dom addition with a maximum tree-ceiling of 500. Taxa were excluded from analyses of partitions for which they had missing data.
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Recovery and Management Options for Spring/Summer Chinook Salmon in the Columbia River Basin

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Construction of four dams on the lower Snake River (in northwestern United States) between 1961 and 1975 altered salmon spawning habitat, elevated smolt and adult migration mortality, and contributed to severe declines of Snake River salmon populations. By applying a matrix model to long-term population data, we found that (i) dam passage improvements have dramatically mitigated direct mortality associated with dams; (ii) even if main stem survival were elevated to 100%, Snake River spring/summer chinook salmon (*Oncorhynchus tshawytscha*) would probably continue to decline toward extinction; and (iii) modest reductions in first-year mortality or estuarine mortality would reverse current population declines.

Dams in the Columbia River Basin of North America almost certainly contributed to severe declines in wild salmon runs (*1*). Some dams in this basin, such as the Hell's Canyon Dam, completely blocked salmon passage, eliminating much spawning habitat (*2*). Other dams allow fish passage, but turbines, predation in reservoirs, and other alterations in the migration corridor presumably increase salmon mortality (*1*). Ecological problems associated with dams are widespread (*1*) and are leading to societal questions weighing the benefits of dams against their costs to depleted fish populations. The most dramatic decision yet faced involves four hydroelectric dams on the lower Snake River.

Salmonid evolutionarily significant units (ESUs) represent genetically distinct collections of populations (*3*). In western North America, 24 salmonid ESUs are listed under the Endangered Species Act; 12 of these are in the Columbia River Basin and four must pass the four lower Snake River dams. The U.S. Army Corps of Engineers is currently considering removing these dams to recover Snake River salmon (*4*). Although most scientists agree that dam removal will help salmon (*5*), it is not known how much benefit would be derived from this action or whether alternative modifications of fish passage could lead to population recovery.

We used an age-structured matrix model (*6*, *7*) for Snake River spring/summer (SRSS) chinook salmon to describe the current situation and explore the demographic effects of reducing mortality at different life stages. Seven index stocks of SRSS chinook salmon have been intensively monitored since the late 1950s (*8*); all are declining (Fig. 1 and Web fig. 1) (*9*), with current spawning populations averaging less than 10% of their 1950 levels (*8*). Using age-specific spawner data, we estimated demographic projection matrices for these index stocks (Table 1). The matrices isolate survival during upriver and downriver migration from survival in other life stages, allowing direct examination of the effect of mortality during in-river migration on population growth. These simple matrix models are density-independent; we found little evidence supporting a density-dependent model (*9*).

We used data for 1990–1994 brood years to estimate parameters for matrices for all index stocks (Table 2), restricting analyses to recent years because these stocks have suffered progressively declining productivity. We thus examined a worst case scenario, taking a precautionary approach to the evaluation of endangered species. The dominant eigenvalues of these matrices indicate the long-term annual rates of population change (assuming that demographic rates remain constant) and all are substantially less than one.

We used these matrices to determine the effect of eliminating all migration mortality except for a small tribal harvest. Although perfect survival during in-river migration is unobtainable, it is a useful numerical experiment because one goal of both dam breaching and modification of intact dams is to reduce in-river migration mortality. Remarkably, even if every juvenile fish that migrated downstream survived to the mouth of the Columbia, and every returning unharvested adult fish survived to reach the spawning grounds, the index stocks would continue to decline (Fig. 2). Thus, management aimed solely at improving in-river migration survival cannot reverse the SRSS chinook decline.

We also tested the effectiveness of three past management actions: (i) reductions of harvest rates, from approximately 50% in the 1960s to less than 10% in the 1990s (*8*); (ii) engineering improvements that increased juvenile downstream migration survival rates from approximately 10% just after the last turbines were installed to 40 to 60% in most recent years (*10*); and (iii) the transportation of approximately 70% of juvenile fish from the uppermost dams to below Bonneville Dam, the lowest dam on the Columbia River (*5*). If such improvements had not been made, the rates of decline would likely have been 50 to 60% annually (Fig. 3), and spring/summer chinook salmon might well have already disappeared from the Snake River. Hence, past management actions have reduced in-river mortality but have not reversed population declines.

