CRI Assessment of Management Actions Aimed at Snake River Salmonids

17 November 1999 Draft

Note that CRI updates its analyses frequently, and that as more analyses are added, there will be new documents and results posted on the website. The methods used in this report are on the Northwest Fisheries Science Center – Cumulative Risk Initiative website as extinction and matrix calculation Excel spreadsheets. A more complete version of this report that includes a synthesis of both CRI and PATH results will be released by the U.S. Army Corps of Engineers as part of its Draft EIS (scheduled for release December 15th).

A Cumulative Risk Analysis

1.1 NMFS has undertaken a new anaytical approach referred to as the CRI.

In lieu of a complex of single model with several hundred parameters that need to be specified, the CRI breaks the analyses into six steps:

1. Estimate the risk of extinction for known populations ("how bad is it?")

2. Construct demographic projection matrices that depict current demographic performance rates and in turn can be used to calculate asymptotic annual population growth rates (assuming a constant environment: "at what stages is mortality occuring")

3. Perform sensitivity analyses to assess where in the life cycles of salmonids there exist the greatest opportunities for promoting recovery, as measured by changes in the annual population growth rate ("where will you get the biggest bang for an improvement")

4. Manipulate the values in baseline matrices to represent hypothesized demographic responses to management actions, and calculate the percent increase in annual population growth rate associated with each management action ("examine HYPOTHETICAL scenarios of management")

5. Relate increases in average population growth rates back to reductions in extinction risks ("how do the scenarios reduce extinction risk?")

6. Explore whether the connection between the management action and the hypothesized demographic response is biologically feasible or those management actions that seem numerically effective ("are the scenarios biologically feasible?")

In addition, so that others can repeat analyses or perform alternative analyses, all data used in analyses and examples of analyses are placed on a public website. CRI purposely separates sensitivity analyses and numerical experiments concerning management scenarios from the question of what is biologically feasible. This approach better draws attention to what data gaps exist and makes the key questions more transparent. The performance measures for the CRI analyses are probabilities of extinction and average annual rates of population change.

1.2 Data Used in Analyses

The salmonid population data that NMFS has analyzed comprise the index stock counts selected by PATH for its analyses (Tables 1, 2, 3). The data for spring/summer chinook are redd counts expanded to estimate total numbers of spawners per reach, while data for fall chinook salmon and steelhead are dam counts. These data provide an agreed upon data set that all scientists can examine as a common ground. At this juncture NMFS did NOT seek different populations or population data upon which to base its analyses, because discrepancies between NMFS conclusions and the conclusions of other analytical exercises would be more difficult to understand if both different methods and different data were used.

One limitation regarding PATH index stock data is that these data are a small fraction of the actual salmonid populations in the Columbia Basin. It is not clear to what extent these index stocks provide a representative sample. NMFS is now looking more broadly at all possible population data from the region. Future analyses will involve data from a broader array of stocks, with two advantages: 1) it may be possible to empirically identify extinction thresholds by looking at situations where stocks have disappeared altogether from specific reaches, and 2) by looking at a broader range of stocks, linkages between habitat conditions and salmonid populations may be more clearly identified.

1.3 If We Do Not Act Quickly, What is the Risk of Extinction for Snake River Salmonids?

Prior to evaluating management options for endangered and threatened ESUs, it is imperative to assess extinction risks over well-specified lengths of time. It is important to quantify extinction risk because one option is always to postpone any decision until more information is known. The risk of this "waiting option" is the risk that an extinction may occur while more is being learned. Unfortunately, analyzing population data to estimate extinction risk is a technically complicated enterprise that typically yields tremendously uncertain answers (Ludwig 1999), due to the variety of models used, the inherent statistical problems of predictions, and the quality of the data used.

Table 1. Number of Spawners (S) (minus jacks) Estimated From Redd Counts and the Number of Recruits (R) to the Spawning Grounds for the Seven Stocks From 1957-1990

	Marsh		Johnson		Imnaha		Bear Valley		Poverty Flats		Sulphur		Minam	
Yr	S	R	S	R	S	R	S	R	S	R	S	R	S	R
80	16	178	55	136	189	561	12	44	42	260	163	324	43	225
81	114	199	102	158	469	677	43	300	151	248	187	367	51	619
82	71	228	93	136	611	521	17	150	83	413	192	264	106	356
83	60	484	152	391	450	664	49	615	171	1210	337	1192	105	835
84	100	60	36	113	574	167	0	59	137	89	220	250	102	232
85	197	86	178	94	721	142	62	117	295	146	341	289	642	250
86	171	102	129	208	479	172	385	252	224	229	233	821	367	364
87	268	56	175	106	448	76	67	42	456	154	554	474	588	105
88	395	274	332	442	606	424	607	261	1109	715	844	1040	507	229
89	80	25	103	90	193	142	43	17	91	75	261	314	203	81
90	101	4	141	17	169	51	170	4	185	18	572	76	342	26
91	73	5	161	29			217	16	184	18	581	95		
92	118	61	191	140			22	71	178	138	586	199		
93	218	222	357	253			264	243	709	502	880	459		

Note: Data were compiled by PATH.

Table 2. Counts of Fall Chinook Spawners and Recruits to the Uppermost Dam

Year	Adult Spawners	Adult Recruits to uppermost dam (minus jacks)
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	

Note: Data were compiled by PATH.

Four extinction-modeling approaches, listed in increasing order of complexity include:

1. simple linear models of population growth without detailed age-structure

2. nonlinear models of population growth without detailed age-structure

3. linear models of population growth with age structure

4. nonlinear models of population growth with age structure

The choice of model depends on the quality of data available and what types of processes appear to be influential. Given the detail of data available for salmonids in the Snake River, 1 and 2 above are the only practical options. Specifically, good estimates of inter-annual variation in age-specific mortality and reproductive rates are lacking. Instead, what is available are counts of spawners and how those counts vary from year-to-year.

Table 3. Counts of Steelhead Spawners and Recruits to the Uppermost Dam

Year	Spawners	Recruits to Uppermost Dam (total)
1983	24,500	18936
1984	24,500	25513
1985	26708	27433
1986	21990	16030
1987	25470	6839
1988	21033	22502
1989	24968	11848
1990	9261	7591
1991	17322	7758
1992	19346	7840
1993	7353	7651
1994	7515	4478
1995	7990	
1996	7304	
1997	8674	

Note: Data were compiled by PATH.

1.3.1 A Simple Model for Estimating Extinction Risk

As a first step, we have adopted the density-independent model and approach developed by Brian Dennis (Dennis et al. 1991). This approach uses a simple linear model of population growth rate, without incorporating age-structure. It requires the least detailed data of any of the four alternatives, and it is thus likely to be the most broadly applicable. This method uses simple census data. It involves calculating a measure of the per capita rate of recruitment (the number of individuals added to the population, adjusted for the number of individuals present). This measure is then used in a simple linear regression, and is regressed against the time period between censuses, while forcing the y-intercept through zero. The slope of this least-squared regression line serves as an estimate of the population growth rate. This value and the mean squared error are then used in a series of calculations to estimate the mean rate of population growth, its 95 percent confidence intervals, and the probability of extinction (Morris et al., 1999).

Assumptions of the Extinction Risk Analysis

The Dennis et al. (1991) approach to extinction risk analysis entails three critical assumptions whose violation can bias the results. These assumptions are:

- The variability from year-to-year in spawner counts is assumed to be due to a fluctuating environment and not due to sampling error.

- 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).
- Over the range of population sizes being examined, the rates of population change are assumed to be independent of the density of fish.

In more technical language, the model assumes that population dynamics are density-independent and result from a temporally homogenous stochastic process with negligible observation error. Although salmonid data violate all of these assumptions to some extent, the magnitude of the violation may be so small that it does not substantively influence the aptness of the model.

Assumption 1: No sampling error

Recent exhaustive numerical simulations indicate that the Dennis et al. (1991) approach provides good estimates of extinction risk, even if sampling error is biased and includes substantial random error (with coefficients of variation up to 50 percent; Fagan and Meir, in press in Conservation Biology). It is worth pointing out that NO MODEL will ever be the correct model for extinction risk, and that the best one can do is explore different models and ask how robust the conclusions are to changes in the underlying model. As time and data allow, salmonid extinction risks will be analyzed using increasingly detailed models. However, as a first step, the Dennis et al. (1991) approach is a widely accepted and frequently used approach in the conservation literature (Morris et al., 1999).

Assumption 2: Trends are homogeneous in time

To satisfy the homogenous in time assumption, the extinction modeling started with data representing brood year 1980. NMFS selected 1980 as the starting point because prior to 1980 dams were either still being built or the transportation and bypass systems were still in a major state of engineering flux. In particular, dams in the mainstem lower Snake and Federal Columbia River Power System were not completed until 1975. In the years following dam completion, the situation remained unstable because in the Snake River, only 3 of 6 possible turbine units were initially installed. Thus, powerhouse capacity was only approximately 60 kcfs and spill of large volumes during the spring outmigration often occurred. This led to frequent instances of dissolved atmospheric gas supersaturation, which in turn led to high mortalities to migrants from gas bubble disease. The full compliment of turbines was completed at Snake River dams in 1979 - which led to decreased levels of spill. Concurrent with completion of the hydropower system, efforts also were made to install flip lips (to change configuration of the flow through spillways to decrease gas supersaturating) at Lower Granite, Little Goose, Lower Monumental, McNary, and Bonneville dams. These efforts were completed by the early 1980's. Because recent years are thought to represent generally poor ocean conditions, with decadal or longer oscillations hypothesized, NMFS has focused on 1980 onward is cautious. With longer time series there would be the opportunity for good ocean years to enter the data and potentially reduce estimated risks of extinction.

Assumption 3: Density-independence

The Ricker function and its many modifications have enjoyed a long history as the premier 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, and it is the model underlying all PATH simulations for Snake River chinook salmon. A critically important parameter for assessing extinction risk is the per capita production of recruits when populations are low (near extinction), which can be estimated from a Ricker model as the intercept of the linear regression relating natural log of "recruits per spawner" to the number of spawners (this is the "A" referred to in the PATH models for Snake River chinook salmon). In practice, estimates of this parameter based on a Ricker function are biased toward producing unduly optimistic portraits of the future for populations (Ginzburg et al., 1990), because they assume that there will be greater recruitment as the number of spawners decreases.

It is worth noting that to date, most extinction risk analyses applied to salmonid populations have relied upon density-dependent models. For example, Emlen (1995) fit Ricker equations to counts of chinook salmon redds (nests) from 1957-1992 and used the estimated productivity at low density (or 'α-value') as a parameter in a stochastic model of population growth. Emlen concluded that the…

> *"present estimated α-value apparently is sufficient to virtually ensure population persistence over the next 100 years, and to lead to considerable increases in the number of redds over present counts… Population recovery, also, might be expected under present α. Indeed, in the absence of adverse weather conditions, environmental deterioration, or unexpected setbacks, the 1957-1961 levels should be regained within about 100 years." Page 1,447.*

In contrast to these predictions, redd counts have continued to decline in these same streams (data for 1993-1995), and several of the populations are perilously close to extinction. For example, the 1995 summed redd count for Bear Valley and Elk was only 8 redds, whereas the summed count for the same areas historically hovered around 1,000 redds. Ratner, Lande, & Roper (1997) similarly incorporated density-dependence in their stochastic population projections of chinook salmon in Oregon. Using a Ricker function to estimate the probability of survival from eggs to smolts, they concluded that "under the assumption of no further habitat destruction, the population is predicted to have a greater than 95 percent probability of persistence for 200 years."

It is not clear how much the assumption of density-dependence may have positively biased the conclusions of these particular simulation efforts. To assess assumptions regarding density-dependence, we examined population data from seven index stocks of Snake River spring/summer chinook salmon for which PATH has developed estimates of the age distribution for each year's spawner population. These data allow straightforward tests of density-dependence. Age frequencies were estimated each year and for each stock based on carcass lengths or scale analysis, and these frequencies were multiplied by the total number of spawners to estimate the number of 3, 4, and 5-year-old spawners (Beamesderfer et al., 1997). The number of recruits, R_t, for a particular brood year, t, is then:

$$R_t = \Sigma N_{x,t+x} \qquad\qquad\qquad \text{equation 1}$$

where $N_{x,t+x}$ is the number of adults of age x that return x years after the brood year (e.g., Table 1).

Simple linear regressions of ln(R/S) versus S provide very little evidence of density dependence in any of these seven index stocks of spring/summer chinook (See Figure 1. Figures are placed at the end of this section (#1). In particular, only 2 of 7 slopes are significantly different from zero and the R^2 values are consistently small (Table 4). Moreover, in all cases simple regression of recruits per spawner versus year explained much more of the variation than did any density-dependent function (Figure 1 versus 2). Productivity, measured as adult recruits per adult spawner has clearly been declining over recent years—yet if one assumed a density-dependent function, then further declines in spawners would be hypothesized to yield <u>increased</u> recruits pers spawner in the future – the exact opposite of the trends revealed in Figure 2. It is also worth noting the huge confidence intervals for the productivity parameter 'a' (Table 4); indeed for 6 of 7 index stocks these confidence intervals range from less than zero to greater than zero (in other words, ranging from a productivity indicative of a declining population doomed to certain extinction to a productivity indicative of an increasing population).

Table 4. Spring/Summer Chinook

Stock	a	lower 95% C.L.	upper 95% C.L.	K	lower 95% C.L.	upper 95% C.L.	e^a	b	R^2
Marsh	0.146	-1.53	1.82	136.0	75.2	196.8	1.16	-0.004 (NS)	0.055
Johnson	0.372	-0.77	1.52	155.2	101.7	208.6	1.45	-0.003 (NS)	0.076
Imnaha	0.203	-1.47	1.87	409.7	260.9	558.4	1.23	-0.002 (NS)	0.113
Bear	0.141	-0.97	1.25	278.7	104.7	452.7	1.15	-0.001 (NS)	0.053
Poverty	0.904	-1.42	1.95	413.7	291.2	536.3	2.47	-0.002 (*)	0.315
Sulphur	0.742	-0.66	2.14	153.0	50.9	255.1	2.10	-0.005 (NS)	0.196
Minam	1.384	0.04	2.72	246.2	142.5	350.0	3.99	-0.006 (**)	0.595
Average							1.94		0.201

Note: Results from regressions that provide estimates of fish productivity and assume density dependent interactions are in operation. ln(recruits per spawner) was regressed against spawner density (see Figure 1). The y-intercept (a) is an estimate of productivity at low spawner density, while the x-intercept is an estimate of carrying capacity (K) for the surveyed areas. Also included are the upper and lower 95 percent confidence limits around a and K, the Ricker function (e^a), regression slope (b) and the amount of variability explained by each regression (R^2). Data for Minam and Imnaha are from 1980-1990, data for all other stocks are from 1980-1993. Data for Sulphur in 1984 were deleted for regressions.

