North American Journal of Fisheries Management 25:446–463, 2005

DOI: 10.1577/M03-145.1

[Article]

Using Simulation Techniques to Estimate Management Parameters on Snake River Steelhead: Declines in Productivity Make Rebuilding Difficult

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Abstract.—We collected adult and juvenile spawner recruit data on wild summer steelhead *Oncorhynchus mykiss* for the Snake River and estimated parameters for fisheries management by partitioning the data into predam and postdam periods and fitting the Ricker and Beverton–Holt models to those time series. The results showed a decline in productivity irrespective of the model chosen and the way in which the pre- and postdam periods were defined. However, the data were noisy and the confidence bounds on parameter estimates were fairly large. To reconcile the different management goals derived from the different data sources (adult or juvenile data) or model choice (Ricker or Beverton–Holt), we used simulation techniques and Bayesian algorithms. The combined approach suggests a recovery management goal (i.e., spawning stock associated with the maximum sustainable yield) of 60,000 steelhead above Lower Granite Dam. At current smolt-to-adult survival rates, the data indicate optimal escapement of between 20,000 and 27,000 adults. We note that Snake River steelhead stocks cannot be managed for recovery escapement levels given current estimates of smolt-to-adult survival rates, and we discuss alternatives for present-day management and rebuilding over time.

Wild Snake River summer steelhead *Oncorhynchus mykiss* have declined in abundance since the early 1960s. This population has two components: the A-run, which enters the Columbia River between June and August and is destined for tributaries all along the Columbia River; and the B-run, which enters between August and October and is destined for tributaries of the Snake River. Both are listed as threatened under the Endangered Species Act (ESA). Schaller et al. (1999) have attributed the decline in out-migrating yearling spring and summer Chinook salmon *O. tshawytscha* in the Snake River to declining productivity coinciding with the completion of the lower Snake River hydropower projects. Schaller et al. (1999) and Deriso (2001) have also shown that the declines in survival rates for Snake River stocks were greater than those for similar stocks on the Columbia River, which migrated through fewer dams.

Both Petrosky et al. (2001) and Wilson (2003) found a significant decline in smolt-to-adult survival (SAR) for Snake River Chinook salmon populations but not in egg-to-smolt survival. Wilson (2003) concluded that neither juvenile habitat degradation nor hatchery impacts caused the Snake River Chinook salmon stocks to decline. It is extremely difficult to pinpoint the cause of the smolt-to-adult decline because it is confounded by a number of factors, such as downstream migration mortality, estuarine mortality, and ocean mortality (Kareiva et al. 2000). Marmorek et al. (1998) evaluated an alternative hypothesis for the distribution of mortality among the different life stages, presenting the strengths and weaknesses of that hypothesis in terms of the available evidence along with the management implications.

To manage in-river fisheries in ways that are consistent with the rebuilding goals for Snake River summer steelhead, we need to address the issues of the productivity and carrying capacity (the latter of which we refer to simply as the ‘‘capacity’’) of the stock. These are key variables, as they are directly related to the maximum sustainable yield for the stock (S_{MSY}; i.e., the spawning stock size at which the yield is maximized) and maximum recruitment (S_{MSP}; the spawning stock size at which recruitment is maximized), as well as to overall abundance. Estimates of S_{MSY} and S_{MSP} are

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Received July 30, 2003; accepted May 17, 2004
Published online March 17, 2005

important in selecting the management options for harvest and hydrosystem operations that will lead to achieving the rebuilding goals for Snake River summer steelhead populations. It is known that alternative management models (such as the Ricker and Beverton–Holt models) provide contradictory goals for the same data set (Hilborn and Walters 1992).

Regardless of model choice, productivity (parameter α in the Ricker curve) is a measure of the density-independent survival of fish from one life stage to the next (Hilborn and Walters 1992). This could be stated as the intrinsic ratios of spawners toadult returns or spawners to smolt recruitment, both of which are analyzed in this paper. Productivity has additional attributes, as it can be directly related to in-river habitat quality for the juvenile life stages (Mobrand et al. 1997). Furthermore, Nickelson and Lawson (1998) showed that population viability is directly related to measures of productivity and that the extinction risk for coho salmon *O. kisutch* becomes higher as habitat quality degrades in coastal ecosystems.

Twnety-five independent summer steelhead populations have been identified in the Snake River (TRT 2003) for the purpose of developing ESA recovery criteria. The data used in this analysis represent the aggregate of the 25 populations (e.g., dam counts and harvest estimates). The inherent productivity of the individual populations varies greatly, as does freshwater habitat. The values of S_{MSY} and S_{MSP} calculated for such an aggregate of populations with varying productivity and capacity tend to be biased downward (Hilborn and Walters 1992). However, real-time monitoring of escapement and harvest by population is not available and the only data available to the fishery manager are for the aggregate of all populations.