Finally, we tested whether improved survival at other life stages could reverse the population declines. Choosing the matrix with the median dominant eigenvalue (Poverty Flat) as a benchmark, we calculated combinations of first-year survival (s_1) and early ocean/estuarine survival (s_e) values that give a dominant eigenvalue of 1.0 [a steady-state population in a deterministic world (Fig. 4)]. We neglected adult mortality because ocean harvest is negligible on these stocks, and

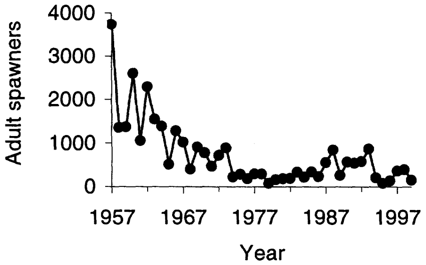

Fig. 1. Total adult (4- and 5-year-old) spawners from 1957–1999 in Poverty Flat index stock of SRSS chinook salmon. Data are based on redd (nest) counts made along a standardized segment of each stream and extrapolated to the full length (*8*). Poverty Flat is presented because it exhibited the median predicted rate of population growth (*9*).

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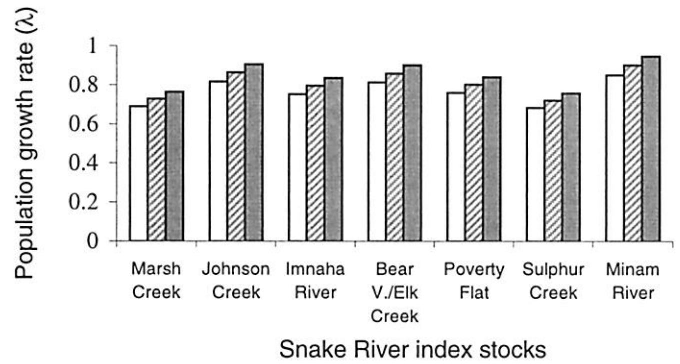
Fig. 2. Numerical experiments exploring 100% survival during in-river migration. Baseline matrices (open columns) were adjusted to simulate 100% survival during downstream migration (hatched columns; $z = 0$ and $s_d = 1.0$) and 100% survival during both downstream and upstream migration (gray columns; $z = 0$, $s_d = 1.0$, and $s_{ms} = 1.0$).



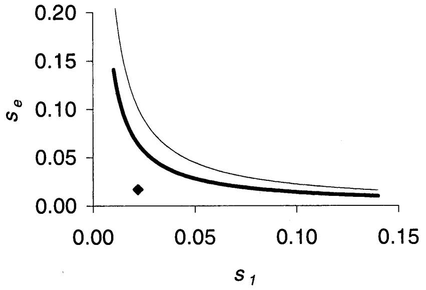
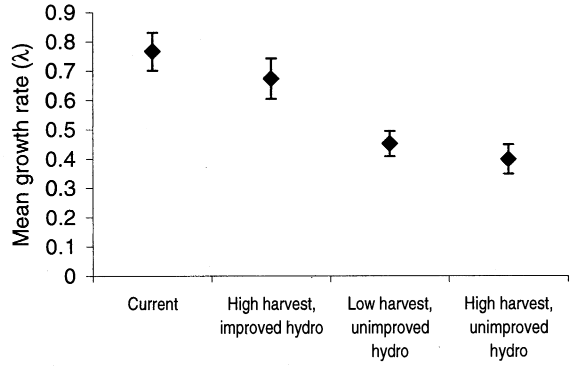


Fig. 4. Isoclines calibrating improvements in s_1 and s_e for Poverty Flat index stock of SRSS chinook salmon. Target λ = 1.0 (thick line) and 1.1 (thin line). To produce isoclines, s_1 was incrementally increased, and values of s_e were searched for the smallest value causing λ to exceed the target λ. Current parameter values are shown for reference.

Fig. 3. Effectiveness of past management actions targeting in-river survival of SRSS chinook salmon. "Unimproved hydro" assumes current conditions except that there is no transportation of juvenile fish ($z = 0$), and survival through the hydrosystem is set at rates estimated for 1977–1979 [$s_d = 0.095$ and average $s_{ms} = 0.511$ (*5*, *8*)]; "High harvest" assumes current conditions except that harvest rates from 1960–1970 are used [average $h_{ms} = 0.390$ and average $h_{sb} = 0.115$ (*9*)]. Error bars are ±1 SD.



