Viability of Sacramento River Winter-Run Chinook Salmon

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Abstract: The winter run of chinook salmon (Oncorhynchus tshawytscha) on the Sacramento River in California (U.S.A.) was the first Pacific salmon stock to be listed under the U.S. Endangered Species Act. We describe some of the characteristics of Pacific salmon populations that require special consideration in viability analysis during development of a model specific to the Sacramento River winter run of chinook salmon. Their anadromous, semelparous life history leads to a special definition of quasi-extinction. Random variability occurs primarily in spawning or early life and is reflected in the “cohort replacement rate,” the number of future spawners produced by each spawner, a measure consistent with the common practice of characterizing salmon population dynamics in terms of stock-recruitment relationships. We determine the distribution of cohort replacement rates from spawning abundance data and life-history information. We then show through simulations that replacing this distribution with a lognormal distribution with the same mean and variance has a negligible effect on extinction rates, but that approximating an indeterminate semelparous life history using a determinate semelparous life history leads to inaccurate estimates of extinction rate. We derive delisting criteria that directly assess the effects of habitat improvement by explicitly including population growth rate (geometric mean cohort replacement rate ≥ 1.0) in addition to abundance (≥10,000 female spawners). These delisting criteria allow for the uncertainty due to limited accuracy in measuring spawner abundance and the finite number of samples used to estimate population growth rate (estimates must be based on at least 13 years of data, assuming spawner abundance is measured with less than 25% error). Because the probability of extinction will generally be very sensitive to the uncertainty involved in meeting delisting criteria, we recommend that similar uncertainty be accounted for in future recovery criteria for all endangered species.

Viabilidad del Salmón Chinook Durante la Corrida Invernal en el Río Sacramento

Resumen: La corrida invernal del salmón Chinook (Oncorhynchus tshawytscha) en Río Sacramento en California (E.U.A.) fue la primera población de salmón del pacifico que se incluyó en el Acta de Especies En Peligro de los Estados Unidos. Describimos algunas características de las poblaciones de salmón del Pacifico que requieren ser consideradas en el análisis de viabilidad al desarrollar un modelo específico para la corrida invernal del salmón Chinook en el Río Sacramento. Su historia de vida anádroma, semelpara conduce a una definición especial de la cuasi-extinción. Principalmente durante el desove o en las primeras etapas de la vida ocurre variabilidad aleatoria que se refleja en la “tasa de reemplazo de coborte,” el número de reproductores producidos por cada reproductor, que es una medida consistente con la práctica común de caracterizar a la dinámica de las poblaciones de salmón en términos de las relaciones de reclutamiento. Determinamos la distribución de tasas de reemplazo de cobortes a partir de datos de abundancia de reproductores e información de la historia de vida. Mediante simulaciones posteriormente mostramos que el cambio de esta distribución por una distribución logarítmica con la misma media y varianza tiene un efecto no significativo sobre las tasas de extinción, pero que la aproximación a una historia de vida semelpara indeterminada mediante una historia de vida semelpara determinada conduce a estimaciones inexactas de la tasa de extinción. Derivamos criterios para retirar de la lista de especies en peligro que directamente evalúan los efectos del mejoramiento del hábitat al explícitamente incluir la tasa de crecimiento poblacional (media geométrica de las tasa de re-

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Debido a que la probabilidad de extinción generalmente será muy sensible a la incertidumbre presente al suponer que la abundancia de reproductores se mide con un error. Debido a que la probabilidad de extinción generalmente será muy sensible a la incertidumbre presente al capturar con los criterios para retirar de la lista de especies en peligro, recomendamos que se debe considerar la incertidumbre similar para los criterios de recuperación futura de todas las especies en peligro de extinción.

Introduction

Pacific salmonids (Oncorhynchus spp.) are a significant component of the natural heritage of western North America, yet many stocks are at risk of extinction. A recent evaluation of extant, naturally spawning native Pacific salmon stocks identified 214 depleted stocks: 101 at high risk of extinction (declining or with spawning runs less than 200), 58 at moderate risk (relatively constant following recent decline), and 54 of special concern for a variety of reasons (Nehlsen et al. 1991). At least 106 additional stocks are known to be extinct. Existing threats and causes of extinction included alteration of flows in spawning rivers, removal of spawning habitat, overfishing in mixed stock fisheries, and hatchery production (Nehlsen et al. 1991; Moyle 1994). Several stocks have now been listed as endangered or threatened under the U.S. Endangered Species Act (ESA), of which the Sacramento River winter-run chinook salmon was the first in 1989.

Under the ESA, Pacific salmon are delineated by distinct population segments rather than by species. This view of salmon populations as groups of separate stocks has a long history in Pacific salmon research (Ricker 1972; Thorpe et al. 1981; review in Nehlsen et al. 1991). For purposes of the ESA a distinct population segment is specifically defined as an evolutionarily significant unit, which is an interbreeding group of fish that is substantially (but not necessarily completely) reproductively isolated and that represents a unique component in the evolutionary legacy of the species (Waples 1991). By this definition, many races of the six Pacific salmon species will require specific consideration under the ESA.

It appears that the declines in Pacific salmon are due primarily to a combination of deterioration of freshwater habitat, high harvest rates, and negative interactions with other fishes, including nonnative hatchery salmon and steelhead (Nehlsen et al. 1991). Restoration efforts will likely involve habitat improvement and harvest reductions, rather than additional hatcheries. Of the declines examined by Nehlsen et al. (1991), most were due to several factors, with 90% involving deterioration of habitat, 50% involving high harvest, and 53% involving negative interactions with other fishes, including nonnative hatchery fish. They joined others in recommending approaches to reversing the broad decline in these stocks, including greater dependence on habitat restoration and ecosystem function rather than artificial production through hatcheries (Healey 1994; Waples 1994). In a review of past performance of the ESA, Tear et al. (1993) recommended habitat restoration as a necessary component of species recovery in general. Hard et al. (1992) outlined the problems associated with hatchery production of endangered salmonids.

