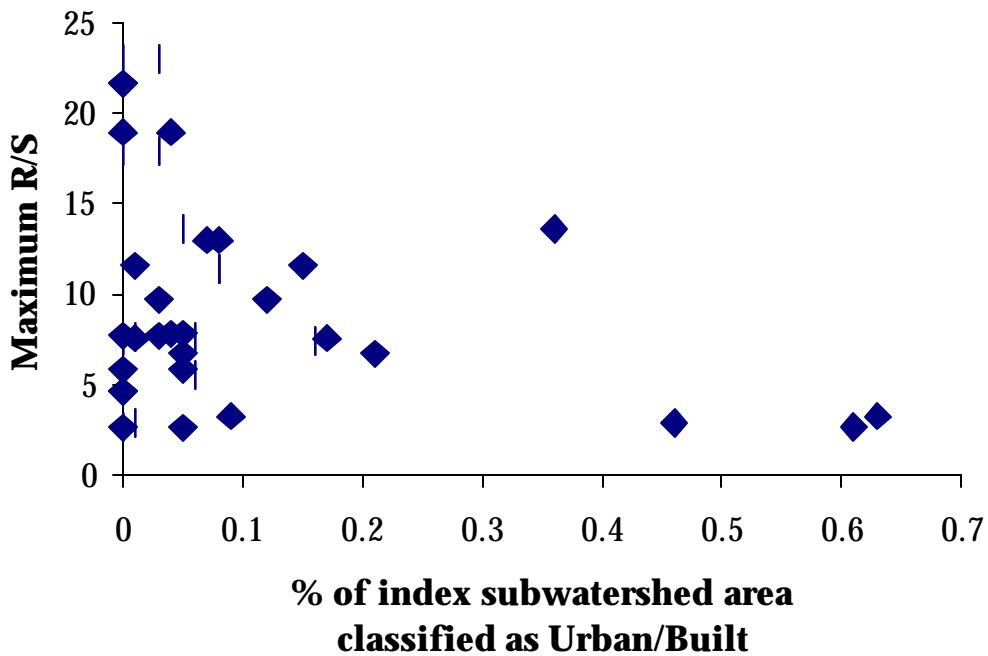


Figure V-17. Plots of maximum *R/S* values, for all 22 index areas, against (a) percent of subwatershed area classified as urban/built, and (b) proportion of subwatershed streamlength listed under EPA 303(d). From Regetz (in review, Conservation Biology)

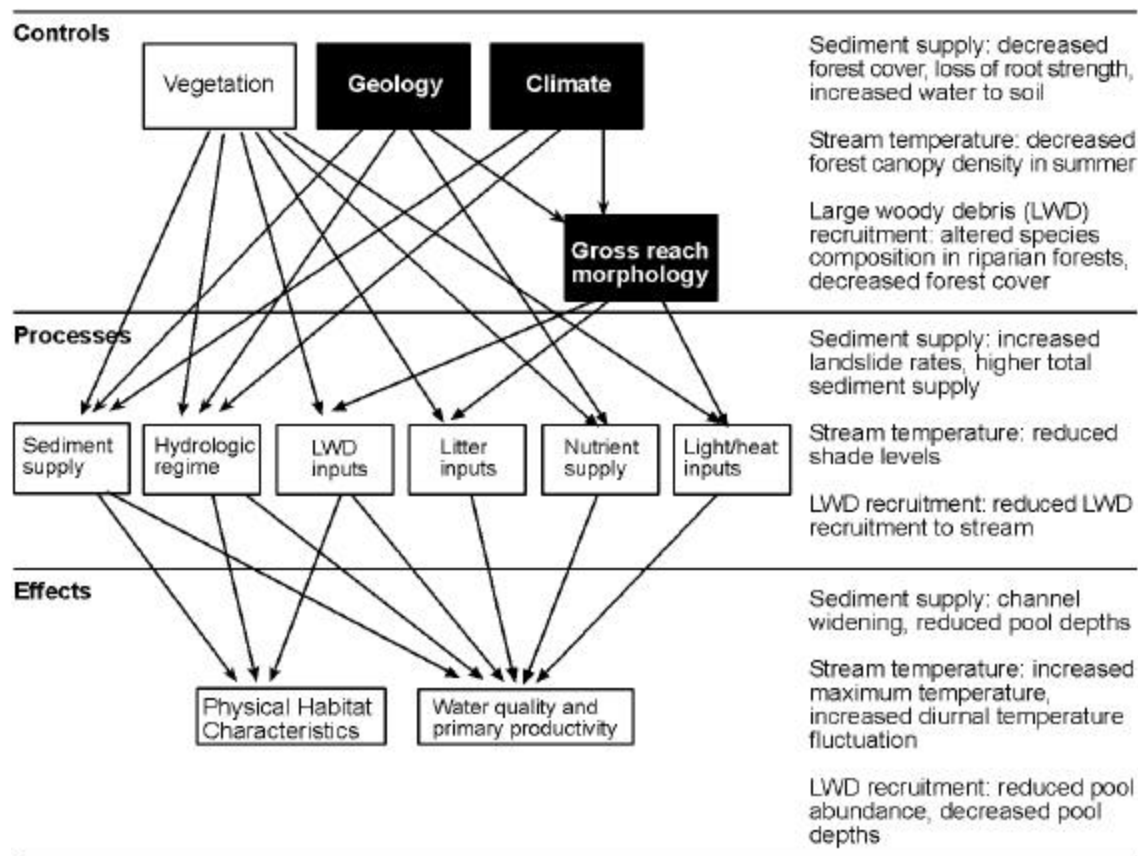


Figure V-18. Schematic diagram of linkages between landscape controls on habitat-forming processes, and between habitat-forming processes and effects on habitat conditions.

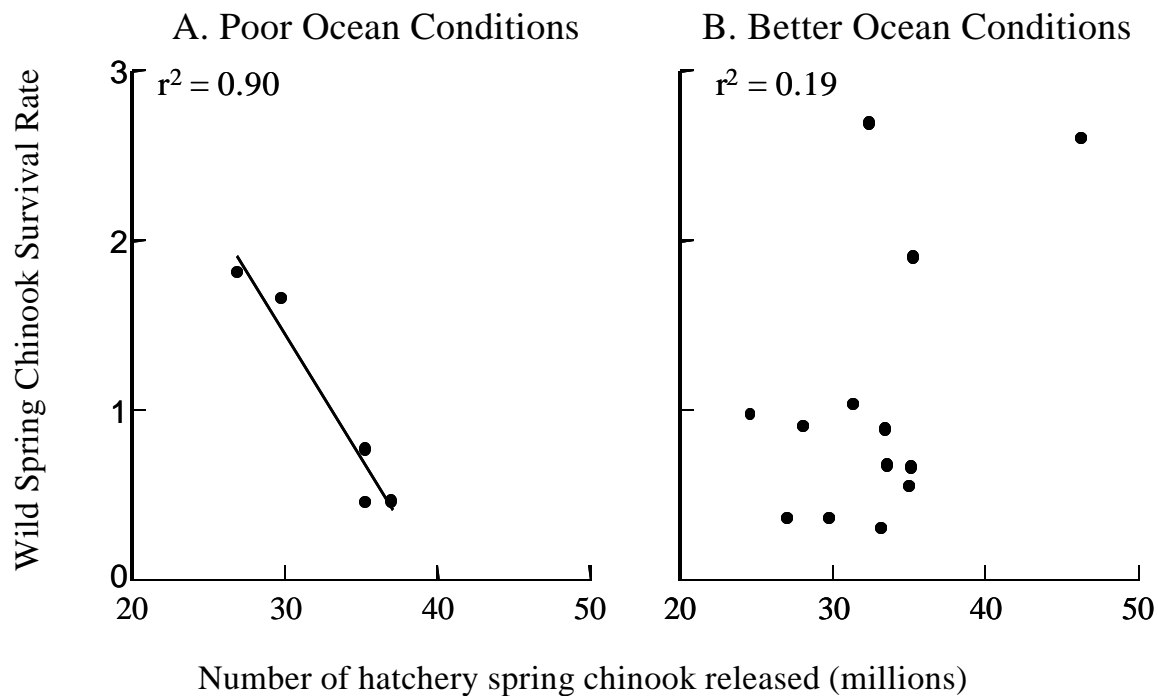


Figure V-19. Survival rates of wild spring/summer Snake River Chinook salmon as a function of the total number of hatchery spring chinook released in the Columbia River Basin during (a) poor ocean conditions and (b) better ocean conditions. Data are from brood years 1975 to present.

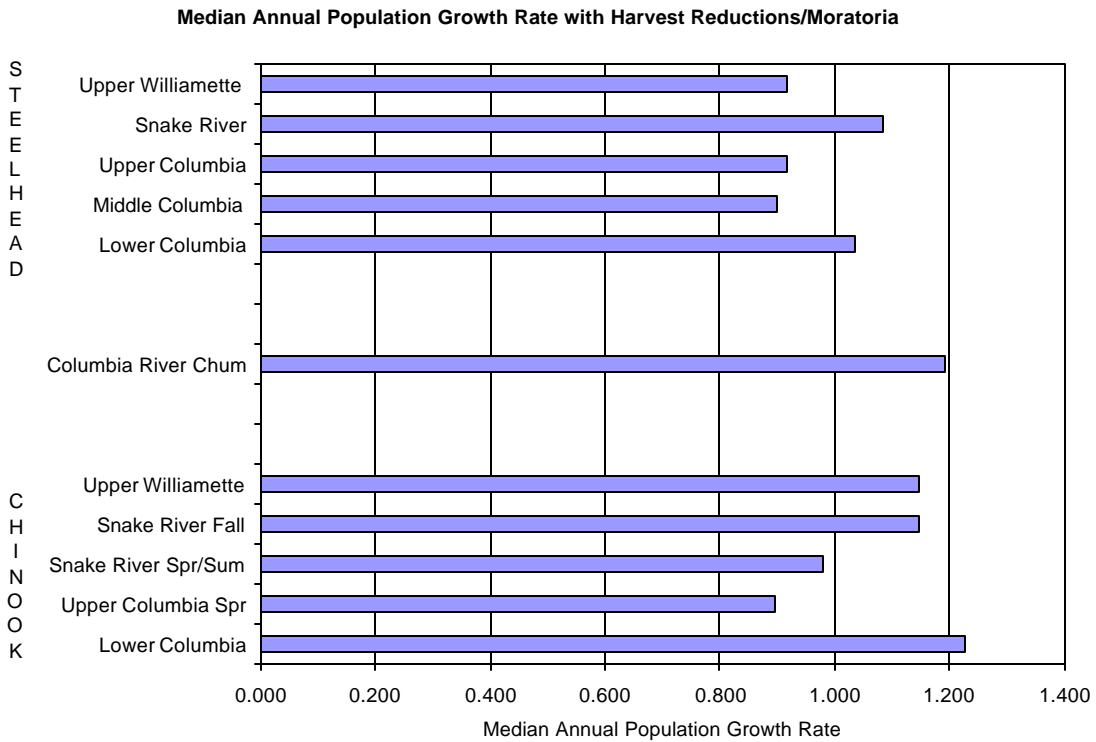


Figure V-20. Predicted values of annual population growth rate (I), with no harvest, using aggregated ESU parameters. This is the maximum benefit that could be obtained through harvest restrictions or moratoria.

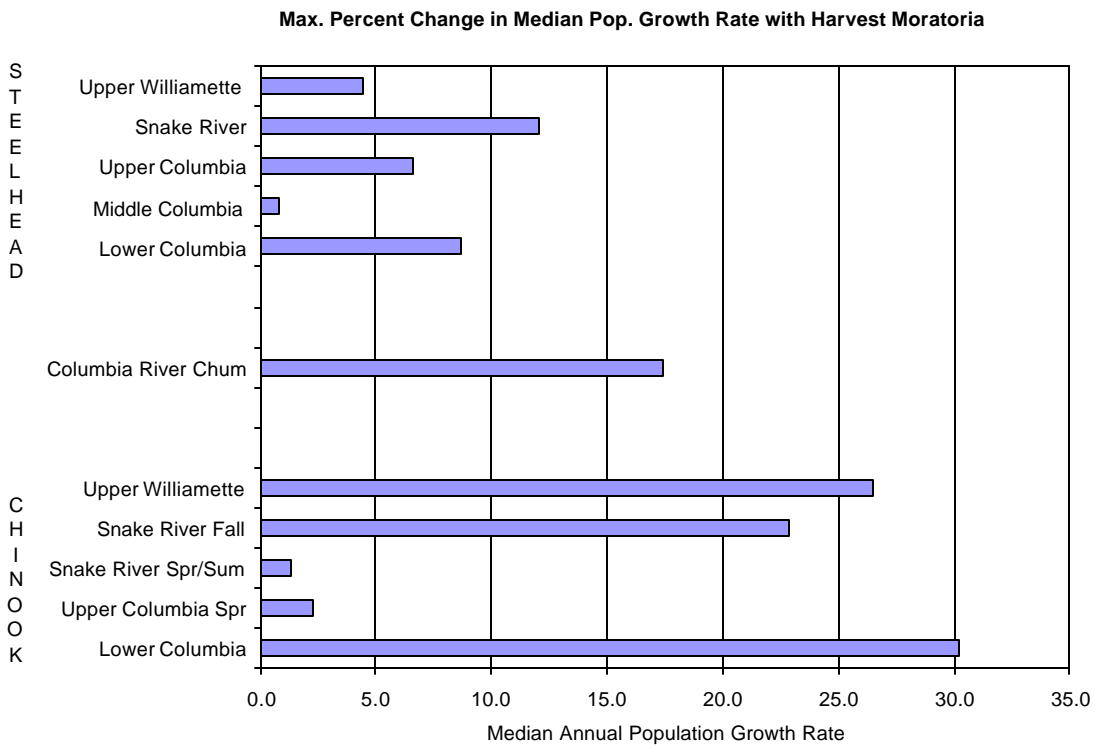


Figure V-21. Predicted percent increase in annual population growth rate (*I*), with no harvest, using aggregated ESU parameters. This is the maximum benefit that could be obtained through harvest restrictions or moratoria.