We present maximum likelihood methods for finding a range of productivity and capacity given the limited data available. We then use Bayesian techniques to derive a management estimate given the data and model choice. The Bayesian simulation used a uniform prior distribution of the parameter values in the stock–recruit relationships that was of sufficient range to incorporate uncertainty in these management estimates (Adkison and Peterman 1996). As discussed by Adkison and Peterman (1996), these estimates are reliable if the choice of priors is adequate.

This paper has three major objectives. The first is to evaluate the effects of dam construction on productivity and capacity for the Snake River steelhead stock. The second is to present the sensitivity of the management goals (i.e., S_{MSY}) to model and data choice. The third is to present a Bayesian approach to reconciling these conflicting data and model choices. To conclude the paper, we discuss the implications of present-day (postdam) estimates of productivity and their relationship to target reference points (S_{MSY} and S_{MSP}) for rebuilding.

Methods

Wild summer steelhead juvenile and adult data.—Snake River summer steelhead rear in freshwater for 2–3 years, migrate past eight dams in the spring, and rear another 1–4 years in the ocean. Summer steelhead returning to the Snake River basin (Figure 1) as adults enter the Columbia River and encounter a lower-river fishery (known locally as Zones 1–5), Bonneville Dam, the Dalles Dam, John Day Dam, and McNary Dam before they find the confluence of the Snake River. Migrating steelhead are also removed in an Indian commercial and subsistence fishery between Bonneville and McNary dams, an area referred to locally as Zone 6. Steelhead then migrate pass four lower Snake River dams: Ice Harbor, Lower Monumental, Little Goose, and Lower Granite, which were constructed between 1961 and 1975. Between 1949 and 1972, a portion of the Snake River summer steelhead run also passed Lewiston Dam on the Clearwater River. Lewiston Dam was removed in 1972. Steelhead eventually spawn in the upper reaches of the Snake River, including the Clearwater and Salmon rivers, the following winter and spring. Hydroelectric dams without fish ladders have reduced upriver summer steelhead habitat in the Snake River basin to that below the Hells Canyon Dam complex (which blocked the Snake River in 1965) and that below Dworshak Dam (which blocked the North Fork of the Clearwater River in 1972).

Estimates of combined hatchery and wild steelhead passage are available for all of the major dams, including the Lewiston Dam. Estimates of wild steelhead at the uppermost passable dam in the Snake River basin, however, were obtained from the Idaho Department of Fish and Game (IDFG 2001). We subtracted the estimated tributary harvest of wild steelhead in the recreational and tribal fisheries (Technical Advisory Committee of *U.S. v. Oregon,* personal communication) to obtain an index of wild steelhead spawning escapement above the uppermost passable dam. The age structure of the adult run (Table 1) was obtained by sampling migrating adults at Lower Granite Dam (Charlie Petrosky, IDFG, unpublished reports). Multiple-spawner rates are less

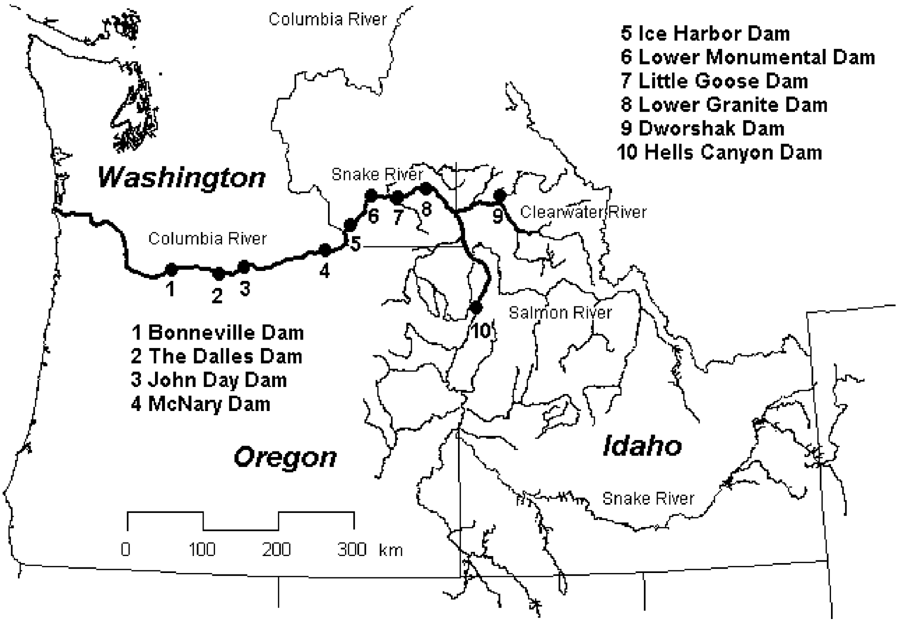

FIGURE 1.—Map showing the locations of dams on the Columbia, Snake, and Clearwater rivers encountered by migrating summer steelhead.

than 2% for wild Snake River summer steelhead (Dan Rawding, Washington Department of Fish and Wildlife, personal communication) and are ignored in our analysis.