The absence of density-dependence evident in Table 4 runs counter to results reported in Schaller et al. (1999 PATH analyses). However, Schaller et al.(1999) detect a strong density signal only when they use data spanning from 1939 until 1990 and when they combine all index stocks into a single aggregate population. For the purpose of extinction analyses aimed at assessing the risk of losing particular stocks, NMFS feels it is better to treat each index stock separately, and to examine the data from 1980 onward as representative of current conditions. If populations rebuild to the very high levels seen prior to 1970, then density-independent analyses would be grossly in error (however, if this were the case, the populations would have recovered), and there would no longer be a need for an extinction risk analysis. The apparent discrepancy between PATH and CRI analyses with regard to density dependence might also be due in part to different definitions of recruits. CRI tabulates recruits at the spawning ground, whereas PATH adds back in losses due to harvest and upstream mortality and tabulates recruits at the mouth of the Columbia River. The CRI data are closer to the actual observations, since they do not require back-calculations involving estimates of upstream losses.

Similar analyses for Snake River fall chinook salmon and Snake River steelhead fail to provide any evidence of density dependence (Figure 3 and Table 5). Specifically, using data from 1980 onward slopes relating recruits per spawner to variations in spawner density were not significant and confidence intervals for the productivity parameter, "a" span zero. The data for fall chinook seem to indicate density-dependence, but when the same recruits per spawner ratios are plotted against year, the temporal trend is far stronger than any density trend (the temporal trend is significant, with an R^2 of 0.45, whereas the density trend is not significant and has an R^2 of only 0.20).

Table 5. Snake River Fall Chinook and Steelhead

	a	lower 95% C.L.	upper 95% C.L.	K	lower 95% C.L.	upper 95% C.L.	e^a	b	R^2
Fall Chinook	0.54	-0.65	1.73	804.9	604.0	1005.7	1.71	-0.001 (NS)	0.20
Steelhead	-0.07	-1.19	1.05	18993.0	12885.1	25100.8	0.93	-0.00002 (NS)	0.05

Note: Results from regressions that provide estimates of fish productivity and assume density dependent interactions are in operation. ln(recruits per spawner) was regressed against spawner density (see Figure 1). The y-intercept (a) is an estimate of productivity at low spawner density, while the x-intercept is an estimate of carrying capacity (K) for the surveyed areas. Also included are the upper and lower 95 percent confidence limits around a and K, the Ricker function (e^a), regression slope (b) and the amount of variability explained by each regression (R^2).

Estimating the Probability of Extinction

NMFS extinction analyses followed the Dennis et al. (1991) approach, with two modifications. First, because the risk of extinction is strongly influenced by current population size and spawner counts vary so dramatically from year to year, NMFS did NOT use point estimates of spawner populations. Instead, for the current baseline population size, the average over the last 5 years (from 1991-1995 or from 1994-1998) was used as the baseline population for all extinction calculations. This reduces the sensitivity of extinction risk estimates to an unusually high or unusually low spawner count. Second,

the method needs to be modified to account for the fact that the abundance of spawners in one year is not directly related to the abundance of spawners the next year, but rather should be related to the adults returning 2-, 3-, 4-, 5-, and sometimes 6-years later (depending on the species and ESU). To get around this problem, use was made of data regarding age distribution of spawners. The number of recruits originating from each group of spawners was calculated using equation 1. The time between censuses was then obtained for each run year as the weighted mean time it took for recruits to return to the spawning grounds.

NMFS has also calculated a quasi-extinction risk, rather than the probability of absolute extinction. Specifically, the Dennis et al. approach was used to calculate the probability that the number of spawners for an index stock will fall to one fish in any single year within a particular time frame (10 years and 100 years). Because the salmonids of concern can live in the ocean for several years, it would actually be possible for a stock to return zero spawners for a number of years in a row, but still have potential spawners alive in the ocean. Of course, from a management perspective, returning one or fewer fish to spawn in any year would be considered extremely undesirable, which suggests that a quasi-extinction level of one is reasonable. Moreover, the Dennis et al. analyses, like most extinction models, neglect catastrophes and therefore tend to underestimate risks. For salmonids, catastrophes that could have a major impact on recruitment, such as major floods and debris flows, appear to occur as often as once every 100 years, but too infrequently to be represented in typical 10-15 year slices of data (see Table 1 in Bisson et al. 1997). Details of the Dennis et al. (1999) calculations are provided on the Northwest Fisheries Science Center – Cumulative Risk Initiative website, but the summary of results appears in Tables 6 and 7. Sockeye in the Snake River are essentially maintained by a captive brood program and have already fallen consistently below the quasi-extinction level.

Extinction Risks

Spring/Summer Chinook Extinction Risks

The most notable conclusion is that extinction risks even on the short term (10 years) are considerable. For example, stocks from both Marsh Creek and Sulphur Creek have at least a 1 in 10 chance of reaching the quasi-extinction level of one spawner during the next 10 years (Table 6). Moreover, when we extend the analyses to 100 years, many stocks show a better than 1 in 2 chance of being extinct (Table 6). There are several caveats. First, the confidence intervals about these estimates are large (as Ludwig 1999 indicates they almost always will be). Second, the Dennis et al. (1997) approach does not deal with the multiple life history paths that salmonids from the same cohort may follow. Nonetheless, as Table 6 indicates, a considerable imminent risk of extinction exists unless conditions improve, albeit with tremendous uncertainty surrounding this estimate of risk.

Fall Chinook Salmon and Steelhead

There is only one Snake River index count for fall chinook salmon and for steelhead, which means there are fewer extinction risks to track. Over the short term of 10 years, both fall chinook and steelhead have very low probabilities of ever declining to as few as one spawner (less than 0.0001 probability). However, over a 100-year time period, the extinction risks are quite high: 27 percent

Table 6. Spring/Summer Chinook

Stock	Avg. λ	avg. N over last 5 years	p(extinction within 10 yrs)	p(extinction within 100 yrs)
Marsh	1.25	60	0.15	0.88
	(0.81-1.92)		(0.01-0.73)	(0.003-1.0)
Johnson	1.08	98	0.001	0.41
	(0.87-1.34)		(<0.001-0.36)	(0.001-1.0)
Bear	1.16	142	0.01	0.59
	(0.85-1.59)		(<0.001-0.53)	(0.002-1.0)
Poverty	1.10	248	<0.001	0.33
	(0.87-1.38)		(<0.001-0.27)	(<0.001-1.0)
Sulphur	1.48	68	0.10	0.56
	(0.89-2.44)		(0.007-0.71)	(0.004-1.0)
Imnaha	0.999	416	<0.001	0.74
	(0.82-1.22)		(<0.001-0.17)	(<0.001-1.0)
Minam	1.40	115	0.04	0.41
	(0.86-2.20)		(0.002-0.72)	(0.002-1.0)

Note: Average population growth rate (λ), populations size (N), and probability of extinction within 10 and 100 years for seven index stocks of spring/summer chinook salmon. Confidence intervals for predictions are listed in parentheses. Analyses for Imnaha and Minam used data from 1980-1995. Analysis for all other stocks used data from 1980-1998.

Table 7. Snake River Fall Chinook and Steelhead

	Avg. λ	avg. N over last 5 years	p(extinction within 10 yrs)	p(extinction within 100 yrs)
Fall Chinook	0.985	706	<0.001	0.65
	(0.4-1.16)		(<0.001-0.05)	(0.001-1.0)
Steelhead	0.91	7767	<0.0001	0.93
	(0.80-1.03)			(0.0004-1.0)

Note: Average population growth rate (λ), populations size (N), and probability of extinction within 10 and 100 years for seven index stocks of spring/summer chinook salmon. Confidence intervals for predictions are listed in parentheses. Snake River Fall chinook analyses used data from 1980-1996 and Snake River steelhead analyses used data from 1983-1997.

for Fall Chinook salmon and 93 percent for steelhead. The reason for such a striking difference between short-term and long-term risks is that both of these stocks are currently at relatively high abundance levels (over 500 fish), which makes it unlikely they can decline so rapidly that they fall below one spawner in only 10 years. On the other hand, when considering a 100-year time scale, the starting population is less important and the extinction risk becomes increasingly dependent on population trends and variability. Snake River steelhead are notable because their extinction risk over

a 100-year time period is estimated to be disturbingly high (93 percent), even though their current population has averaged 7,767 over the last 5 years. This high 100-year risk reflects the fact that the steelhead population has exhibited a steep rate of decline since 1980 (Table 3).

The Connection Between Changing Annual Rate of Population Growth and Extinction Risk

Population recovery is inversely related to a population's risk of extinction. Therefore, to recover a population, its risk of extinction should be small over a 100-year period; exactly how small is a policy decision. Using our current estimates of environmental variability, current population size, and current population trend, it is possible to use the Dennis et al. (1997) approach to associate an increase in the annual rate of population change with a reduction in the extinction risk. Tables 8 and 10 summarize the results of this calculation for the Snake River spring/summer chinook salmon, fall chinook salmon, and steelhead stocks. In addition, Table 9 outlines the reduction in extinction probability associated with particular percent increases in the annual rate of population change for the spring/summer index stock at Marsh Creek. NMFS has focused on Marsh Creek because it is currently the spring/summer chinook index stock at the greatest risk.

In general, substantial increases in the annual rate of population growth are necessary to push 100-year quasi-extinction risks for spring/summer chinook below .01 (50 percent increase for Marsh Creek; 25 percent increase averaged across the seven index stocks of spring/summer chinook). For steelhead, a 10 percent increase in annual growth rate would be required to lower the 100-year extinction probability to below .01. In contrast, fall chinook appear to be much less at risk, since only a 4 percent increase in annual growth rate is needed to reduce their 100-year extinction probability to below .01. For the Snake River spring/summer index stocks, the .01 risk threshold may seem unduly cautious because it is unlikely that these populations are totally independent (and hence incapable of being rescued by strays from other populations). For that reason, NMFS has provided a calculation of what percent increase in annual population growth rate is needed to reduce the probability of extinction to less than 0.1 for each of the seven populations (Table 8).

Table 8. The Percent Change in Population Growth Rate (λ) Required to Lower the Probability of Extinction for Each of the Seven Snake River Spring/Summer Chinook Salmon Index Stocks to Either 0.1 or 0.10 in 100 Years

	% change in λ needed	
Stock	p(extinction within 100 years) = 0.1	p(extinction within 100 years) = 0.01
Marsh	27.2	49.4
Johnson	5.1	11.0
Imnaha	7.6	12.1
Bear	11.1	21.2
Poverty	4.3	10.3
Sulphur	19.3	44.5
Minam	11.3	28.2
Average:	12.3	25.2

Table 9. Extinction Probability for Spring/Summer Chinook in Marsh Creek (the Index Stock with the Highest Probability of Extinction) Associated with Particular Increases in Population Growth Rate (λ)

	probability of extinction within:	
% change in λ	10 years	100 years
5	0.11	0.73
10	0.08	0.54
15	0.06	0.35
20	0.04	0.22
25	0.03	0.13
30	0.02	0.07
35	0.01	0.04
40	0.01	0.03
50	0.004	0.01
100	0.0001	0.0001

Table 10. Extinction Probability for Snake River Fall Chinook and Snake River Steelhead Associated with Particular Increases in Population Growth Rate (λ)

	p(extinction within 100 years)	
% change in λ	Fall Chinook	Steelhead
5	0.13	0.33
10	0.006	0.008
15	8×10^{-5}	1.1×10^{-5}
20	4.8×10^{-7}	9.9×10^{-10}

1.4   Using a Matrix Model to Summarize Demographic Rates and Opportunities for Recovery

The preceding analyses provide estimates of extinction risks. The next steps are to explore what is known about the life cycle of particular stocks and describe where mortality occurs; both steps are needed to identify opportunities for recovery. Demographic matrices are mathematical devices for organizing schedules of mortality and reproduction into a framework that is convenient for data presentation, analysis, and prediction. We have adopted year-class matrices to iterate salmonid populations from one year to the next, as shown in the following example:

$$N(t+1) \quad = \quad A * N(t) \qquad\qquad\qquad\qquad \text{equation } 2$$

where N(t) is a column vector pertaining to the number of individuals in each of the five age classes:

N_1
N_2
N_3
N_4
N_5

with N_x corresponding to number of fish of age x. The matrix A is a 5 by 5 matrix with the following structure:

$$A = \begin{matrix} 0 & 0 & R_3 & R_4 & R_5 \\ a_{12} & 0 & 0 & 0 & 0 \\ 0 & a_{23} & 0 & 0 & 0 \\ 0 & 0 & a_{34} & 0 & 0 \\ 0 & 0 & 0 & a_{45} & 0 \end{matrix} \qquad \text{equation 3}$$

where the above matrix would pertain to fish that live, at most, 5 years, but that could reproduce as early as year 3. The top row represents production of young from 3-, 4- or 5-year-old fish, and the a_{ij}'s along the sub-diagonal represent transitions of fish from the *i*th age class to the *j*th age class. Each element in the matrix may actually be more complicated than displayed above. For example,

$$R_3 = (1-\mu)b_3(m_3/2)s_1 \qquad \text{equation 4}$$

where μ is the mortality of adult females as they swim upstream to spawn, b_3 is the propensity of three year old females to migrate upstream to breed, m_3 is the fecundity of age 3 females, and s_1 is the survival from eggs to 1 year olds. Similarly, instead of a simple a_{ij} transition rate for survival from one age class to the next, we have to account for complications. For instance, when modeling the fate of fish from Snake River stocks between their first and second birthday (a_{12}), we need to recognize the fact that fish may experience different survival rates depending on whether they are barged down the river or swim down the river. Thus, a_{12} for Snake River stocks might be expressed as:

$$a_{12} = ((1-pt) * s_d + pt*s_b)* s_e \qquad \text{equation 5}$$

where pt is the proportion of fish transported in barges, s_d is survival of fish that swim downstream, s_b is survival of barged fish, and s_e is survival of smolts in the estuary and during their first winter in the ocean. Equation 5 neglects the hypothesis favored by some biologists that survival in the estuary and early ocean phases depends on whether fish were barged or swam to the estuary in – but it would be easy to expand s_e into two separate terms that parameterize this hypothesized complication. For the older age classes, the a_{ij} is more straightforward:

$a_{23} = s_3$

$a_{34} = s_4(1-b_3)$ equation 6

$a_{45} = s_5(1-b_4)$

where s_x is the survival from age x-1 to age x, and b_x is the propensity of adults of age x to breed.