VI. Detailed Analyses for Selected ESUs

In this section, we present Leslie matrix-based analyses for Snake River spring/summer, Snake River fall and Upper Columbia River Spring Chinook Salmon, as well as Upper Columbia River steelhead. Our goal in analyzing these matrices and related data for these ESUs is to gain insight into where the greatest opportunities for improving population performance exist. The measure of stock or population performance is annual rate of population change (λ). Improvements are measured in the currency of changes in λ . We do not view these exercises as models of future population growth, but rather as evaluations of likely improvements in population growth as a result of actions that take effect in particular stages of the lifecycle. These sorts of analyses are not possible for additional Columbia River Basin ESUs at this time because of an absence of detailed age-structured data. Even with these age-structured data, we do not feel it is advisable to simulate populations into the future. To do so would require estimates of carrying capacity and density-dependent feedbacks, for which we lack data. In addition, an explicit model of ocean cycles and their impacts on age-specific demography would be necessary – an enterprise that is well beyond our existing database.

VI.A. Snake River Springs/Summer Chinook salmon

VI.A.1. Updates to previous analyses:

We have updated our analyses of Spring/Summer Chinook (in comparison with previous analyses) in several important ways.

First, although we continue to analyze seven “index stocks” (Table VI-1), for which age-structured run-reconstructions have been completed, we have been provided (and include) more recent data than previous analyses included (through brood year 1994). The data for Spring/Summer Chinook are based on redd counts expanded to estimate total numbers of spawners per reach for seven index stocks (Table VI-1). Second, we test for evidence of density-dependence in these stocks using a parametric bootstrap test. Third, we present the standard deviation for numerical experiments. And, finally, we perform several different permutations of numerical sensitivity experiments (using a wide variety of assumptions about baseline demography). Specifically, matrices were calculated and numerical experiments run for all seven index stocks in four different ways (for a total of 28 permutations). The four different approaches for estimating matrices are: (i) using run-reconstruction data for brood years 1980-1994, assuming survival in estuary is 7%, and then solving for first-year freshwater survival to balance Euler’s equation; (ii) using run-reconstruction data for brood year 1990-1994, assuming survival in estuary is 7%, and then solving for first-year survival to balance Euler’s equation; (iii) using run-reconstruction data for brood year 1980-1994 and solving for estuarine survival to produce the smolt-to-adult returns reported by Williams (in review), and then solving for survival in the first year to balance Euler’s equation; and (iv) using run-reconstruction data for brood year 1990-1994 and solving for estuarine survival to produce the smolt-to-adult returns reported by Marmorek et al. (1998), and then solving for survival in the first year to balance Euler’s equation. We single out brood years 1990-1994 to address concerns that by treating the entire time period between 1980 and current, we might misconstrue a situation that has been

progressively declining (that is recruits per spawner have been declining steadily during that time period).

Even though the numerical experiments were performed over a much wider range of baseline matrices than ever before, the results remain essentially unchanged. The conclusions at the end of this section are remarkably similar to the conclusions presented in earlier CRI documents, even though details and numbers have varied and new data have been added. This suggests that the conclusions are quite robust.

Table VI-1. Number of Adult Spawners (S) (minus jacks) Estimated From Redd Counts and the Number of Adult Recruits (R) to the Spawning Grounds for Seven Stocks of Snake River Spring/Summer Chinook (Beamesderfer et al. 1998, and then recently updated by PATH, memo sent in January 2000). For these stocks, adults are age 4 & 5; jacks are age 3. Two entries (the number of Sulphur Creek spawners in 1984 and the number of Marsh Creek recruits in 1994) were changed from 0 to 1 fish.

yr	Marsh		Johnson		Imnaha		Bear Valley		Poverty Flats		Sulphur		Minam	
	S	R	S	R	S	R	S	R	S	R	S	R	S	R
80	16	178	55	130	183	497	42	260	163	318	12	44	43	220
81	115	190	102	151	453	598	151	236	187	323	43	300	50	538
82	71	228	93	125	590	476	83	413	192	218	17	150	104	170
83	60	472	152	387	435	550	171	1200	337	1074	49	598	103	489
84	100	56	36	107	557	141	137	89	220	209	0	57	101	156
85	196	86	178	81	699	99	295	140	341	246	62	116	625	183
86	171	102	129	205	479	104	224	229	233	717	385	252	357	167
87	268	54	175	106	448	52	456	149	554	423	67	38	569	58
88	395	273	332	433	606	339	1109	712	844	904	607	257	493	113
89	80	21	103	79	203	115	91	70	261	278	43	16	197	54
90	101	2	141	17	173	45	185	18	572	56	170	3	331	15
91	72	5	151	29	251	39	181	18	538	90	213	7	189	21
92	114	61	180	138	363	188	173	138	578	192	21	35	102	228
93	216	225	357	244	1178	146	709	499	866	429	263	163	267	198
94	9	0	50	31	115	54	33	43	209	97	0		22	65
95	0		20		97		16		81		4		45	
96	18		49		219		56		135		23		233	
97	110		236		474		225		363		43		140	
98	164		119		159		372		396		140		122	
99	0		49		282		72		153		0		96	

VI.A.2. Testing for density-dependence in the index stock time series of recruits per spawner:

In section V.A. we reported the results of tests for density-dependence across all twelve Columbia Basin ESUs, including Snake River Spring/Summer Chinook salmon. At the aggregated ESU level, there was no evidence of density-dependence for Spring/Summer Chinook salmon in the Snake River. We have also applied the same analyses to recruits per spawner data broken into the separate index stocks (again applying the Dennis and Taper 1994 methods); in this case, seven different sets of bootstrap simulations were performed, one for each index stock. For six of the seven index stocks, the null hypothesis of density-independent population dynamics cannot be rejected (Table VI-2). The absence of density-dependence evident in Table VI-2 runs counter to results reported in Schaller et al. (1999) possibly due to differences in techniques, time series length and the treatment of index stocks as a single or individual populations. Based on the Dennis and Taper (1994) analysis we conclude that it is reasonable to neglect density-dependence for the purpose of the numerical experiments we conduct regarding sensitivity analyses.

Table VI-2. Parametric bootstrap likelihood ratio test for density-dependence for Snake River Spring/Summer Chinook, where a is the y-intercept and b is the slope from a linear regression of ln(recruits per spawner) vs. the density of spawners. (* indicates statistically significant evidence of density-dependence.)

Stock	a1	var1	a2	b2	var2	Test statistic	Critical value
Marsh	-0.5640	2.6927	-0.3488	-0.0016	2.6669	0.1262	6.5125
Johnson	-0.1429	0.7736	0.1674	-0.0021	0.7393	0.6035	7.7120
Imnaha	-0.9043	0.8593	-0.2818	-0.0014	0.7289	2.3248	3.7596
Bear	-0.1395	1.5268	0.1475	-0.0011	1.4378	0.8046	8.3003
Poverty	-0.2380	0.9041	0.5637	-0.0020	0.7001	3.7886	7.2113
Sulphur	0.1717	4.5091	0.9741	-0.0058	3.5568	3.2129	7.4181
Minam	-0.2838	2.4894	1.1399	-0.0060	1.1756	14.5286*	7.0086

VI.A.3 Estimating matrices for Spring/Summer Chinook salmon

Structure of the matrix. Published estimates for stage-specific survival and run-reconstructions were used to derive parameter estimates for Snake River Spring/Summer Chinook projection matrices. For the seven stocks of Snake River Chinook examined here, adults return as 3-, 4-, or 5-year olds to spawn and die -- exceedingly few return at age 6 or older. In addition, these stocks are all stream-type salmon that spend two winters in freshwater before migrating to the ocean. The matrices only keep track of females -- we therefore implicitly assume a 1:1 sex ratio of eggs and equal survival probabilities of males and females. The basic structure of demographic matrices for Spring/Summer Chinook salmon in the Snake River is as follows:

	1	2	3	4	5
1			$(1 - \mathbf{m})s_1b_3m_3/2$	$(1 - \mathbf{m})s_1b_4m_4/2$	$(1 - \mathbf{m})s_1m_5/2$
2	s_2				
3		s_3			
4			$(1 - b_3)s_4$		
5				$(1 - b_4)s_5$	

Where:

- \mathbf{m} is mortality of adult females during their migration upstream.

$$\mathbf{m} = 1 - (ps(1 - \text{harvest}_{sb})\text{BontoBasin}(1 - \text{harvest}_{ms})) \quad [6.1]$$

- ps , the prespawn survival, is set to 0.9 in all years
- BontoBasin is survival of unharvested spawners from Bonneville dam to their spawning basin
- harvest_{sb} , the rate of harvest in the subbasin, was 0 for recent years
- harvest_{ms} is harvest in the mainstem of the Columbia River (Beamesderfer et al. 1997; Table VI-3).
- m_x is the number of eggs per female spawner of age x
 - Estimates of m_x , assuming constant fecundity for all three adult age classes, were obtained from Myers *et al.* (1998; Table VI-3).
- b_x is the propensity of females of age x to breed
- s_x is the probability of survival of females from age $(x-1)$ to age x

Table VI-3. Mean fecundity, upstream survival, and percent female at age for the seven index stocks of Snake River Spring/Summer Chinook using data from 1980-1999.

Stock	mean fecundity	mean Bonto Basin	mean harvest _{ms}	% female ₃	% female ₄	% female ₅
Marsh, Bear, Sulphur	5607	0.581	0.079	0	49	67
Johnson & Poverty	4100	0.681	0.029	11	28	58
Imnaha*	4927	0.631	0.054	11	28	58
Minam*	4086	0.581	0.079	11	28	58

*No data regarding age distribution by sex were available for Imnaha and Minam. We used sex ratios from Johnson & Poverty because Imnaha & Minam have hatchery fish, which are known to spawn at younger age than wild fish.

Estimating specific parameters.

- s_2 – Survival through the 2nd year. This parameter can be decomposed as follows:

$$s_2 = ((1-pt) * s_d + pt*s_b)* s_e. \quad [6.2]$$

where:

- pt is the proportion of smolts transported (Table VI-4)
- s_d is the direct survival of juveniles during downstream migration (Table VI-4)
- s_b is survival of transported fish (assumed to be 0.98, consistent with Marmorek et al., 1998)
- s_e is estuarine and early ocean survival (see below)

Table VI-4. Hydropower corridor parameter estimates for various time periods and for different future scenarios. Estimates of current survival during downstream migration (s_d) and the proportion of smolts transported (p_t) in barges were obtained from Marmorek et al. (1998).

	BY 75-94	BY 90-94	1977-1979	Improved hydro	Draw-down
s_d	0.1448	0.2016	0.0946	0.2400	0.6066
pt	0.5817	0.7285	0	0.7664	0

- s_e – estuarine and early ocean survival.

Few data are available with which to estimate estuarine and early ocean survival, but survival during the first year in the ocean is thought to generally be between 2-10% (Nickelson 1986, Pearcy 1992). We constructed matrices using either of two values for this parameter:

- Assumed a value of 7% (Nickelson 1986, Pearcy 1992).
- Solved for estuarine survival to produce the smolt-to-adult return (SAR) values reported in PATH documents (Marmorek et al., 1998). In other words, we

factored adult mortality and direct juvenile mortality out of SAR estimates, and set s_e equal to the remaining mortality.

Note that in sensitivity analyses we use both methods of estimating s_e . However, in numerical experiments, we present only the results when using the matrices estimated from SAR values.

- s_3, s_4, s_5 – adult survival in the ocean

There are no direct estimates of adult survival in the ocean. As in Ratner et al. (1997), we set $s_3 = s_4 = s_5 = 0.8$.

- b_x – propensity of females of age x to return to breed

Annual age frequencies of spawners (Beamesderfer 1997) were used to calculate b_x . Because these data are for both males and females, the age frequencies were corrected, using sex ratio at age data from Hall-Griswold and Cochnauer (1988), White and Cochnauer (1989), and Elms-Cockrom (1998) to find the proportion of the total returning adults of age x that are female (f_x) (Table VI-3). To find the f_x 's for females only, the age frequencies for each year were multiplied by the % female _{x} , re-scaled so the frequencies summed to one, and averaged across the time series (Table VI-5). Snake River Spring/Summer Chinook salmon are not known to breed beyond age 5, so b_5 was set to 1. Following the procedure outlined in Ratner et al. (1997), b_3 and b_4 were estimated by solving a set of simultaneous equations:

$$f_x = \frac{b_x l_x}{\sum b_i l_i} \text{ for } x = [1,5], l_x = \prod p_x, p_1 = s_1, \quad [6.3]$$

$$\text{and } p_x = (1 - b_{x-1})s_x \text{ for } x > 1$$

Values for this parameter are shown in Table VI-5.

- s_1 – survival through the first year of life, from egg to Lower Granite Dam.

Survival from egg to LGR (s_1) was found by simultaneously solving Euler's equation (Ratner et al. 1997; Table VI-5),

$$(1 - \mathbf{m}) \sum l_x \left(\frac{m_x}{2}\right) b_x \mathbf{I}^{-x} = 1, \quad \text{with } \mathbf{I}^T = e^{\text{avg. ln}(R/S)}$$

$$\text{and } T = (1 - \mathbf{m}) \sum x l_x \left(\frac{m_x}{2}\right) b_x \mathbf{I}^{-x} \quad [6.4]$$

We assumed that productivity does not depend on spawner density, and used the average $\ln(R/S)$ from 1980-1994 as the estimate of productivity (Table VI-5).

Table VI-5. Age distributions of females, age-specific propensity to breed, average productivity, and survival from egg to one year old for seven index stocks of Snake River Spring/Summer Chinook.