Development of methods for assessing population viability specifically for the anadromous forms of the genus Oncorhynchus will require special consideration of some of their life histories. Although the timing and duration of freshwater and marine phases as well as the age of maturity of these anadromous fish all vary greatly (Groot & Margolis 1991), all but the steelhead (Oncorhynchus mykiss) and sea-run cutthroat trout (O. clarki) die after spawning. This indeterminate semelparous life history is common among plants but unusual among fishes. Another departure from standard approaches to viability analysis is the fact that all of the population is not subject to the same risk. For example, returning and spawning adults and outmigrating juveniles can be at higher risk at any one time than adults in the ocean. Because of this, parts of a population (e.g., the spawning run every 3 years) can drop to low abundance somewhat independently of the rest of the population. Also, in most cases abundance of only part of the population (i.e., the spawning run) is assessed each year. Because of these factors, special methods of risk assessment will be required to accomplish three basic functions generally associated with recovery of species at risk: (1) assessing current status, (2) planning strategies for recovery, and (3) establishing delisting criteria. The last purpose, deciding when a species no longer requires special protection, must incorporate fundamental decisions regarding the way in which the risk of extinction is to be reduced, yet it has received little attention in the literature on population dynamics. Also, some of the analytical tools needed to address this aspect of the problem, such as accounting for uncertainty in population abundance estimates, have yet to be developed (but see Taylor & Gerrodette 1993; Taylor 1995; and Ludwig 1996).

The winter run is one of four distinct races of chinook salmon in the Sacramento River, each named for the...
time at which adults enter the river to spawn (fall, late fall, winter, and spring). Genetic studies suggest that in spite of forced overlap of spawning grounds due to flow alteration and the potential for stocks being cross-bred in hatcheries, stocks still appear to be substantially genetically isolated (Fisher 1994; Nielsen et al. 1994). The winter run enters the Sacramento River in January and February and spawns in early summer, juveniles develop during the summer months, migrating to the ocean the following winter or spring. Historically they spawned in the cool, spring-fed streams on the upper Sacramento, Pit, and McCloud Rivers, and on Battle Creek and Hat Creek (Fig. 1). Spawning run sizes before the 1870s were estimated from qualitative observations to be in the hundreds of thousands (Stone 1876); they ranged from 180,000 to 300,000 between 1872 and 1896 based on landings in a gill net fishery. Dam construction began to hamper runs in the early 1900s, and completion of the Shasta Dam in the early 1940s sealed off most of the spawning grounds (Fig. 1). The winter run then began to spawn in the waters downstream from Shasta Dam, which happened to be cooled by dam releases at the appropriate time of year (Fisher 1994). Completion of the Red Bluff Diversion Dam (Fig. 1) in 1967 hampered migration to and from the spawning area but also provided a means of counting almost all spawning adults each year. In recent years the gates of this dam have been open during most of the upstream spawning migration of the winter run to enhance upstream survival. Because migrants are no longer forced to use the counting ladder, the precision of this abundance estimate has declined. The current major, correctable factors affecting this stock are degraded spawning and rearing habitat, dams and flow diversions affecting both upstream and downstream migration, pollution from various sources, and ocean harvest.

Reproduction in Pacific salmon is unusual in that adults die immediately after spawning, and most spawning is typically over two or three ages (Groot & Margolis 1991). This life-history pattern is called indeterminate semelparous (Begon et al. 1990). In a determinate semelparous population spawning at a certain age A, there would be A distinct, independent subpopulations. In indeterminate semelparous species, these subpopulations are not independent. We refer to them here as temporal (as opposed to spatial) subpopulations. The indeterminate semelparity of salmon stocks raises two questions: how the relative degree of indeterminancy affects the probability of extinction and whether a determinate semelparous life history, which is mathematically and statistically simpler than an indeterminate semelparous life history, can be used to simplify the analysis of extinction probabilities.

We developed an approach to the analysis of extinction probabilities specifically for the winter-run chinook salmon. In doing so we addressed issues that may be relevant to viability analyses of other Pacific salmonids (and other species, such as semelparous plants). We formulate an age-structured model of these quasi-semelparous species and evaluate several semelparous approximations. We use this model to determine the current probability of extinction for the winter run of chinook salmon on the Sacramento River and to develop delisting criteria for that species. The latter include explicit accounts of sampling errors and errors in estimation of run size.

A Pacific Salmon Population Model

To assess extinction risk in Pacific salmon, we need a population model that (1) incorporates Pacific salmon life history characteristics, (2) reflects the type of data typically available, and (3) can be used to compute extinction in a random environment under a variety of conditions. We confine our interests to populations for which we can assume that density-dependent effects are not important. This is likely to be the case for endangered...
salmon populations that are at low abundance because of decreased survival through a phase of their life history such as the spawning run. It would not be the case for populations reduced to low abundance by loss of spawning habitat (Botsford 1994).

The information typically available for these stocks is the fraction that spawn at each age, fecundity at each age, and some idea of whether the population is increasing or decreasing. Information on fraction spawning at each age is ideally obtained from tagging studies, but it could also be estimated from the age distributions of spawners over several years. Although ages of spawning among chinook salmon stocks range from 2 to 8 years, the standard deviations of spawning ages within a stock range from 0.206 to 0.698 years for females, indicating that most members of a stock spawn at one or two ages (Healey 1991). For the Sacramento River winter-run chinook, we know fecundity and the fraction of a cohort spawning at each age, but we have no direct estimates of survival rate. In a tagging study conducted on three cohorts of winter-run chinook, 25% of those tagged fish that returned did so to spawn as 2-year-olds, 67% returned to spawn as 3-year-olds, and 8% spawned as 4-year-olds (Hallock & Fisher 1985). Virtually all of the 2-year-old winter-run chinook that spawn are males. We formulate a model of females only, assuming that there are always enough males to fertilize all eggs, so the fraction spawning each year is 89% at age 3 and 11% at age 4. From fish collected at the Coleman National Fish Hatchery over 8 years, the average fecundity is 3353, but the dependence of fecundity on age is unknown. We assume it is the same for ages 3 and 4.