This basic matrix framework is exceptionally flexible and can accommodate:

1. density-dependence in particular matrix elements

2. dispersal between different populations

3. life history variation, with transitions from one life history to another

4. impacts of all four "H" factors

5. environmental variability and uncertainty in parameter estimation

6. demographic stochasticity.

Most importantly, there is a vast tradition of applying this matrix framework to managing endangered and threatened species (e.g., Crouse et al., 1987; Crowder et al., 1994; Doak et al., 1994; Horvitz and Schemske, 1995), with a rich underlying statistical and mathematical theory on which to draw (Caswell, 1989). Given the pace with which NMFS must make progress, it is a tremendous advantage to adopt such a standard tool, without having to invent any new analytical machinery. The most useful application of these demographic matrices involves the calculation of the dominant eigenvalue (or asymptotic rate of population growth, or λ). This rate of growth is conceptually the same as the annual rate of growth referred to in the Dennis et al. analyses, except the two numbers need not agree with one another because they are based on different underlying models and are based on different data. The Dennis et al. growth rate comes only from spawner counts without any age-structure, and included data up to 1998. The matrix-based growth rates require age-specific survival and reproductive rates and were based on data through only 1995.

Estimating the Matrices for Snake River Spring/Summer Index Stocks

In this document, it is demonstrated how the parameter estimates used in the demographic matrices for Snake River spring/summer chinook salmon were obtained (details for how to repeat the calculations are available on the CRI website). These particular salmon stocks have been relatively well studied; for many other stocks, parameterization methods will have to be modified to accommodate far less complete data.

To derive parameter estimates, current demographic data (1980 – present) were used, including redd counts and PIT-tag studies. For the seven stocks of Snake River chinook examined here (Marsh Creek, Sulphur, Bear/Elk, Johnson, Poverty Flat, Imnaha, and Minam), adults return as 3-, 4-, or 5-year olds to spawn and die—none are known to 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			$(1-\mu)s_1b_3m_3/2$	$(1-\mu)s_1b_4m_4/2$	$(1-\mu)s_1m_5/2$
2	s_2				
3		S_3			
4			$(1-b_3)s_4$		
5				$(1-b_4)s_5$	

s_x = probability of survival of females from age (x-1) to age x
m_x = number of eggs/female spawner of age x
b_x = propensity of females of age x to breed
μ = mortality of adult females during their migration upstream

Note that s_2 is actually a more complicated expression given by:

$$s_2 = ((1-pt) * s_d + pt*s_b)* s_e \qquad\qquad \text{equation 7}$$

where pt is the proportion of fish transported in barges, s_d is survival of fish that swim downstream, s_b is survival of barged fish, and s_e is survival of smolts in the estuary and during their first winter in the ocean. In section 1.4.3, S_2 is further modified so it can be used to simulate different hypotheses about mortality below Bonneville Dam due to the presence of the hydrosystem. The resulting seven baseline matrices representing average current conditions are given in Table 11.

Matrices reflecting so-called average conditions can be calculated in many different ways. The matrices in Table 11 used median recruits per spawner rates. Alternatively mean recruits per spawner, or the geometric mean matrix, could be used. All three of these approaches were tried, and the results discussed below are not qualitatively altered by these alternative methods for taking an average. For a detailed population viability analysis, estimates of temporal variation for each matrix entry separately, 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, except slightly more refined estimates of extinction risks. This is not where NMFS believes future research needs to be directed.

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Table 11. Parameterized Matrices and Population Growth Rates (λ) for Seven Index
Stocks of Snake River Spring/Summer Chinook Salmon

Marsh:	1	2	3	4	5	λ = 0.898
1	0	0	0	7.097	38.370	
2	0.058	0	0	0	0	
3	0	0.800	0	0	0	
4	0	0	0.800	0	0	
5	0	0	0	0.652	0	
Johnson:	1	2	3	4	5	λ = 1.017
1	0	0	0.618	13.030	69.120	
2	0.058	0	0	0	0	
3	0	0.800	0	0	0	
4	0	0	0.793	0	00	
5	0	0	0	0.649	0	
Imnaha:	1	2	3	4	5	λ = 0.926
1	0	0	0.418	12.555	43.593	
2	0.058	0	0	0	0	
3	0	0.800	0	0	0	
4	0	0	0.792	0	0	
5	0	0	0	0.570	0	
Bear:	1	2	3	4	5	λ = 0.940
1	0	0	0	8.431	47.635	
2	0.058	0	0	0	0	
3	0	0.800	0	0	0	
4	0	0	0.800	0	0	
5	0	0	0	0.658	0	
Poverty:	1	2	3	4	5	λ = 1.034
1	0	0	0.896	13.471	74.633	
2	0.058	0	0	0	0	
3	0	0.800	0	0	0	
4	0	0	0.790	0	0	
5	0	0	0	0.656	0	
Sulphur:	1	2	3	4	5	λ = 0.983
1	0	0	0	10.678	58.994	
2	0.058	0	0	0	0	
3	0	0.800	0	0	0	
4	0	0	0.800	0	0	
5	0	0	0	0.655	0	
Minam:	1	2	3	4	5	λ = 0.861
1	0	0	0.164	12.086	30.748	
2	0.058	0	0	0	0	
3	0	0.800	0	0	0	
4	0	0	0.796	0	0	
5	0	0	0	0.486	0	

Where in the Spring/Summer Chinook's Life Cycle are the Greatest Opportunities for Recovery?

The relative value of potential changes in the various demographic rates of Snake River spring/summer chinook salmon were assessed in two distinct ways. First, the elasticity of the population growth rate (λ) to small changes in each of the underlying demographic parameters (Caswell, 1989) was examined. Elasticity is a standardized measure of the sensitivity of λ to each of the underlying parameters, where the sensitivity is standardized by the original magnitude of the parameter.

$$\text{elasticity} = (d\lambda/da_{ij})^* \ (\lambda/a_{ij}) \qquad\qquad\qquad \text{equation 8}$$

The best way to think of elasticity is as a measure of the responsiveness of population growth to incremental (small percent) improvements in survival and reproduction. By this measure, the most important parameter is the survival of adults in the ocean (Figure 4). This is not a particularly surprising finding, since survival of individuals near the age of first reproduction is generally among the most important life history parameters for organisms. 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 first reproduction have high reproductive value because they have made it through the long period of lowest survival and are just about to begin contributing offspring.

As a second way of comparing the importance of various life stages and demographic rates, NMFS examined the percent change in λ that would be expected if a management action could somehow save 1 out of every 10 individuals that currently die at each stage. Saving 1of 10 fish that currently die during a lifestage corresponds to a 10 percent reduction in the mortality rate. Sensitivity analyses using the "save 1 in 10 fish" numerical experiment are, in some ways, preferable because it is easier to relate these results to field data and biological intuition than a partial derivative of λ with respect to survival (the elasticities used in Caswell, 1989). Although it is straightforward to translate survival improvement to mortality reductions, the interpretation of a fixed percentage change in either of these parameters can be misleading. A 10 percent change in survival or mortality will yield different absolute numbers of saved fish depending on the starting survival or mortality rate. For instance, note that a 10 percent improvement in a baseline survival of 0.80 saves 8 of 20 fish, whereas a 10 percent improvement in a baseline survival of 0.1 saves 1 of 90 fish. Moreover, the absolute number of saved fish will differ depending on whether survival or mortality is changed. Increasing survival by 10 percent (say from 0.8 to 0.88) implies **saving 8 of 20** fish currently dying, whereas decreasing a mortality rate by 10 percent (say from 0.2 to 0.18) implies **saving only 2 of 20** fish that currently die. In addition to changes in λ that result from reductions in mortality, the percent change in λ that might result from a 10 percent increase in fecundity, or a 10 percent increase in the proportion of smolts transported by barge is reported herein. By the saving 1 in 10 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 5). A 10 percent reduction in mortality during the first year of life is predicted to result in a 20-

30 percent increase in λ (average for the seven stocks = 47.2 percent). A 10 percent reduction in mortality occurring as smolts enter the estuary and during their first year in the ocean (s_e) is expected to result in a 34-57 percent increase in λ (depending on which index stock is being examined). Changes in the other parameters have a much smaller effect on λ (Figure 5). This result is driven in part by the current low values of survival in the first year and in the estuary – and therefore saving 1out of every 10 fish that currently die at these stages would mean saving relatively more individual fish.

It is important to note that both sensitivity measures predict that the survival of inriver 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 reductions in direct mortality from improved fish transportation or improvements in 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, current rates of fish transportation and other improvements to the hydropower system are necessary if stocks are to have any chance of long-term survival (see next section (#2)). In addition, it is also possible that further improvements that influence survival below Bonneville Dam (because they enhance individual fitness or alter run-timing in beneficial ways) could have substantial payoffs.

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

The first impression created by the above sensitivity analyses is that harvest and migration corridor improvements are unimportant. This is not the case. Rather, the situation is that further management actions aimed at harvest and downstream survival for spring/summer chinook salmon (excluding dam breaching) are not likely to be that helpful, but past actions have been crucial; so much has already been done with these two management levers that stocks are now in a region of diminishing returns. To show this clearly, NMFS conducted the following numerical experiment. First, harvest and all other demographic rates were held at their current values, whereas transportation was assumed to be non-existent (pt = 0) and other migration corridor rates impacted by dams were assumed to have not been improved by flow regimes, more turbines, etc. Specifically, s_d and Bon to Basin (survival of adult migrants from the Bonneville Dam back to the basin of origin) survival rates estimated from 1977-1979 run reconstruction data were used as opposed to average rates between 1980 and 1995. 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 0.0093 (down from current average of 0.3225) and the Bon to Basin conversion rate averaged 0.56 (down from current average of 0.63). What is learned from this numerical simulation is that if survival through the hydropower system had remained at the low levels of the 1970s, spring summer/chinook salmon populations in the Snake River would likely have already gone extinct (since the estimated annual decline assuming those unimproved hydrosystem passage conditions is over a 50 percent population loss each year (see the leftmost bar in Figure 6). 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, if 100 percent of the fish were transported, annual rates of population growth would increase on average by only 3.6 percent (much lower than the

needed 25 percent increase). Alternatively, if system survival downstream were elevated to 100 percent, the annual population growth would still increase on average by only 4 percent (which is still far below the needed 25 percent increase). In short, perfect downstream survival by itself would not be enough given the mortality suffered during other life stages of spring/summer chinook salmon.

In a similar vein, another numerical experiment was performed with all rates current except harvest; harvest rates typical of 1960-1970 were imposed (average mainstem harvest rate = 0.3904, average subbasin harvest = 0.1148 compared to current average mainstem harvest rate = 0.065, subbasin harvest = 0). Under harvest rates from the 1960s (yet 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 less than 1). In sum, without the harvest reductions and hydropower system improvements made over the last 20 years, spring/summer chinook salmon would probably have gone extinct by now (Figure 6). However, given current rates, further reductions in harvest or improvements in direct downstream survival are NOT likely to accomplish much by themselves for spring/summer chinook (see the two rightmost bars in Figure 6).

The next question is, **without drawdown can enough improvement come from ALL actions combined to accomplish adequate recovery?** As an initial attack on this question, NMFS simulated the following incremental improvements in Snake River spring/summer chinook demography: no harvest, reduced predation on smolts (with the reduction estimated by studies indicating that hatchery releases of steelhead smolts take as many of 22 percent of chinook smolts and claim this is a lower estimate (Cannamella, 1993); maximum transport, a 10 percent improvement in estuarine survival (perhaps through improved water quality, altered timing of runs, or reduced predation at the mouth of the Columbia and coastal ocean environment), and a 10 percent improvement in first year survival due to habitat improvements. If ALL of these incremental actions are added together, then more than a 14 percent increase in annual population growth rates (Figure 7) could be expected, which is likely to recover the populations of spring/summer chinook salmon. The weak point in this analysis is determining whether these sorts of improvements are technically and logistically feasible. NMFS is currently examining data to determine feasibility. Certainly these results indicate that there is value to implementing suites of management actions that might yield many incremental improvements in different portions of the salmon lifecycle, because added together, the net effect could be substantial.

A final key question **is whether dam breaching by itself is likely to recover 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 PATH for the breaching option), 2) improved upstream survival (here the simulations with four levels of potential improvement in the upstream survival rates were run), and 3) possibly improved survival below Bonneville Dam because differential delayed transportation mortality and/or extra mortality would no longer be an issue. Differential delayed transportation mortality is related to reduced survival of transported fish compared to inriver migrants below Bonneville Dam, whereas extra mortality is a hypothesized reduction in the survival of both transported fish and inriver 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.

The results are summarized in Figure 8. Averaged across the seven spring/summer index stocks, an increase in λ of approximately 12 percent is needed to reduce the current probability of extinction within 100 years to 1 in 10 (Table 8). Using this criterion, and if dam breaching causes no improvement in adult upstream conversion rates, a 120 percent increase in current rates of survival below Bonneville Dam (s_e) is required for dam breaching alone to solve the problem for spring/summer chinook (Figure 8). If upstream migration survival is improved by 30 percent, an 80 percent increase in s_e would be needed, and if upstream migration survival is improved by 45 percent, a 60 percent improvement in s_e would be needed. 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.

When the discussion is phrased in this manner, the key question is obvious: how much would dam breaching increase estuarine survival, upstream conversion rate, and downstream survival 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 NMFS feels is optimistic. For this scenario, the improvements associated with breaching were assumed to result in a 15% 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). To put this drawdown scenario in context, it was compared with a zero-harvest plus a 10 percent improvement in first year survival (s_1) due to habitat improvements. 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 9). **Only in combination do these actions produce an increase in population growth that gets close to what is needed (an 10 percent increase when a 12 percent increase is needed).**

One weakness of this analysis is that dam breaching may in fact alter additional components of the life cycle, beyond the three parameters explored here. For example, dam drawdown could also result in increases in habitat availability and possible improvements in s_1 (because of lower predation rates when reservoirs are drained). Dam breaching could also alter patterns of nutrient cycling and replenishment that, in turn, influence productivity. There could even be delayed effects of dam breaching in terms of increased fitness of fish that would be subtly manifested throughout the life cycle (as opposed to discrete improvements in the survival of any isolated stage).