Stock	avg. f_3	avg. f_4	avg. f_5	b_3	b_4	average $\ln(R/S)$	s_1
Marsh	0	0.256	0.744	0	0.216	-0.564	0.018
Bear	0	0.249	0.751	0	0.210	-0.140	0.027
Sulphur	0	0.247	0.753	0	0.208	0.172	0.037
Johnson	0.015	0.228	0.757	0.010	0.194	-0.143	0.030
Poverty	0.019	0.217	0.764	0.013	0.185	-0.238	0.027
Imnaha	0.016	0.360	0.624	0.011	0.316	-0.904	0.013
Minam	0.010	0.474	0.516	0.007	0.423	-0.284	0.031

Baseline matrices.

The resulting seven baseline matrices representing average current conditions using the 7% estuarine survival approach are given in Table VI-6. An additional set of matrices based only on data from 1990 onward is given in Table VI-7. (The matrices found by solving for estuarine survival to produce PATH SARs are provided on the CRI website.) The sensitivity and numerical experiments are robust to all 28 permutations of the matrices examined; thus, difference in the matrix details among the 28 permutations do not greatly affect the conclusions. As explained above, growth rates associated with the matrices in Tables VI-6 and VI-7 are determined by the average recruits per spawner rates. Although median recruits per spawner, or the geometric mean matrix, could be used, the results discussed below are not qualitatively altered by these alternative methods.

For a detailed population viability analysis, estimates of temporal variation for each matrix entry, as well as some estimate of how the different matrix entries co-vary, would be warranted. There is little chance that such detailed data will be forthcoming for any salmonid stock over the next 10 years. Arguably, it is also unlikely that much would be gained from these more detailed data. The most striking results from these matrix syntheses of run-reconstruction data are:

- 1.) Regardless of the time period (brood year 1980-1994 or brood year 1990-1994), several index stocks appear to be declining at rates in excess of 10% per year. Since the matrices and population growth rates do NOT incorporate the effects of environmental variation, which would increase the rate of decline considerably, the Snake River Spring/Summer Chinook salmon stocks are clearly in substantial peril.
- 2.) The rate of decline has increased in recent years. For example, the average rate of decline for brood years 1990-1994 is an annual decrease of 24%, whereas the average rate of decline for brood years 1980-1994 is a more modest 6% annual decline.
- 3.) The relative performance of different index stocks varies with the time period being analyzed and is not consistent through time. A striking example of this is Sulphur Creek. This stock stands out as the only one showing an annual growth rate greater than 1 for the long time-frame of brood year 1980-1994; yet, over the time period corresponding to brood year 1990-1994, it suffers an annual decline of 32% which is lower than all but one of the index stocks.

Table VI-6. Parameterized matrices and population growth rates (λ) for seven index stocks of Snake River Spring/Summer Chinook salmon based on data from 1980-1999.

Marsh:	1	2	3	4	5	$\lambda = 0.888$
1	0	0	0	5.162	23.914	
2	0.044	0	0	0	0	
3	0	0.800	0	0	0	
4	0	0	0.800	0	0	
5	0	0	0	0.627	0	

Johnson:	1	2	3	4	5	$\lambda = 0.970$
1	0	0	0.370	7.068	36.401	
2	0.044	0	0	0	0	
3	0	0.800	0	0	0	
4	0	0	0.792	0	0	
5	0	0	0	0.645	0	

Imnaha:	1	2	3	4	5	$\lambda = 0.824$
1	0	0	0.189	5.243	16.596	
2	0.044	0	0	0	0	
3	0	0.800	0	0	0	
4	0	0	0.791	0	0	
5	0	0	0	0.547	0	

Bear/Elk:	1	2	3	4	5	$\lambda = 0.971$
1	0	0	0	7.666	36.568	
2	0.044	0	0	0	0	
3	0	0.800	0	0	0	
4	0	0	0.800	0	0	
5	0	0	0	0.632	0	

Poverty:	1	2	3	4	5	$\lambda = 0.951$
1	0	0	0.424	6.134	33.130	
2	0.044	0	0	0	0	
3	0	0.800	0	0	0	
4	0	0	0.790	0	0	
5	0	0	0	0.652	0	

Sulphur:	1	2	3	4	5	$\lambda = 1.037$
1	0	0	0	10.381	49.942	
2	0.044	0	0	0	0	
3	0	0.800	0	0	0	
4	0	0	0.800	0	0	
5	0	0	0	0.634	0	

Minam:	1	2	3	4	5	$\lambda = 0.939$
1	0	0	0.204	12.725	30.055	
2	0.044	0	0	0	0	
3	0	0.800	0	0	0	
4	0	0	0.795	0	0	
5	0	0	0	0.461	0	

Table VI-7. Parameterized matrices and population growth rates (λ) for seven index stocks of Snake River Spring/Summer Chinook salmon based on data from 1990-1999.

Marsh:	1	2	3	4	5	$\lambda = 0.675$
1	0	0	0	1.356	5.313	
2	0.054	0	0	0	0	
3	0	0.800	0	0	0	
4	0	0	0.800	0	0	
5	0	0	0	0.596	0	

Johnson:	1	2	3	4	5	$\lambda = 0.815$
1	0	0	0.131	2.637	12.984	
2	0.054	0	0	0	0	
3	0	0.800	0	0	0	
4	0	0	0.792	0	0	
5	0	0	0	0.638	0	

Imnaha:	1	2	3	4	5	$\lambda = 0.748$
1	0	0	0.124	3.369	8.709	
2	0.054	0	0	0	0	
3	0	0.800	0	0	0	
4	0	0	0.789	0	0	
5	0	0	0	0.491	0	

Bear/Elk:	1	2	3	4	5	$\lambda = 0.812$
1	0	0	0	2.913	12.806	
2	0.054	0	0	0	0	
3	0	0.800	0	0	0	
4	0	0	0.800	0	0	
5	0	0	0	0.618	0	

Poverty:	1	2	3	4	5	$\lambda = 0.757$
1	0	0	0.096	1.719	9.140	
2	0.054	0	0	0	0	
3	0	0.800	0	0	0	
4	0	0	0.792	0	0	
5	0	0	0	0.650	0	

Sulphur:	1	2	3	4	5	$\lambda = 0.681$
1	0	0	0	1.292	5.509	
2	0.054	0	0	0	0	
3	0	0.800	0	0	0	
4	0	0	0.800	0	0	
5	0	0	0	0.612	0	

Minam:	1	2	3	4	5	$\lambda = 0.849$
1	0	0	0.101	6.804	15.569	
2	0.054	0	0	0	0	
3	0	0.800	0	0	0	
4	0	0	0.795	0	0	
5	0	0	0	0.450	0	

VI.A.4. Where in the Spring/Summer Chinook Life Cycle are the Greatest Opportunities for Recovery?

We used sensitivity analyses to identify life stages at which management actions have the greatest potential to influence annual rates of population change, and, as a corollary, to identify life stages for which future research should be a priority.

The relative value of potential changes in various demographic rates was assessed in two ways. First, the elasticity of the population growth rate to small changes in each demographic parameter was calculated. By this measure, the most important parameter is the survival of adults in the ocean (Figure VI-1). This is not a particularly surprising finding, since survival of individuals near the age of reproduction is generally among the most important life history parameters for organisms (Caswell 1989). This occurs because elasticity depends, in part, on reproductive value, which is a measure of an individual's contribution of offspring to future generations. In general, individuals near the age of reproduction have high reproductive value because they have made it through the long period of lowest survival and are just about to contribute offspring. Because of this bias, elasticity analyses can sometimes give misleading results. In fact, in this case, if management actions were targeted at increasing adult survival in the ocean, it would be impossible to produce a stable or increasing population. In order to produce an annual population growth rate of one, survival in the ocean would have to range from 500 to 700% (Figure VI-2)

Therefore, we also conducted a sensitivity analysis based on mortality rates. We calculated the percent change in the population growth rate (λ) that would be achieved if we could save 1 out of every 10 fish that currently die at each lifestage (i.e., we reduced mortality by 10%). By this measure, the most important parameters are survival through the first year of life (s_1) and survival in the estuary and early ocean (s_e) (Figure VI-3). For the 1980-1999 matrices, a 10 percent reduction in mortality during the first year of life is predicted to result in a 41.5 percent increase in λ , on average across the seven stocks. A 10 percent reduction in mortality occurring as smolts enter the estuary and during their first winter in the ocean (s_e) is expected to result in a 19.8 percent average increase in λ . Changes in other parameters have a much smaller effect on λ than changes in s_1 or s_e (Figure VI-3). This result is driven in part by the current low values of first year and estuarine survival; therefore, saving 1 out of every 10 fish that currently die at these stages would mean saving relatively more individual fish. The results displayed in figure VI-3 are the average across all seven index stocks, but there is very little variation in this basic pattern among stocks (note the standard deviations shown in the figure).

We also conducted these analyses using the matrices in which s_e was calculated from PATH SARs. The absolute change in lambda due to a reduction in mortality at the estuary-early ocean stage is larger in comparison with the matrices based on a s_e value of 0.07 (Figure VI-4). Importantly, however, the qualitative result remains the same. The most important parameters, by this measure, are survival through the first year of life and survival in the estuary and early ocean.

It is also important to note that both of these sensitivity measures predict that the survival of in-river migrants (s_d) and the proportion of fish transported in barges (pt) exert little influence on

the rate of population growth. In other words, if our estimates of current demographic rates are correct, we would expect little payoff (in terms of improved population growth) for further improvements in fish transportation or fish guidance systems. This is not to say that fish transportation or improvements in fish guidance systems to date have not been important. In fact, it is quite likely that Snake River Spring/Summer Chinook salmon would currently be extinct if efforts to transport smolts and other improvements to the hydropower system had not been made (see next section). In addition, it is also possible that further improvements in hydrosystem operation that influence survival below Bonneville Dam (because these improvements enhance individual fitness or alter run-timing in beneficial ways) could have substantial payoffs.

VI.A.5. Numerical Experiments as a Means of Evaluating Management Options With Respect to Spring/Summer Chinook Salmon

1. Have past management actions in the harvest arena and hydropower corridor been pointless?

The first impression created by the above sensitivity analyses is that earlier reductions in harvest and historical improvements to the migration corridor have been unimportant, but this is not the case. Rather, these analyses indicate that further management actions aimed at harvest and downstream survival for Spring/Summer Chinook salmon (excluding dam breaching) are not likely to be especially helpful, even though past actions have been crucial. In other words, continued use of these management levers in efforts to increase population growth rates and reduce extinction risk has reached a point of diminishing returns.

To show this clearly, we conducted the following numerical experiments. First, harvest and all other demographic rates were held at their current values, but transportation was assumed to be non-existent ($p_t = 0$) and other migration corridor rates impacted by dams were assumed to have been unaffected by improvements, including altered flow regimes and the addition of turbines. Specifically, s_d and *BontoBasin* (survival of adult migrants from the Bonneville Dam back to the basin of origin) were estimated from 1977-1979 run reconstruction data. The period from 1977-1979 was chosen because all of the currently existing dams were in place by then, but more recent improvements in dam operations had not yet occurred. During the late 1970s (and averaged across the seven stocks), s_d was only 0.0946 (less than the 1990-99 average of 0.2016) and the *BontoBasin* conversion rate averaged 0.56 (less than the 1990-1999 average of 0.64). We based this experiment on the matrices using s_e derived from SAR values.

This numerical simulation demonstrates that if survival through the hydropower system had remained at the low levels of the late 1970s, populations of Spring/Summer Chinook salmon in the Snake River would likely have already gone extinct in the absence of transportation of smolts (since the estimated annual decline assuming unimproved hydrosystem passage conditions is over 50 percent population loss each year; see Figure VI-5). One obvious question is whether transportation or bypass systems could ever be improved to such an extent that, by themselves, these improvements would adequately reduce extinction risks. The answer is no. In particular, even if every smolt made it successfully to the estuary, annual population growth would increase on average by under 6 percent (Figure VI-5). To see the extent to which a 6% increase in lambda “comes up short”, we can examine Figure V-11, which presents the %increase in lambda

required to reduce extinction risk in 100 years to less than 5%. Noting that Sulphur Creek requires a 16% increase in λ to reduce the extinction risk below this 5% value, Minam River requires a 10.5% increase in λ and Marsh Creek requires a 9.5% increase in λ , it is clear that we might expect to lose several stocks even if we could elevate downstream in-river survival to 100%. In short, perfect downstream survival alone would not be enough to prevent extinction, given the mortality suffered during other life stages of Spring/Summer Chinook salmon.

In a similar vein, we conducted another numerical experiment to assess the value of past and hypothetical future harvest reductions. We set all rates at current levels except harvest; harvest rates typical of 1960-1970 were imposed (average mainstem harvest rate = 0.394, average subbasin harvest = 0.142 compared to 1990-1999 average mainstem harvest = 0.053, subbasin harvest = 0). Under harvest rates from the 1960s (and keeping all of the hydrosystem passage improvements and transportation in place), it appears that population growth would be suppressed to a level that would also yield certain extinction (because λ is substantially less than 1; see second bar from the left in Figure VI-5).

In sum, without harvest reductions and hydropower system improvements made over the last 20 years, Spring/Summer Chinook salmon would probably have gone extinct by now (Figure VI-5). However, given current rates, neither elimination of harvest or further improvements in direct downstream survival, by themselves, are likely to sufficiently improve population growth of Spring/Summer Chinook (see the two rightmost bars in Figure VI-5).

2. *Is dam breaching, by itself, sufficient to reduce extinction risk?*

Another key question is whether dam breaching, by itself, is likely to sufficiently reduce extinction risk for Spring/Summer Chinook salmon populations? To answer this question, it was assumed that breaching would have three main effects: 1) altered downstream survival (using the rates assumed by Marmorek (1998) for the breaching option), 2) possibly improved upstream survival (here we simulated four levels of potential improvement in upstream survival rates), and 3) possibly improved survival below Bonneville Dam because differential delayed transportation mortality and/or extra mortality associated with the hydrosystem would no longer be an issue. Differential delayed transportation mortality (D) is related to reduced survival of transported fish compared to in-river migrants below Bonneville Dam, whereas extra mortality is a hypothesized reduction in the survival of both transported fish and in-river migrants that may be attributable to dams. Debate about the importance of these post-Bonneville effects of dams has been highly contentious, and data with which to estimate these parameters are generally poor. We, therefore, examined a broad range of potential improvements in survival below Bonneville Dam that could potentially occur after dam drawdown.