For populations at levels for which density dependence is not important, we can describe the deterministic population dynamics as a linear renewal equation in terms of recruitment \( R_t \):

\[
R_t = \left[ R_{t-2}p_0s_2f_2 + R_{t-3}p_0p_1 \right] \frac{(1 - s_2)s_3f_3 + R_{t-4}p_0p_1p_2}{(1 - s_2)(1 - s_3)s_4f_4},
\]

where recruitment occurs in the summer, shortly after salmon enter the ocean; \( p_a \) is the fraction surviving from age \( a \) to age \( a + 1 \), \( s_a \) is the fraction of the cohort alive at age \( a \) that spawns (then dies) at age \( a \), and \( f_a \) is fecundity at age \( a \) in terms of surviving recruits (Chuma 1981; Caswell et al. 1984; Hankin & Healey 1986; Kope 1987; Kaitala & Getz 1995). This model expresses current recruitment as the result of spawning by each age class present. In the presentation of this model, we include ages 2 through 4; for other Pacific salmon species that also spawn at ages older than 4, the form of additional terms would be similar. This model could be written equivalently in terms of a Leslie matrix. The eventual behavior of this deterministic model is geometric increase at a rate \( \lambda \), where \( \lambda \) is the positive real solution to the characteristic equation (i.e., an Euler equation):

\[
1 = \left[ \lambda - 2p_0s_2f_2 + \lambda - 3p_0p_1 \right] \frac{(1 - s_2)s_3f_3 + \lambda - 4p_0p_1p_2}{(1 - s_2)(1 - s_3)s_4f_4},
\]

One can determine whether the population is increasing, decreasing, or constant from whether lifetime reproduction,

\[
L = \left[ p_0s_2f_2 + p_0p_1 \right] \frac{(1 - s_2)s_3f_3 + p_0p_1p_2}{(1 - s_2)(1 - s_3)s_4f_4},
\]
is respectively greater than, less than, or equal to 1.0.

Salmon biologists rarely describe the potential for population growth in terms of \( \lambda \); rather, they keep track of the number of recruits produced per spawner, with recruits and spawners described in directly comparable terms (both in terms of numbers at the same age, usually the age of spawning). This practice arose out of the common use of stock-recruitment descriptions of the density dependence in salmonid reproduction and recruitment (Ricker 1954; Larkin 1988).

Formulation of a model that will be useful in estimating probabilities of extinction requires an accurate description of the dominant sources of random interannual variability in population dynamics. Although some endangered Pacific salmon populations are at low enough abundance that discrete demographic events must be explicitly treated as random (e.g., the Snake River sockeye), we assume abundance high enough that demographic stochasticity is not important. The main source of random variability in Pacific salmon populations is the random environment in the freshwater phase associated with reproduction. Natural and anthropogenic variability in river flows have a large effect on both upstream and downstream migration (see Kjelson & Brandes [1989] on Sacramento River fall-run chinook), and during these migrations salmon will have greater exposure to a variety of other risks. There is some evidence that even the marine environmental influences occur at the end of this period, at the time of ocean entry (see Kope & Botsford [1990] for Sacramento River fall-run chinook and Pearcy [1992] for other Pacific salmonids). An exception to this would be El Niño events, which have their greatest effect on the growth and survival of adults at any age (Johnson 1988).

To introduce random variability in the reproductive and recruitment phase into this model, we first rewrite equation 1 so that it includes only terms whose values are known. Typically, we do not know survivals \( p_a \) and spawning probabilities \( s_a \), but we know the fraction spawning at each age. We define the total number of spawners per recruit as

\[
P = p_0s_2 + p_0p_1(1 - s_2)s_3 + p_0p_1p_2(1 - s_2)(1 - s_3)s_4.
\]
and then normalize each term in equation 1 by dividing by $P$ to form

$$\sigma_2 = \frac{p_0 \sigma_2}{P}, \sigma_3 = \frac{p_0 \sigma_3 (1 - s_2)}{P}, \sigma_4 = \frac{p_0 \sigma_4 (1 - s_2) (1 - s_3)}{P}. \quad (5)$$

Using these in equation 1 leads to

$$R_t = [R_{t-2} \sigma_2 f_2 + R_{t-3} \sigma_3 f_3 + R_{t-4} \sigma_4 f_4] P. \quad (6)$$

If fecundity is the same at each age, we can call it $f$ and factor it out of the term in brackets (if not, it can be incorporated in the definition of $\sigma$). By then replacing $Pf$ with $E_t$, we add a time-varying factor that incorporates the factor needed to normalize the coefficients ($P$) and fecundity ($f$) and that reflects the influence of the time-varying environment between the time of upstream migration (i.e., the adult census at Red Bluff Diversion Dam) and the first month or so of ocean life. The resulting model is

$$R_t = [R_{t-2} \sigma_2 f_2 + R_{t-3} \sigma_3 f_3 + R_{t-4} \sigma_4 f_4] E_t. \quad (7)$$

The factor $E_t$ is essentially a time-varying version of lifetime reproduction $L$ from the deterministic model. If it had a constant value of 1.0, population abundance would remain constant. Because it reflects the relative amount that a cohort recruited at time $t$ contributes to future recruitment, we refer to it as the cohort replacement rate.

To project probabilities of extinction, we must describe the distribution of the random variability $E_t$. For populations for which a time series of spawning counts is available and the age distribution of spawning is known, the distribution of $E_t$ can be determined empirically. For the winter-run chinook, estimates of spawning run abundance, which we will call $S_t$, are available from a counting station at the Red Bluff Diversion Dam (Figs. 1 & 2). The term in brackets in equation 7 is the number of spawners in year $t$ divided by $P$. Substituting $R_t = (S_t/P) E_t$ for each recruitment in that expression yields an expression for the number of spawners in terms of past spawners:

$$S_t = \sigma_2 E_{t-2} S_{t-2} + \sigma_3 E_{t-3} S_{t-3} + \sigma_4 E_{t-4} S_{t-4}. \quad (8)$$

This expression can be fit to the spawner count data in several ways. One approach is to use the age structure of spawners described above—$\sigma_2 = 0.25$, $\sigma_3 = 0.67$ and $\sigma_4 = 0.08$—to determine the values of cohort replacement rates that minimize the squared differences between logarithms of spawning abundance from the model and the estimates of spawning run abundance (Fig. 2). A problem associated with this estimation procedure is the tendency for occasional negative values of cohort replacement rates. These can be prevented by constraining estimated values to be greater than a small, positive value, but the value chosen influences the subsequent statistical characterization of cohort replacement rate. If the constrained values of cohort replacement rate are omitted from computation of the geometric mean of the cohort replacement rates, they lead to a positive bias; included, they bias the estimate of the geometric mean by an amount dependent on the value chosen as a constraint. The mean natural logarithm (ln) of cohort replacement rate not including values at the constraint was $-0.326$, the standard deviation was 1.031, and the constraint (cohort replacement rate = 0.066) was incurred five times.

