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A LARGE-SCALE, MULTISPECIES STATUS ASSESSMENT: ANADROMOUS SALMONIDS IN THE COLUMBIA RIVER BASIN

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Abstract. Twelve salmonid evolutionarily significant units (ESUs) throughout the Columbia River Basin are currently listed as threatened or endangered under the Endangered Species Act; these ESUs are affected differentially by a variety of human activities. We present a standardized quantitative status and risk assessment for 152 listed salmonid stocks in these ESUs and 24 nonlisted stocks. Using data from 1980–2000, which represents a time of stable conditions in the Columbia River hydropower system and a period of ocean conditions generally regarded as poor for Columbia Basin salmonids, we estimated the status of these stocks under two different assumptions: that hatchery-reared spawners were not reproducing during the period of the censuses, or that hatchery-reared spawners were reproducing and thus that reproduction from hatchery inputs was masking population trends. We repeated the analyses using a longer time period containing both ''good'' and ''bad'' ocean conditions (1965–2000) as a first step toward determining whether recent apparent declines are a result of sampling a period of poor ocean conditions.

All the listed ESUs except Columbia River chum showed declining trends with estimated long-term population growth rates (λ's) ranging from 0.85 to 1.0, under the assumption that hatchery fish were not reproducing and not masking the true λ. If hatchery fish were reproducing, the estimated λ's ranged from 0.62 to 0.89, indicating extremely low natural reproduction and survival. For most ESUs, there was no significant decline in population growth rates calculated for the 1980–2000 vs. 1965–2000 time periods, suggesting that the current population status for most ESUs is not solely a result of changes in ocean conditions, and that without other changes, risks will persist even during upturns in ocean conditions. However, estimated population growth rates for the Snake River spring–summer chinook salmon and steelhead ESUs were significantly lower during the longer time period. This difference may be due to a period of dam building on the Snake River during the 1960s and 1970s. For 33 stocks and seven ESUs, the probability of extinction could be estimated. The estimates were generally low for all ESUs with the exception of Upper Columbia River spring chinook and Upper Willamette River steelhead. The probability of 90% decline could be estimated for all stocks. The mean probability of 90% decline in 50 years was highest for Upper Columbia River spring chinook (95% mean probability across all stocks within the ESU) and Lower Columbia River steelhead (80% mean probability).

We estimated the effects of two different management actions on long-term growth rates for the ESUs. Harvest reductions offer a means to mitigate risks for ESUs that bear substantial harvest pressure, but they are unlikely to increase population growth rates enough to produce stable or increasing trends for all ESUs. Similarly, anticipated improvements to passage survival through the Snake and mainstem Columbia hydropower systems may be important, but additional actions are likely to be necessary to recover affected ESUs.

Key words: *conservation; extinction risk; population growth rates; quantitative risk assessment; salmon; steelhead.*

INTRODUCTION

Evaluating the status of multiple species or populations in large biological systems poses a tremendous challenge to conservation biologists and managers. Large-scale systems not only typically face a variety of threats, but also data quality and extent may be inconsistent across the species or populations of interest. Broad-scale quantitative assessments have the potential to play several extremely important roles in conservation planning in these large systems, especially when standardized assessments can be conducted, with data of variable quality. First, they can provide the opportunity to prioritize conservation needs from a biological standpoint, by expressing status in a common currency across all populations. They can also help prioritize efforts that include economic or social considerations. Second, standardized, quantitative, status assessments can provide the basis for subsequent analyses that evaluate the effect of human actions on status. In particular,

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they can be used in retrospective analyses that explore the relationship between population status and environmental conditions or anthropogenic impacts, or they can provide the starting point from which to gauge the anticipated effects of actions across species and/or populations.

In this paper, we conduct a standardized status assessment for threatened and endangered salmonids in the Columbia River Basin, as an important first step in recovery planning efforts for these species. Following Caswell (2000), we adopted the long-term population growth rate (λ) as the main measure for comparative risk analysis. This is a critical parameter in viability assessment, not least because most population extinctions are the result of steady declines, $\lambda < 1$, (Caughley 1994). We use λ combined with the year-to-year variability to estimate probabilities of extinction and decline using methods that require only simple time series of abundance or density and that have been developed for data sets with high sampling error and age-structure cycles (Holmes 2001). These methods have been extensively tested using simulations (E. Holmes, *unpublished manuscript*), and cross-validated with time series data (Holmes and Fagan 2002). In our analysis, we included currently threatened and endangered populations as well as several stocks widely believed to be at low risk. The inclusion of these nonlisted stocks gives us a basis of comparison for interpreting the estimated status of the more imperiled stocks.

Columbia River salmon and steelhead

The Columbia River Basin spans over 640 000 km^2 and encompasses a diverse variety of ecotypes, from wetlands to coniferous forest to shrub steppes. Twelve salmonid evolutionarily significant units (ESUs) in the Columbia Basin that represent genetically and demographically independent groups of fish (Waples 1991) have been listed as threatened or endangered under the United States Endangered Species Act (ESA). These ESUs, which generally comprise several populations or stocks, belong to four species of anadromous salmonids: chinook salmon (*Oncorhynchus tshawytscha*), sockeye salmon (*O. nerka*), chum salmon (*O. keta*), and steelhead (*O. mykiss*), and are distributed across the wide variety of habitats found in the basin.

The Columbia River once supported one of the most productive salmon fisheries in the world, with an estimated 7–8 $\times$ 10^6 (Chapman 1986) to 15 $\times$ 10^6 (Northwest Power Planning Council [NPPC] 1986) anadromous fish returning to spawn each year. However, the far-ranging distribution of salmon during different parts of the life cycle has made them vulnerable to a wide variety of anthropogenic influences in freshwater, estuarine, and ocean habitats. Heavy fishing pressures initiated a decline in these populations beginning in the 1870s that has been exacerbated by a variety of factors, including continuing fishing pressure on some ESUs. Freshwater habitat throughout the basin has been degraded and lost through agriculture, ranching, mining, timber harvest, and urbanization. Estuarine marshes and swamps have been diked and drained. The construction and operation of hydropower and other dams throughout the basin have made dramatic changes to river systems. In addition, hatchery programs, intended to improve population status, may have worsened the situation, not only by increasing harvest rates on wild populations that are part of mixed-stock fisheries, but also through potential inadvertent negative genetic and ecological interactions (Thomas 1983, NRC [National Research Council] 1996, Williams et al. 1999). As a result of these many factors, wild coho (*Oncorhynchus kisutch*), which were once abundant, are now extinct in the interior basin; Columbia River sockeye, also once abundant, are maintained in a captive broodstock program; and every subbasin of the Columbia currently accessible to anadromous fishes contains at least one threatened or endangered salmonid ESU (Fig. 1).

However, these human factors are not the only influences on salmon population status. Recently, decadal-scale changes in ocean conditions due to climatic cycles (the Pacific Decadal Oscillation or PDO) have been implicated as a factor affecting Pacific salmon populations (e.g., Hare and Francis 1995), with Columbia River stocks experiencing 20–30-year periods of ''good'' ocean conditions associated with cooler temperatures in the northeast Pacific. These alternate with periods of warmer temperatures in the northeast Pacific, which are generally ''bad'' for Columbia River salmonids (Mantua et al. 1997, Hare et al. 1999). Other global climatic events may also affect Pacific salmon populations. In particular, there are El Niño/Southern Oscillation (ENSO) events, which are qualitatively similar to the warmer phase of the PDO, and are correspondingly ''bad'' for Columbia River salmonids. It is anticipated that these will increase in frequency and intensity in the future (Johnson 1988, Hare et al. 1999, Meehl et al. 2001). Global warming is also anticipated to generally worsen conditions for Columbia River salmonids (Chatter et al. 1995). Clearly, projections of population status or risks are likely to be affected by any assumptions about future ocean or climatic conditions.

Although the 12 listed ESUs in the Columbia River Basin have been the focus of many policy decisions affecting harvest management, hydropower dam operations, and a variety of other human activities (e.g., National Marine Fisheries Service [NMFS] 1995, 1999*a b*, 2000), few formal population viability analyses for any Pacific salmon species have been developed (the exceptions being Ratner et al. 1997 and Botsford and Brittnacher 1998). The salmonid species throughout the Columbia River Basin share many habitats and are impacted by many of the same management decisions—sometimes in differing manners. Consequently, there is a tremendous need to determine the status of stocks and ESUs throughout the basin, in a

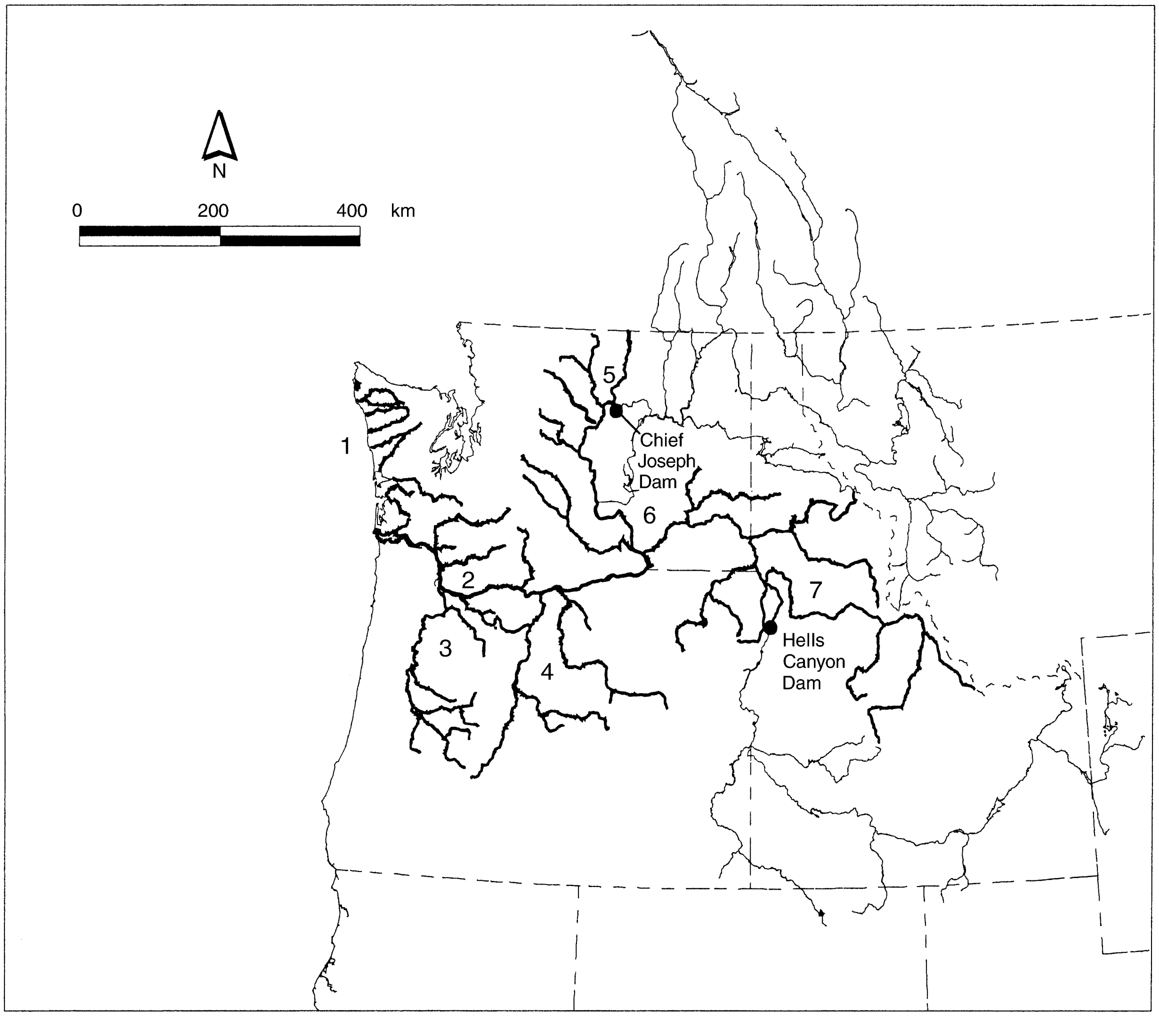

FIG. 1. The Columbia River Basin (Washington, USA). Heavy solid lines denote rivers accessible to anadromous fishes; thin solid lines denote portions of the Columbia and Snake Rivers blocked by dams. Numbers define regions, with analyzed salmonid stocks as follows: (1) Washington coast, nonlisted chinook stocks; (2) lower Columbia River, steelhead, chum, and chinook salmon listed as threatened; (3) upper Willamette River, steelhead and chinook listed as threatened; (4) middle Columbia River, steelhead listed as threatened and spring chinook nonlisted; (5) upper Columbia River, steelhead and spring chinook listed as endangered; (6) upper Columbia River, nonlisted summer/fall chinook stocks; (7) Snake River, steelhead, spring/summer chinook, and fall chinook listed as threatened; sockeye salmon listed as endangered.

manner that allows comparison between stocks, ESUs, and species. Such comparable quantitative reviews of population status are an important component of efforts to prioritize populations for recovery and conservation actions (Allendorf et al. 1997). They can also serve as a foundation for analytical efforts to determine the magnitude of natural anthropogenic impacts on population status or the potential of different restoration actions.

Efforts to determine salmonid population status, however, must deal with the complicating presence of large numbers of hatchery-reared fish, which may be reproducing along with wild-born fish. Regardless of whether the presence of hatchery-reared fish has a negative impact on wild-born fish, reproduction by hatchery fish presents an accounting problem that complicates the estimation of population status. This occurs because the wild population is being supplemented by an external population (the hatchery). Simply removing the hatchery spawners from the time series is not sufficient, since one must account for the hatchery fish offspring, their offspring's offspring, etc. Properly accounting for hatchery fish reproduction requires information on the relative reproductive success of hatchery fish. While it appears that hatchery-reared fish that spawn in the wild generally have lower breeding success than wild-born fish (Fleming 1982, Fleming and Gross 1993, 1994, Berejikian 1995), the estimates of their relative reproductive success are quite variable and range from 10% to 13% of that of wild-born spawners, for nonnative domesticated stock across the entire life cycle (Chilcote et al. 1986) to 80% of the wild fish rate, for local stock in the egg to the yearling stage only (Reisenbichler and McIntyre 1977). In our analyses, we correct for hatchery reproduction by contrasting two different assumptions. In the first case, we assume that hatchery fish have not been reproducing. This gives the most optimistic estimates of population status. In the second case, we assume that hatchery fish have been reproducing at the same rate as wild-born spawners. This gives the most pessimistic estimates. The true rate of hatchery fish reproduction is somewhere between these extremes.

Using these different assumptions, we then conduct a status assessment and analysis that focuses on the following: (1) What is the rate of population decline (or growth) and the associated risk of decline for listed Columbia River stocks and ESUs under the most recent (poor) ocean conditions (1980–2000)? (2) How do those estimates change, given the potential for hatchery fish to reproduce in the wild? (3) Do parameter and risk estimates change significantly if data including both ‘‘good’’ and ‘‘bad’’ ocean conditions (1965–2000) are used in the assessment?

Complete viability analyses will consider other factors in addition to these strictly demographic ones (Soulé and Gilpin 1986). Genetic diversity, the probability of catastrophes, Allee effects or depensation, and a variety of other potential factors can all affect population status. However, many of these concerns, such as the probability of catastrophe, are difficult or impossible to estimate (Coulson et al. 2001). In addition, for the majority of stocks in the region, only the most basic time-series data are available. Thus, we provide these demographic analyses as a first step towards a complete viability analysis.