Figure VI-6 shows the expected increase in population growth rate over a range of increases in adult survival during upstream migration (each of the four panels) and a range of increases in estuarine/early ocean survival (x-axis in each panel). Given a particular upstream survival, we can calculate how much λ would be increased assuming different ranges of improvement in early ocean/estuarine survival. For example, to reduce extinction risk of Sulphur Creek to less than 5% over the next 100 years requires a 16% increase in λ . If upstream survival is

increased by 30%, a doubling (100% increase) in estuarine/early ocean survival due to effects of the hydrosystem would be necessary to achieve that level of risk. [For reference, a 20 percent improvement in s_e corresponds to a D approximately equal to 0.8, a 60 percent improvement in s_e corresponds to $D = 0.5$, and a 160 percent improvement corresponds to $D = 0.2$. An increase in upstream survival of 30% would produce an absolute upstream survival of about 93 percent.]

When the discussion is phrased in this manner, the key question is obvious: how much would dam breaching increase survival of downstream migrants, older fish in the estuary, and upstream migrants compared to current conditions? All of the possibilities can become overwhelming in their many combinations. One way of achieving some clarity is to consider one drawdown scenario that we feel is optimistic. For this scenario, the improvements associated with breaching were assumed to result in a 15 percent improvement in Bonneville to Basin survival, a downstream survival of 62 percent, and an increase in estuarine survival of 60 percent (which roughly corresponds to a $D = 0.5$). This scenario results in an 8 percent increase in I ($I = 0.825$), which is not sufficient by itself to reduce the 100-yr. extinction risk to less than 5%. To put this drawdown scenario in context, it was compared with an alternative scenario combining zero-harvest plus a hypothetical 25 percent improvement in first year survival (s_1). Viewed in this light, drawdown and the habitat/harvest actions are roughly equivalent in their effect on population growth, and neither, by themselves, is likely to recover Snake River chinook salmon (Figure VI-7). One weakness of this analysis is that dam breaching may alter additional components of the life cycle, beyond the three parameters explored here. For example, there is the potential that breaching could result in healthier fish that would experience reduced mortality not only in the estuary but in all subsequent years of adult life in the ocean. Alternatively, dam drawdown might result in increased habitat availability and possible improvements in s_1 (because of lower predation rates when reservoirs are drained). Dam breaching might also alter patterns of nutrient cycling and replenishment that, in turn, influence productivity.

VI.A.6. Estimating the effects of dams on population demographics.

Although dam breaching is a major option likely to offer substantial gains, it is unclear how substantial these gains would be. Some have argued that the magnitude of improvements due to dam breaching can be assessed by comparing upstream and downstream stocks (Schaller et al. 1999). Although this approach is sensible, it has several shortcomings that limit its effectiveness. Chief among the difficult issues facing such assessments is determining what constitutes a “control” for the “treatment” of the hydropower system. Schaller and colleagues use fish stocks residing in lower Columbia River basin, an area with fewer dams, as controls for stocks from upstream regions of the basin with greater numbers of dams. Unfortunately, because they are clumped rather than interspersed, stocks within regions are pseudoreplicates, making the separation of location from treatment effects problematic (Hurlbert 1984, Zabel and Williams in press, Levin in review). Additionally, stocks from different regions are genetically distinct and occupy watersheds of differing potential productivity (Myers et al. 1998, Regetz in review). The presence of differences between down and upriver stocks, therefore, is inconclusive because differences among regions may arise from many factors that vary among locations, only one of which is the number of dams.

Another approach used to estimate the demographic impacts of dam breaching involves examination of survival rates of juvenile downstream migrants over time. Direct effects of the hydropower system should be evident as reduced survival after dam construction relative to survival rates prior to dam construction. Williams et al. (in review, North American Journal of Fisheries Management) conducted such analyses, estimating annual average survival probabilities of Spring/Summer Chinook salmon from 1966 through 1999. They report estimates of survival ranging from 32-56% in the 1960s when only 4 dams were in place. After four additional dams were constructed from 1968 to 1975 survival dropped to 3-30% during the 1970s. After improvements to the hydropower system were put in place survival increased, and during the last 5 years, survival rates of juvenile migrants through eight mainstem dams ranged from 42-59%, a value equal to or greater than that in the 1960s. While survival through the hydropower system in the 1990s is apparently substantially greater than the 1970s, adult return rates have remained low. Consequently, direct mortality of downstream migrant fish through the hydropower system cannot be responsible for the continuing low adult return rates. However, this analysis does not eliminate the possibility that indirect effects of the hydropower system expressed as increased post-Bonneville mortality are important.

A different broad-brush tactic adopted by Regetz (in review, Conservation Biology) also helps put dam passage in perspective. Regetz contrasted the productivity of 22 different Spring/Summer Chinook salmon stocks in the Columbia Basin that differed in habitat attributes and the number of dams they had to pass through before reaching the mouth of the Columbia River. Depending on the way recruit per spawner data was summarized, the number of dams (which ranged from 1 to 9) explained between 1% and 16% of the variation in recruits per spawner data (in no cases a was a statistically significant proportion of the variation explained by number of dams). These analyses indicate that it is not that easy to generate data that clearly and unequivocally point to dam breach as enough of an improvement to recover these stocks. Again, there is no question that dam breaching will provide some marked improvement, but data suggesting that it will be sufficient, by itself, are lacking.

VI.A.7. The Bottom Line and Critical Uncertainties for Snake River Spring/Summer Chinook Salmon

The seven Snake River Spring/Summer Chinook salmon index stocks are experiencing a decreasing trend in population change. This trend appears to have worsened in the most recent years for which we have complete data (1990-1994). Without additional intervention, the long-term prognosis for these stocks is clearly extremely poor. Identifying specific suites of actions that would serve to recover these stocks (or at least mitigate extinction risk), however, is hampered by several important areas of uncertainty. First, while better estimates are becoming available, the magnitude and mechanisms of indirect mortality associated with the hydrosystem or transportation have yet to be conclusively defined. Second, quantitative links between habitat and hatchery management actions and salmon productivity have not yet been established. Finally, the role of changes in ocean conditions in producing patterns of survival is not well understood; nor is the manner in which ocean conditions are likely to change in the future.

Conclusively resolving any of these issues in a short time frame is highly unlikely, given both the generation time of salmonid species and the likelihood of detecting changes in annual rates of

population change within a 10-year period (Section V). In addition, unless dam breaching increases survival below Bonneville Dam by over 100 percent and dramatically improves the survival of upstream migrants, it is unlikely that dam breaching, by itself, can recover Snake River Spring/Summer Chinook. If trends continue to worsen, dam breaching will become even less likely to be sufficient to mitigate extinction risk, (although the likelihood that it will be necessary will increase). Regardless of the hydropower option chosen, therefore, exploring opportunities to improve population trajectories through actions in other arenas will be critical. Equally critical will be conducting our exploration of those opportunities in a statistically sound, scientifically rigorous manner.

VI.B. Snake River Fall Chinook Salmon

The data for fall chinook salmon are counts of fish passing the Lower Granite Dam on the Snake River (Table VI-10).

Table VI-10. Counts of Fall Chinook Adult Spawners (S) and Adult Recruits (R) (Peters et al. 1999). For this ESU adults are 3, 4, 5, & 6; jacks are age 2.

Year	S	R
1980	515	1236
1981	878	951
1982	1209	1201
1983	909	1054
1984	717	856
1985	1080	581
1986	1403	593
1987	1064	318
1988	702	778
1989	815	568
1990	273	233
1991	767	211
1992	674	
1993	883	
1994	448	
1995	226	
1996	964	
1997	1007	

As we did with Spring/Summer Chinook, prior to matrix analyses we tested for evidence of density-dependence in fall chinook. For this ESU, the null hypothesis of density-independent population dynamics cannot be rejected (Table VI-11). A second point worth noting about fall chinook salmon in the Snake River is that a very modest increase in lambda (only 2.5%) is required to mitigate the risk of extinction to below 5% in 100 years (Figure V-11). Because the increase in lambda is modest, this suggests that many management options can substantially benefit fall chinook salmon in the Snake River.

Table VI-11. Parametric bootstrap likelihood ratio test for density-dependence for Snake River fall chinook. a is the y-intercept and b is the slope from a linear regression of ln(recruits per spawner) vs. the density of spawners.

A	b	Var	Test statistic	Critical value
0.5390	-0.00009	0.2951	2.5035	5.5071

VI.B.1. Using a Matrix Model to Summarize Fall Chinook Demographic Rates and Opportunities for Recovery

Snake River Fall Chinook differ from Snake River Spring/Summer Chinook in three important ways: 1) the fall chinook are ocean-type salmonids, migrating to the ocean during their first year of life, 2) fall chinook return to spawn at ages 2 (jacks), 3, 4, 5, and 6, whereas the seven spring/summer index stocks return only at ages 3 (jacks), 4, and 5; 3) fall chinook are subjected to considerable ocean harvest, whereas there is virtually no ocean harvest for the spring/summer stocks. The demographic matrix for fall chinook is, therefore, a six by six matrix, with ocean harvest factored into the adult survival terms:

	1	2	3	4	5	6
1	0	0	$(1 - \mathbf{m})s_1b_3m_3/2$	$(1 - \mathbf{m})s_1b_4m_4/2$	$(1 - \mathbf{m})s_1m_5/2$	$(1 - \mathbf{m})s_1m_6/2$
2	$(1-h_2)s_A$	0	0	0	0	0
3	0	$(1-h_3)s_A$	0	0	0	0
4	0	0	$(1-b_3)(1-h_4)s_A$	0	0	0
5	0	0	0	$(1-b_4)(1-h_5)s_A$	0	0
6	0	0	0	0	$(1-b_5)(1-h_6)s_A$	0

Parameters are defined as for Spring/Summer Chinook salmon.

h_x = ocean harvest rate of individuals of age x

Parameter estimates.

To derive parameter estimates for Snake River fall chinook, we used annual counts of natural-origin jacks and adults at Lower Granite Dam (1980-present) and age frequencies of spawners based on year-specific proportion at age calculated from Lyons Ferry Hatchery fall chinook CWTs (Peters et al. 1999; Table VI-13). Mainstem harvest, ocean harvest, and *BontoBasin* conversion rates were also obtained from Peters et al. (1999). For harvest rates and survival during upstream migration, data from 1993-1996 were used, because there were reductions in harvest starting in 1993 under ESA management (Table VI-13). Although there are potential problems involved with using data from hatchery fish, the best available information on age-specific fecundity and sex ratio at age comes from fish at Lyons Ferry Hatchery (Mendel et al., 1996; Table VI-13).

Table VI-13. Age-Specific Parameters Used in Snake River Fall Chinook Analyses.

	2	3	4	5	6
Age frequency of females (f_x)	0	0.129	0.652	0.198	0.020
93-96 Ocean harvest rate (h_x)	0.0123	0.0465	0.1368	0.1838	0.1953
Eggs per female spawner (m_x)		2885	3133	3251	3251
Propensity to breed (b_x)	0	0.081	0.650	0.863	1.0
93-96 Mainstem adult harvest rate		0.174			
93-96 adult <i>BontoBasin</i> conversion rate		0.471			
S_1		0.0044167			

Age-specific propensity to breed (b_x) and survival during the first year (s_1) were calculated using methods similar to those described for Spring/Summer Chinook. However, because fall chinook are ocean-type salmonids, s_1 includes everything beginning from egg hatching and including downstream migration, survival in the estuary and entry into the ocean environment. Because data regarding survival during downstream migration and the proportion of smolts transported are generally much poorer for fall chinook than for Spring/Summer Chinook, no attempt was made to break s_1 down into all of its component pieces.

Table VI-14. Parameterized Matrix and Population Growth Rate (λ) for Fall Chinook Salmon.

	1	2	3	4	5	6	$\lambda = 0.980$
1	0	0	0.182	1.573	2.170	2.513	
2	0.790	0	0	0	0	0	
3	0	0.763	0	0	0	0	
4	0	0	0.634	0	0	0	
5	0	0	0	0.229	0	0	
6	0	0	0	0	0.088	0	

Sensitivity analyses.

As was done for the Spring/Summer Chinook, the sensitivity of the matrix for fall chinook was evaluated in two ways: 1) elasticity analysis, and 2) numerical experiments investigating the percentage improvement associated with saving 1 out of 10 salmon that currently die at each stage. The elasticity results for fall chinook (Figure VI-8) closely mirror those for Spring/Summer Chinook salmon (Figure VI-1). In particular, the most sensitive parameter is the survival of adults in the ocean, again because individuals at this stage have survived periods of high mortality and are close to the age of reproduction. Results of the saving 1 of 10 experiments for fall chinook (Figure VI-9) are also quite similar to those for Spring/Summer Chinook (Figure VI-3). Specifically, reducing mortality during the first year of life produces the largest change in population growth rate (recall that for fall chinook, s_1 includes survival in the rearing habitat, downstream migration, and entry into the estuary and ocean environments). This

result can be largely attributed to the low estimated survival during the s_1 stage. Simply stated, because survival of s_1 fish is so low, saving 1 out of 10 fish that die at this stage would save many more fish than for any of the other stages.

Numerical assessments.

It is more difficult to assess the potential benefits of dam breaching for Snake River Fall Chinook salmon because data regarding survival during downstream migration and the proportion of smolts transported are not as abundant. However, the majority of effects would likely occur in the s_1 stage, which includes both downstream migration and post-Bonneville survival in the estuarine environment (where latent effects of dams are likely to accrue). We examined the percent increase in lambda expected to result from a broad range of potential changes in s_1 survival. Again, an approximate 2.5 percent increase in lambda is expected to lower the probability of dropping to less than one spawner within 100 years to 5%. This level of improvement in lambda could be achieved with as little as a 15 % percent increase in s_1 (Figure VI-10). Whether or not such a change in s_1 would actually occur under dam drawdown is unknown, but it seems highly likely.