A second approach is to assume values of $\sigma_2$, $\sigma_3$, and $\sigma_4$ corresponding to a determinate semelparous population ($\sigma_2 = 0.0$, $\sigma_3 = 1.0$, $\sigma_4 = 0.0$). This approach guarantees positive values of cohort replacement rates and produces an exact fit to the spawning run abundance data. We used the distribution of cohort replacement rates from this approach in subsequent calculations (Fig. 3). The mean and variance of this distribution are $-0.631$ and $1.059$ respectively, and it differs little from the distribution obtained by the other approach, except for the constrained values. This approach to estimation enables one to obtain a distribution of cohort replacement rates that is close to the actual in a situation in which the actual distribution cannot be recovered from spawning abundance data. There was no correlation between values of cohort replacement rate in different years, so we were able to choose independent values in simulations.

Analyses of extinction probabilities for Pacific salmon will require a specific definition of extinction. For mathematical and biological reasons we use a quasi-extinction approach (Ginzburg et al. 1982). Quasi-extinction occurs when a population falls below a specified level. The mathematical reason for using this approach is that the random matrix model as structured here will not reach an abundance of zero. Biologically, a quasi-extinc-

Figure 2. Count of winter-run chinook salmon spawners traversing the Red Bluff Diversion Dam (solid line), along with the fit to these data used to estimate cohort replacement rates (dashed line). The inset shows the same information on a logarithmic scale.
tion approach makes sense because it can reflect existing population mechanisms that dramatically increase population jeopardy at low numbers. These mechanisms are Allee effects, in which recruitment drops to near zero before spawner abundance declines to zero (Allee 1931; Dennis 1989). In Pacific salmon, the most likely Allee effects would be failure to find mates at low abundance and predator satiation during the downstream migration or at ocean entry (Peterman 1987 and references therein).

Pacific salmon differ from most other populations in that only part of the population—spawners—is at risk of falling below a quasi-extinction threshold at any one time. For Pacific salmon, therefore, only those currently spawning should be compared to a threshold level at any one time. The number we compare to the threshold level is the current number of spawners (the abundance of the spawning run), not the total number in the population. We chose a value of 100 females as the quasi-extinction level below which we defined complete failure of a spawning run to occur. In an attempt to detect depensatory effects at low population levels of a number of fish species, Myers et al. (1995) found depensation in only a few. Among the few were several salmon stocks, and in the most convincing case depensation occurred at 100 females.

Defining extinction to depend on spawning runs dropping below a specific level presents a problem when one is trying to combine the effects of spawners going extinct in various years into a definition of extinction of the whole population. A reasonable approach is to define population extinction to have occurred when all of the 4 temporal subpopulations have gone extinct, where 4 is the age at which most individuals spawn. Because Pacific salmon populations are indeterminate semelparous, not determinate semelparous, this approach incurs a potential problem: by the time the last subpopulation has dropped below the extinction level, one or more of the other temporal subpopulations may have increased to a level such that it is no longer below the extinct level. The likelihood of this obviously depends on how each individual extinction of a spawning run is treated. We chose to set the reproduction by a spawning run to zero each time a spawning run dropped below the extinction level.

A consequence of relevance to Pacific salmon in general is that, on the time scales commonly considered in computing extinction probabilities (less than 100 years), once a temporal subpopulation has become "extinct" (not spawned at the age of maximum reproduction) it appears to increase from zero to above the extinction level within 100 years only rarely. We demonstrated this for the spawning age distribution of the winter-run chinook, and for other distributions in general, by simulating populations that all had the same probability of extinction (set by adjusting the geometric mean of the cohort replacement rates). The number of cases in which cohorts that were counted as extinct and set to zero subsequently rose to above the extinction level was always less than 2% (Table 1). Because of this, in computing probabilities of extinction for winter-run chinook salmon, most of which spawn at age 3, we needed only to keep track of the time at which the third temporal subpopulation went below the quasi-extinction threshold.

With extinction defined, we turn to evaluating the sensitivity of extinction to the values of spawning distribution used and the distribution of environmental variability, cohort replacement rate. We evaluate these aspects for mean values of cohort replacement rate in the range that will be of most interest to analysts. In work with endangered species, neither a rapidly decreasing population in danger of imminent extinction nor an increasing population in no danger of extinction will typically be the focus of this kind of analysis. We therefore explore behavior for geometric mean values of cohort replacement rate near 1.0.

**Table 1. Simulations of winter-run chinook salmon.***

<table>
<thead>
<tr>
<th>Spawning age distribution (years)</th>
<th>Threshold abundance</th>
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<tbody>
<tr>
<td></td>
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</tr>
<tr>
<td>2 3 4</td>
<td></td>
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<tr>
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</tr>
<tr>
<td>0.00 0.89 0.11</td>
<td>1.40</td>
</tr>
</tbody>
</table>

*Beginning at spawning runs of 10,000, the years (%) in which an extinct cohort increases to above the extinction level for thresholds of 100 and 50 spawning females. In all cases mean ln (cohort replacement rate) was adjusted so that the probability of population extinction in 50 years was 0.05.
The first question we asked was whether we could approximate the indeterminate semelparous population with a determinate semelparous population that spawned at the age of maximum spawning. It would be mathematically and numerically much simpler to determine probabilities of extinction of determinate semelparous populations because of the lack of age structure and the independence of temporal subpopulations (using the results of Lewontin and Cohen [1969]). We tested this by simulating populations with different age structures, starting from an initial abundance of 10,000. We chose a distribution of cohort replacement rates with mean in logarithms of −0.2 and standard deviation in logarithms of 1.0 so that we could easily see differences within a reasonable time period. The results show that extinction probabilities for Pacific salmonids are sensitive to the distribution of spawning over age. Probabilities of extinction for determinate semelparous populations increase much more rapidly with time than those for populations that have even the smallest number of individuals spawning at other ages (Fig. 4). In addition to the importance this result has for comparing life histories, it has a disappointing effect on prospects for analysis. Approximating indeterminate semelparous populations with determinate semelparous populations does not appear feasible.