1.5 What Is the Bottom Line and What Are the Critical Uncertainties for Spring/Summer Chinook Salmon?

Unless dam breaching increases survival below Bonneville Dam by upwards of 60 percent, it seems unlikely that dam breaching by itself can recover spring/summer chinook stocks. It might seem surprising that dam breaching does not yield a dramatic and clear effect with minimal uncertainty, given the obvious impacts of dams. The reason for this is that the fish passage systems and barging of fish (most spring/summer chinook salmon are barged) are effective at getting fish to below Bonneville Dam. In a sense, engineering has replaced nature for that portion of the salmon life cycle. There may be many ecological reasons to favor natural processes and natural rivers, but in terms of demographic accounting for spring/summer chinook salmon, those reasons have to be found outside the direct impacts of dams on fish migrating through the hydrosystem. PATH analyses have

hypothesized that the place to look for these effects is below Bonneville Dam, in terms of extra mortality caused by the hydrosystem. Experimental approaches that manipulate the location of offshore releases, such as those of McNeil et al. (1991), would be an effective way of understanding and thereby minimizing this extra mortality resulting from transportation. Alternatively, it could be that the hydropower system alters survival during the first year because it impedes processes by which nutrients are replenished and the productivity of rearing habitats is maintained. If solutions outside the hydropower system are considered (habitat improvements, harvest reductions, hatchery modifications, predator control) a similar paucity of data relating management action to demographic improvements exists. It is easy to produce plausible simulations showing that many incremental actions can add up to produce greater than 10 percent enhancements of annual population growth rates (and hence likely recovery). But there are very few data to determine whether these incremental improvements are actually feasible. For example, it is not known whether habitat improvements could possibly increase first-year survival by 10 percent, or whether any management action could effectively enhance estuarine survival. Minimally, these analyses make clear what is yet needed to learn—the biology of inriver predation, estuarine predation, the effects of stress from hydro passage on physiological and reproductive performance, hatchery interactions, and habitat-dependent productivity that appear to play the most crucial roles for spring/summer chinook demography in the Snake River.

Given the substantial risk of extinction over the short term, a totally risk averse policy would recommend dam breaching, a moratorium on harvest, and vigorous improvements in all other areas as well. Alternatively, policy makers may want to accept the 1-in-7 odds of short-term quasi-extinction for Marsh Creek stocks if no action is taken quickly and explore whether aggressive management without dam breaching could recover the stocks. The risks for Marsh Creek may be accepted because the risks of short-term extinction for other spring/summer chinook stocks are substantially lower (e.g., less than .001 for the Johnson Creek and Imnaha stocks). Finally, breaching by itself is likely to recover spring/summer chinook salmon only if the negative impacts of dams beyond fish passage obstruction and fish passage mortality are large (and at this point in time there are no data with which to assess whether these sorts of extensive effects outside the migration corridor exist). Certainly, there are no data to suggest dam removal can be viewed as the silver bullet that will recover threatened salmonid stocks.

1.6   Estimating Projection Matrices for Fall Chinook Salmon and Management Experiments

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, 4, 5, and 6); 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 (see below).

To derive parameter estimates for Snake River fall chinook, NMFS used annual counts of natural origin jacks and adults at the uppermost 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). Mainstem harvest, ocean harvest, and Bon to Basin 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. 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).

Age-specific parameters used in Snake River fall chinook analyses are shown in Table 12.

Table 12. 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
Female eggs per female spawner (m_x)		1442.5	1566.5	1625.5	1625.5
Propensity to breed (b_x) (solved as in Appendix A)	0	0.081	0.650	0.863	1.0
93-96 Mainstem adult harvest rate	0.174				
93-96 adult Bon to Basin conversion rate	0.471				
s_1	0.0044167				

These parameters are then substituted into the following matrix where, as previously, $\mu = 1-(0.9 *$ Bon to Basin $* (1\text{-mainstem harvest})$.

	1	2	3	4	5	6
1	0	0	$(1-\mu)s_1b_3m_3$	$(1-\mu)s_1b_4m_4$	$(1-\mu)s_1m_5$	$(1-\mu)s_1m_6$
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

Data regarding survival during downstream migration and the proportion of smolts transported are generally much poorer for fall chinook than for spring/summer chinook. Therefore, s_1 includes everything from egg hatch, downstream migration, and survival in the estuary and entry into the ocean

environment. Due to the lack of data, no attempt was made to break s_1 down into all of its component pieces.

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 l if 1 out of 10 salmon that currently die at each stage. The elasticity results for fall chinook (Figure 10) closely mirror those for spring/summer chinook salmon (Figure 4). 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 11) are also quite similar to those for spring/summer chinook. Specifically, reducing mortality during the first year of life produces the largest change in population growth rate (Figure 5; Recall that for fall chinook, s_1 includes survival in the estuary and entry into the ocean environment). 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 involve saving a great many more fish than for any of the other stages.

After 1993, ESA management has led to decreases in rates of harvest for Snake River fall chinook salmon. However, one potential management option would be to enforce further reductions in either ocean or mainstem harvest or in both (i.e., more than those examined in the save 1 of 10 experiments). An approximately 4 percent increase in λ would required to lower the probability of quasi-extinction within 100 years for fall chinook to less than 1 in a 100. This magnitude of change could be accomplished with a 75 percent reduction in ocean harvest, a 75 percent reduction in mainstem harvest, or a 50 percent reduction in both ocean and mainstem harvest (Figure 12). Thus harvest reductions can yield a biologically reasonable management option for Snake River fall chinook.

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 λ expected to result from a broad range of potential changes in s_1 survival. Again, an approximate 4 percent increase in λ is expected to lower the probability of quasi-extinction within 100 years to 1 in a 100. This level of improvement in λ could be achieved with a less than 20 percent increase in s_1 (see Figure 13). Whether or not such a change in s_1 would actually occur under dam drawdown is unknown. Lastly, as noted in the PATH analysis, dam breaching would open up habitat for fall chinook salmon. Expansion of populations to fill this habitat will still require an increase in annual population growth rates above current levels.

1.7   Steelhead Analyses

There are not adequate data for Snake River steelhead to build stage-structured demographic matrices. However, the simple Dennis et al. extinction analyses afford the opportunity to examine the implications of harvest reductions. First, it is important to note that when steelhead spawner counts are analyzed for density dependence, the data do not suggest even the slightest hint of density-dependence in recruits per spawner, with an r-squared of only 0.05 for the density-dependent

regression (Table 5). This suggests that as a first approximation, a simple density-independent model, such as the Dennis et al. model, can be used to ask by how much should harvest be reduced to sufficiently increase the annual rate of population change such that the probability of extinction falls below 0.01 over a 100-year period. The estimated harvest rate during the time period between 1983 and 1994 (the last year of recruits to spawning grounds for which data were available, see Table 3) is 23 percent. If a harvest rate of 0.23 yields an estimated annual population growth of 0.91 (see Table 7), then reducing harvest to zero would produce an annual population growth of 0.91/(1-0.23), or 1.18. This is a huge increase in the annual growth rate (i.e., a 30 percent increase). More modest reductions in harvest are also effective. For example, reducing steelhead harvest to 10 percent would increase annual population growth from 0.91 (which is a 9 percent decline per year) to 1.06 (a 6 percent increase per year). When the average growth rate of 1.06 is adjusted for environmental variability, it is still a substantial enough increase in growth to reduce the extinction risk to less than 0.001 over 100 years. If the A- and B-runs for the Snake River steelhead are analyzed separately, the same qualitative conclusion holds (details are in Annex F). The average harvest on the A-run has been 14 percent over the last 10 years, and reducing that harvest to 5 percent increases the rate of population change from an annual 5 percent decline to an annual 4 percent increase. The average harvest for the B-run over the last 10 years has been 25 percent and reducing that harvest to 10 percent increases the rate of population change from an annual 7 percent decline under the 25 percent harvest rate to an annual 9 percent growth under the 10 percent harvest rate. Thus, as was the case with fall chinook, it appears that harvest reductions alone could reduce extinction risks in steelhead to acceptably low levels. The impact of dam breaching on steelhead is much harder to evaluate because their life cycle is so complicated and data on the age-class of smolts are generally lacking. By analogy to other salmonids, it is not unreasonable to think that dam breaching without any harvest reductions could enhance survival by 20 percent, which would be enough to increase annual rate of growth to levels that would produce acceptably low risks of extinction.

1.8 Limitations of the CRI Analytical Framework

There are several limitations of the CRI analytical framework. First, CRI has not yet developed effective approaches for estimating carrying capacity; hence, while CRI analyses may be apt for populations at low density, as stocks rebuild the analyses will need to be modified. Second, CRI cannot address questions about refinements in the hydropower systems because the hydropower system does not appear explicitly in CRI models; this means that instead of mechanistic relationships between flow regimes and survival, CRI treats flow variability as simply unexplained environmental variability. Third, CRI has not yet developed adequate analyses of the feasibility of achieving particular demographic improvements as a result of specific management actions. This will be the hardest challenge for CRI. The hope is that by isolating these feasibility studies from population projection models, the research and data needs will become more apparent. It remains to be seen whether this hope is warranted. Fourth, by focusing so much on current conditions, CRI fails to incorporate potential influences of decadal oscillations in ocean conditions and infrequent catastrophes. Finally, CRI has thus far essentially treated each population as independent and has built up its risk analyses without attention to ESU-wide meta-population structure. Many of these limitations are not necessary attributes of CRI, but rather represent its early stages of development. The challenge will be in keeping it simple and transparent, while addressing the above limitations.

1.9   Synthesis of Results Across All Salmonids

The CRI analyses attempt to put dam breaching in the context of a menu of other management actions and to account for extinction risks. From the perspective of extinction risks alone, it appears that harvest reductions (or moratoriums) would be adequate to sufficiently increase annual rates of population growth for both steelhead and fall chinook; it also appears that modest survival improvements due to dam breaching could accomplish the same goals. Of course, dam breaching would also increase the availability of habitat for fall chinook salmon and hence the carrying capacity; whereas harvest reductions have no such possibility.

The situation for spring/summer chinook is much more complicated. First of all, for spring/summer chinook salmon, there is no silver bullet that is likely to adequately reduce extinction risks. For dam breaching alone to recover spring/summer chinook salmon, very optimistic scenarios would need to be assumed about how much survival below Bonneville Dam could be improved due to the elimination of latent mortality not measured during inriver downstream and upstream migration. For aggressive habitat management and other management actions alone to be sufficient, magnitudes of habitat improvements that are not known to be achievable would have to be assumed, as well as reductions in predation impacts for which data are still scant.

Figure Legends

Figure 1. Relationship between log (recruits per spawner) and total number of spawners for seven index stocks of spring/summer chinook salmon, between 1980 and 1993. (Data from Minam and Imnaha stocks extend only until 1990). Only slopes for the Minam and Poverty stocks are significantly different from zero; R^2 values are consistently low (Table 4).

Figure 2. Relationship between log (recruits per spawner) and year for seven index stocks of spring/summer chinook salmon. All slopes are significantly different from zero. R^2 values range from 0.38 to 0.85.

Figure 3. Relationship between log (recruits per spawner) and total number of spawners for steelhead (a) and fall chinook salmon (b). Slopes for both species are not significantly different from zero. R^2 for steelhead is 0.05, for fall chinook $R^2 = 0.20$ For both species, a temporal trend explains more of the observed variation than this density relationship.

Figure 4. Average elasticity (sensitivity of population growth rate to changes in demographic parameters) for seven index stocks of spring/summer chinook. Pt = percent of smolts transported in barges; sd = survivorship of smolts swimming downstream; se = survivorship in the estuary and ocean until the fish's second birthday; sA = survivorship of adults in the ocean; mx = fecundity of females of age x; s1 = survivorship to the fish's first birthday; B to B = survivorship of upstream migrants from Bonneville Dam to the Snake River Basin; harvest = mainstem harvest. Survivorship of adults in the ocean has the highest elasticity because these individuals have survived periods of high mortality and are near the age of reproduction.

Figure 5. Average percent change in population growth rate with a 10 percent reduction in mortality at each life stage for seven index stocks of spring/summer chinook. (A 10 percent increase in fecundity, and a 10 percent increase in the proportion of smolts transported in barges was also analyzed). Pt = percent of smolts transported in barges; sd = survivorship of smolts swimming downstream; se = survivorship in the estuary and ocean until the fish's second birthday; sA = survivorship of adults in the ocean; mx = fecundity of females of age x; s1 = survivorship to the fish's first birthday; Bon to Basin = survivorship of upstream migrants from Bonneville Dam to the Snake River Basin; harvest = mainstem harvest. Spring/summer chinook population growth rate shows the greatest sensitivity, by this measure, to reduced mortality during freshwater rearing, and during the estuary and early ocean phases because these are periods during which there is very high mortality.

Figure 6. Population growth rate (top), and average percent change in population growth rate (bottom) for spring/summer chinook under current conditions and hypothetical management scenarios. 77-79 hydro survivals = current conditions, but survivorship through the hydrosystem set at the levels occurring between 1977-1979 (after dams had been constructed, but before improvements to bypass and transportation. no transport = current conditions, but no smolts transported in barges; 60-70 harvest = current conditions, but mainstem harvest rates set equivalent to those between 1960 and 1970; no harvest = current conditions, with mainstem harvest entirely eliminated; max pt = current conditions, with the proportion of smolts transported in barges increased to the maximum possible. With hydrosystem survivorship set to 1977-1979 levels, population growth rate decreases by about 60 percent. Increased transportation, or eliminating mainstem harvest each yields an approximately 1 percent increase in population growth rate.

Figure 7. Population growth rate (top), and average percent change in population growth rate (bottom) for spring/summer chinook under current conditions and hypothetical management scenarios. No harvest = current conditions, with mainstem harvest entirely eliminated; no steelhead predation = elimination of predation on chinook fry by hatchery released steelhead smolts (estimated at 22 percent, Cannamella, 1993); max pt = current conditions, with the proportion of smolts transported in barges increased to the maximum possible; 1.1*se = 10 percent increase in estuarine and early ocean survivorship; 1.1*s1 = 10 percent increase in first-year survivorship; all combined = all 5 potential management actions in place. Combining each of these 5 actions yields an increase in population growth rate of about 14 percent.