METHODS

We estimated population trends and risk estimates for 152 stocks in 11 ESUs listed as threatened or endangered throughout the Columbia River Basin and for 24 stocks in three nonlisted ESUs regarded as ‘‘healthy.’’ We did not assess the status of Snake River sockeye, the 12th listed ESU, because this entire ESU is currently maintained in a captive broodstock program. Estimation of the long-term population growth rate (λ) was one of the main foci of our analysis. ‘‘Managing for λ’’ has been suggested as a strategy of achieving species viability and productivity (Caswell 2001), since any population with a declining growth rate ($\lambda < 1$) will eventually go extinct, regardless of initial size. Populations with a positive trend ($\lambda > 1$) increase in number and ultimately have a lower extinction risk. In addition, ESUs in the Columbia River Basin are severely depleted and one current management objective is to recover these populations to higher levels, which necessarily entails a $\lambda > 1$.

Time periods analyzed

We assessed the status of stocks and ESUs over two time periods: 1980–2000 and 1965–2000. Regime shifts in the Pacific Decadal Oscillation occurred in 1947 and 1977 (Francis and Hare 1994). Thus, the 1980–2000 time period gave an estimate of population growth rates during ocean conditions that are considered to have been poor for Columbia River salmonids (Mantua et al. 1997). Risk estimates projected from population growth rates using 1980–2000 time series thus carry the assumption that the warm ocean conditions characteristic of this time period persist indefinitely into the future. Note that most models of global climate change suggest that ENSO events (which are superficially similar to the warm phase of the PDO) will increase in frequency and intensity (Meehl et al. 2001). Thus, projections using the 1980–2000 period may be a surrogate for continued warm conditions due to global climate change. The configuration of the Columbia and Snake River hydropower system (including water storage capacity, which affects the Columbia plume and estuarine conditions) was also relatively uniform during this time period. Survival of juvenile chinook from the Snake River through the hydropower system did improve over these 20 years, but in comparison with the larger change in passage survival between the mid–late 1970s and early 1980s, it was relatively constant (Williams et al. 2001).

The longer time period (1965–2000) encompasses both ‘‘good’’ and ‘‘bad’’ ocean conditions. Risk estimates or projections of population growth rates from this time period implicitly incorporate the assumption that ocean conditions will cycle between these two regimes into the future, meaning that the poor ocean conditions of the late 20th century will not persist indefinitely. The 1965–2000 period also includes an episode of dam construction, particularly focused on the Lower Snake River; risk estimates for this area therefore also include a substantial perturbation. The 1965–1980 data were available for approximately half of the stocks we examined, in all ESUs except Upper Willamette River chinook and steelhead, Upper Columbia River steelhead, Washington Coastal chinook, and Columbia River chum. However, data prior to 1965 were not widely available, making pre-1965 analyses for the majority of stocks impossible.

Data used in analyses

Our analyses required, at the minimum, a time series of spawner abundance. Spawner abundance data consisted of either direct counts of returning adults at dams or weirs, index counts of spawner numbers, or estimates of total returning spawners. Index counts, such as ‘‘redds per mile’’ (a redd is the gravel nest made by spawning female) give a relative index rather than an absolute count of the total number of spawners. At the stock level, spawner estimates were typically derived from redd surveys of a portion of a particular river or creek, although dam or weir counts were available for some stocks. For seven ESUs (Snake River steelhead, fall chinook and spring/summer chinook, Upper Columbia River spring chinook and steelhead, and Upper Willamette River chinook and steelhead), total spawner estimates for the entire ESU were available via dam counts at the downstream end of the ESU. In order to best represent the number of fish on the spawning grounds, we subtracted fish from the time series that were harvested in-river or taken into hatcheries upstream, after dam counts. For three other ESUs (Lower Columbia River chinook and steelhead and Middle Columbia River steelhead), we created an ESU-level index count by aggregating all stocks within that ESU for which a total live spawner time series was available. No ESU-level counts were possible for Columbia River chum or the three nonlisted ESUs since the majority of time series within these ESUs were index counts.

Estimates of the proportion of hatchery-reared spawners in the time series were available for approximately half of the stocks analyzed. Estimates of the proportion of hatchery fish on the spawning grounds were based either on direct observations of fin-clipped fish or were derived from estimated hatchery stray rates. When the proportion of hatchery and wild spawners was unknown, we conducted our analyses on the total spawner counts, which include both wild- and hatchery-reared spawners.

The age at which individuals return to spawn varies by species and stock, and not all individuals within a given species and stock return at the same age. The distribution of the spawning age was available for most ESUs but variably available for individual stocks. A generic ESU-level spawner age distribution was used for those stocks without data. The raw spawner count, age, and hatchery-fraction data are supplied in the Supplement.

Estimating population-level parameters

We used time series of spawner counts to estimate population growth rates and risks by fitting a stochastic exponential decline model:

$$N_{t+1} = N_t \exp(\mu + \varepsilon) \tag{1}$$

[where ε is distributed Normal$(0, \sigma^2)$] to the data and then using diffusion approximation methods (Dennis et al. 1991) to estimate risks. However, the parameter estimation methods described by Dennis et al. (1991) were not appropriate for raw spawner counts for several reasons. First, spawner counts represent only a single life stage and are therefore not a representative sample of the entire population. In addition, salmon life history, particularly iteroparity and delays between birth and reproduction, make salmon prone to boom and bust cycles in annual spawner numbers. These cycles confound parameter estimation. Second, sampling error is likely to be very high in spawner count data (Hilborn et al. 1999). Large sampling error results in overestimates of the environmental variance, which lead to correspondingly poor estimates of any risk metrics that incorporate this measure of variance (Holmes 2001, Holmes and Fagan 2002). We used the following approach to deal with these issues.

First, we used a uniform running sum of four consecutive counts to filter out sampling error and age-structure cycles:

$$R_t = \sum_{j=1}^{4} S_{t+j-1}. \tag{2}$$

We tested the running sum transformed counts for their fit to the assumptions of the underlying stochastic process: (1) that the relationship between the variance and the lag, τ, in $\ln(R_{t+\tau}/R_t)$ was linear, using the R^2 of a least-squares fit through the variance data; (2) that $\ln(R_{t+1}/R_t)$ was distributed normally and there were no significant outliers (using the dffits statistic >2 [Chatterjee and Hadi 1988]); (3) that density-dependent processes were not apparent (following Dennis and Taper 1994); (4) that statistically significant temporal trends in μ were not present (using a method analogous to Dennis and Taper's test for density dependence); and (5) that there was no significant serial autocorrelation in the R_{t+1}/R_t ratios (by detrending the ratios and using Spearman's rank correlation test). All tests were done at the $P < 0.05$ significance level with no adjustment for the fact that multiple tests were conducted. We found a good fit to all assumptions with the following exceptions: the Upper Columbia spring chinook ESU-level data showed a downward trend in R_{t+1}/R_t ratios, as do most of the stocks within that ESU. This downward trend was also seen in a few stocks in most other ESUs. It should be kept in mind that simulations (ours and Shenk et al. 1998) indicate that significant trends appear by chance 25–30% of the time in 20-year samples of stochastic age-structured processes. Several stocks also showed evidence of density-depensatory or compensatory processes (Table 1). Risk estimates will tend to be overly optimistic when there is depensatory density dependence or declining trends in R_{t+1}/R_t ratios. A handful of stocks and the Upper Columbia River summer/fall chinook ESU showed evidence of first order autocorrelation in R_{t+1}/R_t ratios. When autocorrelation is present, σ^2 is underestimated using our methods, but μ should be unaffected (Tuljapurkar 1989).

While we have not conducted sensitivity analyses for each of these factors, a recent cross-validation study of diffusion approximation (DA) methods (Holmes and Fagan 2002) used long-term salmon time series to look implicitly at the effects of violations of simple DA model assumptions, such as no density-dependent processes, low autocorrelation, and no trends. This study found that DA methods gave unbiased estimates of λ and of the probability of decline. Only for rapidly increasing populations were biases in the estimation of

λ seen that were sufficient to cause overestimation of the risk of decline.

We estimated μ for each stock and ESU from the ratios of consecutive running sums:

$$\hat{\mu}_{\text{run}} = \text{mean}[\ln(R_{t+1}/R_t)]. \tag{3}$$

This method gives an estimate of μ that is resistant to severe age-structure perturbations and sampling error (Holmes 2001). We used a slope method to estimate σ^2

$$\hat{\sigma}^2_{\text{slp}} = \text{slope of var}\left[\ln\left(\frac{R_{t+\tau}}{R_t}\right)\right] \text{ vs. } \tau \tag{4}$$

for $\tau = 1, 2, 3$, and 4. This estimate of σ^2 is significantly less biased in the face of severe sampling error (Holmes and Fagan 2002). These parameter estimation methods have been cross validated using a large collection of west-coast salmon time series by Holmes and Fagan (2002).

Using estimates of μ and σ^2, we calculated the following metrics of risk to assess the status of these populations.

Long-term rate of population change.—The estimate of the long-term rate of population change (denoted $\hat{\lambda}$) is

$$\hat{\lambda} = \exp(\hat{\mu}). \tag{5}$$

Note that we use λ to denote the long-term population growth rate, defined as $\lambda = N_{t+\tau}/N_t^{1/\tau}$ as $\tau \to \infty$. If λ is less than 1, the population will go extinct with certainty over the long term, and over the short-term λ denotes the median observed growth rate. Our use of λ follows the concept of the time-averaged long-term rate of stochastic growth suggested by Caswell (2001). In Dennis et al. (1991), λ is used to indicate the mean (rather than median) annual growth rate ($= \exp[\mu + \sigma^2/2]$); however, we do not use the mean as our metric since the mean is not the long-term growth rate nor does $\exp(\mu + \sigma^2/2) < 1$ indicate extinction with certainty.

A range of underlying stochastic processes (with different μ and σ^2) could have produced the observed time series. The 95% confidence intervals on λ give an estimate of the range of true λs that could have produced the observed data. From Holmes and Fagan (2002), Eq. 4, the 95% confidence intervals on λ are

$$\begin{gathered}\exp\left[\hat{\mu} - t_{0.025,\text{df}}\sqrt{\hat{\sigma}^2/\gamma(n-4)}\right] \\ \exp\left[\hat{\mu} + t_{0.025,\text{df}}\sqrt{\hat{\sigma}^2/\gamma(n-4)}\right]\end{gathered} \tag{6}$$

where γ is a constant ($\approx$1) and $t_{\alpha,\text{df}}$ is the quantile of a student's t distribution at probability α and degrees of freedom df. The degrees of freedom for the t distribution are given by the degrees of freedom of the $\hat{\sigma}^2_{\text{slp}}$: df $\approx 0.333 + 0.212\, n - 0.387\, L$, where L is the number of counts summed together to form R_t (in our case $L = 4$) and n is the time series length (following Holmes and Fagan 2002).

Probability of extinction.—To estimate extinction probabilities, we required an estimate of population size. For this, we estimated the total number of wild-born fish alive at year t that do eventually return to spawn. We denote this TS_t. We can calculate TS_t using the mean age distribution of returning spawners:

$$\begin{aligned}\text{TS}_t = {} & w_t S_t + (1 - F_1) w_{t+1} S_{t+1} \\ & + (1 - F_1 - F_2) w_{t+2} S_{t+2} + \cdots\end{aligned} \tag{7}$$

where S_t is the spawner count at year t, F_i is the fraction of spawners that return at age i, and w_t is the fraction of year t spawners that were wild-born (vs. hatchery-reared). Note $F_0 = 0$, that is, no individuals return to spawn the same year that they are born.

The probability of reaching a given threshold population size, TS_e, before the end of t_e years (Eq. 16 × Eq. 84 in Dennis et al. [1991]) is

$$\begin{aligned}G\pi' = {} & \pi'\Phi\left[\frac{-\ln(\text{TS}_0/\text{TS}_\text{e}) + |\hat{\mu}|t_\text{e}}{\hat{\sigma}\sqrt{t_\text{e}}}\right] \\ & + \exp\left[\frac{2\ln(\text{TS}_0/\text{TS}_\text{e})|\hat{\mu}|}{\hat{\sigma}^2}\right] \\ & \times \Phi\left[\frac{-\ln(\text{TS}_0/\text{TS}_\text{e}) - |\hat{\mu}|t_\text{e}}{\hat{\sigma}\sqrt{t_\text{e}}}\right], \qquad t_\text{e} > 0\end{aligned} \tag{8}$$

where

$$\pi' = \begin{cases} 1 & \hat{\mu} \le 0 \\ \exp[-2\hat{\mu}\ln(\text{TS}_0/\text{TS}_\text{e})/\hat{\sigma}^2] & \hat{\mu} > 0. \end{cases}$$

The function Φ is the standard normal cumulative distribution function. The most recent TS_t estimate for each stock is denoted TS_0 and is given in Table 1. For extinction, we used $\text{TS}_\text{e} = 1$ and $t_\text{e} = 50$ years.

Probability of 90% decline.—In many cases, the probability of extinction could not be calculated, since TS_t requires total spawner counts rather than index counts, an estimate of the age distribution of returning spawners, and an estimate of the fraction of spawners in the time series that are wild born. Therefore, we also calculated the probability that the population is 90% lower at the end of t_e years = 50 years (cf. Eq. 6 in Dennis et al. 1991):

$$\Pr\left(\frac{\text{TS}_{t_\text{e}}}{\text{TS}_0} < \frac{10}{1}\right) = 1 - \Phi\left[\frac{\ln(10/1) + \hat{\mu}t_\text{e}}{\hat{\sigma}\sqrt{t_\text{e}}}\right]. \tag{9}$$

This risk metric could be calculated when only index counts were available or if spawner age data or hatchery fraction data were missing. The risk of 90% decline also gives another risk perspective for large populations that have a low extinction probability due to their size while still having a substantial probability of severe declines due to underlying dynamics.

We used parametric bootstrapping to estimate the confidence intervals on the probability of extinction and 90% decline by sampling from the estimated distributions of $\hat{\mu}$ and $\hat{\sigma}^2$ (Holmes and Fagan 2002). The estimated distribution of $\hat{\mu}$ is specified by $\hat{\mu}$ +

TABLE 1. Parameter estimates, risk of extinction and 90% decline in abundance in 50 years, and needed percentage increases in λ to achieve $\lambda = 1$ and to reduce 50-year risk of decline or extinction to below 5%.