In contrast to other proposed management actions, it is incontrovertible that harvest reductions will save fish from dying, and in fact save adult fish with far greater reproductive value than fry or smolts. Despite listing under the Endangered Species Act, harvest continues to be a significant source of risk to Snake River Fall Chinook salmon. Importantly, harvest reductions can take effect immediately, whereas dam breaching or habitat restoration will likely include time lags of 5-10 years before any effect is realized. The question then is, could harvest moratoriums attain the desired increase in annual population growth needed to mitigate the imminent risk of extinction of fall chinook salmon? Using a deterministic, stage-structured matrix model for fall chinook salmon, the required 2.5% increase in lambda is certainly achieved with a 75% reduction in mainstem harvest alone and may be accomplished with even a 50% reduction in mainstem harvest alone (Figure VI-11).

Lastly, dam breaching would open up spawning habitat for fall chinook salmon, which, unlike Spring/Summer Chinook, tend to spawn in the mainstem of the Snake River. However, expansion of populations to fill this habitat would not by itself reduce extinction risks; longer term increases in annual population growth rates above current levels would still be required. But the increased availability of habitat is a benefit not attainable through management of hatcheries or harvest actions.

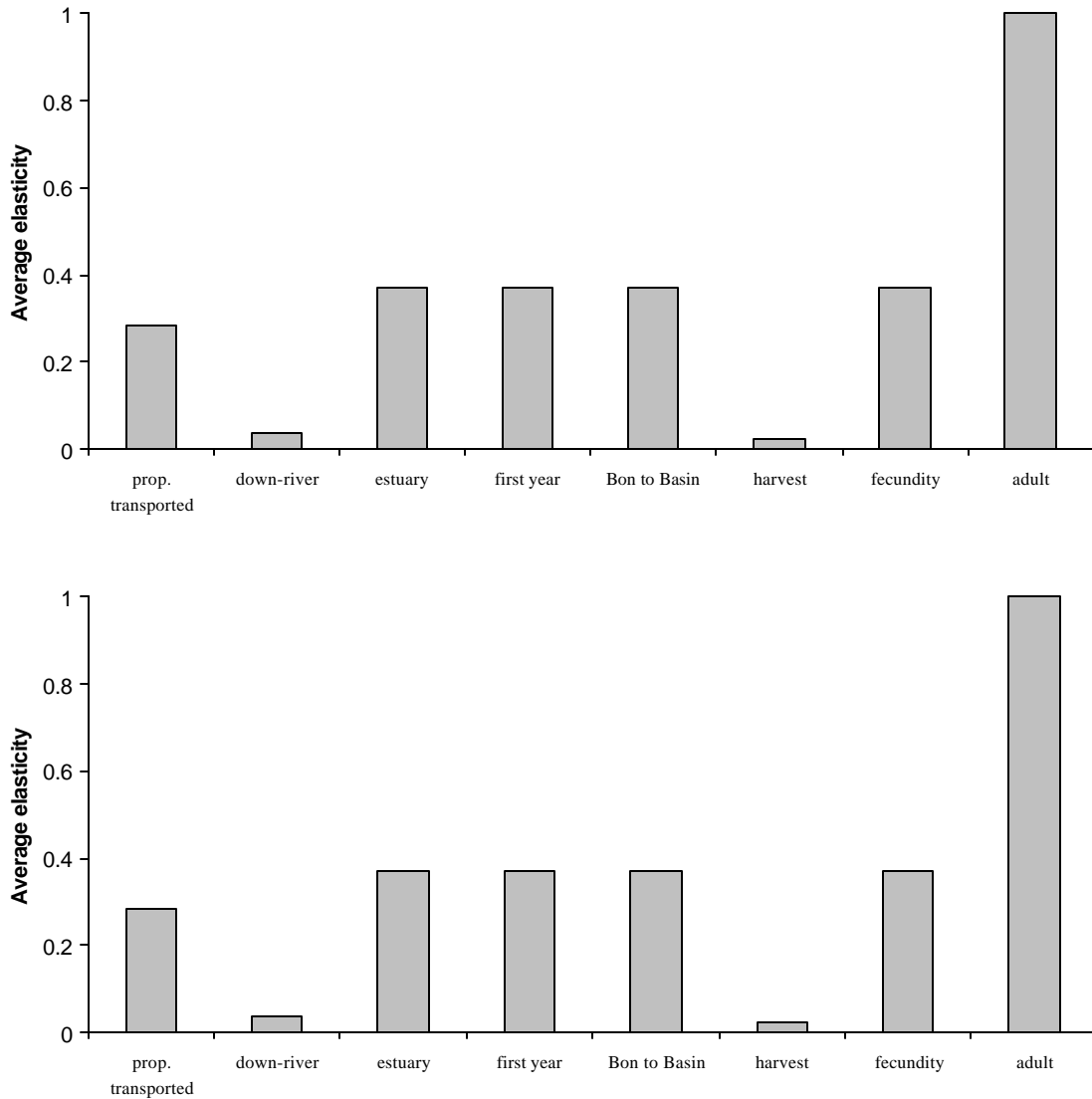


Figure VI-1. Sensitivity of annual population growth to small changes in components of the Spring/Summer Chinook salmon demographic projection matrix. The top panel is derived from brood years 1980-1994, while the bottom panel is derived from brood years 1990-1994. Average elasticities, relative to the largest value, are shown.

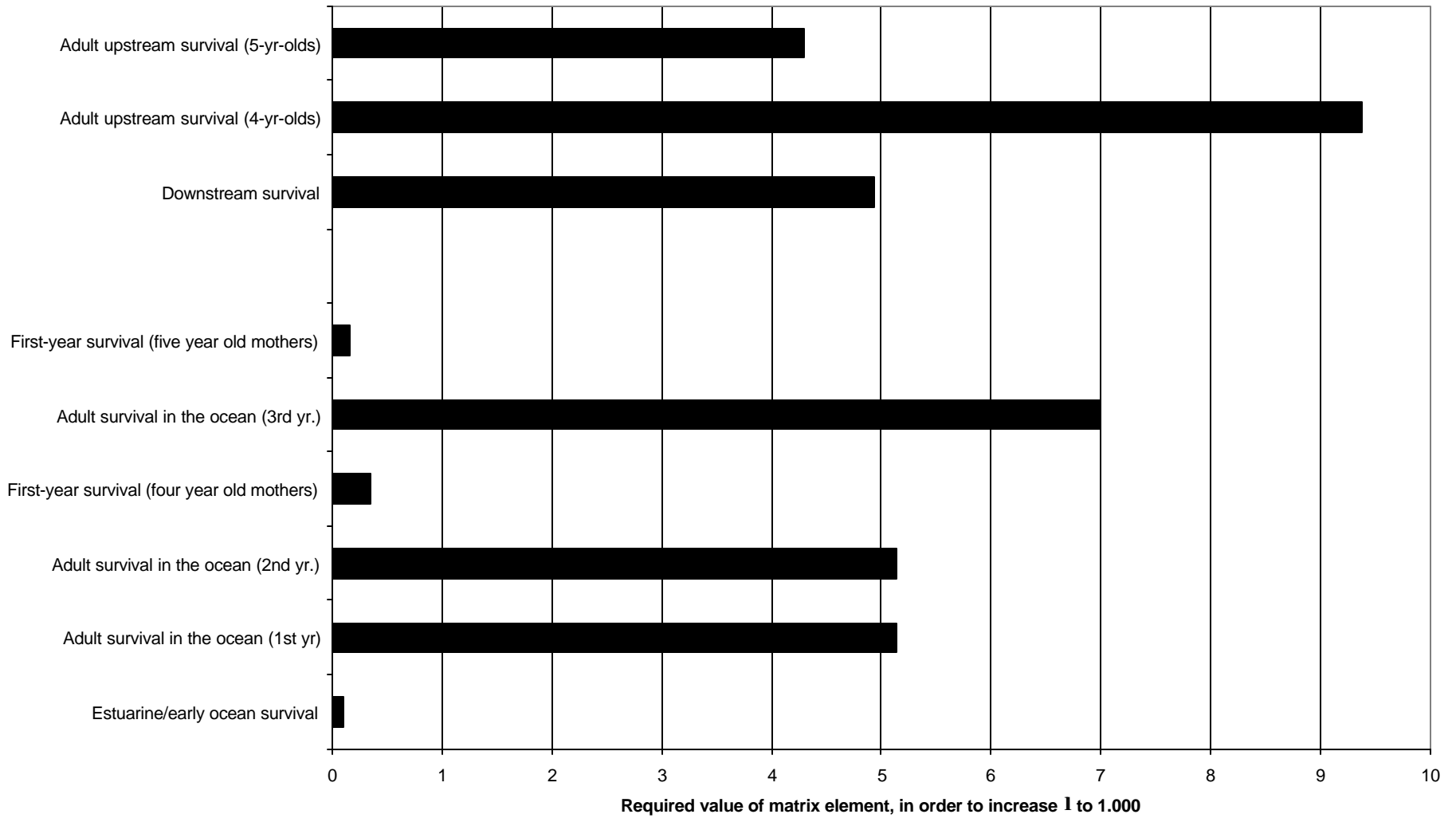


Figure VI-2. Necessary changes in single matrix elements to yield an annual rate of population change =1. Example presented here is the Marsh Creek index stock, using λ calculated from SAR values, and λ calculated from brood years 1990-1994.

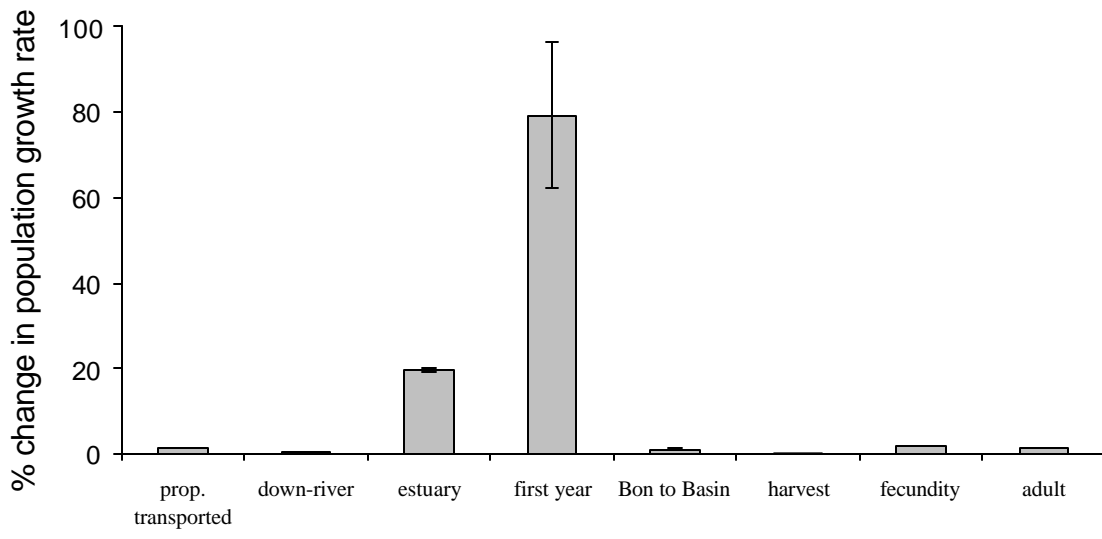
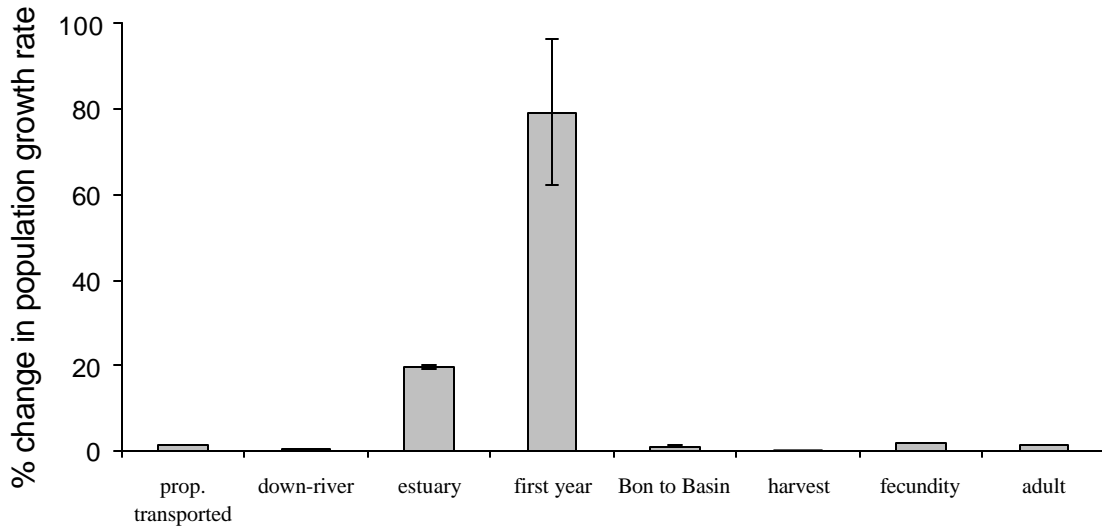


Figure VI-3. Average increase in annual population growth with a 10 percent reduction in mortality during different life stages for Spring/Summer Chinook salmon assuming estuarine survival is 7%. A 10 % increase in fecundity, and a 10% increase in the proportion of smolts transported in barges were also simulated. The top panel is derived from brood years 1980-1994, while the bottom panel is derived from brood years 1990-1994. Error bars are ± 1 standard deviation.