Figure 8. Average percent change in population growth rate over a range of percent improvements in estuarine and early ocean survival, and a range of percent improvements in survivorship during adult upstream migration from the Bonneville Dam to the Snake River Basin.

Figure 9. Population growth rate (top), and average percent change in population growth rate (bottom) for spring/summer chinook under hypothetical management scenarios. No harvest plus 1.1*s1 = current conditions, but no mainstem harvest, and a 10 percent increase in estuarine and early ocean survivorship; drawdown = breaching of dams, yielding a Bonneville to Basin adult migration survivorship of 80 percent, a smolt downstream migration survivorship of 62 percent, and a 30 percent increase in estuarine survivorship (equivalent to D = 0.7); combo = effect of both scenarios combined. Each scenario individually yields an approximately 4 percent increase in population growth rate; combined they yield an approximately 8 percent increase in population growth rate.

Figure 10. Elasticity (sensitivity of population growth rate to changes in demographic parameters) for fall chinook. s1 = survivorship to the fish's first birthday (note that this includes freshwater rearing and estuarine survival); Bon to Basin = survivorship of upstream migrants from Bonneville Dam to the Snake River Basin; mainstem harvest = mainstem harvest rate; mx = fecundity of females of age x; sA = survivorship of adults in the ocean; ocean harvest = ocean harvest rate. Survivorship of adults in the ocean has the highest elasticity because these individuals have survived periods of high mortality and are near the age of reproduction.

Figure 11. Percent change in population growth rate with a 10 percent reduction in mortality at each life stage for fall chinook. (A 10 percent increase in fecundity was also analyzed). s1 = survivorship to the fish's first birthday (note that this includes freshwater rearing and estuarine survival); Bon to Basin = survivorship of upstream migrants from Bonneville Dam to the Snake River Basin; mainstem harvest = mainstem harvest rate; mx = fecundity of females of age x; sA = survivorship of adults in the ocean; ocean harvest = ocean harvest rate. Fall chinook population growth rate shows the greatest sensitivity, by this measure, to reduced mortality during the first year of life (which includes freshwater rearing, estuarine and early ocean survivorship) because these are periods during which there is very high mortality.

Figure 12. Percent increase in fall chinook population growth rate with a range of reduction in ocean harvest (top), mainstem harvest (middle) and ocean and mainstem harvest (bottom).

Figure 13. Percent increase in population growth rate for fall chinook with a range of increases in first year survivorship.

Figure 1. Recruits Per Spawner Versus Spawner Density for Spring/Summer Chinook Salmon Index Stocks
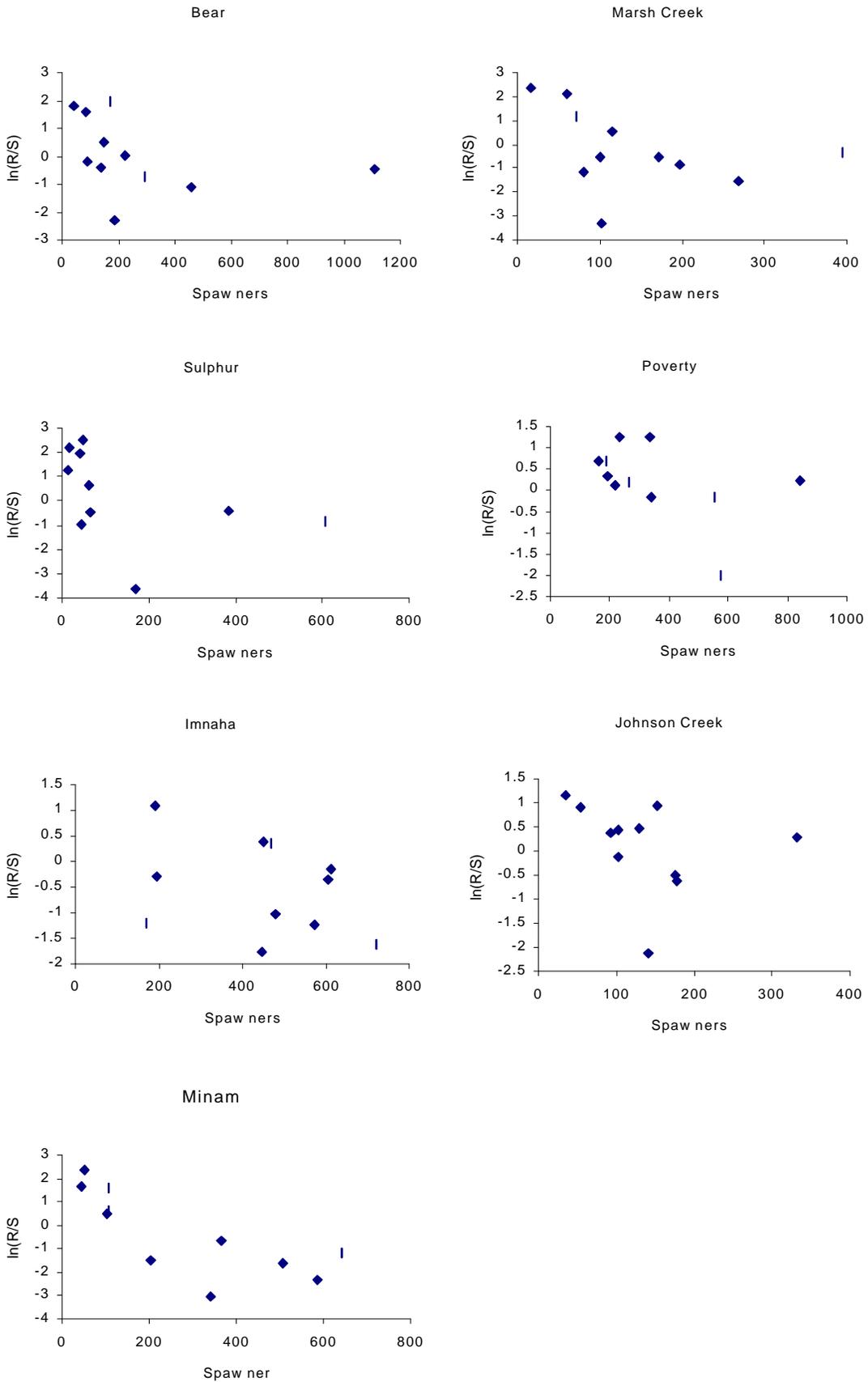
Figure 2. Recruits Per Spawner Versus Year for Spring/Summer Chinook Salmon Index Stocks
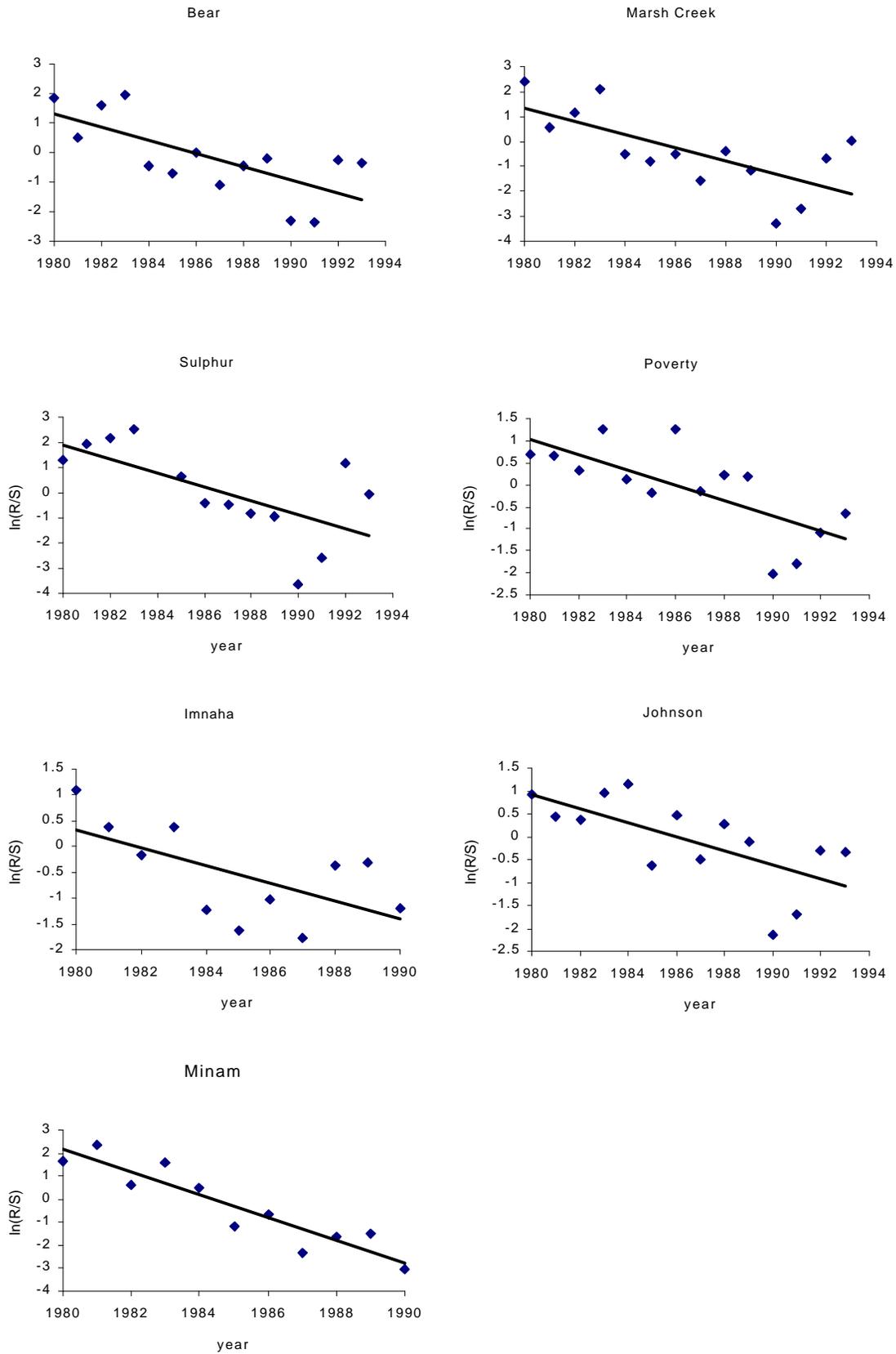
Figure 3. Recruits Per Spawner Versus Spawner Density for Steelhead and Fall Chinook
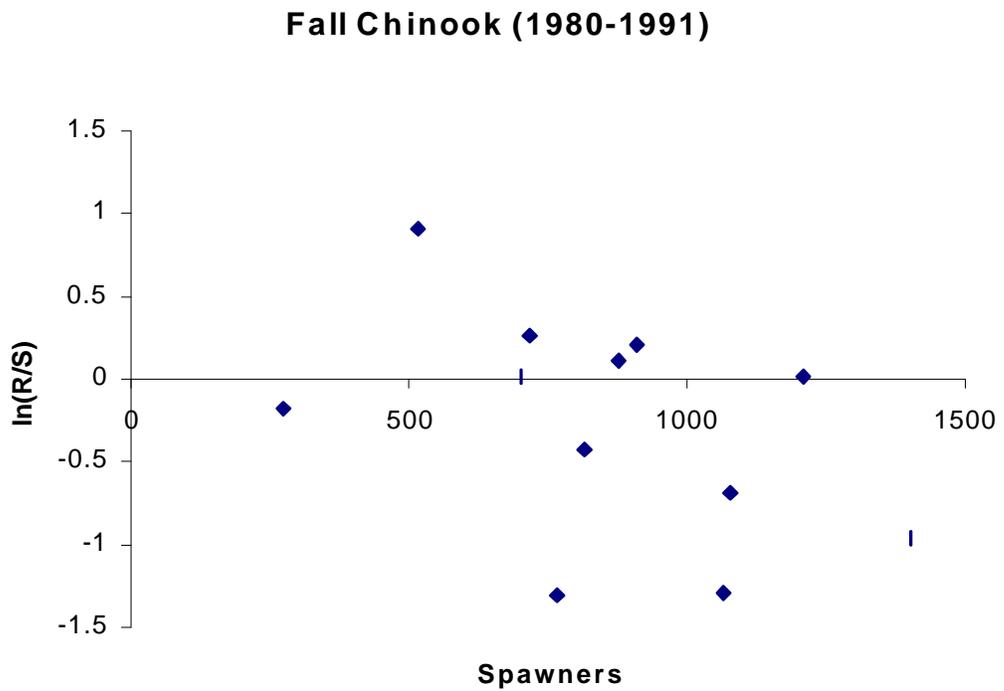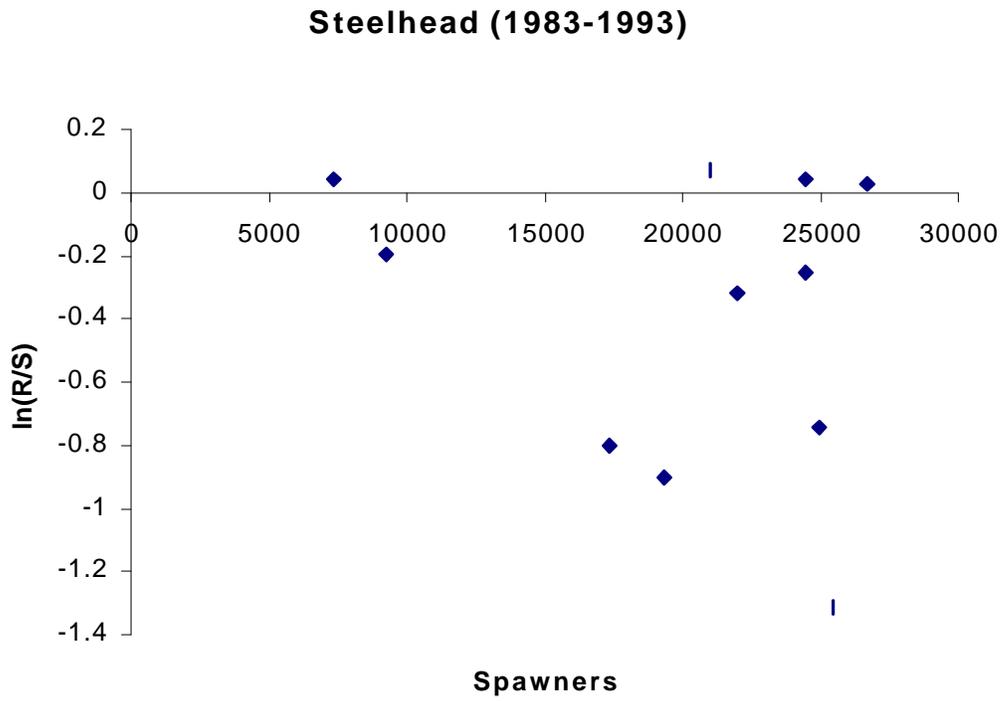Salmon