The next question addressed was how sensitive the probabilities of extinction were to the actual shape of the distribution of cohort replacement rates. We wanted to know whether in simulating this population we needed to sample from the distribution of cohort replacement rates indicated in Fig. 3 or whether we simply use a Gaussian distribution of ln(cohort replacement rate) with the same mean and standard deviation of ln(cohort replacement rate). The distribution of ln(cohort replacement rates) (Fig. 3) is not Gaussian using the logarithmic test appropriate for data that may not match in the tails (p < 0.001; Zar 1984). To test whether we could use a Gaussian distribution, we compared extinction probabilities from simulated populations with the cohort replacement rates in Fig. 3 to those obtained from simulations using a Gaussian distribution with the same mean and standard deviation. The results indicated that a Gaussian distribution gives probabilities of extinction very close to the values obtained with the estimated distribution. In this case, therefore, probabilities of extinction appear to be relatively insensitive to the distribution of randomness in environmental effects about any specified mean near 1.0. For the following analyses we used Gaussian distributions of ln(cohort replacement rates).

Viability and Recovery of Winter-Run Chinook

We applied our model of extinction of a salmon population to the practical problems associated with recovery of the winter-run chinook stock. Of the three functions that viability modeling can fulfill, (1) assessment of the current probability of extinction, (2) formulation of delisting criteria, and (3) evaluation of strategies for recovery, the first is trivial for the winter-run chinook salmon. We focus on the second and make only qualitative comments regarding the third. Based on the geometric decline in spawning abundance in Fig. 2, the computation involved in the first task is merely a formality for this population. Based on the distribution of female spawning over age and the distribution of cohort replacement rate estimated above, the probability of the winter-run chinook salmon going extinct soon is essentially 1.0.

Delisting Criteria

The delisting criteria are a complete, quantitative specification of the conditions that the listed stock must meet to be considered recovered to the point that it is no longer likely to be in immediate danger of extinction in the near future. Quantitative specification of the danger of extinction requires definition of the time period and probability level we will consider safe from extinction. For the winter-run chinook, we decided on a probability near 0.1 over a period of 50 years. This is less conservative than criteria used for some other species, but we consider it safe because we specifically account for uncertainty in estimates of population parameters when delisting and because this population is likely to be
closely monitored, not just brought to the delisting level and assumed recovered, without further attention.

The choice of conditions to be met for delisting is a critical one. In most recovery plans for the ESA, only population abundance has been specified. But current abundance alone does not completely reflect future prospects for population abundance and extinction; some specification of population growth rate is required. This is especially important for salmon stocks for a couple of reasons. First, salmon stocks can be increased to high abundance fairly quickly and easily through artificial propagation. It would not make sense to specify a delisting abundance that could easily be met by construction of a temporary hatchery. Second, natural population growth rate is an integrated reflection of the various factors affecting habitat quality. Hence, including it in delisting criteria specifies general habitat improvement as suggested for salmonid stocks (Nehlsen et al. 1991; Healy 1994; Waples 1994) as well as for endangered species in general (Tear et al. 1993).

Construction of the delisting criteria thus requires specifications of the population growth rate as well as abundance. Here we use the geometric mean of cohort replacement rate as the definition of population growth rate. One could choose the values of population growth rate and abundance required for delisting based on the trade-offs involved in their combined effects on probability of extinction (Fig. 5). For the definitions used here, a decline in the mean of the ln(cohort replacement rate) of 0.2 requires an increase in specified initial abundance of roughly an order of magnitude to maintain the same probability of extinction. While this figure demonstrates the trade-off between growth rate and initial population abundance, we did not use it directly to choose an acceptable combination because it does not include the effects of estimation and sampling errors on probability of extinction (Fig. 5). For the definitions used here, a decline in the mean of the ln(cohort replacement rate) of 0.2 requires an increase in specified initial abundance of roughly an order of magnitude to maintain the same probability of extinction. While this figure demonstrates the trade-off between growth rate and initial population abundance, we did not use it directly to choose an acceptable combination because it does not include the effects of estimation and sampling errors on probability of extinction. We chose a population growth rate of ln(cohort replacement rate) = 0.0 somewhat arbitrarily because it corresponds to a constant deterministic population. We then chose a level of spawning abundance to satisfy the condition on probability of extinction (less than 0.1 over 50 years). A spawning abundance of 10,000 females yields a probability of extinction near 0.1 when sampling and estimation error are accounted for. We use that spawning abundance in the following calculations to demonstrate how accounting for sampling and estimation error increase the corresponding probability of extinction from the value less than 0.01 shown in Fig. 5 to near 0.1.

Sampling Error

Direct use of the relationships in Fig. 5 is limited by the fact that at the time of possible delisting we would not know the geometric mean of cohort replacement rate but rather would have to estimate it from recently observed values of spawning abundance. Because that estimation would involve some error, we must include the effects of that imprecision on the resulting probability of extinction. To include the error in the estimate of cohort replacement rate, we write the probability of extinction as the probabilities of extinction for each possible value of cohort replacement rate, summed over the probability of occurrence of each value:

\[
p[\text{extinction}] = \sum_{E} p[\text{extinction}|E]p[E|E = 1.0],
\]

where \(E\) = the geometric mean of cohort replacement rate and \(E\) = the estimate of the geometric mean of cohort replacement rate. To investigate the effects of sampling variability on the probability of extinction, we note that the effect of many estimates of \(E\) of 1.0 would be a distribution of true values of \(E\) equal to \(p[E|E = 1.0]\), so that we can represent \(p[E|E = 1.0]\) in equation 9. One could estimate the probability distribution of the estimate \(p[E|E = 1.0]\) from a description of the errors incurred in the estimation of cohort replacement rates described above. But the relative insensitivity of the probability of extinction to the distribution of cohort replacement rates and the age distribution used to estimate the distribution of cohort replacement rates (including a determinate semelparous distribution) suggest a simpler, approximate approach. Estimation of the geometric mean of cohort replacement rate in the semelparous case can be accomplished by estimating the mean of the logarithm of the cohort replacement rates, an esti-
mate whose sampling statistics are well known. The variance of an estimate of a mean is the variance of the samples divided by the number of samples, and the distribution of errors is Gaussian if the variance is known, and Student t if it is not. Because future habitat improvement will be likely to lead to less variability in the environment, we have made the conservative assumption that the variance in the samples will be the same as the current variance, and we have not estimated it. Thus the variance in the estimate of the mean of the logarithm of the cohort replacement rates is the variance in ln(cohort replacement rate) divided by the number of samples used to estimate the mean of ln(cohort replacement rate).