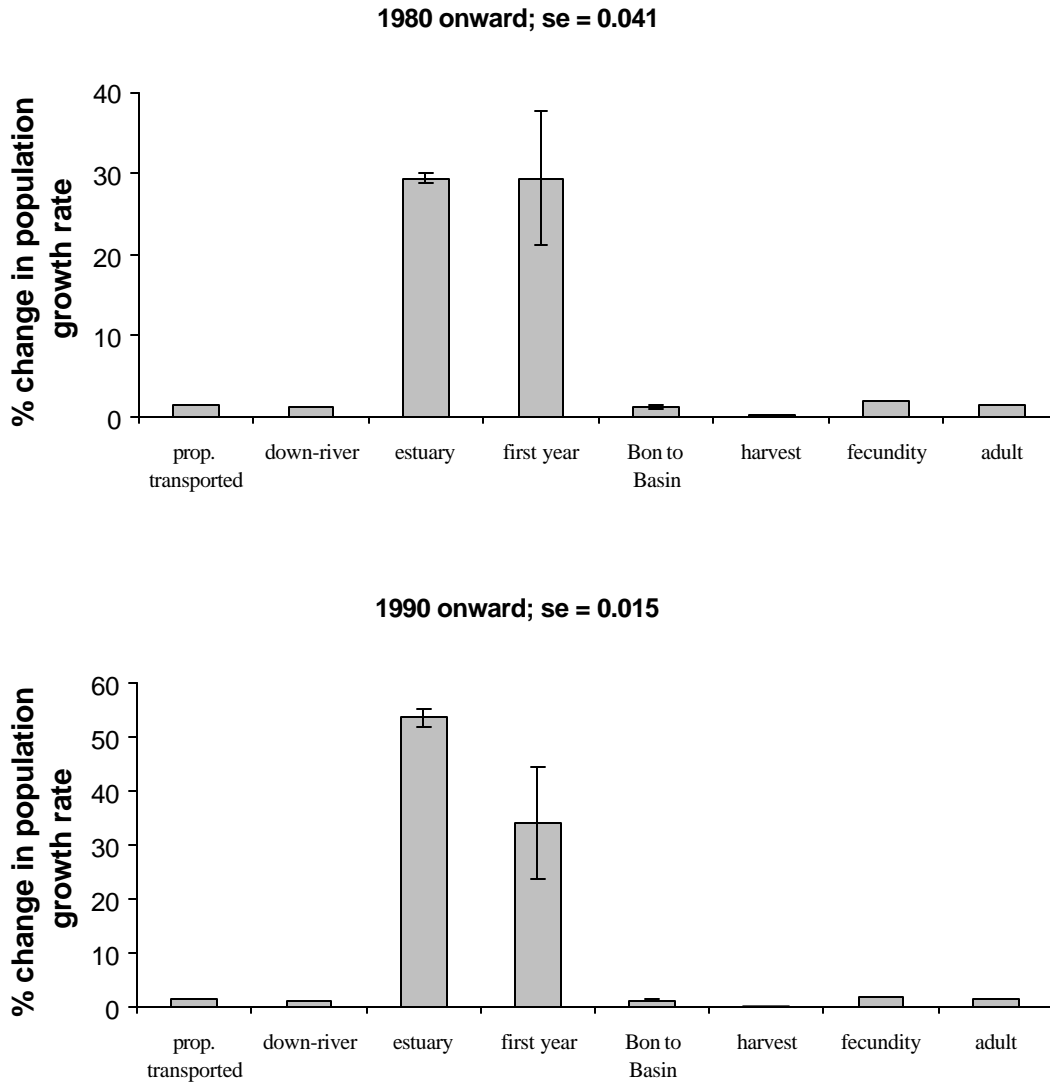


Figure VI-4. Average increase in annual population growth with a 10% reduction in mortality during different life stages for Spring/Summer Chinook salmon. Estuarine survival (s_e) was calculated to produce the smolt-to-adult returns reported by PATH. The top panel is derived from brood years 1980-1994, while the bottom panel is derived from brood years 1990-1994. Error bars are ± 1 standard deviation.

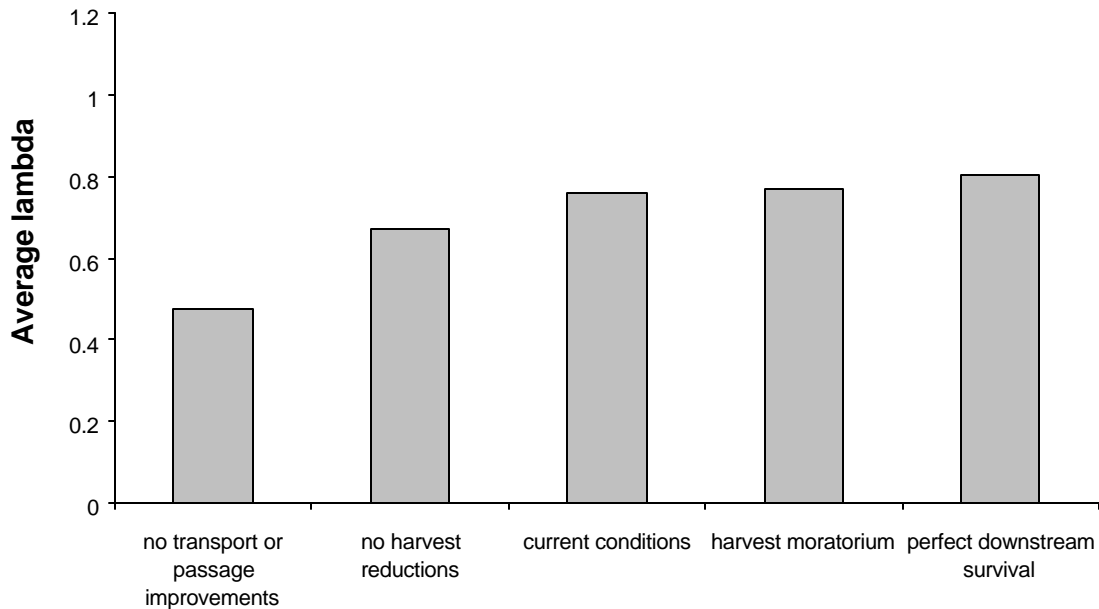


Figure VI-5 Average rate of population growth for Snake River Spring/Summer Chinook salmon assuming different management scenarios. “No transport or passage improvements” equals current conditions, except $pt = 0$ and survivorship through the hydrosystem is set at rates observed between 1977-1979 (after dams had been constructed, but before improvements to bypass and transportation). “No harvest reductions” equals current conditions, except mainstem and subbasin harvest rates set to those seen between 1960 and 1970. “Harvest moratorium” equals current conditions, but with mainstem harvest entirely eliminated. “Perfect downstream survival” equals current conditions, except $pt = 0$ and $s_d = 1.0$.

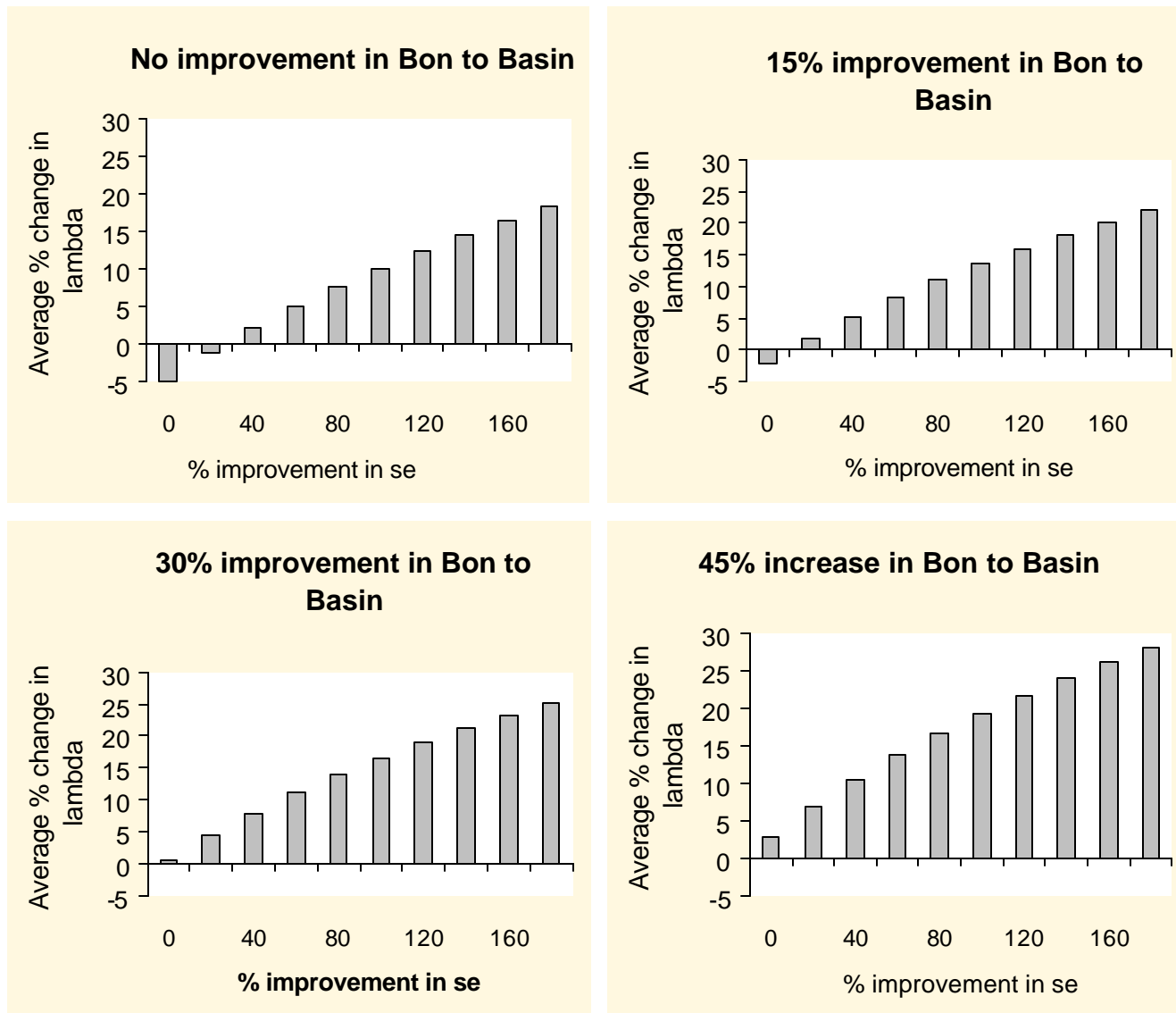


Figure VI-6. Possible Breaching Effects on Spring/Summer Chinook salmon Estimated Through Improved Estuarine and Ocean Survival in Conjunction with Improved Upstream Survival.

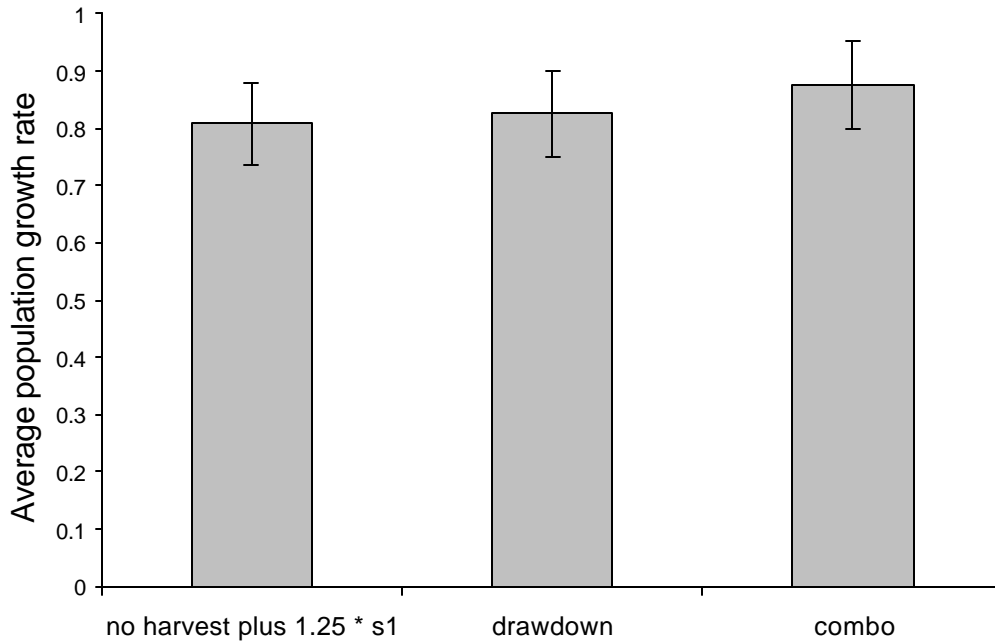


Figure VI-7. Average Population Growth for Spring/Summer Chinook Salmon: Gauging the Effectiveness of Breaching Versus an Alternative Management Scenario. “No harvest plus $1.25 * s1$ ” represents current conditions without mainstem harvest but with a 10% increase in first year survivorship. Drawdown implies that dam breaching yields a 15% improvement in survival of adults migrating upstream, a smolt downstream migration survivorship of 62%, and a 60% increase in estuarine survivorship (roughly equal to $D = 0.5$). “Combo” is the combination of both scenarios.