Steelhead (1983-1993)

Fall Chinook (1980-1991)

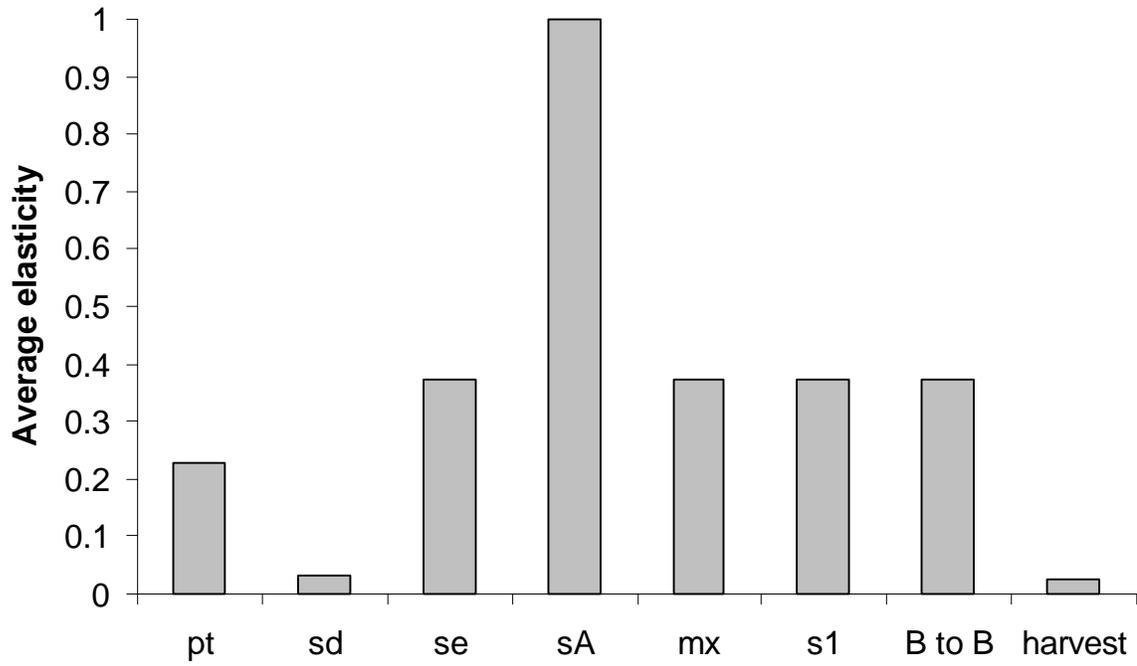**Figure 4.** Sensitivity of Annual Population Growth to Small Changes in Components of Spring/Summer Chinook Salmon Demographic Projection Matrix

Figure 5. Average Increase in Annual Population Growth with a 10% Reduction in Mortality During Different Life Stages for Spring/Summer Chinook Salmon
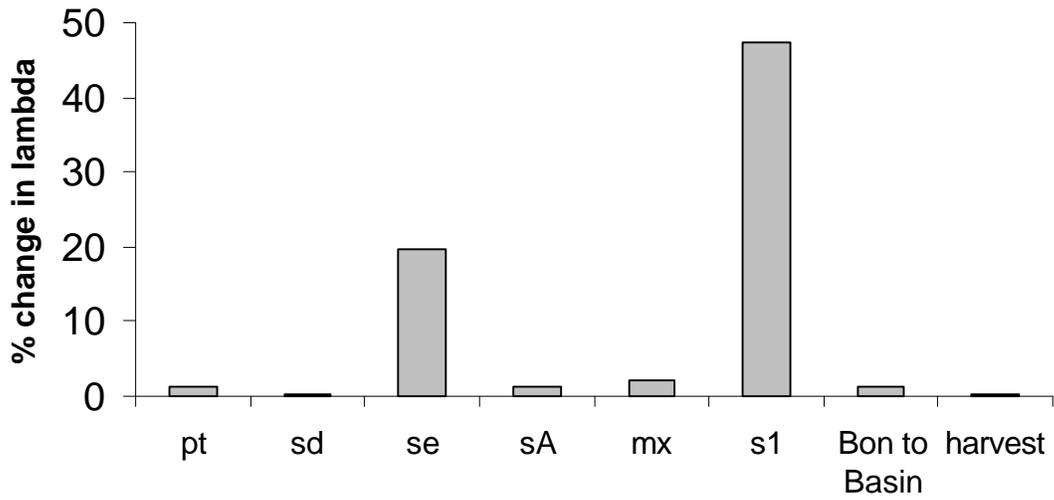
Figure 6. Average Population Growth Rate for Spring Summer Chinook Salmon and Percent Change From Baseline After Different Hydrosystem Management Scenarios Are Simulated
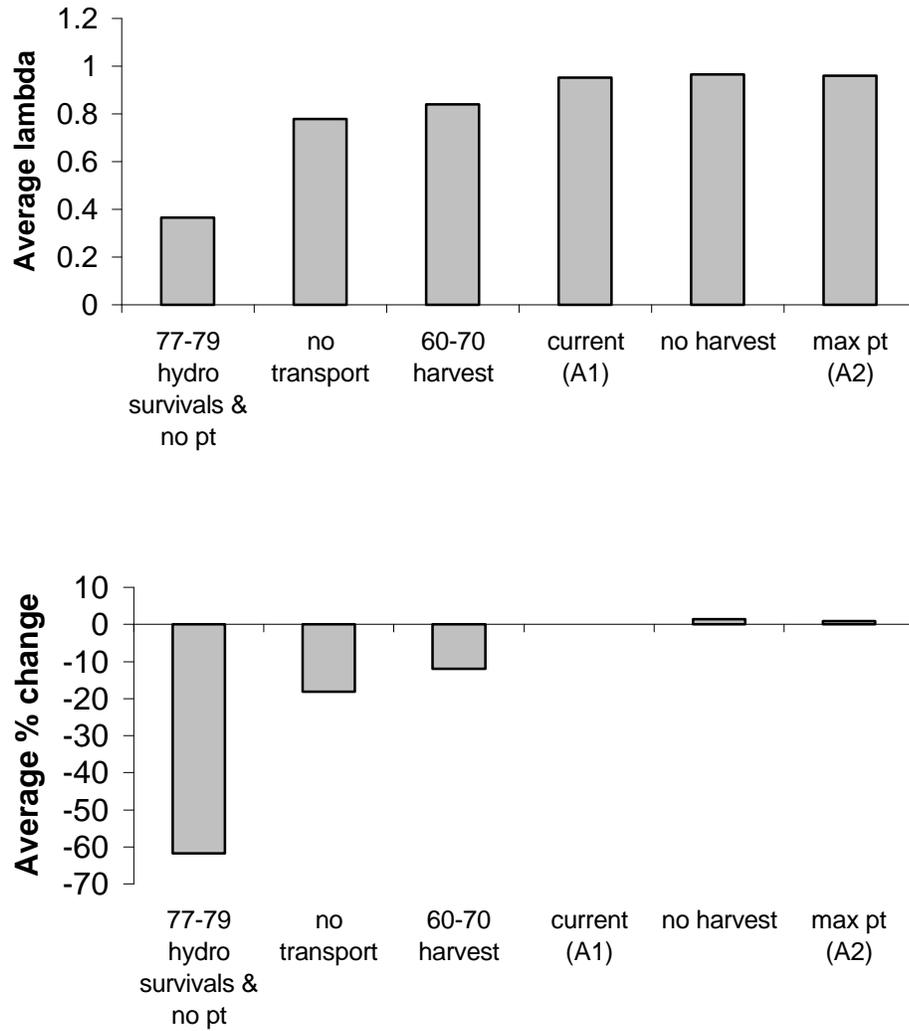
Figure 7. Average Population Growth Rate for Spring Summer Chinook Salmon and Percent
Change From Baseline After Mixtures of Hydrosystem Alterations and Other
Management Actions Are Simulated
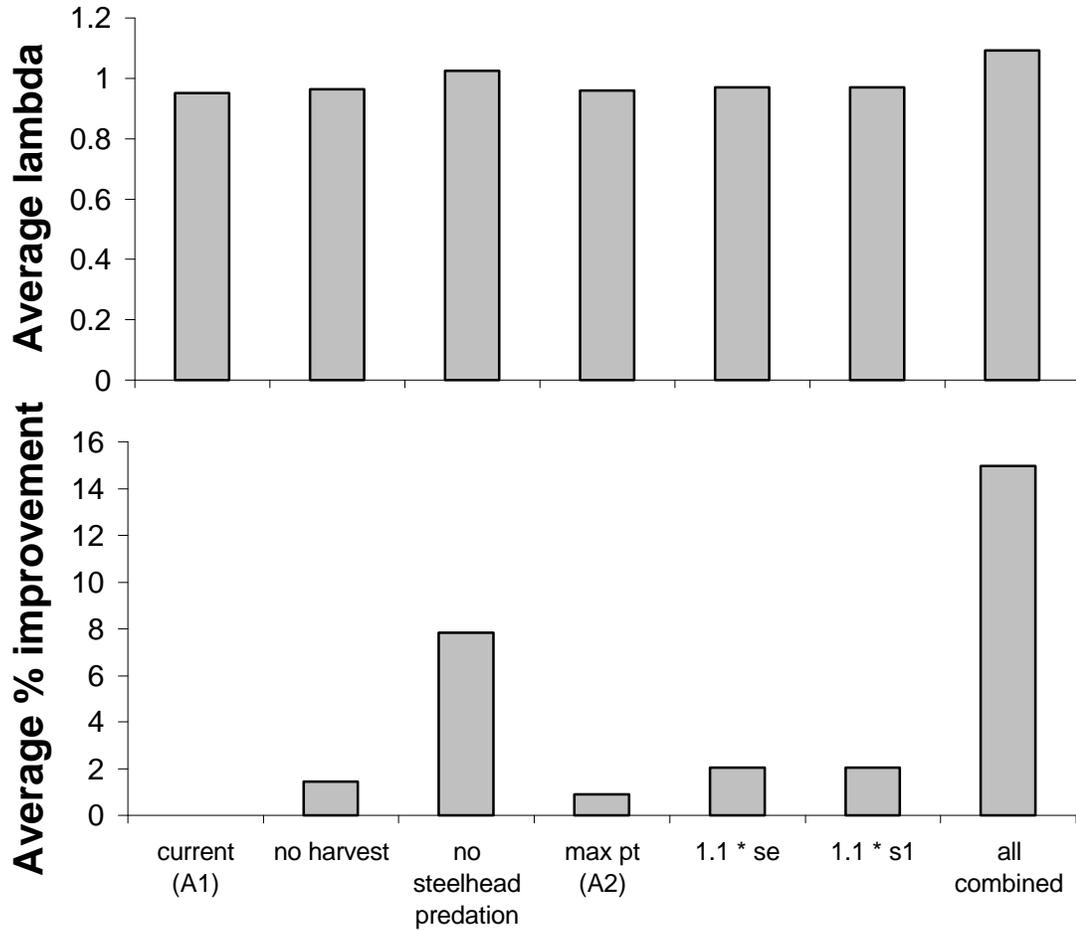
Figure 8. Possible Breaching Effects on Spring/Summer Chinook Salmon Estimated Through Improved Estuarine and Ocean Survival

No improvement in Bon to Basin

15% improvement in Bon to Basin

30% improvement in Bon to Basin

45% increase in Bon to Basin
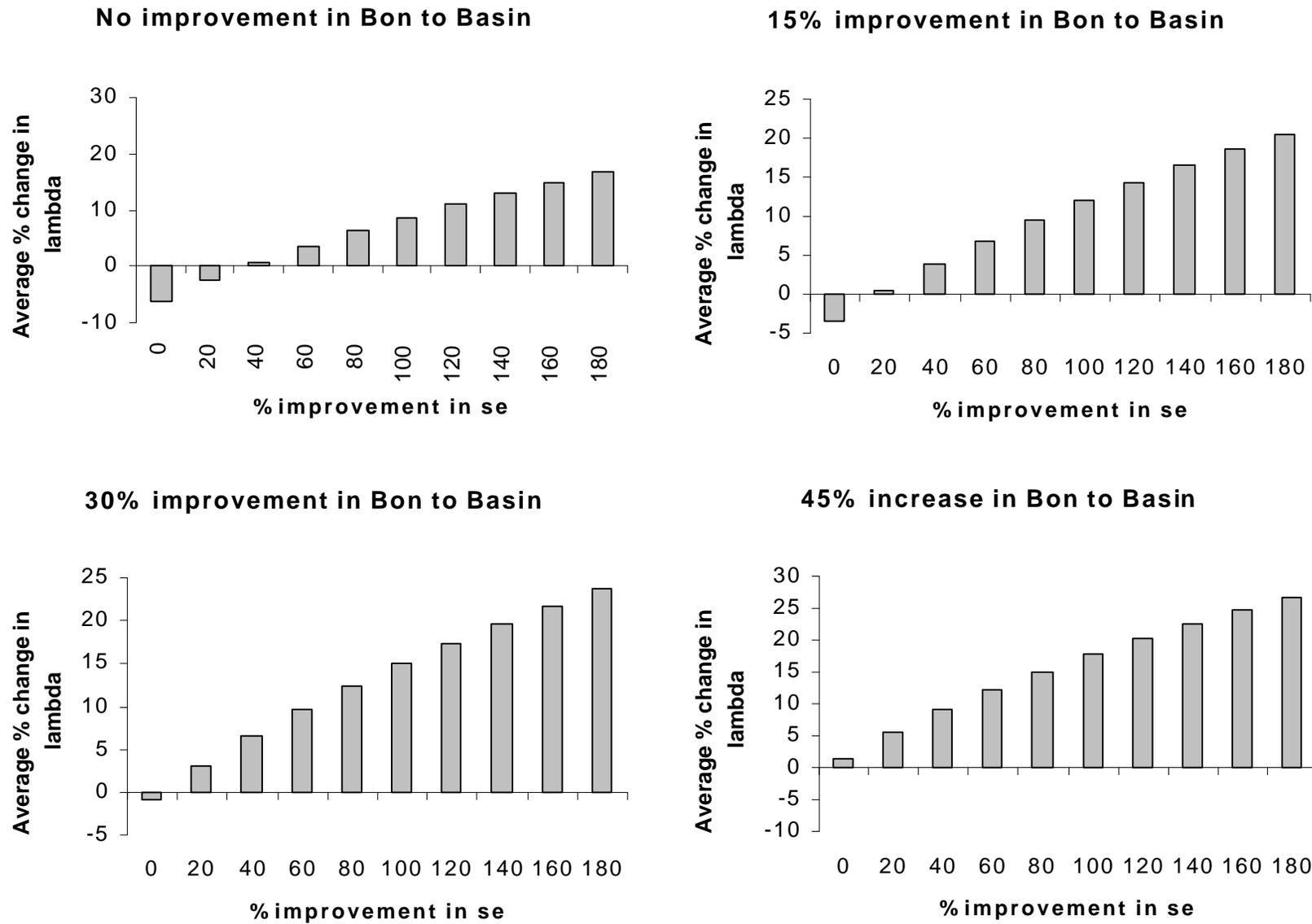
in Conjunction with Improved Upstream Survival