ESU and stock (population size estimate)	Population parameter estimates†					
				Pr (λ)		Increase needed (%)
	μ	σ^2	λ (95% CI)	<1.0	<0.9	
Lower Columbia River chinook	**0.00**	**0.03**	**0.99 (0.68, 1.44)**	**0.50**	**0.27**	**0**
Abernathy Creek f-t (1587)	−0.03	0.02	0.98 (0.82, 1.15)	0.58	0.23	3
Bear Creek fall	−0.14	0.28	0.87 (0.45, 1.66)	0.71	0.54	15
Big Creek fall	−0.06	0.07	0.94 (0.76, 1.16)	0.68	0.33	6
Clackamas River fall	−0.04	0.04	0.96 (0.71, 1.30)	0.59	0.31	4
Clatskanie River fall	−0.02	0.68	0.98 (0.50, 1.93)	0.52	0.34	2
Coweman River f-t (2923)	0.23	0.19	1.26 (0.82, 1.94)	0.14	0.07	0
Cowlitz River f-t (7903)	−0.03	0.10	0.97 (0.71, 1.33)	0.56	0.29	3
Cowlitz River spring	−0.03	0.03	0.97 (0.83, 1.14)	0.61	0.23	3
Elochoman River f-t	0.05	0.40	1.05 (0.57, 1.96)	0.40	0.24	0
Germany Creek f-t	0.01	0.14	1.01 (0.67, 1.52)	0.47	0.26	0
Gnat Creek fall	−0.03	0.40	0.97 (0.56, 1.71)	0.54	0.34	3
Grays River f-t	−0.10	0.42	0.90 (0.48, 1.70)	0.65	0.47	11
Kalama River spring	−0.11	0.22	0.90 (0.57, 1.42)	0.69	0.48	11
Kalama River f-t	0.02	0.47	1.02 (0.52, 2.00)	0.46	0.29	0
Klickitat River f-t	0.08	0.13	1.08 (0.73, 1.59)	0.32	0.16	0
Lewis River f-b (34652)	−0.02	0.05	0.98 (0.79, 1.22)	0.55	0.24	2
Lewis River spring	−0.04	0.46	0.96 (0.50, 1.85)	0.56	0.38	4
Lewis East Fork f-t (853)	−0.01	0.02	0.99 (0.85, 1.15)	0.53	0.18	1
Mill Creek f-t	−0.10	0.26	0.91 (0.37, 2.24)	0.64	0.46	10
Plympton Creek fall	−0.02	0.11	0.98 (0.73, 1.32)	0.54	0.28	2
Sandy River fall	0.17	0.33	1.19 (0.74, 1.90)	0.20	0.10	0
Sandy River f-l (3790)	0.00	0.02	1.00 (0.82, 1.23)	0.47	0.21	0
Sandy River f-t (398)	−0.21	0.10	0.81 (0.14, 1.78)	0.74	0.61	23
Skamokawa Creek f-t	−0.10	0.14	0.90 (0.63, 1.30)	0.71	0.47	11
Washougal River f-t	0.04	0.02	1.04 (0.90, 1.21)	0.31	0.11	0
White Salmon River f-t	−0.13	0.12	0.88 (0.62, 1.23)	0.77	0.55	14
Wind River f-t	−0.10	0.81	0.90 (0.37, 2.18)	0.63	0.46	11
Wind River spring	0.01	0.05	1.01 (0.81, 1.27)	0.43	0.18	0
Youngs River fall	−0.03	1.21	0.97 (0.39, 2.40)	0.53	0.37	3
Upper Columbia River chinook (3381)	**−0.16**	**0.13**	**0.85 (0.62, 1.17)**	**0.82**	**0.63**	**17**
Entiat River spring (168)	−0.14	0.04	0.87 (0.73, 1.03)	0.86	0.64	15
Methow River spring (486)	−0.14	0.35	0.87 (0.51, 1.47)	0.73	0.54	15
Wenatchee River spring (1466)	−0.17	0.08	0.84 (0.65, 1.09)	0.86	0.68	18
Snake River spring/summer chinook (21683)	**−0.03**	**0.01**	**0.97 (0.89, 1.06)**	**0.68**	**0.14**	**3**
Alturas Lake Creek spring	−0.26	0.07	0.77 (0.62, 0.96)	0.94	0.86	29
Bear Valley/Elk Creek (713)	0.03	0.16	1.03 (0.74, 1.44)	0.42	0.22	0
Beaver Creek spring	−0.14	0.25	0.87 (0.53, 1.41)	0.74	0.56	15
Big Creek spring	0.00	0.18	1.00 (0.69, 1.45)	0.49	0.27	0
Big Sheep Creek spring	−0.08	1.77	0.93 (0.34, 2.55)	0.59	0.43	8
Camas Creek spring	−0.14	0.12	0.87 (0.62, 1.22)	0.71	0.58	15
Cape Horn Creek spring	0.02	0.22	1.02 (0.64, 1.61)	0.34	0.25	0
Catherine Creek spring	−0.10	0.15	0.91 (0.68, 1.22)	0.73	0.46	10
Catherine Creek North Fork spring	−0.06	0.25	0.94 (0.58, 1.53)	0.60	0.39	6
Catherine Creek South Fork spring	−0.11	0.86	0.90 (0.36, 2.22)	0.63	0.47	11
Chamberlain Creek spring	−0.10	0.09	0.91 (0.46, 1.81)	0.66	0.46	10
Grande Ronde River spring	−0.09	0.18	0.92 (0.66, 1.27)	0.70	0.44	9
Imnaha River spring (610)	−0.06	0.06	0.94 (0.77, 1.15)	0.67	0.35	6
Johnson Creek summer (432)	0.01	0.05	1.01 (0.83, 1.22)	0.45	0.17	0
Knapp Creek spring	−0.20	0.28	0.82 (0.49, 1.36)	0.81	0.66	23
Lake Creek summer	0.03	0.09	1.04 (0.78, 1.38)	0.39	0.18	0
Lemhi River spring	−0.02	0.32	0.98 (0.62, 1.56)	0.53	0.32	2
Lookingglass Creek spring	−0.20	0.15	0.82 (0.61, 1.10)	0.88	0.73	22
Loon Creek summer	0.00	0.03	1.00 (0.88, 1.14)	0.46	0.13	0
Lostine River spring	−0.01	0.07	0.99 (0.82, 1.21)	0.51	0.19	1
Marsh Creek spring (286)	0.01	0.15	1.01 (0.73, 1.39)	0.47	0.25	0
Minam River spring (322)	0.01	0.23	1.01 (0.68, 1.49)	0.47	0.26	0
Minam River Upper spring	0.01	0.12	1.01 (0.76, 1.34)	0.45	0.21	0
Minam River Lower spring	0.10	0.31	1.11 (0.70, 1.75)	0.30	0.16	0
Poverty Creek (951)	0.01	0.08	1.01 (0.80, 1.28)	0.45	0.20	0
Salmon River EF summer	−0.06	0.28	0.95 (0.61, 1.45)	0.61	0.38	6
Salmon River SF summer	0.06	0.12	1.07 (0.80, 1.41)	0.32	0.14	0
Salmon River Upper spring	−0.09	0.05	0.91 (0.76, 1.08)	0.79	0.45	10
Salmon River Upper summer	−0.11	0.10	0.90 (0.66, 1.23)	0.74	0.49	11
Secesh River summer	−0.02	0.00	0.98 (0.94, 1.03)	0.68	0.07	2
Sulphur Creek spring (200)	0.03	0.47	1.03 (0.59, 1.81)	0.43	0.26	0

TABLE 1. Extended.

Risk of extinction‡			Risk of 90% decline§			
50 years (95% CI)	Pr(VHER)	Increase needed (%)	50 years (95% CI)	Pr(VHRD)	Increase needed (%)	Additional notes‖
NA	**NA**	**NA**	**0.05 (0, 1)**	**0.51**	**0**	**i**
0.00 (0, 0.43)	0.28	0	0.17 (0, 1)	0.55	2	l
NA	NA	NA	0.90 (0, 1)	0.77	25	l,h,i
NA	NA	NA	0.63 (0, 1)	0.69	8	h,i
NA	NA	NA	0.40 (0, 1)	0.60	5	t,l,h,i
NA	NA	NA	0.41 (0, 1)	0.60	22	h,i
0.00 (0, 0.13)	0.13	0	0.00 (0, 0.67)	0.18	0	
NA	NA	NA	0.33 (0, 1)	0.59	6	h
NA	NA	NA	0.25 (0, 1)	0.57	3	l,h
NA	NA	NA	0.14 (0, 1)	0.47	7	h
NA	NA	NA	0.15 (0, 1)	0.51	4	h
NA	NA	NA	0.41 (0, 1)	0.61	16	h
NA	NA	NA	0.72 (0, 1)	0.72	25	h
NA	NA	NA	0.82 (0, 1)	0.74	19	l,d,h,f
NA	NA	NA	0.25 (0, 1)	0.53	13	h
NA	NA	NA	0.01 (0, 0.99)	0.36	0	l,h
0.00 (0, 0.08)	0.19	0	0.19 (0, 1)	0.54	3	
NA	NA	NA	0.49 (0, 1)	0.63	19	t,a,h
0.00 (0, 0.27)	0.26	0	0.06 (0, 1)	0.48	1	
NA	NA	NA	0.77 (0, 1)	0.69	20	l,h
NA	NA	NA	0.3 (0, 1)	0.58	6	
NA	NA	NA	0.01 (0, 0.98)	0.26	0	t,h,i
0.00 (0, 0.01)	0.24	0	0.01 (0, 1)	0.44	0	l
0.98 (0, 1)	0.76	19	1.00 (0, 1)	0.78	27	l
NA	NA	NA	0.85 (0, 1)	0.75	16	h
NA	NA	NA	0.00 (0, 0.94)	0.30	0	h
NA	NA	NA	0.96 (0, 1)	0.80	19	h
NA	NA	NA	0.67 (0, 1)	0.71	36	h
NA	NA	NA	0.03 (0, 1)	0.44	0	h
NA	NA	NA	0.45 (0, 1)	0.62	35	h,i
0.54 (0, 1)	**0.65**	**10**	**0.99 (0.01, 1)**	**0.89**	**22**	**t,d**
0.93 (0, 1)	0.83	10	1.00 (0.22, 1)	0.88	16	a,d
0.69 (0, 1)	0.76	21	0.87 (0, 1)	0.78	28	t,d
0.76 (0, 1)	0.76	11	1.00 (0.01, 1)	0.88	21	t,d
0.00 (0, 0)	**0.09**	**0**	**0.15 (0, 1)**	**0.53**	**1**	**l**
NA	NA	NA	1.00 (0.92, 1)	0.96	32	l,h,i
0.01 (0, 0.95)	0.37	0	0.09 (0, 1)	0.46	2	
NA	NA	NA	0.92 (0, 1)	0.79	25	h,i
NA	NA	NA	0.22 (0, 1)	0.54	6	t,h,i
NA	NA	NA	0.57 (0, 1)	0.69	53	i
NA	NA	NA	0.97 (0, 1)	0.81	20	i
NA	NA	NA	0.16 (0, 1)	0.81	5	d,i
NA	NA	NA	0.82 (0, 1)	0.77	15	i
NA	NA	NA	0.56 (0, 1)	0.66	14	h,i
NA	NA	NA	0.68 (0, 1)	0.71	38	i
NA	NA	NA	0.89 (0, 1)	0.70	13	t,h,i
NA	NA	NA	0.75 (0, 1)	0.74	16	i
0.03 (0, 1)	0.49	0	0.66 (0, 1)	0.69	8	
0.00 (0, 0.59)	0.30	0	0.05 (0, 1)	0.44	0	
NA	NA	NA	0.98 (0.01, 1)	0.85	33	d,h,i
NA	NA	NA	0.03 (0, 1)	0.42	0	d,h,i
NA	NA	NA	0.37 (0, 1)	0.59	13	h,i
NA	NA	NA	1.00 (0.10, 1)	0.91	29	i
NA	NA	NA	0.02 (0, 1)	0.40	0	l,h,i
NA	NA	NA	0.14 (0, 1)	0.50	3	i
0.03 (0, 0.99)	0.46	0	0.17 (0, 1)	0.51	4	
0.07 (0, 0.99)	0.48	1	0.21 (0, 1)	0.52	6	
NA	NA	NA	0.11 (0, 1)	0.48	3	i
NA	NA	NA	0.04 (0, 1)	0.36	0	h,i
0.00 (0, 0.84)	0.30	0	0.08 (0, 1)	0.47	2	
NA	NA	NA	0.56 (0, 1)	0.67	15	h,i
NA	NA	NA	0.01 (0, 0.98)	0.35	0	d,h,i
NA	NA	NA	0.94 (0.01, 1)	0.80	11	h,i
NA	NA	NA	0.91 (0, 1)	0.77	15	t,h,i
NA	NA	NA	0.00 (0, 0.86)	0.34	0	l,h,i
0.17 (0, 1)	0.55	8	0.21 (0, 1)	0.51	11	

TABLE 1. Continued.

ESU and stock (population size estimate)	Population parameter estimates†					
	μ	σ^2	λ (95% CI)	Pr (λ) <1.0	Pr (λ) <0.9	Increase needed (%)
Valley Creek Upper spring	0.04	0.63	1.04 (0.54, 1.99)	0.43	0.26	0
Valley Creek Upper summer	−0.08	0.20	0.92 (0.59, 1.43)	0.66	0.43	9
Wallowa Creek spring	−0.07	0.62	0.93 (0.51, 1.69)	0.61	0.43	8
Wenaha River South Fork spring	0.03	0.10	1.03 (0.81, 1.31)	0.39	0.17	0
Yankee Fork summer	−0.19	0.31	0.83 (0.48, 1.43)	0.79	0.63	21
Yankee West Fork summer	0.00	0.24	1.00 (0.62, 1.61)	0.49	0.28	0
Yankee West Fork spring	−0.17	0.14	0.84 (0.58, 1.22)	0.81	0.63	19
Snake River fall chinook (1946)	**−0.05**	**0.04**	**0.95 (0.76, 1.18)**	**0.65**	**0.32**	**5**
Up. Willamette River chinook (8770)	**−0.01**	**0.23**	**0.99 (0.65, 1.53)**	**0.50**	**0.29**	**1**
McKenzie River (5112)	0.01	0.20	1.01 (0.68, 1.51)	0.46	0.25	0
Columbia River chum	**NA**	**NA**	**NA**	**NA**	**NA**	NA
Grays River WF	0.21	0.23	1.23 (0.81, 1.88)	0.15	0.07	0
Grays River fall	−0.03	0.10	0.97 (0.73, 1.29)	0.58	0.30	3
Hardy Creek fall	0.04	0.06	1.04 (0.86, 1.26)	0.34	0.13	0
Crazy J Creek	0.14	0.03	1.15 (0.98, 1.34)	0.11	0.05	0
Hamilton Creek fall	−0.08	0.05	0.92 (0.75, 1.13)	0.74	0.40	8
Hamilton Springs	0.09	0.51	1.10 (0.61, 1.97)	0.33	0.19	0
Lower Columbia River steelhead	**−0.04**	**0.00**	**0.96 (0.94, 0.98)**	**0.84**	**0.10**	**4**
Clackamas River summer (2155)	−0.09	0.09	0.91 (0.71, 1.17)	0.73	0.46	10
Clackamas River winter (1041)	−0.10	0.06	0.91 (0.73, 1.13)	0.77	0.46	10
Green River winter (450)	−0.15	0.25	0.86 (0.17, 4.46)	0.67	0.52	16
Kalama River summer (6445)	−0.04	0.14	0.96 (0.67, 1.38)	0.57	0.34	4
Kalama River winter (4975)	−0.02	0.01	0.98 (0.87, 1.09)	0.61	0.19	2
Lewis River East Fork winter	−0.17	0.02	0.84 (0.15, 4.84)	0.76	0.61	19
Sandy River winter (4535)	−0.06	0.03	0.94 (0.79, 1.11)	0.71	0.32	6
Sandy River summer	−0.04	0.09	0.96 (0.75, 1.22)	0.62	0.31	5
Toutle River SF winter	−0.10	0.00	0.91 (0.88, 0.93)	0.79	0.43	10
Trout Creek summer	−0.25	0.03	0.78 (0.08, 0.95)	0.80	0.69	28
Washougal River summer	−0.12	0.01	0.89 (0.64, 1.24)	0.73	0.51	12
Wind River summer (1218)	−0.06	0.00	0.95 (0.51, 1.76)	0.64	0.34	6
Middle Columbia River steelhead	**−0.06**	**0.14**	**0.94 (0.69, 1.27)**	**0.65**	**0.38**	**6**
Bear Creek summer	−0.08	0.07	0.92 (0.69, 1.22)	0.71	0.43	9
Beaver Creek North Fork summer	−0.06	0.17	0.95 (0.69, 1.29)	0.63	0.36	6
Beech Creek summer	−0.02	0.17	0.98 (0.70, 1.38)	0.54	0.29	2
Beech Creek East Fork summer	−0.02	0.17	0.98 (0.71, 1.34)	0.54	0.29	2
Camp Creek summer	−0.01	0.16	0.99 (0.73, 1.35)	0.51	0.26	1
Canyon Creek summer	−0.03	0.17	0.97 (0.71, 1.33)	0.56	0.30	3
Canyon Creek Mid. Fork summer	−0.06	0.16	0.94 (0.69, 1.29)	0.64	0.37	6
Deep Creek summer	−0.03	0.18	0.97 (0.70, 1.34)	0.56	0.30	3
Deer Creek summer	−0.04	0.40	0.96 (0.60, 1.56)	0.56	0.36	4
Deschutes River summer (3052)	−0.06	0.16	0.94 (0.70, 1.27)	0.64	0.38	6
Eightmile Creek winter	−0.08	1.62	0.92 (0.15, 5.89)	0.57	0.43	8
Fields Creek summer	−0.11	0.11	0.90 (0.70, 1.15)	0.78	0.51	12
Fifteen Mile Creek winter	−0.01	0.03	0.99 (0.81, 1.20)	0.54	0.22	1
Kahler Creek summer	−0.02	0.51	0.98 (0.57, 1.68)	0.53	0.34	2
Mcclellan Creek summer	−0.05	0.15	0.95 (0.70, 1.28)	0.63	0.36	6
Mill Creek summer	−0.03	0.00	0.97 (0.91, 1.03)	0.69	0.17	3
Murderers Creek summer	−0.18	0.25	0.83 (0.57, 1.22)	0.82	0.65	20
Olive Creek summer	−0.02	0.19	0.98 (0.70, 1.37)	0.55	0.30	2
Parrish Creek summer	−0.03	0.51	0.97 (0.57, 1.68)	0.54	0.34	3
Ramsey Creek winter	0.06	1.65	1.06 (0.16, 6.83)	0.44	0.30	0
Riley Creek summer	−0.06	0.24	0.94 (0.61, 1.46)	0.61	0.39	6
Shitike Creek summer	−0.06	0.03	0.94 (0.80, 1.10)	0.73	0.33	7
Tex Creek summer	−0.15	0.33	0.86 (0.56, 1.34)	0.76	0.57	16
Umatilla River summer (5384)	−0.01	0.05	0.99 (0.84, 1.17)	0.51	0.19	1
Wall Creek summer	−0.02	0.22	0.98 (0.69, 1.40)	0.53	0.29	2
Warm Springs summer (729)	−0.06	0.08	0.94 (0.74, 1.19)	0.66	0.36	6
Wind Creek summer	−0.06	0.03	0.94 (0.83, 1.06)	0.78	0.28	7
Yakima River summer	0.14	0.21	1.15 (0.59, 2.24)	0.27	0.15	0
Upper Columbia River steelhead (2822)	**0.00**	**0.15**	**1.00 (0.66, 1.52)**	**0.50**	**0.27**	**0**
Snake River steelhead (41035)	**−0.04**	**0.03**	**0.96 (0.84, 1.10)**	**0.65**	**0.23**	**4**
Butte Creek summer A	0.06	0.65	1.07 (0.57, 1.97)	0.39	0.23	0
Camp Creek summer A	0.02	0.18	1.02 (0.73, 1.40)	0.45	0.22	0
Crow Creek summer A	0.03	0.25	1.03 (0.70, 1.50)	0.42	0.22	0
Devils Run Creek summer A	0.05	0.25	1.05 (0.72, 1.55)	0.37	0.19	0
Five Points Creek summer A	0.00	0.11	1.00 (0.78, 1.30)	0.47	0.21	0
Fly Creek summer A	0.00	0.28	1.00 (0.67, 1.50)	0.48	0.27	0
McCoy Creek summer A	0.08	0.10	1.09 (0.85, 1.39)	0.25	0.10	0