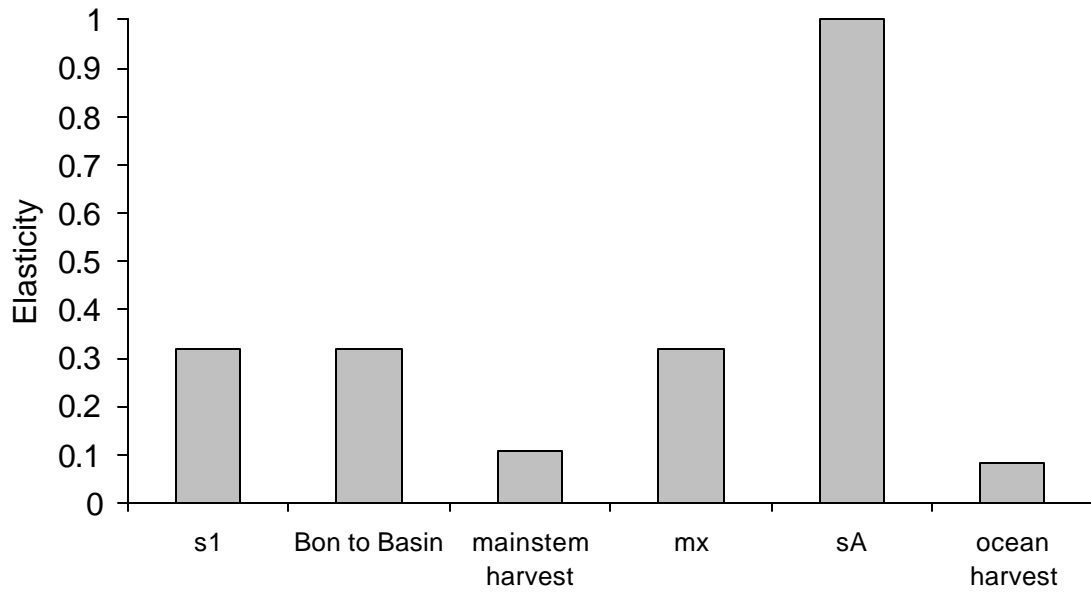


Figure VI-8. Sensitivity of annual population growth to small changes in the components of the Fall Chinook salmon demographic projection matrix.

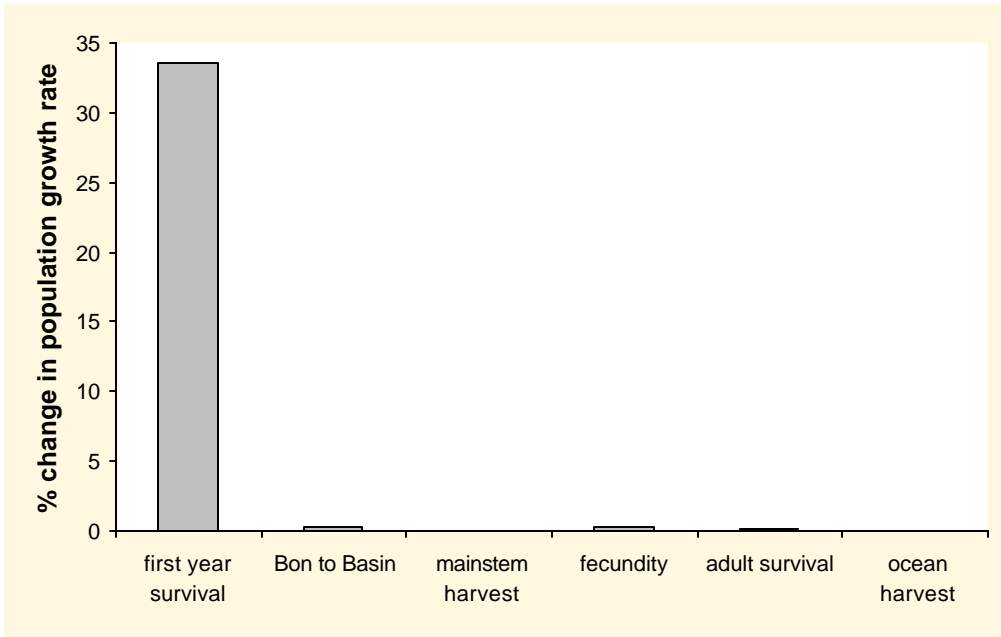


Figure VI-9. Improvements in Fall Chinook Salmon Annual Population Growth with 10 Percent Reductions in Mortality During Different Lifestages. A 10% increase in fecundity was also analyzed.

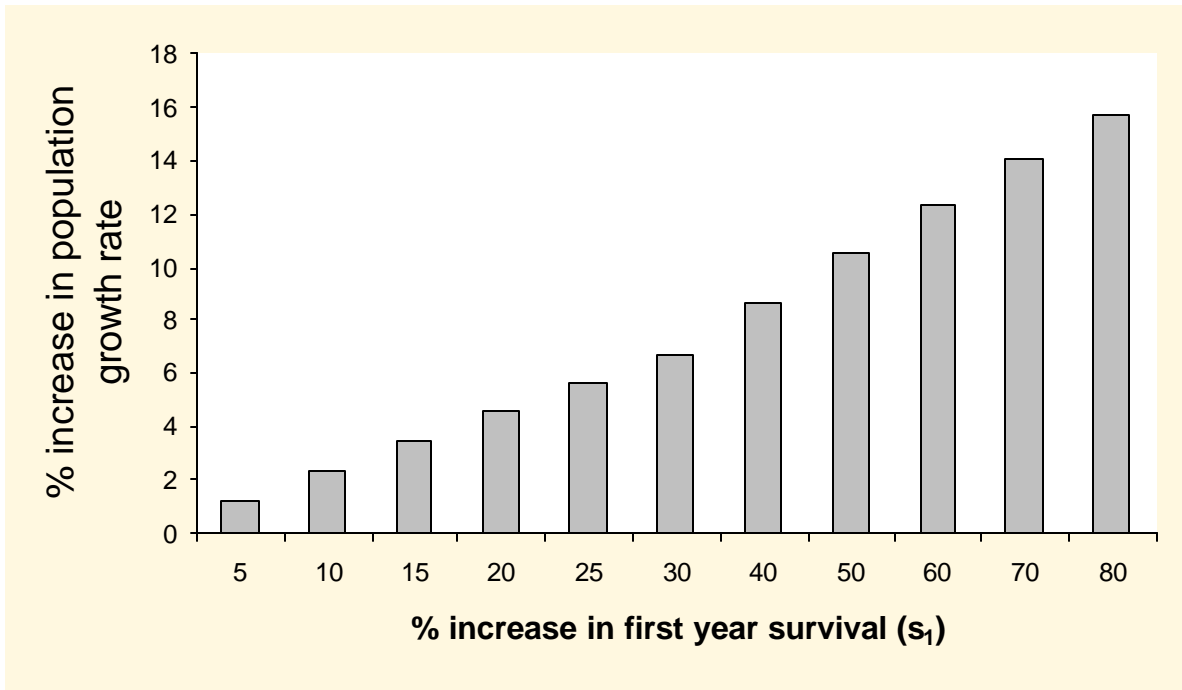


Figure VI-10. Increase in Fall Chinook Annual Population Growth with a Range Of Increases in First Year Survivorship.

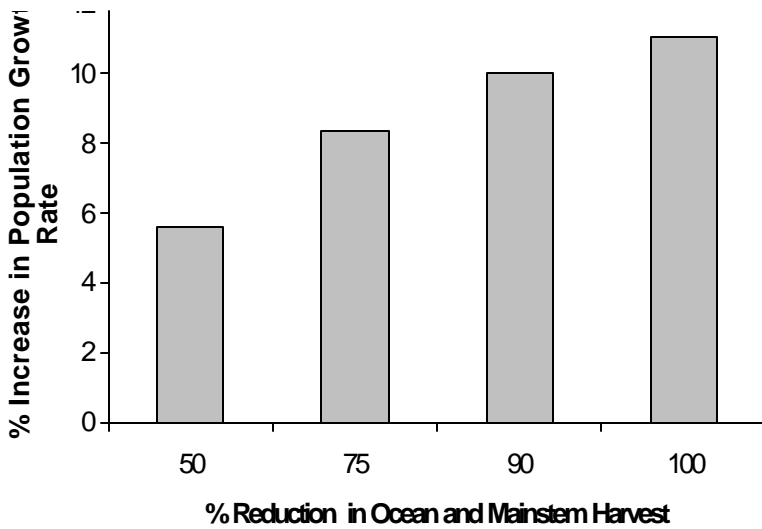
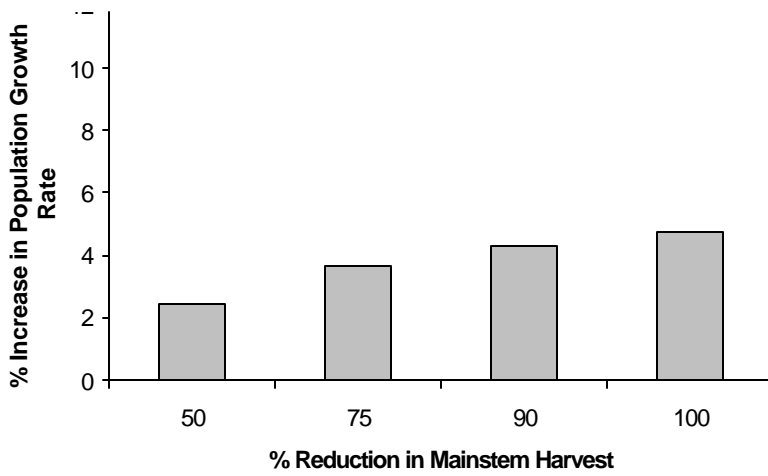
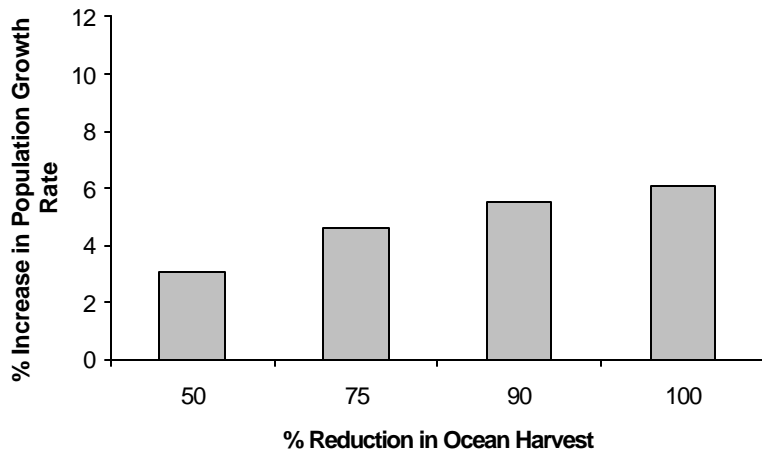


Figure VI-11. Results of a deterministic, stage-structured matrix model showing effects of harvest reduction on population growth.

VII. Summary of Key Findings: The Ten Most Important Points.

- 1) Comparisons among and within ESUs requires a standardized analytical approach. From such an approach, it is possible to draw general conclusions using a common currency about the relative risks faced by stocks within and among ESUs. Standardization also allows an assessment of the relative level of demographic improvement needed for different ESUs to mitigate extinction risk.
- 2) ESU and populations within ESU vary greatly in their risk and their rate of decline (spanning more than an order of magnitude of variation).
- 3) While Snake River Chinook salmon are clearly at risk and worthy of concerted efforts, it is worth noting that these ESUs are not the most imperiled ESUs; more specifically, steelhead in general and stocks from the Upper Columbia (steelhead and chinook) are facing the greatest relative risks.
- 4) A major uncertainty in estimating these risk measures involves information (or documentation of information) regarding the presence and influence of hatchery fish on the spawning grounds. Data on the proportion of naturally spawning fish that are of hatchery origin and the reproductive contribution of these fish are largely lacking. In the absence of such data, estimates of true population trends of wild fish may be obscured.
- 5) One way of using standardized assessments of risk is to identify “targets for improvement.” Clearly the specification of such targets is a policy decision. However, the use of a common metric derived using the same methodology highlights those populations in the most dire circumstances. Moreover, matrix models provide the life history stage that management action should target.
- 6) Harvest reductions offer plausible way to reduce risk for the few ESUs that presently bear substantial harvest burdens. Harvest reductions improved λ by 1% to 30% depending on current harvest pressure and generation time. ESUs that may be particularly likely to benefit from harvest reductions include Lower Columbia Chinook, Upper Willamette Chinook and Snake River Fall Chinook.
- 7) However, for the majority of the ESUs, harvest reductions alone are unlikely to adequately mitigate risks. For these ESUs, there is a need to ensure that the methods and data for identifying needed actions in other H’s are in place.
- 8) The most recent data for Snake River Spring/Summer Chinook salmon reveal that this ESU may be doing worse than was previously thought. It is now even less likely that dam breaching BY ITSELF will mitigate imminent risks faced by Snake River Spring/Summer Chinook salmon. Importantly, there are no data to indicate that improvements in any of the other H’s (i.e., habitat, harvest, or hatcheries) could BY

THEMSELVES, mitigate the extinction risks faced by the Snake river Spring/Summer Chinook ESU.

9) The data and metadata are generally inadequate for a more detailed analysis than we have conducted here. In particular, the quality of the data is rarely documented, and consequently sampling error is unknown. The design of monitoring and evaluation efforts is hindered by the absence of information about sampling error. Standardization and consistency are largely lacking in both methodology and documentation.

10) The emphasis now needs to shift from determining relative risk to feasibility studies that link specific management actions to likely demographic improvements. Unfortunately, the region has suffered from an inattention to standardized reporting of data and analyses, and as a result currently lacks the scientific information required to make quantitative assessments of management scenarios. It is imperative that this last point be emphasized to the public and policy makers: collectively we have failed to manage Columbia River Basin salmonid populations and are now forced to undertake management actions as experiments, accepting that some will fail, but if they are properly designed, we can learn from our mistakes.