To estimate the effect of varying sample size on probability of extinction, we simulated populations with an initial abundance of 10,000, the baseline spawning distribution and the estimated standard deviation of cohort replacement rates. For each sample size, we computed the standard error as the standard deviation divided by the square root of the sample size, then the probability of extinction for every possible estimated value in that distribution, assuming a mean ln(cohort replacement rate) = 0.0. We summed over all of these as indicated by equation 9. The results show the dramatic effect of sample size on the probability of extinction (Fig. 6). At least seven samples are required to reach the range of probabilities less than 0.1. Note that because an estimate of cohort replacement rate requires 4 years of data, an indication of n samples in this figure would require n + 4 years of spawning abundance data to permit estimation of the required number of values of cohort replacement rate.

**Measurement Error**

These results assume that spawning abundance is known exactly, whereas for most endangered salmonids estimating spawning abundance will involve an error, which we term measurement error. For the winter-run chinook, for example, spawning runs were known with negligible error from 1967 through 1985 from counts taken at the Red Bluff diversion Dam. Since 1985, however, the gates of that dam have been open during the early portion of the migration of winter run, so spawning counts are available only during the last 13 weeks of the 35-week run, and abundance must be estimated with associated error.

We can determine the impact of measurement error on our estimate of the geometric mean of cohort replacement rate by approximating it with the value that would correspond to a determinate semelparous population. If all individuals reproduced at the same age, $E_t = N_t/N_{t-4}$. Because most methods of population estimation have a certain percent error, errors in logarithms of cohort replacement rate would be additive, resulting in a variance in ln($E_t$) of $2\sigma^2_{E_t}$, where $\sigma^2_{E_t}$ is the variance of the measurement error involved in estimating the logarithm of spawning abundance. The impact of this error on the estimation of extinction probabilities associated with estimating ln(cohort replacement rate) can be determined by simply adding $2\sigma^2_{E_t}$ to the error-free environmental variance (assuming measurement error is independent of environmental variability). The resulting relationship can be displayed as extinction rate in terms of both sample size and estimation error (Fig. 7). From these results one can choose the combination of sample sizes and estimation errors required for recovery.

For the winter-run chinook salmon, for example, we chose an estimation error of 25%, which is achievable in many population estimates in general and which corresponds to a requirement of nine samples. Because each estimate of cohort replacement rate requires 4 years of data, this would correspond to 13 years of escapement. An estimation error of 25% requires that a new method...
of estimating spawner abundance be implemented. Note, however, that we could have used the current method of estimating spawner abundance and required additional samples. The precision of the current method can be estimated from a regression of complete counts (weeks 49–32) from 1967 to 1985 on counts from the current counting period (weeks 20–32). A regression of natural logarithms with slope 1.0 yields a mean-squared-error of 0.831, which corresponds to an approximate percentage error of a little over 100% (the 1 SD range is from 0.44 to 2.22 times the estimate). Continued use of those counts would require about 18 samples (Fig. 7).

From these considerations, delisting criteria were chosen for the winter-run chinook salmon that specified population growth rate in addition to abundance and accounted for sampling as well as estimation error. The abundance level chosen was 10,000 female spawners per run, and the geometric mean cohort replacement rate was chosen to be 1.0. The number of samples of spawning abundance was chosen to be 13 (9 estimates of cohort replacement rate), assuming an estimate of spawning abundance with error less than 25% if that error could not be achieved, the number of samples was specified to increase by one sample for every 10% error greater than 25%. These are not the only choices that yield a probability of extinction of 0.1 over 50 years. The combinations of number of years for which estimates of spawning abundance are required, the spawning abundance, and standard error (in logarithms) of measurement error are shown in Fig. 8. Specifying higher mean abundance in spawning runs would require fewer years of sampling to obtain an adequate estimate of population growth rate. On the other hand, mean abundances less than 10,000 quickly begin to require a prohibitive number of samples.

Discussion

These results were obtained in the formulation of a model for assessing risk specifically for the winter run of chinook salmon in the Sacramento River, but some of them apply to anadromous Pacific salmon in general, whereas others have important implications for endangered species in general.

Winter-Run Chinook

Although the model developed for the winter race of chinook salmon on the Sacramento River may provide some basis for the analysis of population viability of Pacific salmon in general, some of the characteristics of this stock are unique. Because the geometric decline in abundance indicates low constant survival rather than density dependence and a rapid decline in a limiting resource such as the amount of spawning area, the model developed does not include density dependence. It therefore would not apply to populations currently at low abundance due to reduction in spawning area, for example. Emlen (1995) included density dependence in recruitment in a model of the spring run of chinook salmon on the Snake River and found that while abundance depended on a parameter reflecting carrying capacity, extinction depended primarily on the density-independent parameter.

Because the winter run can be considered isolated from the other major runs and because there is currently only one spawning location for this stock, the model developed was for a single population. Some Pacific salmon stocks, in particular those that are not mainstem spawners, will require metapopulation models with straying between subpopulations. A third, somewhat special, characteristic of the winter run is the availability of a time series of spawning abundance. For some stocks, such as most coastal coho salmon stocks in California, there will be only aggregate catch data from the fishery, whereas for others, such as some spring-run and summer-run chinook salmon on the Columbia River and the Snake River, the information on age structure and harvest necessary for complete run reconstruction will be available.
Most of the results obtained here employ the life-history characteristics of winter-run chinook salmon and hence apply directly only to a stock with that spawning distribution. The winter run tends to be closer to determinant semelparous than the other Sacramento River runs (Fisher 1994), and probably to most chinook stocks (Hankin & Healey 1986; Healy 1991). The shape of this age distribution is in part due to harvesting. Harvest rates in the 1970s and 1980s are not known but there are recent indications that current rates, which would be similar, are substantial. The values of $\sigma_a$ may change in the future if harvest rates are decreased. We have in several instances evaluated the sensitivity to specific parameter values, but prudent use of this approach will require evaluation of specific parameter values. For the sake of clarity, we did not present the age-structured model in terms of completely general sums over an arbitrary number of age classes, but the extensions are straightforward.