TABLE 1. Continued, Extended.

Risk of extinction‡			Risk of 90% decline§			
50 years (95% CI)	Pr(VHER)	Increase needed (%)	50 years (95% CI)	Pr (VHRD)	Increase needed (%)	Additional notes‖
NA	NA	NA	0.22 (0, 1)	0.51	14	h,i
NA	NA	NA	0.72 (0, 1)	0.71	16	h,f,i
NA	NA	NA	0.60 (0, 1)	0.69	28	h,i
NA	NA	NA	0.05 (0, 1)	0.42	0	i
NA	NA	NA	0.96 (0, 1)	0.83	33	t,l,h,i
NA	NA	NA	0.24 (0, 1)	0.54	7	h,i
NA	NA	NA	0.99 (0, 1)	0.85	24	h,i
0.00 (0, 0.99)	**0.37**	**0**	**0.58 (0, 1)**	**0.65**	**6**	
0.01 (0, 0.99)	**0.35**	**0**	**0.29 (0, 1)**	**0.56**	**8**	
0.00 (0, 0.97)	0.33	0	0.18 (0, 1)	0.51	5	
NA	**NA**	**NA**	**NA**	**NA**	**NA**	**i**
NA	NA	NA	0.00 (0, 0.86)	0.26	0	l,i
NA	NA	NA	0.38 (0, 1)	0.61	7	l,i
NA	NA	NA	0.01 (0, 0.99)	0.35	0	l,i
NA	NA	NA	0 (0, 0.001)	0.13	0	l,i
NA	NA	NA	0.86 (0, 1)	0.75	10	i
NA	NA	NA	0.10 (0, 1)	0.41	6	t,a,l,i
NA	**NA**	**NA**	**0.05 (0, 1)**	**0.49**	**0**	**l**
0.11 (0, 1)	0.53	2	0.87 (0, 1)	0.76	13	t
0.13 (0, 1)	0.55	2	0.93 (0, 1)	0.78	12	t
0.73 (0, 1)	0.70	18	0.93 (0, 1)	0.72	25	t
0.01 (0, 1)	0.39	0	0.42 (0, 1)	0.61	8	d
0.00 (0, 0)	0.19	0	0.07 (0, 1)	0.51	1	l
NA	NA	NA	1.00 (0, 1)	0.78	18	i
0.00 (0, 0.71)	0.30	0	0.73 (0, 1)	0.70	6	
NA	NA	NA	0.49 (0, 1)	0.64	7	t,h
NA	NA	NA	1.00 (1, 1)	0.80	6	l,i
NA	NA	NA	1.00 (0, 1)	0.83	28	t,h
NA	NA	NA	1.00 (0, 1)	0.75	10	l,h,i
0.00 (0, 1)	0.38	0	0.91 (0, 1)	0.61	3	l
NA	**NA**	**NA**	**0.62 (0, 1)**	**0.69**	**11**	**i**
NA	NA	NA	0.85 (0, 1)	0.73	11	h,f,i
NA	NA	NA	0.57 (0, 1)	0.67	12	i
NA	NA	NA	0.34 (0, 1)	0.59	8	f,i
NA	NA	NA	0.34 (0, 1)	0.59	8	f,i
NA	NA	NA	0.25 (0, 1)	0.55	6	f,i
NA	NA	NA	0.37 (0, 1)	0.60	8	f,i
NA	NA	NA	0.58 (0, 1)	0.68	12	f,i
NA	NA	NA	0.38 (0, 1)	0.60	9	l,f,i
NA	NA	NA	0.47 (0, 1)	0.64	17	f,i
0.06 (0, 0.99)	0.47	1	0.61 (0, 1)	0.68	12	
NA	NA	NA	0.57 (0, 1)	0.66	50	i
NA	NA	NA	0.91 (0, 1)	0.80	16	t,f,i
NA	NA	NA	0.11 (0, 1)	0.52	2	h,f,i
NA	NA	NA	0.41 (0, 1)	0.52	19	a,f,i
NA	NA	NA	0.56 (0, 1)	0.67	11	f,i
NA	NA	NA	0.02 (0, 1)	0.50	0	l,f,i
NA	NA	NA	0.97 (0, 1)	0.86	29	f,i
NA	NA	NA	0.36 (0, 1)	0.60	9	f,i
NA	NA	NA	0.42 (0, 1)	0.62	19	f,i
NA	NA	NA	0.29 (0, 1)	0.52	32	i
NA	NA	NA	0.58 (0, 1)	0.67	14	f,i
NA	NA	NA	0.79 (0, 1)	0.71	6	h,i
NA	NA	NA	0.89 (0, 1)	0.81	28	f,i
0.00 (0, 0.05)	0.21	0	0.10 (0, 1)	0.50	2	d
NA	NA	NA	0.33 (0, 1)	0.58	9	f,i
0.06 (0, 1)	0.50	1	0.63 (0, 1)	0.68	9	
NA	NA	NA	0.79 (0, 1)	0.74	6	f,i
NA	NA	NA	0.01 (0, 1)	0.32	0	t
0.00 (0, 1)	**0.36**	**0**	**0.19 (0, 1)**	**0.53**	**5**	**t**
0.00 (0, 0.003)	**0.16**	**0**	**0.38 (0, 1)**	**0.61**	**4**	
NA	NA	NA	0.17 (0, 1)	0.47	12	a,i
NA	NA	NA	0.15 (0, 1)	0.50	4	i
NA	NA	NA	0.15 (0, 1)	0.49	5	a,i
NA	NA	NA	0.08 (0, 1)	0.43	2	t,i
NA	NA	NA	0.15 (0, 1)	0.55	3	h,i
NA	NA	NA	0.26 (0, 1)	0.55	9	i
NA	NA	NA	0.00 (0, 0.94)	0.28	0	i

TABLE 1. Continued.

ESU or stock (population size estimate)	Population parameter estimates†					
				Pr(λ)		Increase needed (%)
	μ	σ^2	λ (95% CI)	<1.0	<0.9	
Meadow Creek summer A	0.00	0.14	1.00 (0.75, 1.33)	0.48	0.23	0
Peavine Creek summer A	0.07	0.29	1.07 (0.69, 1.67)	0.35	0.19	0
Phillips Creek summer A	−0.03	0.09	0.97 (0.77, 1.23)	0.57	0.26	3
Prairie Creek summer A	0.16	0.38	1.18 (0.74, 1.88)	0.21	0.11	0
Snake River A (39585)	−0.03	0.03	0.97 (0.85, 1.11)	0.60	0.20	3
Snake River B (9115)	−0.08	0.07	0.93 (0.76, 1.14)	0.68	0.41	8
Summit Creek summer A	0.03	0.36	1.03 (0.65, 1.63)	0.43	0.24	0
Swamp Creek summer A	0.01	0.11	1.01 (0.78, 1.31)	0.45	0.20	0
Wallowa River summer A	−0.11	0.10	0.89 (0.64, 1.26)	0.74	0.50	12
Upper Willamette River steelhead (9898)	**−0.07**	**0.05**	**0.93 (0.75, 1.16)**	**0.70**	**0.37**	**7**
Agency Creek winter	0.00	0.46	1.00 (0.52, 1.94)	0.49	0.31	0
Calapooia River late (196)	−0.07	0.21	0.93 (0.60, 1.46)	0.63	0.41	7
Mill Creek winter	0.04	0.10	1.04 (0.76, 1.41)	0.39	0.19	0
Mollala River late (573)	−0.14	0.10	0.87 (0.68, 1.11)	0.84	0.61	15
N. Santiam River late (2286)	−0.12	0.05	0.89 (0.75, 1.06)	0.84	0.54	12
S. Santiam River winter (1061)	0.01	0.02	1.01 (0.90, 1.14)	0.39	0.10	0
S. Santiam River late (1202)	−0.13	0.07	0.88 (0.72, 1.08)	0.84	0.58	14
Willamette River winter	−0.08	0.08	0.92 (0.73, 1.16)	0.72	0.41	8
Washington Coast chinook	**0.00**	**0.10**	**1.00 (0.76, 1.32)**	**0.47**	**0.22**	**0**
Hoh River fall	−0.02	0.03	0.98 (0.85, 1.14)	0.57	0.19	2
Hoh River spring	0.00	0.09	1.00 (0.79, 1.26)	0.50	0.21	0
Queets River fall (16333)	0.05	0.04	1.05 (0.77, 1.42)	0.28	0.21	0
Willapa River fall	0.01	0.05	1.01 (0.68, 1.50)	0.47	0.25	0
Upper Columbia River summer/fall chinook	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**
Hanford Reach fall	0.04	0.16	1.04 (0.70, 1.55)	0.39	0.21	0
Methow River summer	0.01	0.01	1.01 (0.92, 1.11)	0.41	0.12	0
Okanogan River summer	0.10	0.15	1.11 (0.72, 1.70)	0.29	0.15	0
Similkameen River summer	0.08	0.15	1.09 (0.72, 1.65)	0.32	0.16	0
Wenatchee River summer	0.00	0.02	1.00 (0.86, 1.16)	0.47	0.17	0
Middle Columbia River spring chinook	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**
American River	−0.05	0.08	0.95 (0.72, 1.26)	0.63	0.34	5
Beaver Creek	−0.05	0.06	0.95 (0.77, 1.16)	0.67	0.31	5
Bull Run Creek	0.03	0.03	1.03 (0.89, 1.18)	0.35	0.10	0
Clear Creek	0.01	0.07	1.01 (0.82, 1.23)	0.46	0.17	0
Granite Creek	0.02	0.02	1.02 (0.92, 1.14)	0.33	0.08	0
John Day River	0.06	0.04	1.06 (0.92, 1.22)	0.24	0.08	0
John Day River Middle Fork	0.06	0.13	1.07 (0.81, 1.40)	0.31	0.13	0
John Day River North Fork	0.05	0.07	1.05 (0.86, 1.29)	0.31	0.12	0
Klickitat River	0.05	0.23	1.06 (0.66, 1.69)	0.38	0.21	0
Mill Creek	0.00	0.07	1.00 (0.80, 1.23)	0.50	0.20	0
Naches River	0.05	0.18	1.05 (0.39, 2.78)	0.42	0.26	0
Shitike Creek	−0.02	0.01	0.98 (0.90, 1.07)	0.62	0.12	2
Warm Springs River	−0.03	0.06	0.97 (0.79, 1.19)	0.59	0.25	3
Wind River	0.01	0.05	1.01 (0.81, 1.27)	0.43	0.18	0
Yakima River	0.00	0.00	1.00 (0.99, 1.01)	0.48	0.18	0

Notes: The most recent TS_t estimates for stocks with total spawner counts are noted in parentheses after the stock or ESU name. Abbreviations: f-t, fall thules; f-b, fall brights. ESU-level estimates are in bold. Estimates were made assuming no hatchery fish reproduction. When hatchery fraction data were available, the hatchery input correction was used. Otherwise estimates used the total (wild + hatchery) spawner count data. Population size estimate is an estimate of the total spawner population. The first 11 ESUs are listed under the U.S. Endangered Species Act; the three nonlisted ESUs follow.

† ''Increase needed'' refers to the percentage increase in λ needed to achieve $\lambda = 1$.

‡ Pr(VHER) is the probability of very high extinction risk (the probability that extinction risk in 50 years is over 25%). ''Increase needed'' refers to the percentage increase in λ needed to reduce the 50-year risk of extinction to below 5%.

‖ Tests for underlying assumptions were made on the running sums of wild-spawner-only counts where possible; otherwise total mixed counts were used. The codes designate tests that failed at ($P < 0.05$). Note that a number of the ''fails'' are false fails since the P value was not adjusted for 152 tests being conducted. If the P value is adjusted ($P < 0.001$) to reduce the probability of a false positive to less than 5%, none of the time series fail the diagnostic tests. Definitions of codes are as follows: a, significant first-order autocorrelation in $\ln(R_{t+1}/R_t)$ was found; d, a model with depensatory density dependence fit the data significantly better than a model with no density dependence (this indicates that the risk estimates are pessimistic); t, a model with a trend in μ fit the data significantly better than the model with no trend (this indicates that the risk estimates are optimistic); l, the variance vs. τ plot was nonlinear ($R^2 < 0.7$), indicating an underestimate of σ^2. Reasons for NA in the extinction estimates column: i, index data, no extinction estimates possible; h, no hatchery data, no extinction estimates possible, risk estimates calculated on (wild + hatchery) spawner count; f, no age of spawners data, no extinction estimates possible.