Figure 9. The Effect of Combining Different Management Actions on Annual Population Growth Rate for Spring/Summer Chinook Salmon
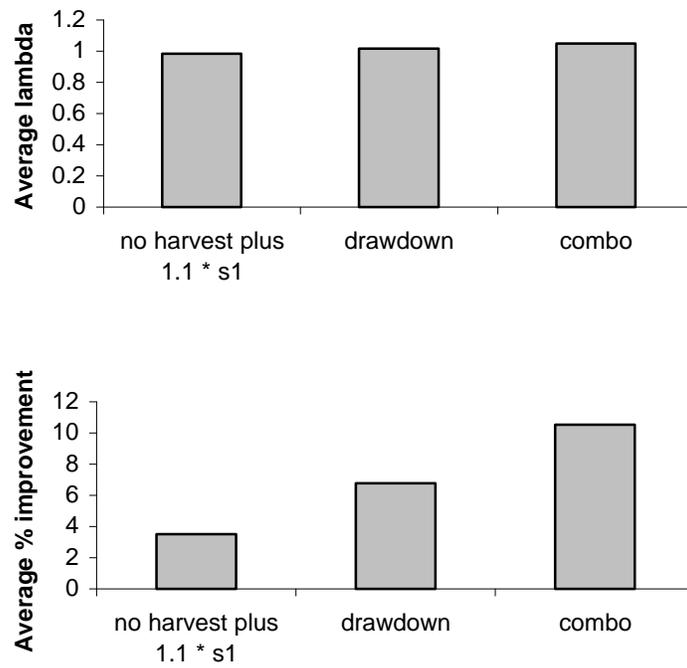
Figure 10. Sensitivity of Annual Population Growth to Small Changes in Components of Fall Chinook
Salmon Demographic Projection Matrix
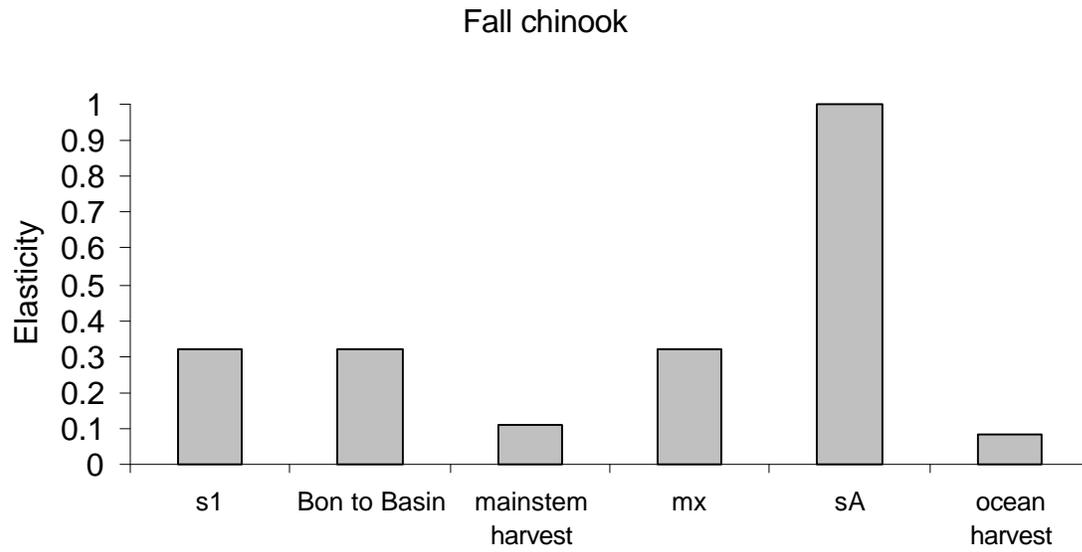
Fall chinook

Figure 11. Improvements in Fall Chinook Salmon Annual Population Growth with 10% Reductions in Mortality During Different Lifestages
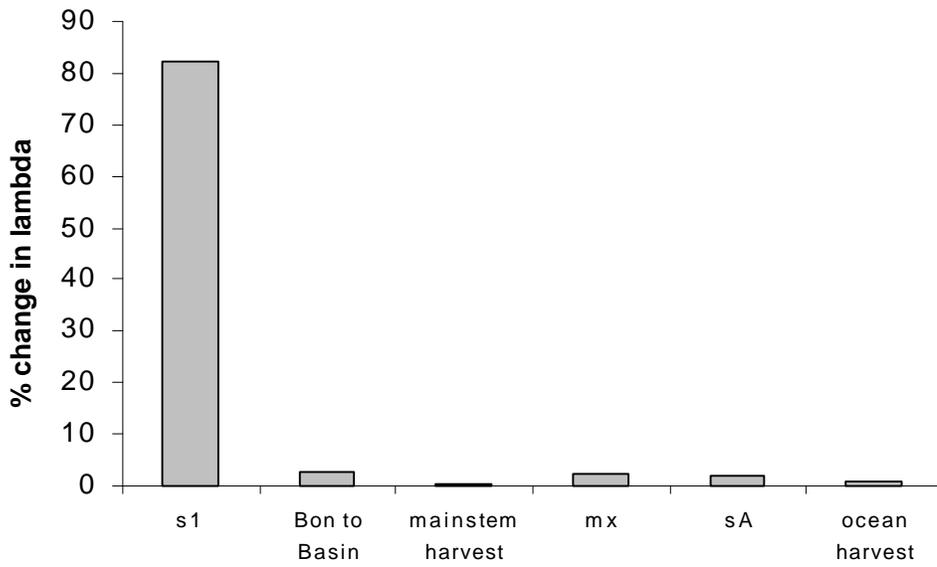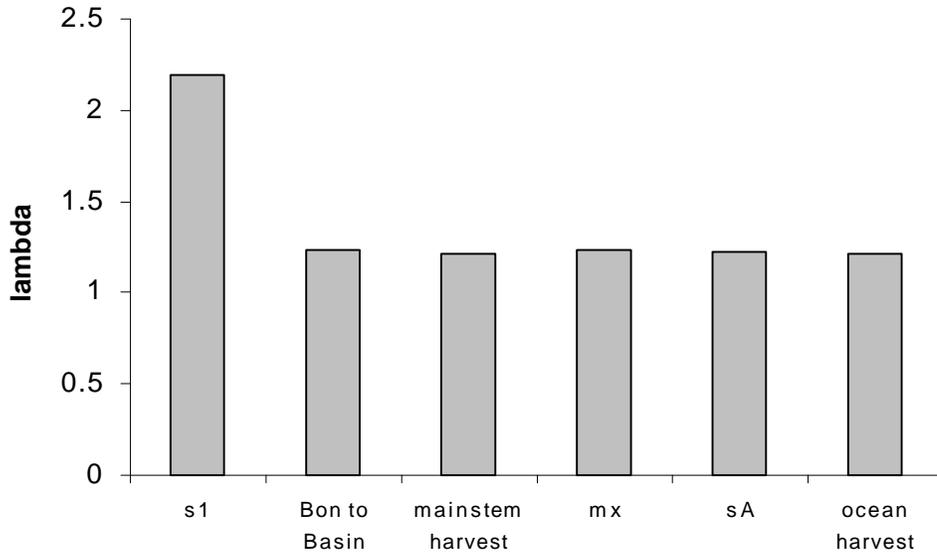
Figure 12. Increase in Fall Chinook Annual Population Growth with a Range Of Harvest
Reductions
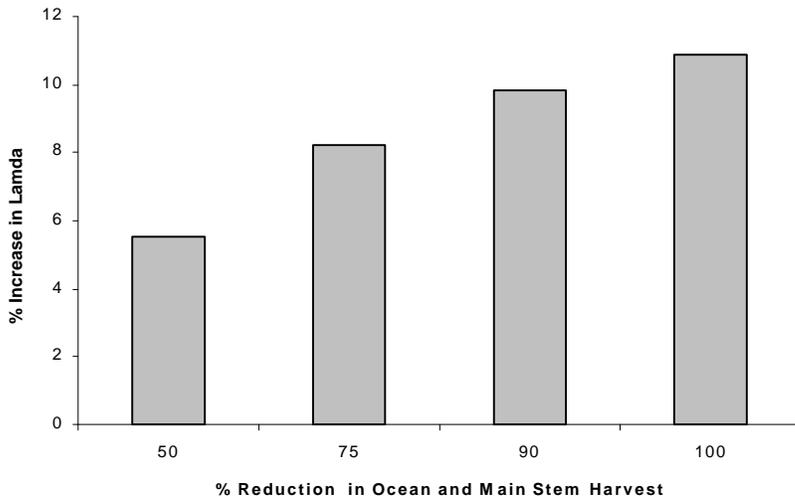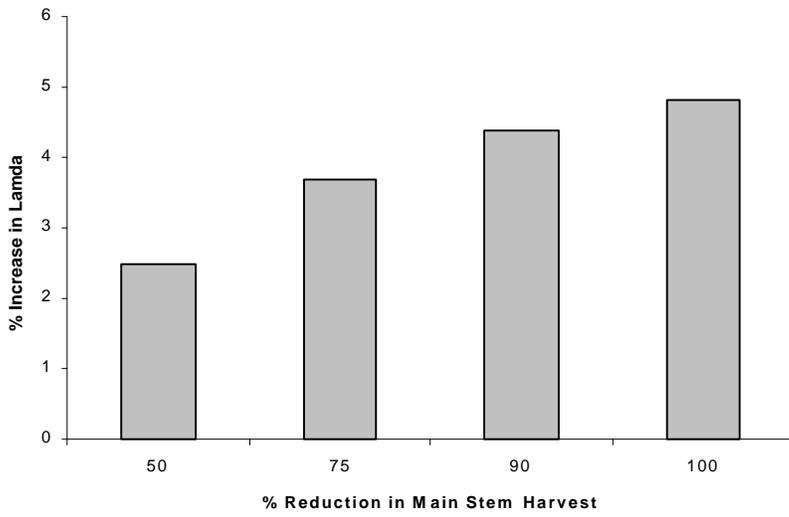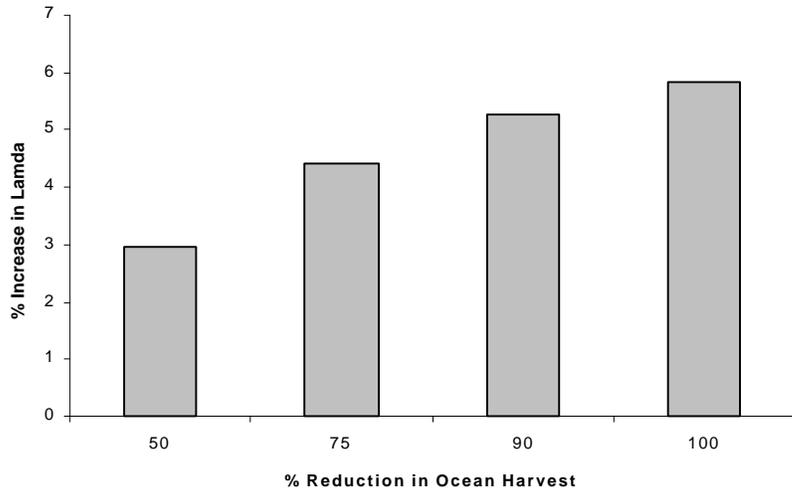
Figure 13. Increase in Fall Chinook Annual Population Growth (lamda) with a Range of Increases in First Year Survivorship (S1)
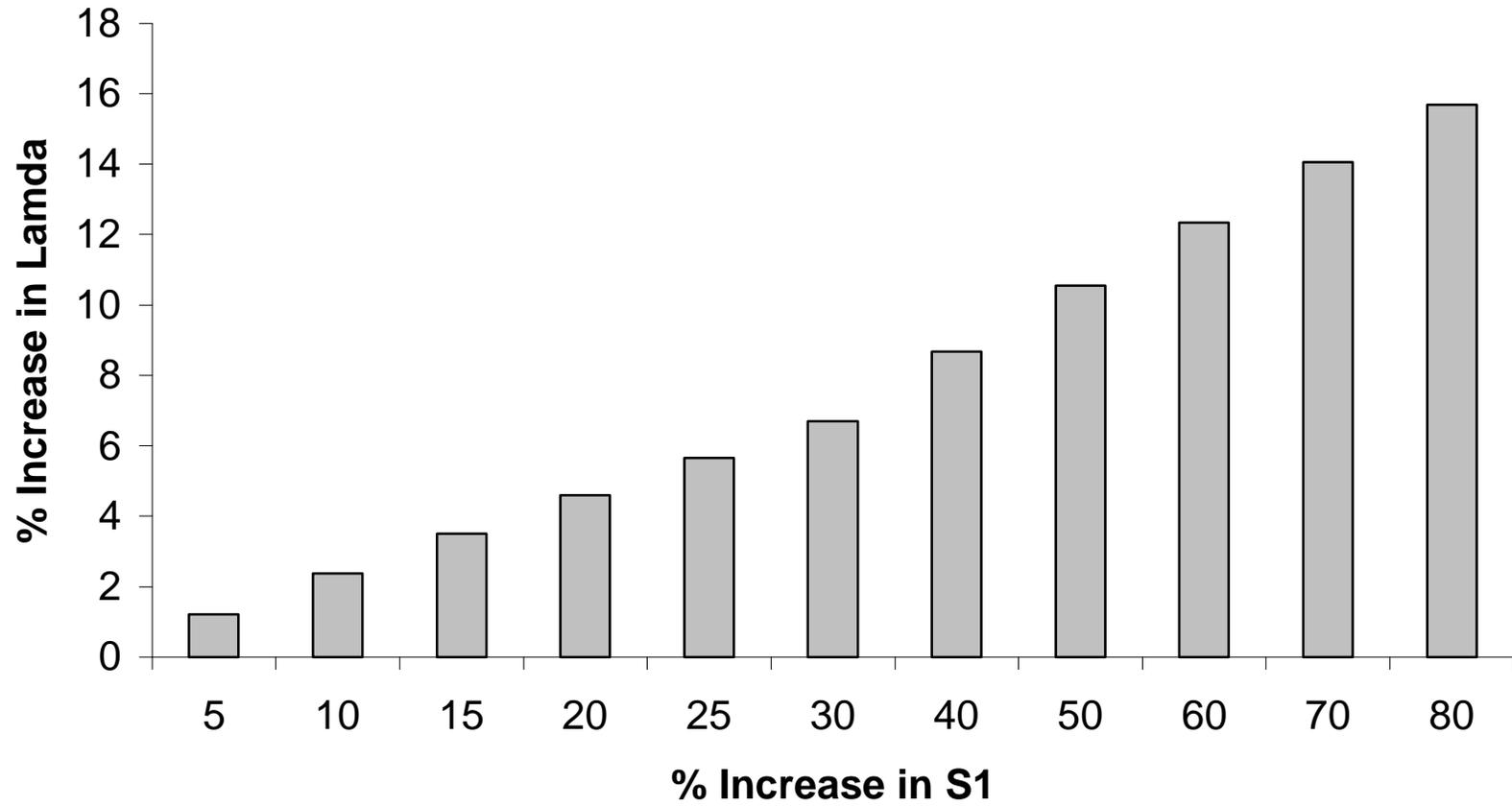
2. Summary of Results, Uncertainties, and Opportunities for Resolving the Uncertainties