Some of the specific numerical values chosen in the viability analysis of the winter-run chinook salmon deserve comment. That the time period (50 years) and the threshold extinction probability (0.1) are respectively on the low and high sides of the ranges of commonly used values may appear risky, but there are several other aspects of the formulation that tend to be conservative. The most significant is the inclusion of the effects of uncertainty in estimation of parameters for delisting. From the low probabilities of extinction corresponding to high numbers of samples on Fig. 6, one can see that, if we ignored the effects of uncertainty, the stated probability of extinction would be less than 0.01. Also, we assume that the winter-run chinook salmon will be a closely monitored population. The presence of three other salmon stocks in this system, one of which has been proposed for listing under the ESA, another listed species, several other proposed species, and the central importance of these waters to California’s agricultural economy all imply that this population will be closely watched.

Because there have been some changes in flow management since the mid-1980s, we were concerned that the samples of cohort replacement rate since then might have inordinately influenced our estimate of natural variability. There was, however, no significant difference between estimates of the variance of cohort replacement rates for the periods before and after 1983.

One of the ongoing and important aspects of viability analysis of the winter-run chinook salmon not described here is use of this model to formulate recovery strategies. Recovery strategies require determination of the effects on cohort replacement rate of controllable influences (e.g., river flows, harvest) and uncontrollable influences (e.g., precipitation, ocean conditions). These can be determined either by assessing covariability between cohort replacement rates and environmental time series or by incorporating environmental time series directly in the estimation of cohort replacement rate. Recovery strategies can then be formulated from the combined effects of these various influences and consideration of extraneous factors. The fact that extraneous factors for one salmonid stock may involve other salmonid stocks linked either through migration and a metapopulation structure, a common harvest, or a common source of water for dam releases may lead to consideration of several stocks at once. Recovery strategies require consideration of the combination of actions that will lead to two levels of population growth, one during the recovery phase and a second during the recovered, sustained population phase. Use of artificial rearing may be considered in the former. Uncertainty in the estimation of the effects of various factors on population growth rate suggest close monitoring and adaptive responses during the increasing phase.

It is difficult to estimate the time to recovery for this species. The time required for the population to reach a level at which it could be considered for delisting will depend on the specific actions taken to reach a female spawning abundance of 10,000. Beyond that, the time required to accumulate enough samples for delisting will be that required to obtain nine samples of cohort replacement rate, or 13 years. Simulation results indicate that a population that should qualify for delisting—one for which female abundance is 10,000 and the mean ln(cohort replacement rate) is 1.0—will satisfy the criteria in the first possible year more than 60% of the time.

**Pacific Salmon**

We have assumed that in a population of anadromous Pacific salmon the individuals currently spawning are in greater jeopardy of falling below a critically dangerous level than the rest of the population, so we use spawning abundance as the fundamental unit to be tested against a quasi-extinction criteria, rather than using total abundance as is done in most models of population viability. A primary reason for this is that most Allee effects considered for Pacific salmon depend on numbers in a spawning run as opposed to total numbers in the population. As a consequence of these effects, one cannot take the typical quasi-extinction approach (Ginzburg et al. 1982) of computing the probability of total abundance being less than a threshold; rather, one must compute the probability of a segment of the population (current spawners) being below a threshold. The fact that an Allee effect can depend on abundance of only part of a population is not completely unique to Pacific salmon. Although rarely mentioned, it would be true of any population in which, for example, failure to find a mate is the purported Allee mechanism underlying the threshold (see Cisneros-Mata et al. [1997] for some of the implications).

Recent findings indicate that shifts in atmospheric and oceanographic regimes may have a dramatic impact on
salmon in the marine phase of their lives. For example, an intensification and shift in the position of the Aleutian low-pressure zone in the mid-1970s apparently led to a fundamental shift in the physical state of the north Pacific (Miller et al. 1994), and to an increase in salmon stocks in the Gulf of Alaska, and it may possibly have contributed to a decline in stocks in the contiguous U.S. (Pearcy 1992; Beamish 1993; Hare & Francis 1995). The possibility of such regime shifts in marine salmonid habitat on decadal time scales has important implications for the recovery of endangered salmon. Formulation of recovery strategies will require the ability to differentiate between natural and anthropogenic causes in order to recommend changes in the latter (e.g., the last dams on the upper Snake River where the endangered spring/summer chinook salmon spawn were completed in the mid-1970s, about the same time as the regime shift). Also, changes in marine survival on these decadal and shorter time scales may need to be considered as another source of random variability in viability analysis. To the extent that they are similar to El Niño events, they would tend to add variability in adult survival (Johnson 1988).

The accuracy of estimating cohort replacement rates from time series of spawning abundance of Pacific salmon will depend on the age structure (the values of $\sigma_a$), as well as on measurement and structural errors in the data. The estimation procedure is essentially a deconvolution of the age-aggregated spawning data, so the numerical properties of deconvolution (Kope & Botsford 1988) can be used to assess these dependencies. Declining age structures ($\sigma_1 < \sigma_2 < \sigma_3$) will lead to better estimates of cohort replacement rates than those with partial recruitment of younger age classes ($\sigma_2 < \sigma_3$). The age structure used here to estimate the cohort replacement rates is particularly error-prone, but others may not be. Measurement errors for the direct counts available for winter-run chinook salmon are probably quite small and will probably be greater where other methods are used. Structural errors (i.e., temporal variability in values of $\sigma_a$) could be large in Pacific salmon. The age of maturity can vary from year to year in Pacific salmon (Peterman 1985). Some forms of structural variability, such as varying harvest rates, may be known for some species and hence can be used to improve estimates. Although these problems may affect the precision of estimates of individual values of cohort replacement rates, because of the relative insensitivity of probabilities of extinction to the exact form of the distribution of cohort replacement rates, we do not expect that they influenced our results.