§ Pr(VHRD) is the probability of very high risk of decline (the probablility that the risk of 90% decline in 50 years is over 25%). ''Increase needed'' refers to the percentage increase in λ needed to reduce the 50-year risk of decline to below 5%.

TABLE 1. Continued, Extended.

Risk of extinction			Risk of 90% decline			
50 years (95% CI)	Pr(VHER)	Increase needed (%)	50 years (95% CI)	Pr(VHRD)	Increase needed (%)	Additional Notes‖
NA	NA	NA	0.18 (0, 1)	0.52	4	i
NA	NA	NA	0.07 (0, 1)	0.41	2	i
NA	NA	NA	0.32 (0, 1)	0.59	6	i
NA	NA	NA	0.02 (0, 0.96)	0.28	0	a,h,i
0.00 (0, 0)	0.14	0	0.21 (0, 1)	0.56	3	
0.00 (0, 0.94)	0.41	0	0.79 (0, 1)	0.71	10	
NA	NA	NA	0.19 (0, 1)	0.50	8	i
NA	NA	NA	0.11 (0, 1)	0.47	3	i
NA	NA	NA	0.93 (0, 1)	0.77	15	h,i
0.00 (0, 0.97)	**0.33**	**0**	**0.78 (0, 1)**	**0.71**	**8**	
NA	NA	NA	0.31 (0, 1)	0.56	14	h,f,i
0.40 (0, 1)	0.67	10	0.64 (0, 1)	0.68	14	
NA	NA	NA	0.03 (0, 1)	0.42	0	h,f,i
0.69 (0, 1)	0.76	11	0.98 (0.01, 1)	0.86	19	t
0.14 (0, 0.99)	0.54	2	0.99 (0.05, 1)	0.86	14	t
0.00 (0, 0)	0.15	0	0.00 (0, 0.77)	0.33	0	
0.40 (0, 1)	0.66	6	0.98 (0.01, 1)	0.86	16	
NA	NA	NA	0.8 (0, 1)	0.74	11	h,f
NA	**NA**	**NA**	**0.12 (0, 1)**	**0.50**	**2**	**i**
NA	NA	NA	0.13 (0, 1)	0.52	2	h
NA	NA	NA	0.16 (0, 1)	0.51	3	a,h
0.00 (0, 0.07)	0.23	0	0.00 (0, 1)	0.41	0	
NA	NA	NA	0.04 (0, 1)	0.49	0	h
NA	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**
NA	NA	NA	0.06 (0, 1)	0.44	1	t,a,h
NA	NA	NA	0.00 (0, 0.69)	0.32	0	l,h,i
NA	NA	NA	0.01 (0, 0.96)	0.33	0	h,i
NA	NA	NA	0.01 (0, 0.99)	0.36	0	h,f,i
NA	NA	NA	0.01 (0, 1)	0.43	0	h,i
NA	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**
NA	NA	NA	0.55 (0, 1)	0.65	8	h,i
NA	NA	NA	0.57 (0, 1)	0.67	7	l,h,f,i
NA	NA	NA	0.00 (0, 0.95)	0.32	0	l,h,f,i
NA	NA	NA	0.08 (0, 1)	0.46	1	h,f,i
NA	NA	NA	0.00 (0, 0.69)	0.28	0	l,h,f,i
NA	NA	NA	0.00 (0, 0.75)	0.24	0	h,i
NA	NA	NA	0.01 (0, 0.99)	0.35	0	h,i
NA	NA	NA	0.01 (0, 0.94)	0.33	0	h,i
NA	NA	NA	0.07 (0, 1)	0.44	2	h
NA	NA	NA	0.13 (0, 1)	0.50	2	h,f,i
NA	NA	NA	0.06 (0, 1)	0.47	1	h,i
NA	NA	NA	0.05 (0, 1)	0.47	1	h,f,i
NA	NA	NA	0.32 (0, 1)	0.59	5	h,i
NA	NA	NA	0.03 (0, 1)	0.44	0	h
NA	NA	NA	0.55 (0, 1)	0.65	0	l,h,f,i

$\sqrt{\hat{\sigma}^2/\gamma(n-4)} \times t_{\mathrm{df}}$, where t_{df} is a t-distributed random variable with df degrees of freedom. The estimated distribution of $\hat{\sigma}^2$ is a chi-squared (df) random variable multiplied by $\hat{\sigma}^2/\mathrm{df}$, where df is specified as discussed for Eq. 6. Confidence intervals on these risk metrics are generally very large. For example, the 95% confidence intervals on probabilities of 90% decline or extinction are often 0 to 1 (Table 1). However, cross-validation work suggests that within a collection of populations, the mean probability of decline gives an unbiased estimate of the fraction of populations that will decline (Holmes and Fagan 2002)—although one does not know which populations will decline. The variability of the mean is much less than the variability of individual estimates, and thus we use the mean probability of decline or extinction of all stocks within an ESU to give us a relatively tight estimate of the mean risk to those stocks.

Presenting levels of support for different risk metrics.—The bootstrapped confidence intervals indicate how variable the risk estimates are, but they do not necessarily give a good sense of the degree to which the data support different conjectures about the risk levels, for example, whether the true rate of population decline is $\lambda < 0.95$, say. To examine the data support for different risk levels, we used Bayesian techniques with uniform priors to calculate the probability that the true risks were above or below certain thresholds.

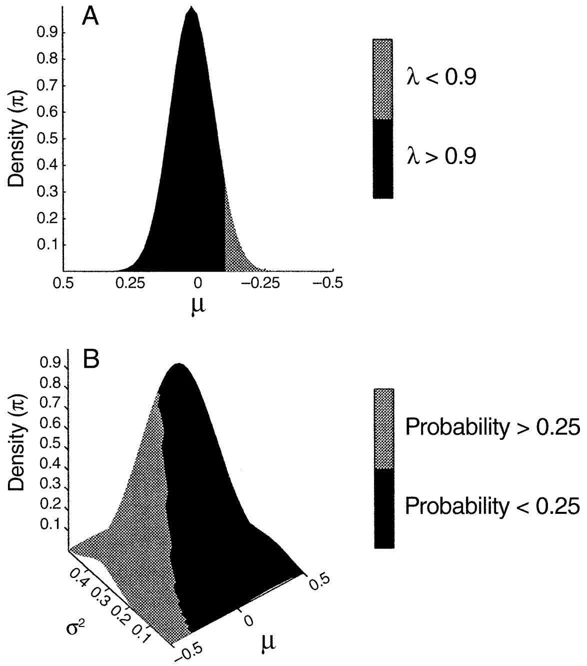

FIG. 2. Illustration of the Bayesian risk metrics, the probability that the true λ is less than 0.9 and the probability that the true risk of decline or extinction is very high. This requires first calculating the posterior probability density functions (π) of the parameters. The surfaces in panels (A) and (B) are illustrations of π's. (A) The probability that λ is less than 0.9 is calculated by integrating the π for μ over those μ for which $\lambda < 0.9$. (B) The probability that the true risk of decline or extinction is very high is calculated by integrating the joint π's for μ and σ^2 over those values of μ and σ^2 for which the probability of 90% decline (VHDR) or probability of extinction (VHER) is greater than 25%.

Bayesian approaches are commonly used in conservation biology to express risks in this manner (Wade 2000), and E. Holmes (*unpublished manuscript*) gives algorithms for calculating the probability that λ is less than some threshold given the observed data and the probability that the risk of the population declining or going extinct is greater than some threshold. Using these methods, we estimated the probability that the stock has a very high extinction risk (VHER) or a very high decline risk (VHRD). VHER is defined as a >25% probability of extinction in 50 years. VHRD is defined as a >25% probability of 90% decline in 50 years. To calculate the probability that a stock falls in the VHER or VHRD category, we first calculated the posterior probability distributions of the parameters μ and σ^2 and then integrated over the distributions, assuming uniform priors, over those values of μ and σ^2 that gave a VHER or VHRD. This is shown diagrammatically in Fig. 2.

Adjusting parameter estimates for inputs from hatchery-origin spawners

The introduction of reproducing hatchery-born spawners (in effect, fish from another population) confounds the parameter estimates of the long-term population growth rate due to natural reproduction and survival. If hatchery fish reproduce successfully instream, we must account for these inputs, otherwise μ (and any risk estimates incorporating μ) will be overestimated. Our adjustment responds to an accounting problem rather than a negative ecological or genetic effect of the hatchery fish. Because information on hatchery fish reproductive success is sparse and variable, we estimated parameters under two assumptions that, taken together, bracket the range of possible situations:

(1) Hatchery fish were assumed not to reproduce. That is, all wild-born spawners observed had wild-born parents. Parameters were estimated using Eqs. 3 and 4 with hatchery spawners removed from the time series before analysis. When no estimates of the fraction of hatchery fish were available, the parameters were estimated using the total spawner or index count, which may include hatchery-reared spawners. If the proportion of hatchery fish in the time series does not change substantially through time, and those hatchery fish do not reproduce, the resulting estimates of μ and σ^2 will be the same as if the hatchery fish had been removed from the time series prior to parameter estimation.

(2) Hatchery fish were assumed to reproduce at a rate equal to that of wild fish, and thus, wild spawners in the time series may have had wild- or hatchery-born parents. Our estimates of μ in this case were

$$\hat{\mu} = \text{mean}\left[\frac{1}{T}\ln(\hat{w}_t) + \ln\left(\frac{S_{t+1}}{S_t}\right)\right] \qquad (10)$$

where w_t is the proportion of the spawning population that was born in the wild (of wild- or hatchery-reared parents), S_t is the total number of spawners (wild plus hatchery-born) at year t. Our estimates of σ^2 were not adjusted since simulations indicated that $\hat{\sigma}^2_{\text{slp}}$ corrected for the extra variability due to variable hatchery inputs. E. Holmes (*unpublished manuscript*) gives a derivation of Eq. 10.

Comparing time periods

To assess the effect of a parameterization time period that included cooler, ''good'' ocean conditions, we repeated the analyses for the 83 stocks with data beginning in 1965 (Appendix B), and we then compared these estimates to the estimates using 1980–2000 data. We compared the mean λ between the two time periods for stocks within each ESU using a two-tailed paired t test. Only the 83 stocks with both 1965–2000 and 1980–2000 data were used in this comparison.

RESULTS

In many of the listed ESUs, the estimated total spawner population (TS) showed marked decline since 1980 (Fig. 3). While it is apparent from these trends alone that these populations are at considerable demographic risk if such declines continue into the future,

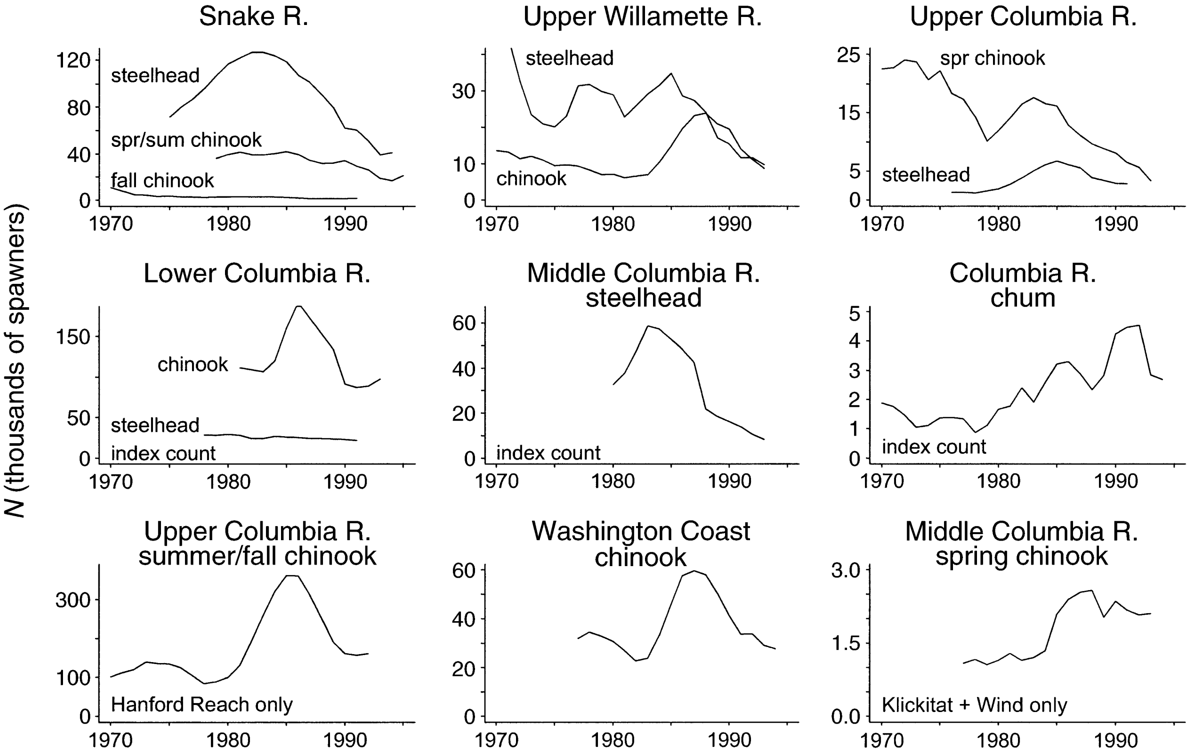

FIG. 3. Time series of TS_t, the estimated total living current or future spawner population size, for each ESU in the Columbia River basin, plus Hanford Reach and coastal chinook. In these plots, R_t was estimated from total (wild + hatchery origin) spawner-count time series spanning 1980–1999. All y-axis numbers are in thousands.

a quantitative assessment of this status allows us to compare formally the status of listed and unlisted stocks; to estimate the wild population growth rate with masking from hatchery inputs; and finally, to study whether these downward trends have been persistent through periods of both good and bad ocean conditions. When presenting the results, we contrast three different levels of estimates: (1) the ESU-level estimate. This is the estimate of the risk to the ESU as a unit, i.e., the risk estimated from the total number of spawners within the ESU; (2) the stock-level estimate. This is the risk estimate for a single stock, generally the fish spawning in a single creek or section of a larger river; (3) the mean risk to stocks within the ESU. This mean stock status is different than the ESU-level risk. For example, the ESU as whole may appear to be at low risk due to a few large, relatively healthy, stocks even though the ESU as a whole contains mostly smaller, rapidly declining, stocks.

Population trends from 1980 to the present

Given the trajectories seen at the ESU level (Fig. 3), it is not surprising that, for most ESUs, the estimated long-term population growth rate indicated a declining population. We had an ESU-level time series and thus were able to estimate an ESU-level λ, for 10 of the 11 ESUs; the exception was Columbia River chum. For nine of these, the point estimate of λ was less than 1.0 (Table 1, Fig. 4a), and for four ESUs, the estimated λ was <0.95. The ESU in the worst apparent condition was Upper Columbia River spring chinook, for which the ESU-level λ was <0.9. At the stock level, the λ estimates were more variable, and most ESUs contained some stocks with estimated λ's greater than 1.0. However, in all listed ESUs, except Columbia River chum, the majority of stock-level λ's were <1.0. In addition, two ESUs, Lower Columbia River steelhead (with 12 stocks), and Upper Columbia River spring chinook (with three stocks), did not have a single stock with an estimated $\lambda > 1.0$, and the Middle Columbia River steelhead ESU had only two stocks (out of 28) with an estimated $\lambda > 1.0$.

In contrast, the majority of λ estimates for stocks in the unlisted ESUs were ≥ 1.0 (Table 1), with a mean value of 1.02. In fact, the population growth rates of the unlisted ESUs and stocks were significantly higher than those of the listed stocks (one-tailed t test, $P < 0.001$). The estimated risks faced by these populations were correspondingly lower (Figs. 4–6).