In general, the CRI analyses indicate substantial risks of extinction for spring/summer chinook salmon, fall chinook salmon, and steelhead over the next 100 years if current conditions hold. CRI analyses also indicate significant extinction risks for spring/summer chinook salmon within the next 10 years. The extinction calculations estimate the probability of quasi-extinction (escapement falling to one fish in any one year), and are therefore relatively conservative measures of extinction risk.

Unlike PATH, the CRI analyses suggest that no single management action is likely to result in sufficiently improved demography for spring/summer chinook salmon. For dam breaching alone to recover spring/summer chinook salmon, it would have to produce improvements in estuarine and early ocean survival as high as 80 to 100 percent, as well as an approximate 30 percent improvement in survival during upstream migration. On a more optimistic note, the CRI analyses suggest that a combination of improvements spread throughout the life cycle, and attained by a mixture of different management actions, could promote adequate annual population growth for spring/summer chinook salmon. Numerical experiments that correspond to manipulations of "current demography" indicate that small improvements in estuarine and early ocean survival or in the survival of newly born fish, will yield the greatest rewards in terms of enhanced population growth. Moreover, if many improvements are added together, CRI analyses suggest that annual rates of population growth could be increased enough that stocks of spring/summer chinook salmon could rebuild. The management actions that might produce these demographic improvements include habitat restoration, reducing predation pressure in reservoirs and the estuary, potentially manipulating the time and release position of downstream migrants, improved water quality, mitigation of negative hatchery impacts, continued harvest restrictions, and, of course, dam breaching. But no single silver bullet solution is supported by the data when it comes to spring/summer chinook salmon.

The situation for fall chinook salmon and steelhead is not as difficult as that discussed above for spring/summer chinook salmon. For these threatened stocks, single management actions may sufficiently improve population growth. For example, harvest reductions alone would likely increase annual rates of population growth to levels that would sufficiently reduce extinction risks. Alternatively, in the absence of harvest reductions, if dam breaching were assumed to improve the survival of fall chinook salmon during their first year of life by only 20 percent, then breaching alone is likely to adequately reduce extinction risks. For fall chinook salmon, which are mainstem spawners, dam breaching would also open up new habitat, thereby increasing the total potential number of fall chinook salmon that might exist after breaching.

2.1 Critical Uncertainties About the Feasibility of Attaining Required Demographic Improvements

The major uncertainty for the CRI analyses is the biological feasibility of using particular management actions to achieve sufficient demographic improvements. Harvest reductions, which are

clearly and undeniably converted into survival improvements, are the one management action for which the feasibility of achieving a specific demographic effect is not contentious. In contrast, the demographic consequences of virtually every other management action are uncertain.

CRI sensitivity analyses of stage-structured demography for fall and spring/summer chinook salmon indicate that improvements in survival of fish during the first year of life before migrating downstream or during entry into the estuary and ocean are likely to have the greatest impacts on annual population growth rates. This sensitivity analysis thus points toward the need for feasibility studies aimed at how to attain improvements in survival during these key life stages. Critical uncertainties regarding the connection between management actions and improvement in fish demography or fitness are discussed below, along with specific suggestions for research that could help resolve these uncertainties.

2.1.1 Could Habitat Restoration Help Recover Threatened Snake River Salmonids?

Improved habitat conditions might lead to substantial improvements in the survival of fish during their first year of life, but a better understanding of the relationship between habitat quality and salmonid population dynamics is required. This knowledge would enable an accurate assessment of the role freshwater habitat can play in recovery. Key research questions include:

1. What is the relationship between habitat quality and the abundance, survival, and productivity of salmonids in the Snake River Basin? Although researchers have previously asked this question, population levels of key species have been very low, possibly masking the influence of habitat quality on survival and productivity. Continuing to collect data on the interaction between habitat condition and fish production as population levels increase will provide a clearer indication of the role habitat plays in determining stock productivity. Using the 22 PATH index stocks for spring/summer chinook salmon in the Columbia Basin, Regetz (1999, in review) found that a combination of only three habitat variables explained 62 percent of the variation in mean recruits per spawner (which is one possible measure of productivity, especially pertinent given the apparent absence of density dependence discussed earlier). Especially interesting is Regetz's finding that EPA 303(d) compliance and Mean Watershed Sensitivity Indices predicted a significant proportion in the landscape level variation in recruits per spawner. These results suggest that it may be feasible to enhance chinook salmon stock productivity by strict habitat measures, although more research is needed. Analyses by Bilby et al. (1999 and Annex G) reveal that only a few subwatersheds account for the bulk of salmon productivity in any given river basin. Using this fact, it may be possible to identify the habitat features that promote productivity, as well as target particular subwatersheds that are prime candidates for restoration.

2. What are the effects of carcass-derived organic matter and nutrients on trophic productivity of rearing habitat? Delivery of carcass organic matter and nutrients to the Snake River watershed is about 0.2 percent of historical levels. The extent to which the elimination of this annual nutrient subsidy has contributed to the decline in salmon and steelhead populations is not known. Likewise, the extent to which these low input levels may retard recovery is unknown. However, in other systems, materials provided by spawning salmon do substantially increase primary and secondary production, including fishes. Understanding the significance of these materials in the

Snake River system may assist in developing approaches to habitat and harvest management that will contribute to recovery of these depressed stocks.

Of course, for any of the above studies to be useful, we need basic information on the location and population size of all salmon stocks in the Columbia River Basin.

2.1.2 Could Reductions or Alterations in Hatchery Releases Help Recover Threatened Snake River Salmonids?

Considerable scientific uncertainty surrounds most aspects of the genetic and ecological interactions among hatchery and wild fish. Research that could help resolve some of these uncertainties includes:

1. Comparing the spawning and rearing index areas that have been exposed to significant numbers of hatchery fish to others that have been relatively free of hatchery influence.

2. Determining the ecological interactions and possible effects of hatchery fish releases on wild fish. Research should examine possible detrimental effects (e.g., displacement of wild fish by hatchery fish, the transmission of disease from hatchery to wild fish, size-selective predation, the attraction of predators by large concentrations of hatchery fish, and aggression) and suggest methods to minimize them. CRI researchers are currently exploring statistical relationships between magnitude and type of hatchery release and recruits per spawner data; unfortunately these analyses will have a problem separating cause and effect.

3. Producing a hatchery fish with characteristics more similar to those of wild fish may aid recovery of wild fish. However, a great deal of research is need to produce hatchery fish more like wild fish in morphology, body coloration, physiology, and behavior. It is critical to develop a hatchery fish that is prepared for the receiving environment and that will have increased survival to adulthood. Studies should focus on improving the operational efficiency of hatcheries, both in terms of their cost efficiency and adult survival. In general, these studies should aim to improve the biological efficiency through better husbandry.

4. In many cases, conservation hatcheries release adults and offspring from captive broodstocks. However, the reproductive success of these animals and their potential interactions with wild animals are largely unknown. Because captively reared and wild salmon experience dramatically different developmental forces, they are likely to differ in their physiology, morphology, and behavior, all of which can substantially influence their reproductive success. Comparative research on the adult reproductive behavior of captive-reared and wild salmon will elucidate potential deficiencies of captive-reared salmon and their offspring and suggest ways to mitigate for such deficiencies through improved rearing technology.

5. Hatchery fish may improperly imprint during rearing or after release, potentially resulting in straying of returning adults and, thus, genetic introgression on wild stocks. Research should directly address a number of concerns over the potential effects of homing and imprinting of hatchery fish on natural gene pools and aim at providing data and hatchery management schemes to ensure that the genetic integrity of spawning stocks is maintained.

2.1.3   Are Differential Delayed Transportation Mortality or Latent and Extra Mortality Caused by Factors that Indicate Dam Breaching Could Successfully Recover Snake River Salmonids?

The extent to which transported fish suffer differential delayed mortality is a crucial question because the answer strongly influences the possible advantage to be accrued by dam drawdown. Ongoing direct experiments that contrast the return rates of tagged fish that pass through the hydrosystem versus the return rates of transported fish can resolve this question in a clear and unambiguous manner. It will, however, require several years to obtain sufficient data because sample sizes of recaptured returning fish are typically low, the magnitude of differential delayed transportation mortality may vary with climate, and measurements from only a few years may fail to capture extreme values that could have important ecological effects.

One possible cause of extra mortality is that dams, by altering the range and quality of habitats which fry, parr, and smolts occupy, may also alter the ultimate fitness of these fish. One way to examine whether dams are an important source of extra mortality would involve comparing the size and fecundity of individuals completing their freshwater rearing in the hydropower corridor to those completing this life stage under more normative conditions. For example, fall chinook on the Hanford Reach could be compared with fall chinook from the Snake River to provide an estimate of the impact of the four lower Snake River dams on that species. Because there is a relationship between size and fecundity in fishes, comparing the length of individuals from both groups at the juvenile, outmigrating smolt, and returning adult stages would provide: 1) an estimate of the growth rates and survivorships of both groups during the freshwater rearing stage and 2) an estimate of the relationship between size at the juvenile stage and adult fecundity. This would allow an assessment of not only whether the hydropower corridor and more riverine areas provide different quality rearing habitats, but also whether those differences translate to differences in adult fecundity. Determining whether the timing of spawning differs between the groups would also be important to monitor, since fecundity of older females is likely to be greater due to their greater size. This type of analysis can provide insight into more subtle, but potentially important effects of dams on salmonid populations that comparisons of survivorship alone cannot yield.

2.1.4   Could Management of Predators Yield Substantial Benefits for Threatened Salmonids?

Predators have major impacts on salmonids throughout their life cycle. Bass and other exotic predator eat salmonids in reservoirs, Caspian terns consume smolts at the mouth of the Columbia River, and marine predators (marine mammals and fish) are a major source of mortality as well. Two significant questions are:

1. What is the impact of different predators in terms of the percentage of salmonids eaten? If that were known, their impact on annual population growth would be straightforward to calculate.

2. What are the management options for reducing the impact of predators on salmon populations that are at risk?

These questions require research that involves multiple species and is less salmonid-centric than has been typical in the past. Importantly, predation is tied up with hatcheries, habitat, harvest, and

hydropower – since all of these "H-factors" can influence the type of predators present, the numbers of predators present, and the behavior or feeding efficiency of predators.

2.1.5 How do Changing Ocean Conditions Affect Chances for Successful Recovery of Snake River Salmonids?

CRI analyses suggest that survival of adults in the ocean is a key life history stage. Unfortunately, ocean conditions are little more than a black box for all salmonids, and there is a need for long-term research focused on the relationship between ocean conditions and salmonid population dynamics. This research will not help inform decisions over the next few years, but could help place population fluctuations in a broader context over the long term, so management actions might better respond to those threats that are best mitigated by non-ocean actions. There is, however, a more fundamental scientific challenge posed by the effects of ocean conditions. It is very difficult to assign mortality and salmonid declines to factors such as hydrosystem effects without making some assumptions about ocean conditions. Although data regarding the marine mortality of Columbia River Basin salmonid stocks are scare, data from other sources at least make clear how important the problem can be. Welsh (1998) calculated the average marine survival of Oregon coastal coho for three ocean regime periods: 1960 to 1977 (6.1 percent), 1978 to 1990 (3.3 percent) and 1991 to 1995 (0.5 percent). In 1991 and later years, average survival declined to less than $1/5^{th}$ the rate evident during the 1978 to 1990 period, and only $1/10^{th}$ that observed prior to 1977. The magnitude of these changes is more striking when considered that for these coho stocks, there are no potential effects of extra or delayed mortality attributable to dams. Given such dramatic changes in SARs (albeit for stocks outside the Snake River Basin), there is a risk of not being able to discriminate non-ocean factors against a backdrop of large variations in ocean conditions.

2.2 Conclusions Regarding Critical Uncertainties

Clearly, there are important uncertainties with substantial consequences for decisions about alternative management actions. It is equally clear that research can help resolve some of these uncertainties. However, research involves delay, and delay involves risk. The CRI extinction analyses provide a concrete measure of the risk of delaying action while learning more (see Tables 6 and 7). These risks, which can be substantial, must be weighed against the value of identifying the feasibility of using particular management actions to achieve demographic improvements. Management itself represents an experiment, and there is certainly an opportunity to test the feasibility of options by careful monitoring and evaluation. Any management decisions that are made for the Snake River salmonids must be viewed as experiments from which we can learn information that might be applied to the many other populations of threatened and endangered salmonids throughout the west coast. It needs to be emphasized that the quasi-extinction risks for several Snake River chinook salmon population are so high that extinction is a real threat for this ESU. This argues for vigorous action.

3. References

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