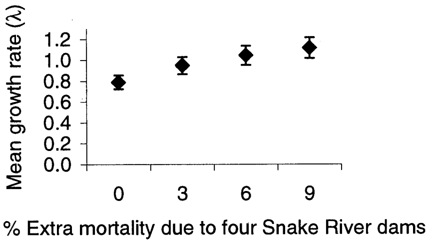


Fig. 5. Potential effects of dam breaching on SRSS chinook salmon index stocks. In addition to straightforward improvements in migration survival, breaching the four lower Snake River dams might also improve survival in postmigration stages. Delayed transportation mortality is conventionally measured as *D*, a ratio of survival of transported fish relative to that of nontransported fish; the current best estimate for this ESU is $D = 0.7$ (transported fish survive at 70% the rate of nontransported fish) (*12*). Extra mortality results from the physiological stress of passing through dams. Baseline mortality (*m*) is increased by a percentage, *e*, such that mortality observed in the estuary today is $m + em$. If the four lower Snake River dams were breached, the hypothesized *e* would go to zero, causing s_e to increase. For this figure, we assumed no fish transportation ($z = 0$); improved survival during downstream ($s_d = 0.607$) and upstream ($s_{ms} = 0.913$) migration; $D = 0.7$; and that the "extra mortality" indicated along the ordinate axis becomes 0, corresponding to the following values: $s_e = 0.022$ for $e = 0\%$, $s_e = 0.052$ for $e = 3\%$, $s_e = 0.082$ for $e = 6\%$, and $s_e = 0.112$ for $e = 9\%$.

Table 1. Structure of demographic matrices for female SRSS chinook salmon. s_x is the probability of survival from age ($x - 1$) to age x, b_x is age-specific propensity to breed, μ is survival during upstream migration, and m_x is the number of eggs per female spawner of age x. The parameters s_2 and μ were further defined as follows: $s_2 = [zs_z + (1 - z)s_d]s_e$, where z is the proportion of fish transported, s_d is survival during in-river migration, s_z is survival during transport, and s_e is survival in the estuary and during entry into the ocean. $\mu = (1 - h_{ms})s_{ms}(1 - h_{sb})s_{sb}$, where h_{ms} is harvest rate in the main stem of the Columbia River, s_{ms} is survival of unharvested spawners from Bonneville Dam to their spawning basin, h_{sb} is harvest rate in the subbasin, and s_{sb} is survival of unharvested adults in the subbasin before spawning.

	1	2	3	4	5
1			$\mu s_1 b_3 m_3/2$	$\mu s_1 b_4 m_4/2$	$\mu s_1 b_5 m_5/2$
2	s_2				
3		s_3			
4			$(1 - b_3)s_4$		
5				$(1 - b_4)s_5$	

management opportunities for enhancing open ocean survival are limited (*5*). For Poverty Flat, management actions that reduce mortality during the first year by 6%, or reduce early ocean/estuarine mortality by 5%, would be sufficient. If reductions in mortality are simultaneously accomplished in both the first year of life and the early ocean/estuarine stage, then the combinations of mortality reductions required to produce an eigenvalue ≥1.0 are as modest as a 3% reduction in first-year mortality and a 1% reduction in estuarine mortality. These required improvements are surely underestimates because the analyses are deterministic. Although we lack data to parameterize a stochastic matrix model, environmental variability reduces long-term population growth as compared to deterministic analogs (*6*). To accommodate this effect, we repeated the calculation with a target of 10% annual growth. When we made this precautionary adjustment for stochasticity, we found that first-year mortality must be reduced by 11% or early ocean/estuarine mortality must be reduced by 9%. In addition, our conclusions are qualitatively robust to a wide range of parameter values for chinook salmon.

The challenge of increasing first-year and estuarine survival shifts scientific inquiry from demographic modeling to identifying management actions that might produce the desired improvements. Because SRSS chinook salmon spawn in the upper reaches of Snake River tributaries, dam breaching is unlikely to affect available spawning habitat or first-year survival but could improve estuarine survival considerably. Although survival of juvenile fish during barging is quite high, barging might reduce the subsequent survival of barged fish relative to those that swim downstream. Breaching the lower Snake River dams would mean the end of fish transportation operations and would therefore eliminate any delayed mortality from transportation. Additionally, the removal of four of the eight dams encountered by Snake River salmon might increase the physiological vigor of salmon that swim downriver, thus improving survival during the critical estuarine phase. If

Table 2. Parameter values used in the baseline matrix developed for Poverty Flat index stock of SRSS chinook salmon. The corresponding population growth rate λ is 0.760 (*9*).