The confidence intervals on λ estimates were generally wide, primarily due to our uncertainty in estimation of σ^2. Thus, we cannot rule out the possibility that the underlying dynamics in the listed ESUs are positive ($\lambda > 1.0$) and that the declining trends were observed by chance as can occur when σ^2 is large. The consistent declining trend estimates across the listed

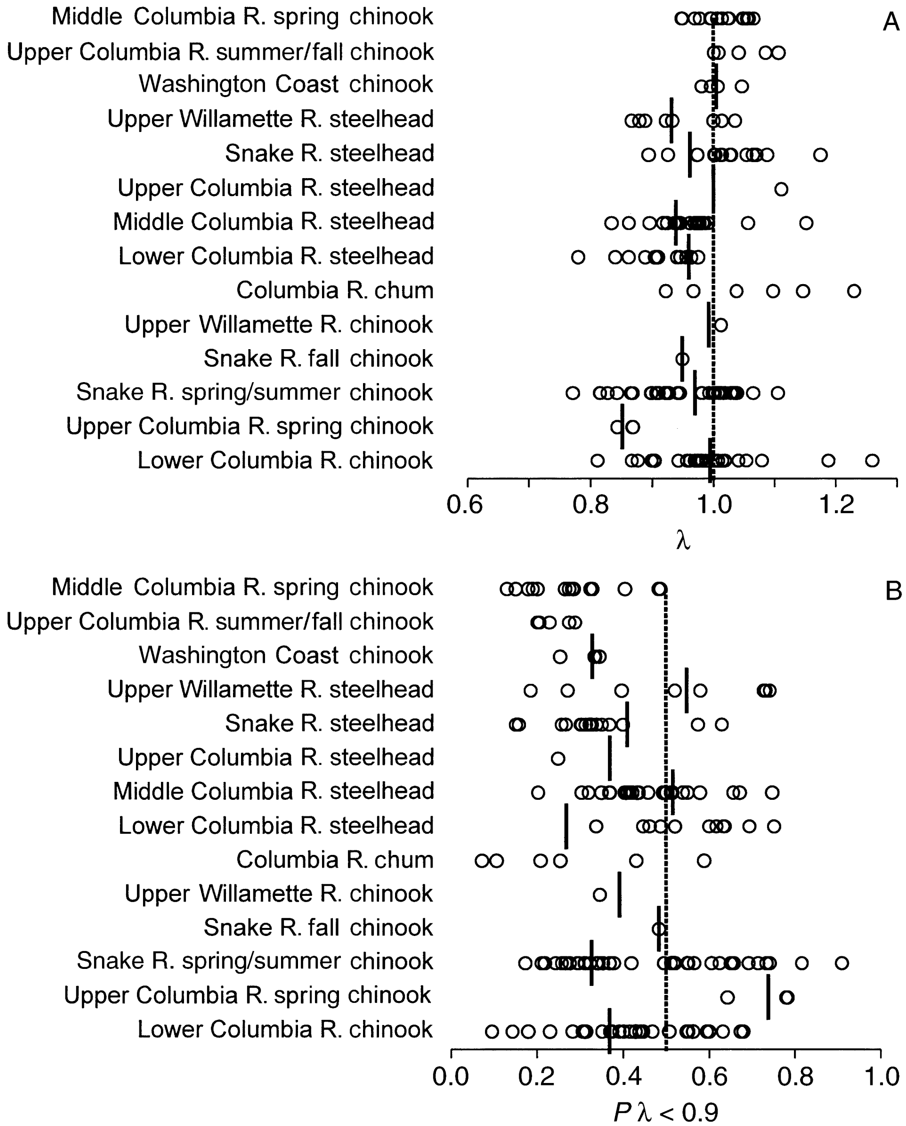

FIG. 4. Estimated long-term rate of population decline, λ, at the individual stock level (circles) and at the ESU level (bar). (A) Estimates assuming that no masking of the parameter μ occurred due to hatchery fish reproduction (i.e., hatchery reproduction = 0). The dotted line shows $\lambda = 1.0$. Below 1.0, the population is estimated to be declining. Above 1.0, the population is estimated to be increasing. (B) Estimated probability that the stocks have a true λ of less than 0.9. A λ of less than 0.9 translates to a mean yearly decline of at least 10%. The dotted line indicates the level of 50% data support; above 50%, the data give more support to the conjecture that $\lambda < 0.9$.

ESUs but not in the unlisted ESUs, however, makes such a conjecture seem unlikely, at least for most of the listed ESUs. In addition, when we made a quantitative assessment of our uncertainty, by calculating the probability that $\lambda < 1.0$, we found that for almost half the listed stocks and seven of the listed ESUs, there was considerable data support (>60% probability) for a long-term declining trend (Table 1). For the conjecture that the stocks and ESUs are undergoing rapid decline, $\lambda < 0.90$, there was generally low but not negligible data support, roughly a 20% probability for most ESUs. Upper Columbia River chinook was the exception with high data support (72% probability) for a $\lambda < 0.90$. For perspective, populations with a long-term population growth rate of 0.9 are declining rapidly enough that the population can be anticipated to halve in less than seven years.

These low estimates of population growth rate translate into substantial risks of decline and extinction. At the broad scale, all ESUs except Lower Columbia River steelhead had a probability greater than 50% of VHRD (Fig. 5, Table 1), indicating that the data gave more support than not to the possibility that there is a 25% chance of serious decline in the next 50 years. At the stock level, the picture was similar. For every ESU except Columbia River chum, the mean probability of

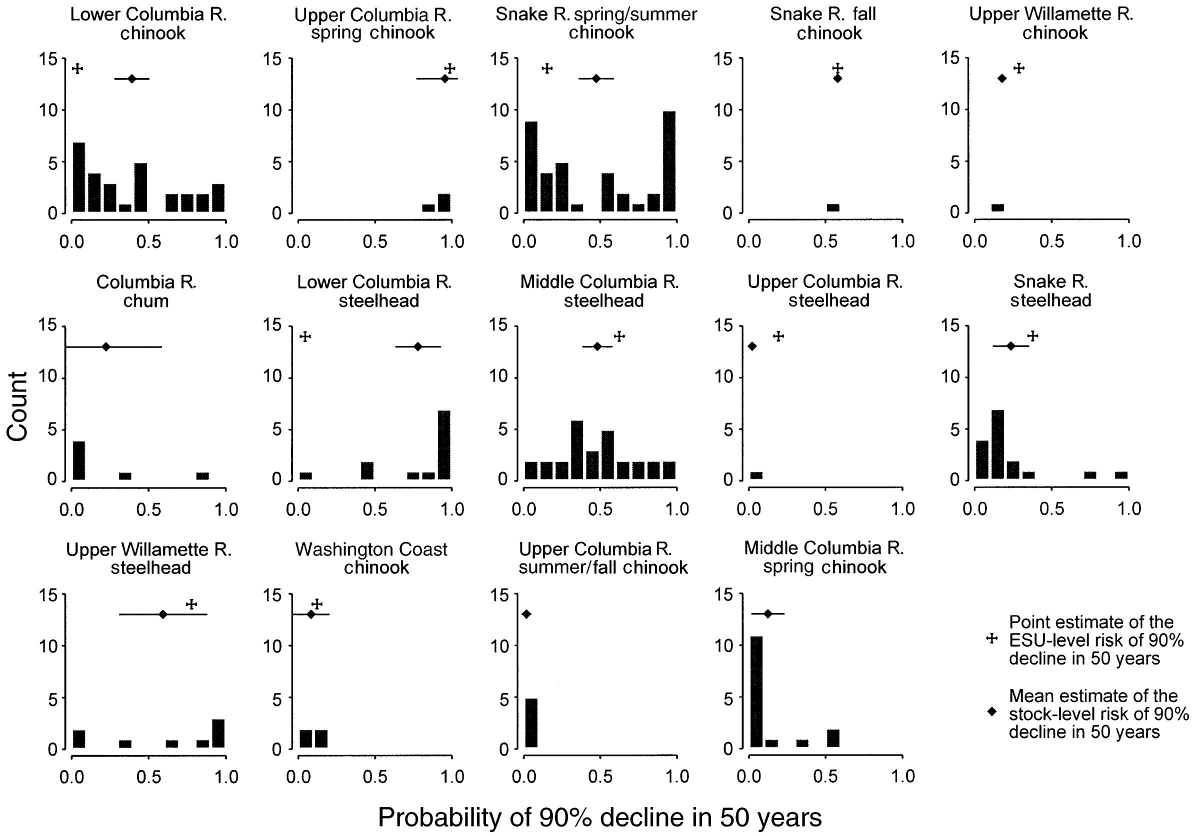

FIG. 5. Histograms of the stock-level estimates of the probability of 90% decline in 50 years for each ESU including three nonlisted ESUs: Washington coast chinook, upper Columbia summer/fall chinook, and middle Columbia River spring chinook. The mean probability of 90% decline is shown above the histogram bars (diamonds). The 95% confidence intervals on the mean probabilities, $\bar{x}$, of the n stock estimates for an ESU are shown ($\bar{x} \pm t_{0.025,n-1}\, s/\sqrt{n-1}$) where s is the unbiased sample variance of the n estimates. If $n = 1$ (only one stock estimate in the ESU), the mean probability of 90% decline was plotted with no error bars. The point estimate for the ESU as a whole is shown by the cross above the histogram bars.

VHRD at the stock level was also >50% (Fig. 5, Table 1). In addition to the risk of decline, we were also able to estimate extinction risk for seven ESUs with total spawner estimates from dam counts. There was high (69%) support for a >25% chance of extinction (VHER) for the Upper Columbia River chinook ESU. However, the probability of VHER for the remaining ESUs was generally low, ranging from 9% to 37% (Fig. 6, Table 1). Estimates of extinction probability and decline have wide confidence intervals (Table 1). Rather than focusing on the precise point estimates for an individual ESU or stock, one should focus on the overall patterns within the basin across multiple ESUs or of stocks within an ESU. The mean risk estimated across multiple ESUs or stocks gives a broad picture of the risk and has much smaller confidence intervals than the individual point estimates (Figs. 5 and 6).

We also used our estimates of long-term population growth and risk to determine how much change in population growth rate would be necessary to mitigate the current risks. At both stock and ESU levels, we calculated the percent change required to achieve a point estimate of $\lambda = 1.0$, as well as the change necessary to reduce the probability of 90% decline in 50 years to <5%. When estimates of total population size were available, we also calculated the percentage increase in λ necessary to reduce the risk of extinction to <5% in 50 years. Although these calculations do not suggest specific management actions, they can contribute to establishing management goals by giving rough estimates of the magnitude of changes required. We did not evaluate the potential for changes in variance to reduce risks of decline or extinction for these stocks, although this may present another way in which management actions might alter the status of the stocks.

To reduce the risk of a 90% decline in 50 years to <5%, the necessary improvements in λ at the stock level ranged from 0% to 53%, with a mean of 10% (Fig. 7, Table 1). Reducing the long-term risk of extinction required improvements ranging from 0% to 41%, with a mean of 4% (Table 1). The slightly greater improvements required to avoid long-term declines are due in part to the fact that larger, less steeply declining populations can have a low probability of reaching the extinction threshold over the analyzed time frame, but

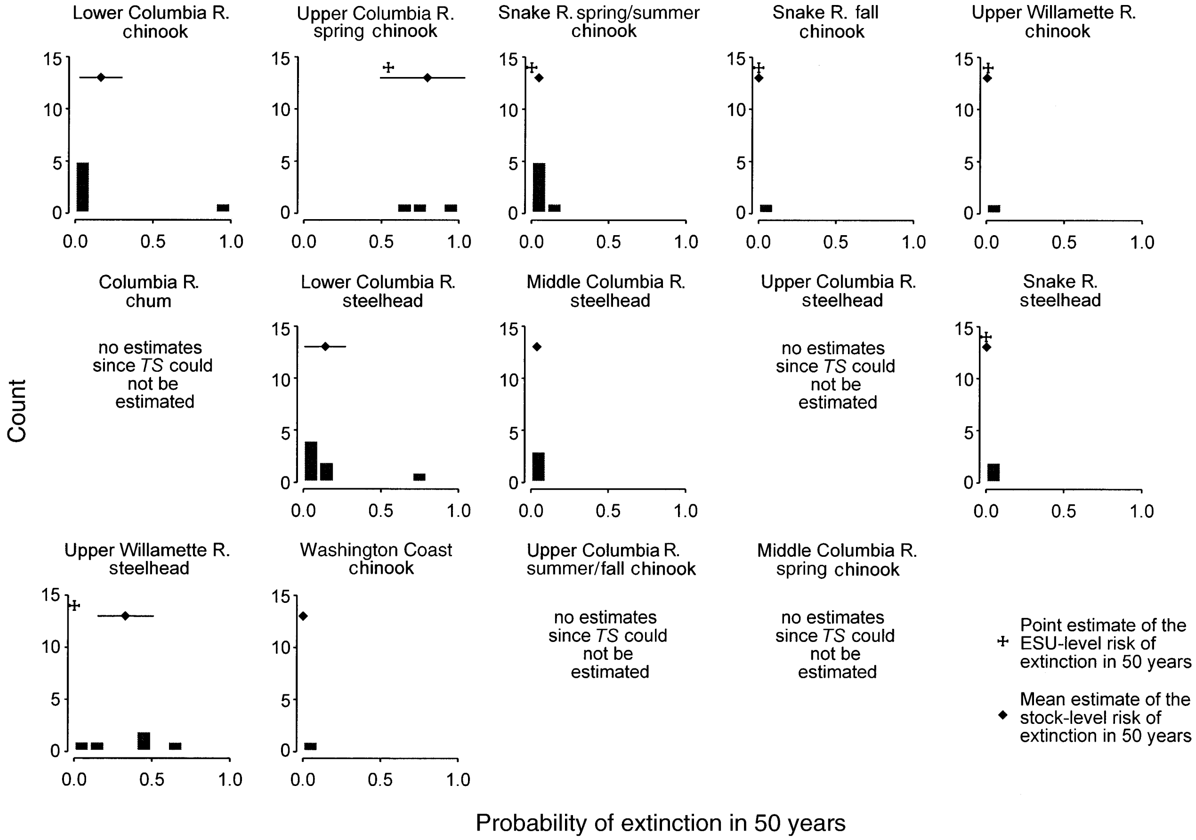

FIG. 6. Histogram of the stock-level estimates of the probability of extinction in 50 years. See Fig. 5 for a description of the error bars.

still have a reasonably high probability of a substantial decrease in abundance.

There are several considerations for specific stocks or ESUs that are worth noting when interpreting these results. First, Upper Columbia River chinook had the lowest estimated λ ($\lambda = 0.85$) by far and the highest consequent risks. Also the stocks within this ESU appear to have an increasing rate of decline through time, which will cause both λ and risk estimates to be overly optimistic. In addition, none of the three stocks within this ESU had a point estimate of λ corresponding to an increasing or stable trend. This combination of factors suggests that the Upper Columbia River spring chinook ESU may be an ESU that is disproportionately at risk within the Columbia River Basin. Second, when considering the stock-level estimates in the Snake River steelhead ESU, note that stock-level data were available only for ''A-run'' stocks in the state of Oregon. The majority of these stocks are experiencing stable growth trajectories. However, counts at the Lower Granite Dam, which encompass the entire ESU, and include Idaho and ''B-run'' stocks, show a decidedly negative trend. Because the stock-level data from this ESU are not a representative sample of the ESU, estimates from the stock data should be viewed with caution. Given the trends in counts at Lower Granite Dam, actual risks faced by this ESU are likely to be larger than is apparent from the stock-level data.

Accounting for possible hatchery fish reproduction

We next examined the potential for the true status of the population to be obscured or masked by hatchery fish reproducing naturally. The effect we evaluated is not due to an impact of the hatchery fish on wild populations, although such negative interactions may certainly exist. Rather, it is a matter of determining the population growth rate due to wild reproduction alone when the wild population receives an infusion of fish from another population (namely, the hatchery) each year. If hatchery fish reproduce, their reproduction effectively masks the component of population growth due to reproduction and survival in the wild.