VIII. References and Acknowledgements

- Anderson, J.R., E.E. Hardy, J.T. Roach, and R.E. Witmer. 1976. A land use and land cover classification system for use with remote sensor data. U.S. Geological Survey Professional Paper # 964. 28 p.
- Beamesderfer, R.C.P., H.A. Schaller, M.P. Zimmerman, C.P. Petrosky, O.P. Langness, and L. LaVoy. 1998. Spawner-recruit data for spring and summer chinook salmon populations in Idaho, Oregon, and Washington. Section 2, Chapter 1 in Marmorek, D.R. and C.N. Peters (eds). J. Anderson, R. Beamesderfer, L. Botsford, J. Collie, B. Dennis, R. Deriso, C. Ebbesmeyer, T. Fisher, R. Hinrichsen, M. Jones, O. Langness, L. LaVoy, G. Matthews, C. Paulsen, C. Petrosky, S. Saila, H. Schaller, C. Toole, C. Walters, E. Weber, P. Wilson, M.P. Zimmerman. 1998. Plan for Analyzing and Testing Hypotheses (PATH): Retrospective and Prospective Analyses of Spring/Summer Chinook Reviewed in FY 1997. Compiled and edited by ESSA Technologies Ltd., Vancouver, B.C.
- Beechie, T., E. Beamer, B. Collins, and L. Benda. 1996. Restoration of habitat-forming processes in Pacific Northwest watersheds: a locally adaptable approach to salmonid habitat restoration. Pages 48-67 in D. L. Peterson and C. V. Klimas, eds. The role of restoration in ecosystem management. Society for Ecological Restoration, Madison, WI.
- Beechie, T.J. and S. Bolton. 1999. An approach to restoring salmonid habitat-forming processes in Pacific Northwest watersheds. *Fisheries* 24(4): 6-15.
- Bisson, P, et al. 1997. Watershed management and Pacific Salmon: desired future conditions. pp 447-474 in Strouder et al (eds), *Pacific Salmon and their Ecosystems*.
- Bradford, M.J. 1997. Partitioning mortality in Pacific Salmon. In Emmett, R.L., and M.H. Schiewe (editors). 1997. Estuarine and ocean survival of Northeastern Pacific salmon: Proceedings of the workshop. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-NWFSC-29.
- Breiman, L., J. H. Friedman, R. Olshen, and C. J. Stone. 1984. Classification and Regression Trees. Wadsworth, Belmont, CA. 358 pp.
- Brodeur, R.D., and D.M. Ware. 1992. Interannual and interdecadal changes in zooplankton biomass in the subarctic Pacific Ocean. *Fish. Oceanogr.* 1:32-38.
- Brook, B. W., J. O'Grady, A. Chapman, M. Burgman, H. Resit Akcakaya and R. Frankham. 2000. Predictive accuracy of population viability analysis in conservation biology. *Nature* 404: 385-386.
- Burnham, K.P. and D.R. Anderson. 1998. Model Selection and Inference. Springer-Verlga, New York. 353 pages.

- Busby, P.J., T.C. Wainwright, G.J. Bryant, L.J. Lieber, R.S. Waples, F.W. Waknitz, I.V. Lagomarsino. 1996. Status Review of West Coast Steelhead from Washington, Idaho, Oregon, and California. National Marine Fisheries Service, Seattle, WA.
- Cairns, J., Jr. 1990. Lack of theoretical basis for predicting rate and pathways of recovery. *Environ. Manage.* 14(5):517-526.
- Chapman, D.W. 1986. Salmon and steelhead abundance in the Columbia River in the nineteenth century. *Trans. Am. Fish Soc.* 115: 662-670.
- Caswell, H. 1989. *Matrix Population Models*. Sinauer: Sunderland, Mass.
- Caswell, H. 2000. *Matrix Population Models*. Second Edition. Sinauer: Sunderland, Mass.
- Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage-based population model of loggerhead sea turtles and implications for conservation. *Ecology* 68:1412-1423.
- Crowder, L. B., D. T. Crouse, S. S. Heppell, and T. H. Martin. 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. *Ecological Applications* 4:437-445.
- Dennis, B. and M. L. Taper. 1994. Density dependence in time series observations of natural populations: estimation and testing. *Ecological Monographs* 64:205-224.
- Dennis, B., P. L. Munholland, and J. M. Scott. 1991. Estimation of growth and extinction parameters for endangered species. *Ecological Monographs* 61:115-143.
- Doak, D., P. Kareiva, and B. Klapetka. 1994. Modeling population viability for the desert tortoise in the western Mojave desert. *Ecological Applications* 4:446-460.
- Doppelt, B., M. Scurlock, C. Frissell, and J. Karr. 1993. *Entering the watershed*. Island Press, Covelo, CA.
- Elms-Cockrom, T. J. 1998. *Salmon Spawning Ground Survey, 1997*. Idaho Fish and Game.
- Emlen, J. M. 1995. Population viability of the Snake River chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 52:1442-1448.
- Fagan et al. 1999. Variation thresholds for extinction and their implications for conservation strategies. *American Naturalist*. 154:510-520.
- Francis, R. C., and S. R. Hare 1994. Decadal-scale regime shifts in the large marine ecosystems of the Northeast Pacific: a case for historical science. *Fish. Oceanogr.* 3: 279-291

- Fieberg J. and S. Ellner. in press. When is it meaningful to estimate extinction probability? *Ecology*.
- Frissell, C. A., and R. K. Nawa. 1992. Incidence and causes of physical failure of artificial habitat structures in streams of western Oregon and Washington. *North American Journal of Fisheries Management* 12:182-197.
- General Accounting Office (GAO). 1998. Public Rangelands: some riparian areas restored but widespread improvement will be slow. U.S. General Accounting Office, Washington, D.C. GAO/RCED-88-105. 85pp.
- Ginzburg, L. R., S. Ferson, and H. R. Akcakaya. 1990. Reconstructibility of density dependence and the conservative assessment of extinction risks. *Conservation Biology* 4:63-70.
- Hall-Griswold, J. and T. Cochnauer. 1988. Salmon Spawning Ground Survey. Idaho Fish and Game.
- Hare, S. R.; Mantua, N. J., and Francis, R. J. Inverse production regimes: Alaska and West Coast Pacific Salmon. *Fisheries*. 1999; 24:6-15.
- Healey, M. C. 1991. Life history of chinook salmon (*Oncorhynchus tshawytscha*). Pages 311-394 in C. Groot and L. Margolis, eds. *Pacific salmon life histories*. University of British Columbia Press, Vancouver.
- Holmes, E. (2000, in review). Modifying diffusion models of extinction risk to deal with sampling error and subsampled populations.
- Johnson, O.W., T.A. Flagg, D.J. Maynard, G.B. Milner, F.W. Waknitz. 1991. Status Review for Lower Columbia River Coho Salmon. National Marine Fisheries Service, Seattle, WA.
- Kauffman, J. B., R. L. Beschta, N. Otting, and D. Lytjen. 1997. An ecological perspective of riparian and stream restoration in the western United States. *Fisheries* 22(5):12-24.
- Korman, J. and P.S. Higgins. 1997. Utility of escapement time series data for monitoring the response of salmon populations to habitat alteration. *Can. J. Fish. Aquat. Sci.* 54:2058-2067.
- Lichatowich, J., L. Mobrand, L. Lestelle, and T. Vogel. 1995. An approach to the diagnosis and treatment of depleted Pacific salmon populations in Pacific Northwest watersheds. *Fisheries* 20(1):10-18.
- Ludwig, D. 1998. Management of stocks that may collapse. *Oikos* 83:397-402.
- Ludwig, D. 1999. Is it meaningful to estimate extinction probabilities? *Ecology* 80:298-310.
- Ludwig, D. and C.J. Walters. 1985. Are age-structured models appropriate for catch-effort data? *Canadian Journal of Fisheries and Aquatic Science* 42: 1066-1072.

- Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific - interdecadal climate oscillation with impacts on salmon production. *Bull. Amer. Meteor. Soc.* 78: 1069-1079.
- Marmorek, D.R. and C.N. Peters (eds). J. Anderson, R. Beamesderfer, L. Botsford, J. Collie, B. Dennis, R. Deriso, C. Ebbesmeyer, T. Fisher, R. Hinrichsen, M. Jones, O. Langness. L. LaVoy, G. Matthews, C. Paulsen, C. Petrosky, S. Saila, H. Schaller, C. Toole, C. Walters, E. Weber, P. Wilson, M.P. Zimmerman. 1998. Plan for Analyzing and Testing Hypotheses (PATH): Retrospective and Prospective Analyses of Spring/Summer Chinook Reviewed in FY 1997. Compiled and edited by ESSA Technologies Ltd., Vancouver, B.C.
- Matthews, G. and R.S Waples. 1991. Status Review for Snake River Fall Chinook Salmon. National Marine Fisheries Service, Seattle, WA.
- McElhany, P., M. Ruckelshaus, M. J. Ford, T. Wainwright, and E. Bjorkstedt. 2000. Viable salmonid populations and the recovery of evolutionarily significant units. National Marine Fisheries Service, Seattle.
- McNeil, W. J., R. Gowan and R. Severson. 1991. Offshore release of salmon smolts. *American Fisheries Society Symposium* 10:548-553.
- Meir, E. and W. F. Fagan. 2000. Will observation error and biases ruin the use of simple extinction models? *Conservation Biology* 14: 148-154.
- Miller, R., and E. Brannon. 1982. The origin and development of life history patterns in Pacific salmonids. Pages 296-306 in E. L. Brannon and E. O. Salo, eds. *Proceedings of the Salmon and Trout Migratory Behavior Symposium*, School of Fisheries, University of Washington, Seattle.
- Mendel, G.J. Bumgarner, D. Milks, L. Ross, and J. Dedloff. 1996. Lyons Ferry Hatchery Evaluation: Fall Chinook. 1995 Annual Report. Washington Dept. of Fish and Wildlife. Hatcheries Program Assessment and Development Division.
- Morris, W., D. Doak, M. Groom, P. Kareiva, J. Fieberg, L. Gerber, P. Murphy, and D. Thomson. 1999. A practical handbook for population viability analysis. The Nature Conservancy.
- Myers, J.M., R.G. Kope, G.J. Bryant, L.J. Lierheimer, R.S. Waples, F.W. Waknitz, T.C. Wainwright, W.S. Grant, K. Neely, and S.T. Lindley. 1998. Status Review of Chinook Salmon from Washington, Idaho, Oregon, and California. National Marine Fisheries Service, Seattle, WA.
- National Marine Fisheries Service (NMFS). 1999. ESA Listing Maps. Northwest Region - Protected Resources Division. 525 NE Oregon Street, Suite 500. Portland, OR 97232-2737. Tele 503/230-5400.
<http://www.nwr.noaa.gov/1salmon/salmesa/mapswitc.htm>

- National Research Council (NRC). 1996. *Upstream; Salmon and Society in the Pacific Northwest*. National Academy Press, Washington, D.C
- Northwest Power Planning Council (NPPC). 1982. *Columbia River Basin Fish and Wildlife Program*. Northwest Power Planning Council, Portland, OR
- Nickelson, T. E. 1986. Influences of upwelling, ocean temperature, and smolt abundance on marine survival of coho salmon (*Oncorhynchus kisutch*) in the Oregon production area. *Journal of Fisheries and Aquatic Sciences* 43:527-535.
- Pearcy, W. G. 1992. *Ocean ecology of north Pacific salmonids*. University of Washington Press, Seattle, Washington.
- Peters, C.N., D.R. Marmorek, and I. Parnell (eds.). 1999. *PATH Decision Analysis Report for Snake River Fall Chinook*. Prepared by ESSA Technologies Ltd., Vancouver, B.C.
- Ratner, S., R. Lande, and B. B. Roper. 1997. Population viability analysis of spring Chinook salmon in the South Umpqua River, Oregon. *Conservation Biology* 11:879-889.
- Reeves G. H., J. D. Hall, T. D. Roelofs, T. L. Hickman, and C. O. Baker. 1991. Rehabilitating and modifying stream habitats. *American Fisheries Society Special Publication* 19:519-558.
- Reeves, G., L. Benda, K. Burnett, P. Bisson, and J. Sedell. 1995. A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionarily significant units of anadromous salmonids in the Pacific Northwest. Pages 334-349 in *Evolution and the aquatic ecosystem: defining unique units in population conservation*. American Fisheries Society Symposium 17, Bethesda, MD.
- Ricker, W.E. 1972. Hereditary and environmental factors affecting certain salmon populations. Pages 27-160 in *The stock concept in Pacific salmon*. MacMillan Lectures in Fisheries, Univ. British Columbia, B.C. 231 p.
- Schaller, H. A., C. E. Petrosky, and O. P. Langness. 1999. Contrasting patterns of productivity and survival rates for stream-type chinook salmon (*Oncorhynchus tshawytscha*) populations of the Snake and Columbia rivers. *Canadian Journal of Fisheries and Aquatic Science* 56:1031-1045.
- Stearns, S.C. 1992. *The Evolution of Life Histories*. Oxford University Press, Oxford, UK.
- Sugimoto, T., and K. Tadokoro. 1997. Interannual-interdecadal variations in zooplankton biomass, chlorophyll concentration, and physical environment in the subarctic Pacific and Bering Sea. *Fish. Oceanogr.* 6:74-93.

- Thomas, D.W. 1983. Changes in Columbia River estuary habitat types of the past century.
Columbia River Estuary Study Tasforce (CREST), Astoria, OR. 51pp.
- Waples, R.S., Orly W. Johnson, and R.P. Jones, Jr. 1991. Status Review for Snake River Sockeye Salmon. National Marine Fisheries Service, Seattle, WA.
- Waples, R.S., R.P. Jones, Jr., B.R. Beckman, and George A. Swan. 1991. Status Review for Snake River Spring and Summer Chinook Salmon. National Marine Fisheries Service, Seattle, WA.
- White, M. and T. Cochnaue. 1989. Salmon Spawning Ground Surveys. Idaho Fish and Game.
- Zabel, R.W., Williams, J.G. 2000. Comments on "Contrasting patterns of productivity and survival rates for stream-type chinook salmon (*Oncorhynchus tshawytscha*) populations of the Snake and Columbia rivers" by Schaller et al. (1999). Can. J. Fish. Aquat. Sci. In press.

Acknowledgements

This synthesis of data would not have been possible without the support and use of facilities provided by NCEAS, a center funded by the National Science Foundation (Grant DEB 94-21535), the University of California-Santa Barbara, the California Resources Agency, and the California Environmental Protection Agency. We thank O.J. Reichmann and M. Snowball for providing support and encouragement while using NCEAS facilities to conduct a data synthesis and analysis workshop.