Parameter	Value	Reference no.
s_1	0.022	(*13*)
s_2		
z	0.729	(*14*)
s_z	0.98	(*14*)
s_d	0.202	(*14*)
s_e	0.017	(*15*)
s_3, s_4, s_5	0.8, 0.8, 0.8	(*16*)
b_3, b_4, b_5	0.013, 0.159, 1.0	(*17*)
μ		
h_{ms}	0.020	(*8*)
s_{ms}	0.794	(*14*)
h_{sb}	0	(*8*)
s_{sb}	0.9	(*8*)
m_3, m_4, m_5	3257, 4095, 5149	(*18*)

this indirect mortality were 9% or higher, then dam breaching could reverse the declining trend of SRSS chinook salmon (Fig. 5). Unfortunately, estimating the magnitude of any indirect mortality from passage through the Snake River dams is difficult; identifying fish appropriate as a "control" for the potential effects of these dams is problematic. Also, even if the Snake River dams were removed, the fish would still have to negotiate four Columbia River dams, and baseline mortality would still include any indirect mortality attributable to passage through those dams.

For the Snake River, deliberation regarding dam removal will require us to examine the effects of dams that may be manifested outside the migration corridor. Given the current uncertainty, policy-makers may have to view the decisions they make as large experiments, the outcomes of which cannot be predicted but from which we can learn a great deal pertaining to endangered salmonids worldwide.

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13. Productivity of each stock, *P*, was estimated as
$$\sum_{t=1}^{n} \ln(R_t/N_t)/n, \qquad \text{where } R_t = \sum_{x=4}^{5} N_{x,t+x}$$
is the number of recruits for a particular brood year; t, $N_{x,t+x}$ is the number of adults of age x that spawn x years after the brood year; and n is the number of data years used. s_1 was found by simultaneously solving the Euler equation
$$\mu \sum_{x=1}^{5} l_x(m_x/2)b_x\lambda^{-x} = 1$$
(*17*) and $\lambda^T = e^P$, where the generation time
$$T = \mu \sum_{x=1}^{5} l_x(m_x/2)b_x\lambda^{-x} \qquad (7)$$
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15. To calculate s_e, we used annual counts of smolts for the aggregate run of SRSS chinook made at Lower Granite Dam [C. E. Petrosky, H. Schaller, in *PATH Weight of Evidence Report*, D. Marmorek, C. Peters, Eds. (ESSA Technologies, Vancouver, Canada, 1998), submission 10]. We accounted for all estimated mortality occurring below this dam until spawning and attributed remaining mortality to the period when salmon enter the estuary and nearshore ocean.
16. No direct estimates of adult survival in the ocean exist for this ESU. We set $s_3 = s_4 = s_5 = 0.8$ [W. E. Ricker, *J. Fish. Res. Board Can.* **33**, 1483 (1976)].
17. To find f_x, the fraction of spawners of age x for females only, we multiplied the annual age frequencies of spawners (*8*) by the proportion of age x fish that are female (*11*), rescaled so the frequencies summed to 1, and averaged across the time series. Because these stocks rarely breed beyond age 5, we set $b_5 = 1$. We estimated b_3 and b_4 by solving a set of simultaneous equations:
$$f_x = b_x l_x \Big/ \sum_{i=1}^{x} b_i l_i \text{ for } x = 1 \text{ to } 5$$
$$\text{where } l_x = \prod_{i=1}^{x} p_i$$
$p_1 = s_1$, and $p_x = (1 - b_{x-1})s_x$ for $x > 1$ (*7*).
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19. We thank M. Schiewe, G. Matthews, D. Dey, R. Zabel, C. Toole, and J. Williams for comments and S. Kiefer for fecundity data. The views expressed in this paper are not the official view of the National Marine Fisheries Service or of Santa Clara University.

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VirB/D4-Dependent Protein Translocation from *Agrobacterium* into Plant Cells

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The *Agrobacterium* VirB/D4 transport system mediates the transfer of a nucleoprotein T complex into plant cells, leading to crown gall disease. In addition, several Virulence proteins must somehow be transported to fulfill a function in planta. Here, we used fusions between Cre recombinase and VirE2 or VirF to directly demonstrate protein translocation into plant cells. Transport of the proteins was monitored by a Cre-mediated in planta recombination event resulting in a selectable phenotype and depended on the VirB/D4 transport system but did not require transferred DNA.

The Gram-negative soil bacterium *Agrobacterium tumefaciens* causes crown gall disease on plants. During the infection process, a segment of the bacterial tumor-inducing (Ti) plasmid, the T region, is transferred to recipient plant cells, ultimately resulting in phytohormone overproduction (*1–3*). Transfer of the T region occurs as a single-stranded DNA-protein complex, resembles conjugation in many ways, and is mediated by a set of Virulence (Vir) proteins, which are encoded by the Ti plasmid. Transport requires the 11 VirB proteins, which constitute the proposed channel, and the coupling factor VirD4 (*4*, *5*).

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