Given the large numbers of hatchery fish in the Columbia River Basin, population trends and associated risks certainly have the potential to be substantially masked by hatchery fish reproduction. We had hatchery fraction data for nine of the 11 listed ESUs. When we corrected for hatchery fish in the ESU-level time series and assumed that hatchery- and wild-born fish reproduce at the same rate, the estimated λ's were <0.9 for every ESU and were <0.8 for four of the nine (Appendix A). For two ESUs with especially high numbers

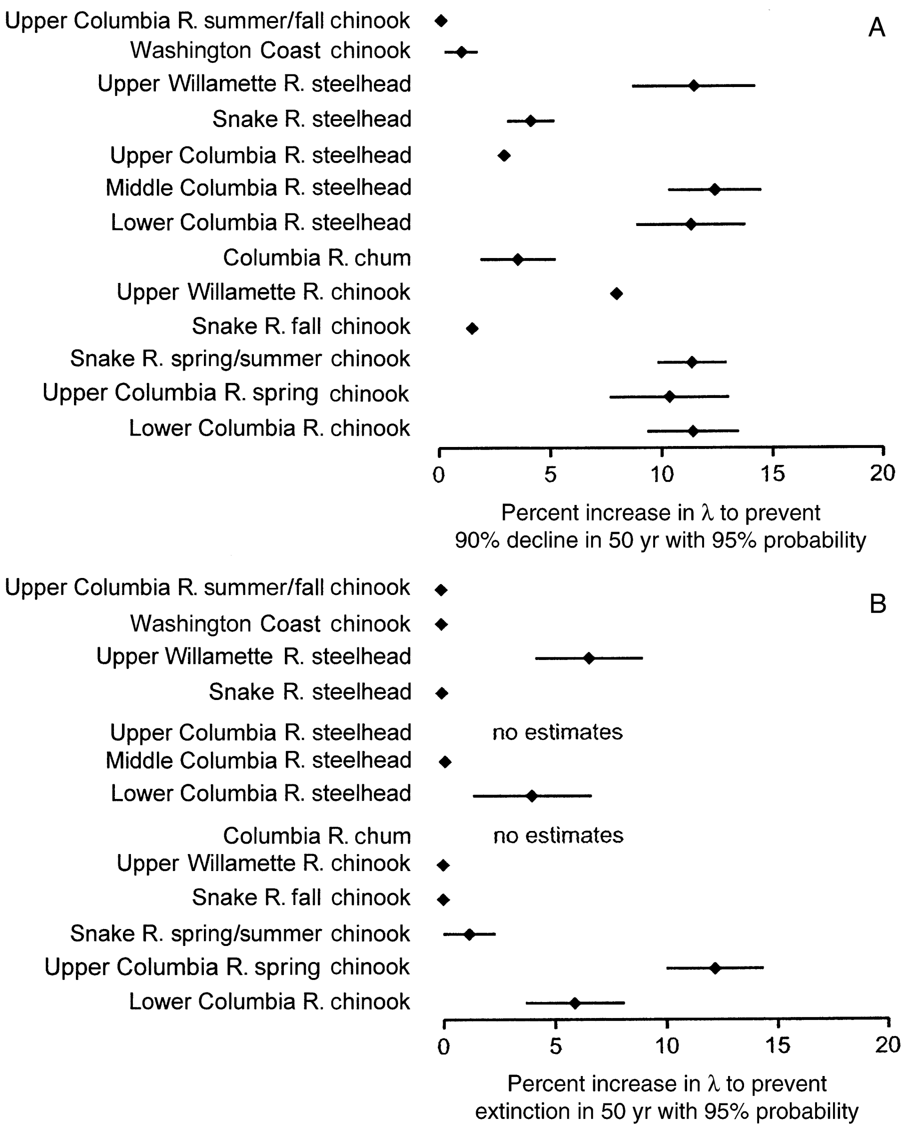

FIG. 7. Mean percentage increases in λ required to reduce the risk of (A) 90% decline or (B) extinction in 50 years to below 5%. The error bars show the standard errors. No error bars were plotted when only one estimate was available for the ESU. In (B), the results only include those stocks and ESUs for which a population size estimate was possible (when total live spawner counts, hatchery fractions, and spawner ages were available). The parameters were estimated assuming that no masking of the parameter μ occurred due to hatchery fish reproduction (i.e., hatchery reproduction = 0).

of hatchery spawners (Upper Willamette River chinook and Upper Columbia River steelhead), the estimated λ's dropped from near 1.0 to 0.62 and 0.69 respectively. At the stock level (Table 2), the changes were similar. Such severely low estimated λ's indicate that if the hatchery-reared spawners have been reproducing, then the underlying reproduction and survival in the wild for the listed salmonids in the Columbia River Basin has been extremely low. The ESUs with the lowest estimate of long-term growth also shifted with the assumption of 100% effective hatchery-fish reproduction. Upper Willamette River chinook stood out with an especially low estimate ($\lambda = 0.62$) while most of the rest of the ESUs had λ estimates in the range of 0.77–0.89.

Derived risk estimates were similarly changed for the worse when hatchery reproduction was assumed. Probability of extinction could be estimated for seven of the ESUs. For six of these, the point estimates of extinction risk in 50 years increased from near zero, assuming no hatchery fish reproduction, to a mean 62% probability of extinction, assuming equal hatchery fish reproduction (Appendix A). The probability of 90% decline in 50 years could be estimated for eight ESUs. The point estimates indicated a greater than 90% probability of severe decline for all eight ESUs when hatchery fish were assumed to be reproducing. Because extinction and decline risk estimates are highly variable, we present these values to suggest the magnitude of

TABLE 2. Comparison of the estimated in-stream λ under different assumptions about hatchery fish reproduction.

ESU	Mean λ estimates: Hatchery fish do not reproduce	Mean λ estimates: Hatchery fish reproduce at the same rate as wild-born fish
Lower Columbia River chinook	0.99	0.95
Upper Columbia River spring chinook	0.86	0.83
Snake River spring/summer chinook	0.97	0.93
Snake River fall chinook	0.95	0.88
Upper Willamette River chinook	1.01	0.86
Columbia River chum	1.07	1.07
Lower Columbia River steelhead	0.92	0.81
Middle Columbia River steelhead	0.97	0.95
Upper Columbia River steelhead	1.00	0.63
Snake River steelhead	1.02	0.96
Upper Willamette River steelhead	0.91	0.85
Washington Coast chinook†	1.05	1.03
Upper Columbia River summer/fall chinook†	no hatchery data	
Middle Columbia River spring chinook†	no hatchery data	

Notes: Mean λ estimates are shown for those stocks where hatchery fraction information is available. Mean λ is defined as exp(mean of the stock μ's).

† Not listed under the U.S. Endangered Species Act.

change in risk that is possible, rather than to provide a precise estimate of that change. The true rate at which hatchery-born fish spawn in the wild lies between the two extremes of no reproduction and reproduction equal to wild fish. Thus the risk estimates shown in Figs. 4–7 and Table 1, which assume no hatchery fish reproduction, should be viewed as somewhat optimistic and those in Appendix A, which assume hatchery fish reproduction is equivalent to wild fish reproduction, should be viewed as somewhat pessimistic.

When interpreting these low estimates of the ''natural'' λ and high risk estimates, it is important to note that our analysis cannot distinguish between whether the hatchery fish are supporting collapsing wild populations (playing a positive role) or are instead causing low natural reproduction and survival (playing a negative role). A relationship between the natural λ and hatchery fraction cannot be examined since we were only able to estimate the minimum natural λ by assuming 100% hatchery fish reproduction. In reality, reproduction by hatchery-reared fish is not 100% as effective as reproduction by wild-born fish and the reproductive effectiveness of hatchery-reared fish almost certainly varies across ESUs and species.

Ocean cycles and population status

Finally, we calculated population growth rates and associated risk over two time periods, 1980–2000 and 1965–2000, that reflect different ocean conditions for most Columbia River salmonids (Mantua et al. 1997; Appendix B). This comparison is a simple test of the sensitivity of our status and risk estimates to the time period we evaluated. We had sufficient data from 86 stocks in nine ESUs for this comparison. We did not have ESU-level data before 1979 in most cases and thus we compared mean stock-level λ estimates. For four ESUs, the mean population growth rate was slightly higher over the longer time period as might be expected if pre-1977 years were under ''good'' ocean conditions. However, the difference was only significant for Upper Columbia River spring chinook (Table 3); this ESU shows a steady declining trend in productivity since the 1970s. Higher growth rates in the 1980–2000 period (the opposite expectation based on ocean conditions) were seen in five of the nine ESUs with significant differences seen in the Snake River spring/summer chinook, Snake River steelhead, and Middle Columbia River chinook ESUs (Table 3). In addition, Upper Columbia River summer/fall chinook ''healthy'' stocks had a lower mean λ over the 1965–2000 time period than during the 1980–2000 time period; this difference was nearly significant (Table 3).

Potential for management actions to mitigate risk

Determining whether specific management actions can achieve the changes necessary to mitigate the risks currently faced by threatened and endangered populations in the Columbia River Basin is an enormous challenge, in no small part because the effects of most recovery or restoration activities on salmon survival are not well quantified. However, there are two cases in which human-caused salmonid mortality has been relatively well documented. The first is harvest of adult fish, in both commercial and sport fisheries. The second is the survival rate of juveniles and adult spawners migrating through the Columbia River and Snake River hydropower dams. As a first step toward addressing the potential for specific management actions to achieve the needed improvements in population growth rate, λ, we assessed the maximum possible change to λ that could be achieved by reducing harvest and by implementing the proposed improvements to fish passage

TABLE 3. Paired *t* test for differences between the mean λ for stocks within ESUs from 1965 to the present and from 1980 to the present.

ESU	No. stocks	λ, 1965–2000	λ, 1980–2000	*P*
Lower Columbia River chinook	12	0.99	1.00	0.45
Upper Columbia River spring chinook	3	0.89	0.86	**0.03**
Snake River spring/summer chinook	36	0.91	0.95	**0.01**
Snake River fall chinook	1	0.90	0.95	n/a
Upper Willamette River chinook		no early data available		
Columbia River chum		no early data available		
Lower Columbia River steelhead	1	0.96	0.91	n/a
Upper Columbia River steelhead		no early data available		
Middle Columbia River steelhead	7	0.93	0.91	0.23
Snake River steelhead	9	0.97	1.03	**0.02**
Upper Willamette River steelhead		no early data available		
Washington Coast chinook†		no early data available		
Upper Columbia River summer/fall chinook†	5	1.00	1.05	0.06
Middle Columbia River spring chinook†	6	1.00	1.04	**0.02**

Notes: All stocks with complete time series for both time periods were included. Mean λ is defined as exp(mean of the stock μ's). Bold *P* values indicate that the two time ranges are significantly different.

† Not listed under the U.S. Endangered Species Act.

through the dams outlined in the NMFS Biological Opinion on the Federal Columbia River Power System (NMFS 2000).

We can use the approximation, $\lambda = R_0^{1/T}$ where T is the mean generation time (Caswell 2001), to explore the potential impacts on λ of changes in harvest rates or survival through the hydropower system. Exploitation rates for salmon are expressed in terms of the fraction of spawners that did not return but would have without harvest, e.g., an exploitation rate of 0.80 indicates that number of returning spawners is 20% of what it would be if there had been no harvest. Exploitation rates are expressed in this way so that harvest that occurs in-stream vs. in-ocean can be compared via a common currency. Given that the exploitation rate is expressed this way, the reproductive rate is

$$R_0 = s_1F_1(1 - h)R + s_1(1 - F_1)s_2F_2(1 - h)R + s_1(1 - F_1)s_2(1 - F_2)s_3F_3(1 - h)R \cdots \quad (11)$$

where h is the exploitation rate, s_i is the survival from age $i - 1$ to i, and F_i is the fraction of spawners that return at age i, R is the mean offspring per spawner. Using the relationship between λ and R_0, we can calculate the proportional change in λ from a change in h alone

$$\frac{\lambda_{\text{new}} - \lambda_{\text{old}}}{\lambda_{\text{old}}} = \left(\frac{R_{0,\text{new}}}{R_{0,\text{old}}}\right)^{1/T} - 1 = \left(\frac{1 - h_{\text{new}}}{1 - h_{\text{old}}}\right)^{1/T} - 1. \quad (12)$$

To estimate the impact of harvest over the 1980–1999 time period, we calculated the mean total (ocean and in-river) exploitation rates for each ESU (or component of an ESU that is subject to different harvest regulations) for those years (Table 4). For most ESUs, there has been a substantial reduction in harvest in the mid-to-late 1990s in response to conservation concerns and ESA-listings; the average harvest rates include this reduction. We then determined the effect on λ of completely eliminating harvest, $h_{\text{new}} = 0$, using Eq. 12. We did not assess the impact of harvest on the Columbia River chum ESU, since we did not have total population size estimates, and therefore could not estimate total harvest rate.

The potential response of ESUs or components of ESUs to this hypothetical change in harvest management varied with exploitation rate and current population status. At a broad scale, harvest moratoria had the largest effect on the Lower Columbia River chinook, Upper Willamette River chinook, and Snake River fall chinook ESUs, resulting in >15% increases in λ (Table 4). For context, the optimistic point estimates of λ for these ESUs, which assume no hatchery fish reproduction, require a 1–5% increase to be equal to 1.0 (Table 1) and the pessimistic point estimates of λ, which assume high hatchery fish reproduction, require a 1–23% increase with most required increases much less than 15% (Appendix A).

Improving the survival of both juvenile and adult fish migrating through the Columbia and Snake River dams has been the focus of much effort, and is another human impact that has been relatively well-quantified. NMFS (2000) has recently required that agencies operating the Federal Columbia River Power System implement a variety of activities, including increased spill, improved passage facilities, and increased transportation as a means of improving that survival. The dams affect survival during both downstream migration as juveniles pass through the hydropower system on their way to the ocean and again during upstream migration as adults return to their natal streams to spawn. Denoting adult spawner and juvenile survival through the hydropower system as d_s and d_j, respectively, the reproductive rate is given by the following:

TABLE 4. Harvest rates for ESUs in the Columbia River Basin, from 1980 to 1999, and expected changes if no fish were harvested.

ESU	λ, 1980–2000	Mean return time	Mean exploitation rate, 1980–1999	Percentage increase in λ with no harvest	Current allowable total exploitation rate†	Additional notes‡
Lower Columbia River chinook						
Fall Tule	0.97	3.7	0.56	25	0.65	a
Fall Bright	0.98	3.8	0.41	15	no specific limit	b
Spring	0.96	3.8	0.84	62	<0.15	c
Upper Columbia River spr chinook	0.86	4.3	0.09	2	<0.06–0.19	d
Snake River spring/summer chinook						
Spring	0.94	4.5	0.08	2	<0.06–0.19	d
Summer	0.96	4.3	0.03	1	<0.06	
Snake River fall chinook	0.95	3.7	0.62	30	~0.50	e
Upper Willamette River Spring chinook	0.99	4.4	0.48	16	in development; max. likely to be 0.15, expected 0.09–0.11	f c
Lower Columbia River steelhead						
Summer	0.94	5.2	0.26	6	expected <0.10	
Winter	0.90	4.5	0.29	8	expected <0.10	
Middle Columbia River steelhead	0.96	4.8	0.19	4	max. 0.20, expected <0.15	
Upper Columbia River steelhead	1.00	3.8	0.25	8	no specific limits	
Snake River steelhead						
A-run	0.97	5.0	0.16	4	expected <0.17	g
B-run	0.92	6.5	0.36	7	expected 0.17	
Upper Willamette River steelhead	0.94	4.0	0.12	3	<0.02	

Notes: Harvest impact on chum was not assessed, because the total population size (and thus harvest rate) was unknown. Exploitation rate data were obtained from the NMFS Sustainable Fisheries Division, CTC (2001), ODFW (2001*a–e*), WDFW (2001), Beamesderfer et al. (1998), Chilcote (2001), and Cooney (2000). Estimates of λ for subgroups within an ESU are the mean of all stocks in that subgroup, or a dam count of that subgroup when available. The λ calculation assumed zero hatchery fish reproduction. Estimates of λ for ESUs without subgroups are the ESU-level λ estimates. Note that most wild steelhead fishing has been catch-and-release since 1992. Currently allowable mortality rates on steelhead result from hooking mortality and incidental take in other fisheries and are generally not met.