The large difference in probabilities of extinction between the determinate and indeterminate semelparous models (Fig. 4) implies that there may be a broad range of extinction risk among Pacific salmon with different life histories. Cognizance of this fact provides a rationale for organizing and justifying different levels of protection for the various stocks. This result also implies that the effect of harvesting on the age structure of a Pacific salmon, which is to skew the age distribution to fewer, lower ages, will be to increase the risk of extinction. This result for indeterminant semelparous populations is consistent with the idea in life-history theory that distribution of reproduction over several ages leads to greater persistence in semelparous populations (Murphy 1968; Stearns 1992). Hankin and Healy (1986) obtained a related but different result. They showed that the growth rate of deterministic, density-dependent salmon populations became negative at lower harvest rate in populations with spawning over a broad range of ages than in populations with spawning over a narrow range of ages. That result is due to a differential effect of harvest rate on reproduction per individual, which we hold constant in Fig. 4.

The fact that a determinate semelparous model fails to approximate an indeterminate semelparous model that differs only marginally is also disappointing from a methodological point of view. Being able to approximate an indeterminate semelparous population with a determinate semelparous population would make a variety of simple approaches useful (Lewontin & Cohen 1969). Furthermore, the indeterminate semelparous life history of Pacific salmon casts doubt on the applicability of some otherwise useful general results (e.g., expressions for the distribution of abundance of age structured populations [Tuljapurkar & Orzack 1980; Tuljapurkar 1982] and the consequent diffusion approximation [Lande & Orzack 1988] assume iteroparous populations). Analytical methods that assume either determinate semelparous or strictly iteroparous populations should be carefully evaluated before use in the gray area of indeterminate semelparous populations. Viewing these indeterminate semelparous populations as temporal metapopulations with marginal "dispersal" between them is probably a useful metaphor.

**Endangered Species**

The importance of explicitly including effects of uncertainty in parameter estimates in projections of probability of extinction is becoming more widely recognized (Botsford 1994; Taylor 1995; Ludwig 1996). Here, the dramatic difference between probabilities of extinction computed from an estimated value of population growth rate and a known population growth rate (e.g., extinction probabilities for a few samples versus the probability for 1000 samples in Fig. 6) implies that similar uncertainties should be explicitly accounted for in delisting criteria for other species. Estimates of extinction probability that do not account for uncertainty can substantially underestimate probability of extinction (for other examples see Ludwig 1996, 1997). The sensitivity of extinction rate to uncertainty in the estimated value of mean
population growth rate results from the fact that the probability of extinction depends sharply on the mean population growth rate (in the case addressed here, \( dP[E]/dE \ll 1 \) near \( \ln(\text{cohort replacement rate}) = 0.0 \)). Therefore, any uncertainty in the value of average population growth rate increases the probability of extinction dramatically. This result is not specific to the use of cohort replacement rate but would also be true for other measures of population growth rate such as the rate of geometric increase, \( \lambda \). Accounting for such uncertainties is not without problems, both conceptual and real. In computing the impact of uncertainty in the mean value of \( \ln(\text{cohort replacement rate}) \) on the probability of extinction, we needed the conditional distribution of actual values of \( \ln(\text{cohort replacement rate}) \) given the estimated value of 1.0, which is unknown. Because it is unknown, we used the conditional distribution of estimates given a true value of 1.0. Because this is one of the terms in the desired conditional distribution expressed by Bayes theorem, this is a reasonable approximation, especially considering that there is no prior knowledge of the mean value of \( \ln(\text{cohort replacement rate}) \) under current conditions.

The effects of uncertainty on estimates of extinction probability can be described in several ways (Ludwig 1996). Here we characterize these effects directly as an increase in the probability of extinction over the “inherent” probability of extinction so that we can use this measure to determine the required number of samples and the estimation error. This is justified because the uncertainty in estimation is merely an extension of the uncertainty implied in our usual expression of the “inherent” probability of extinction of a species. The inherent probability of extinction is an explicit acknowledgement of uncertainty; if we could predict the environment of the population in the future, we could predict when extinction would occur. Because we can’t, we resort to probabilistic statements. Knowledge of the mean cohort replacement rate limited by low sample size is merely an additional source of uncertainty.

A second recommendation for delisting criteria for endangered species in general is the inclusion of some measure of population growth rate. This allows the delisting decision to depend on the direct consequences of improvement in the quality of the habitat and environment of the listed species. The improvement of natural habitat has been a de facto recommendation associated with almost all listed species, but delisting criteria have not typically included a specific measure of habitat improvement, except insofar as it might be reflected in current total abundance. Specifying abundance may in some cases adequately reflect habitat quality, but not as specifically and comprehensively as specification of population growth rate. This is particularly important for Pacific salmon and other species that are easily cultured artificially.

There is little special in our choice that the average growth rate be 1.0 (i.e., that the geometric mean of cohort replacement rate be 1.0). It has some appeal because of its deterministic equivalent of a self-sustaining population, but other values could be chosen. Managers should be aware that because the distribution of abundance is lognormal, such a specification implies only that the median population has a growth rate of 1.0; the mode may be less. At some point the balance between extremely low probabilities of extremely high populations and populations with growth rates less than 1.0 becomes meaningless, and an adaptive approach with close monitoring becomes more reasonable.

One notable, theoretical aspect of the use of a criterion involving population growth rate is the privileged status given to the first few years and the last years used in the estimation of the average growth rate, which in this case is the mean of \( \ln(\text{cohort replacement rate}) \). This effect is strongest and can be most easily seen in the deterministic semelparous case, in which estimation of cohort replacement rate involves dividing the number of spawners in one year by the number spawners in the year that would have produced them. In the geometric mean of these, all abundances would cancel, except for the first \( A \) years and last \( A \) years, where \( A \) is the age of maturity. A similar situation arose in the method used for estimating \( \lambda \) developed by Heyde and Cohen (1985), but they found that none of their attempts to incorporate intervening values improved the estimate of the mean.

We have developed, evaluated, and applied a model for viability analysis of the winter-run chinook salmon in the Sacramento River. The facts that density dependence is not important in this species and that it is a single population rather than a metapopulation make this stock, and the model, special. But it illustrates many of the issues relevant to recovery of the many depleted stocks of Pacific salmon, and it at least presents a null case that can provide a context in which to evaluate the more complex situations appropriate for other Pacific salmon. Some aspects of this formulation may be advantageous for endangered species in general. These include specific accounting for uncertainty in estimating population parameters and the direct specification of habitat improvement in terms of its effect on population growth rate.

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