† As set by the National Marine Fisheries Service or state agencies.

‡ Explanation of codes: a, harvest rates on fall-tule stocks have been much lower (0.45) than allowable limits in recent years, maximum allowable exploitation rate likely to be lowered to 0.50; b, fishery managed for 5700 fish escapement to N. F. Lewis River; c, fishery selective for marked hatchery fish only; d, allowable harvest depends on returns of aggregate upriver Columbia and wild Snake River stocks; e, harvest rate has been below allowable limits in recent years; f, ocean exploitation has been substantially below allowable levels in recent years, current allowable exploitation rate represents a 30% reduction from 1988–1993 period); g, fishery on A-run managed through limits on B-run fishery.

$$R_0 = d_j s_1 F_1 d_s R + d_j s_1 (1 - F_1) s_2 F_2 d_s R + d_j s_1 (1 - F_1) s_2 (1 - F_2) s_3 F_3 d_s R \cdots . \quad (13)$$

If we denote the product of the dam survivals, $d_s \times d_j$, as d, then the proportional change in λ due to change in d can be calculated as

$$\frac{\lambda_{\text{new}} - \lambda_{\text{old}}}{\lambda_{\text{old}}} = \left(\frac{R_{0,\text{new}}}{R_{0,\text{old}}}\right)^{1/T} - 1 = \left(\frac{d_{\text{new}}}{d_{\text{old}}}\right)^{1/T} - 1. \quad (14)$$

Using Eq. 14, anticipated improvements in λ due to the proposed changes in the hydropower system operation ranged from 1% to 9% across all ESUs (Table 5). For most ESUs, the estimated increase in λ represented one-quarter to one-half of the estimated required increase in λ to achieve $\lambda = 1$, under the optimistic assumption of zero hatchery fish reproduction. The exception was Snake River fall chinook for which the estimated increase in λ was 3–9%, comparing favorably to the estimated required increase of 5%.

DISCUSSION

Columbia River Basin anadromous salmonid status

Regardless of the risk metric chosen, our estimates of the risks faced by the threatened and endangered salmon populations in the Columbia River Basin suggest that the majority of these populations are unlikely to be viable. Even under the optimistic assumption of zero hatchery fish reproduction, nine of the 11 listed ESUs had point estimates of long-term population growth rate, indicating declining trends. We had sufficient data to estimate the extinction risk for seven of these ESUs. The estimated probability of extinction in 50 years was zero or nearly so for six of the seven, with the striking exception being Upper Columbia River chinook with a 54% estimated probability of extinction in 50 years. Despite the predominance of zero point estimates for the risk of extinction, there was much higher estimated risk that the ESUs are severely (90%) below current levels in 50 years. This risk could

TABLE 5. Potential impact of anticipated improvements to the hydropower system, aimed at increasing adult and juvenile migration survival (NMFS 2000).

ESU	λ 1980–2000	Mean return time	Anticipated increase in juvenile and adult (combined) migration survival (%)	Increase in λ (%)
Lower Columbia River chinook				
Spring	0.96	3.8	5–6	1
Fall	0.98	3.7	6–14	2–4
Upper Columbia River chinook	0.85	4.3	16–21	4–5
Snake River chinook				
Spring/summer	0.97	4.3	5–6	1
Fall	0.95	3.7	11–39	3–9
Upper Willamette River chinook	0.99	4.4	0	0
Columbia River chum	1.06	3.6	6–14	2–4
Lower Columbia River steelhead	0.96	4.7	1–4	0–1
Upper Columbia River steelhead	1	3.8	8–17	2–4
Snake River steelhead	0.96	5.2	6–10	1–2
Middle Columbia River steelhead	0.94	4.8	8–17	2–3
Upper Willamette River steelhead	0.93	4.1	0	0

Notes: Estimates of λ were made assuming hatchery fish do not reproduce. The range of anticipated improvements for Snake River ESUs includes estimated indirect mortality attributable to barging. The Columbia River chum value is the mean of the stock estimates.

be estimated for 10 of the 11 listed ESUs. For six of these, the probability was a >25% that the ESUs will be one-tenth of current levels in 50 years. The point estimates give an estimate of the most likely probability of extinction or severe decline given the available data. However, both the extinction and decline probability metrics tend to be highly sensitive to parameter uncertainty. Thus, given the uncertainty in our analyses, the true risks may be high, even when the point estimates were low.

Most scientific and political attention to date has been focused on the threatened Snake River spring/summer chinook stocks. However, our results suggest that this ESU is not necessarily the management unit most at risk. Rather, Upper Columbia River stocks and steelhead throughout the basin had the lowest mean long-term population growth rates at the ESU level. In fact, the Upper Columbia River chinook and the Lower Columbia River steelhead ESUs did not include a single stock with a point estimate of λ greater than 1.0. The Snake River spring/summer chinook ESU, on the other hand, included 16 (out of 38) stocks with point estimates of population growth rates equal to or greater than one. Obviously, this is not to say that the Snake R. spring/summer chinook ESU is viable under current conditions (in fact, the λ estimated at ESU-level and for many of the component stocks is less than 1), but rather that attention should be directed toward the status of stocks throughout the Columbia River drainage.

In contrast to the threatened and endangered ESUs in the Columbia River Basin are the Washington Coastal, Middle Columbia River spring chinook and Upper Columbia River summer/fall chinook stocks widely (and apparently appropriately) regarded as ‘‘healthy.’’ The mean λ value of these stocks was not only >1, with correspondingly low probabilities of VHER and VHRD, but also significantly greater than the mean λ for listed stocks. Demographically, at least, these unlisted ESUs appear to be more viable than their listed counterparts.

One important consideration for this, or any other status assessment, is appropriate population definition. Salmon data have been traditionally collected on a stream-by-stream basis and treated as de facto populations. However, little work has been done to verify this assumption, and fish in multiple streams or rivers may belong to a single population, or may behave as sources and sinks. Alternatively, a single stream may contain more than one population. Either case may complicate the interpretation of adult census data (Brawn and Robinson 1996). Because recovery-planning efforts depend on estimates of the status of populations, it is critical that demographically independent populations be defined (McElhany et al. 2000).

Naturally spawning hatchery fish—an additional layer of uncertainty

Our results also suggest that our lack of information about the reproductive success of hatchery-reared fish spawning in the wild is a critical information gap for Columbia River salmonids. Our population growth rate estimates varied widely depending on our assumption about hatchery fish spawning success. This variation has a cascading effect on other risk estimates. Without knowing the proportion of hatchery spawners in a population count and the actual relative reproductive success of those fish, it is only possible to determine the best and worst case scenarios for population status, and not the true population status. Without knowing whether wild populations are stable or declining, or by how much they are declining, it will be challenging (at best) to determine appropriate management actions to remedy the situation. Recently, National Marine Fisheries Service (NMFS; 2000) has required that many hatchery fish in the Columbia River Basin be marked. Although the nature of this marking program has not yet been established, when implemented, it will enable managers to determine the proportion of hatchery spawners spawning in the wild more reliably for many stocks. A complete marking program would improve our ability to determine population growth rates even further. However, the reproductive success of hatchery fish is still largely unknown. It will be important to conduct paternity studies of wild and hatchery-reared fish spawning in the wild to reduce this uncertainty.

Ocean conditions and the status of Columbia River salmonids

Changes in oceanographic conditions are often implicated in salmon population regulation (Francis and Hare 1994, Mantua et al. 1997). We evaluated population status across two time periods: one that included only years from the warm (''bad'') phase of the PDO, and a second that included years from both the warm and cold (''bad'' and ''good'') phases of this climatic cycle as one means to assess the possibility that recent declines are primarily a result of the most recent (post-1977) downturn in ocean conditions. For most ESUs with sufficient data for analysis, we found that there was either no significant difference in the mean population growth rate of stocks between the two time periods or a significant increase in the growth in the more recent period. There was hydropower dam building during the 1970s which could have offset the effects of good ocean conditions during that period; however, the dam building mainly affected stocks in the Snake River Basin. If we look only at the ESUs least affected by the dam construction during this period, namely Lower and Middle Columbia River ESUs, there is no indication that the λ estimates using the 1980–2000 period have been skewed lower due this time period being in a PDO cycle with poor ocean conditions. Overall our results suggest that the declines seen over the last 20 years are not solely due to a temporary period of poor ocean conditions, but are more likely to be a more long-term phenomenon. Indeed, salmon in the Columbia River Basin have maintained a steady decline since the late 1800s (National Research Council [NRC] 1996). Regime shifts to more positive ocean conditions for Columbia River salmon, such as those believed to have occurred in 1998, will certainly help listed ESUs in this region. In fact, record runs (including the hatchery component) have been recorded at Bonneville Dam in 2000 and 2001. However, given our results, we suggest that recovery is unlikely to be achieved by relying on improvements in ocean conditions alone.

Snake River spring/summer chinook and Snake River steelhead stocks both had significantly lower population growth rates over the 1965–present time period than over the more recent 1980–present time period. The single Snake River fall chinook stock also experienced a large drop in population growth rate (0.97 in the recent time period; 0.89 in the longer time period). The period from 1965 to 1977 was a period of dramatic change in the hydropower system for these ESUs, as three major dams on the Snake and one on the mainstem Columbia were constructed. The lower population growth rates seen during this period are likely to be at least in part, a reflection of this large perturbation. Snake River spring/summer chinook also experienced an increase in productivity in the early 1980s. This may have caused the mean population growth rate to be overestimated in the 1980–present time period. This is not true for Snake River steelhead, however, or for Snake River fall chinook. If a precautionary approach to status assessment is desired, it may be appropriate to use population growth rates derived from the longer time periods for the ocean-type ESUs, and for Snake River spring/summer chinook (due to the increase in productivity in the early 1980s that this ESU experienced).

Mitigating risks

Using estimates of the potential magnitude of harvest reductions and increases in survival through the Columbia Basin hydropower system, we did a coarse evaluation of the potential improvements in λ from these actions. These analyses suggest that both harvest reduction and hydropower passage improvements provide biologically viable means of improving population growth rates. Changes in the harvest levels could have relatively large effects on the population growth rates of the Upper Willamette River, Snake River fall, and Lower Columbia River chinook ESUs. These three ESUs are subject to harvest both in the ocean and in-river, resulting in higher overall harvest rates than those seen in other ESUs. Changes from past harvest levels could also have a moderate (4–7%) impact on several steelhead ESUs (Table 4). However, it should be kept in mind that harvest rates have already been reduced recently (1992–1996) for many ESUs due to conservation concerns, and the mean exploitation rate for the 1980–1999 time period which we used in our analysis is, in many cases, higher than current exploitation rates. Thus some portion of the potential improvements in λ from harvest reduction may have already been achieved via recent reductions.

Improving survival for adults and juveniles as they migrate through the hydropower corridor is another avenue by which population growth rates might be increased. In fact, past improvements to the passage system appear to have been important in increasing overall survival for Snake River spring/summer chinook (Kareiva et al. 2000). Anticipated additional improvements to the hydropower system are less likely to produce large changes in population growth rates for most ESUs (Table 5). One exception to this generalization is the Snake River fall chinook ESU, which currently has very poor survival through the hydropower system (NMFS 2000). Given the challenge of finding other actions that produce ESU-wide improvements in survival, these improvements, even if they result in relatively moderate λ increases, can be an important component of a suite of actions aimed at recovery.

Unfortunately, evaluating the potential for other management actions to improve population growth rates is extremely challenging. In particular, breaching the four lower Snake River dams has been proposed as a high-profile means of recovering Snake River ESUs. Determining the magnitude of response to dam breaching is complicated by the potential for indirect mortality that could be attributable to the hydropower system (Marmorek et al. 1999). Schaller et al. (1999) compared the productivity of stocks upstream and downstream of the Snake River dams and concluded that there was substantial indirect mortality caused by the dams. However, a more recent analysis comparing those stocks in a formal BACI design suggests that patterns of productivity in the Snake River were similar to those seen in the control (downstream) region, suggesting that dams are not currently causing a substantial reduction in population growth rates of Snake River salmon stocks (Levin and Tolimieri 2001). Clearly, evaluating definitively the potential for removal of the four lower Snake River dams to improve population status is problematic.

In the hatchery and habitat arenas, there is a dearth of studies that quantitatively link specific actions or impacts with fish population responses. In many cases, we lack information even about the distribution of impacts and efforts to reduce them. Because of this lack of information, it will be critical for future recovery actions (including dam breaching, if this option is chosen) to be conducted as formal experiments. The quantitative and mechanistic links that such experiments can provide will be a crucial component of conservation planning for these fishes.

Lack of knowledge about the impact of various management actions is not the only uncertainty important when mitigating risks to listed ESUs. Continuing degradation in environmental conditions due to human activities will affect the magnitude of improvement that is needed to recover listed ESUs. As human impacts on the landscape increase, they have the potential to offset benefits achieved through other means, thus requiring additional improvements. For example, harvest rates on several ESUs, including the Snake River spring/summer chinook and Upper Columbia River spring chinook were reduced well before 1980. Increased mortality through the hydropower system, however, may have worked together with a variety of other factors (such as ocean conditions) to continue the decline of these ESUs even after harvest was reduced.

Beyond status assessment: using standardized comparative risk analyses

This status assessment is clearly not a final recovery plan for Columbia Basin salmon and steelhead. Rather it is a first step that quantifies the status of listed ESUs with respect to a repeatable and standard metric (λ) that is critical for population viability. It also begins to assess the impact of two important anthropogenic sources of mortality across ESUs. However, this type of assessment is also likely to play an role as a starting point for additional analyses that contribute to a more complete recovery planning analysis.

For instance, many recovery planning prioritization schemes will include economic and political considerations as well as biological ones. Identifying situations where only minor improvements are necessary, and those where drastic action will be required is important to economic and political planning. Similarly, many conservation efforts seek to preserve areas that are currently in the best biological condition, as these efforts are both biologically and economically expedient (Allendorf et al. 1997). Having biological criteria in a common currency allows more ready integration of different considerations, especially when that common currency incorporates uncertainty, for example the probability that λ is less than a certain value. In addition, these standard metrics have the potential to contribute to analyses linking environmental or other conditions to population status. There are a variety of efforts in the U.S. Pacific Northwest to quantify the distribution of geologic and climatic factors as well as the distribution and magnitude of anthropogenic impacts on anadromous fishes. Combining these locally explicit assessments of habitat and other factors with a standard description of population status can provide the opportunity to begin to link fish population responses to specific environmental conditions.

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APPENDIX A

Parameter and risk estimates assuming that hatchery-born spawners reproduce as well as wild-born spawners are available in ESA's Electronic Data Archive: *Ecological Archives* A013-015-A1.

APPENDIX B

Parameter and risk estimates using all 1960–present data (rather than only 1980–present) is available in ESA's Electronic Data Archive: *Ecological Archives* A013-015-A2.

SUPPLEMENT

A table showing spawner counts, age structures, and the fraction of wild fish in each population used in the analysis is available in ESA's Electronic Data Archive: *Ecological Archives* A013-015-S1.