Estimates of wild smolt out-migration in the Snake River between 1964 and 1996 were obtained from Marmorek et al. (1998). We use the freshwater age from the Lower Granite Dam adult age composition to calculate the age composition of the smolt out-migration (Table 1). We assumed that the smolt-to-adult survival rates were the same for smolts of ages 2–4.

Spawner recruit analysis.—We compared two spawner recruitment models in which recruitment could be measured as either adult returns or smolt recruits. The first model was the lognormal form of the Ricker curve, that is,

$$R = \alpha S e^{-(s/\beta)}, \tag{1}$$

where α is the estimate of density-independent productivity and β is the estimate of spawners associated with maximum recruitment, which we will refer to as $S_{\max}$. Optimum escapement (S_{MSY}) based on the Ricker curve and adult return data was estimated as a function of the Ricker curve's α and parameters with $0 < \alpha < 3$ (Hilborn 1985), namely,

$$S_{\text{MSY}} = \frac{\log_e \alpha}{1/\beta}(0.5 - 0.07 \log_e \alpha). \tag{2}$$

The second model was the nonlinear form of the Beverton–Holt curve,

$$R = \frac{S}{1/p + S/c}, \tag{3}$$

where p = productivity (recruits per spawner) and c = capacity in terms of maximum recruitment, either adult or smolt (Moussalli and Hilborn 1986; Hilborn and Walters 1992).

Optimum escapement based on the Beverton–Holt curve and adult return data was estimated as a function of the Beverton–Holt curve's p and c parameters (Moussalli and Hilborn 1986), namely,

$$S_{\text{MSY}} = \frac{c}{p}(\sqrt{p} - 1). \tag{4}$$

For the juvenile data, we used optimization techniques to find S_{MSY}.

Parameter uncertainty.—Likelihood ratio methods were used to determine the 95% confidence intervals around the Ricker α and β and Beverton–Holt p and c parameters (Hilborn and Mangel 1997). From the lognormal probability density function,

TABLE 1.—Escapement indices (count at the uppermost dam less tributary harvest) for wild Snake River adult summer steelhead, smolt production, and adult returns by escapement year (see the Appendices for run reconstruction details).

Escapement year	Escapement index	Smolt production		Total smolt production per escapement	Wild adult returns[a]				Total wild age-3–7 returns[a] per escapement
		Age 2	Age 3		Age 4	Age 5	Age 6	Age 7	
1954								1,094	
1955							47,357	723	
1956						112,661	31,332	676	
1957					63,812	74,538	29,263	622	
1958					42,219	69,615	26,956	592	
1959					39,431	64,126	25,633	434	
1960			703,763		36,322	60,980	18,783	812	
1961		892,290	659,778		34,540	44,683	35,150	665	
1962	62,061	836,522	703,763	24.9	25,309	83,619	28,816	496	2.23
1963	42,418	892,290	791,733	39.8	47,363	68,551	21,481	540	3.26
1964	37,494	1,003,827	791,733	48.0	38,828	51,103	23,367	417	3.04
1965	35,363	1,003,827	571,807	44.7	28,945	55,590	18,078	293	2.92
1966	32,726	724,986	703,763	43.8	31,487	43,005	12,698	115	2.67
1967	16,033	892,290	791,733	105.2	24,359	30,208	4,997	115	3.74
1968	51,958	1,003,827	483,837	28.7	17,110	11,889	4,981	82	0.66
1969	34,827	613,450	571,807	34.2	6,734	11,850	3,545	203	0.65
1970	30,681	724,986	615,793	43.8	6,712	8,432	8,811	138	0.79
1971	35,859	780,754	351,882	31.7	4,776	20,960	5,957	170	0.89
1972	24,560	446,145	615,793	43.4	11,872	14,170	7,376	197	1.37
1973	17,065	780,754	219,926	58.8	8,026	17,547	8,526	163	2.01
1974	9,570	278,841	395,867	70.9	9,939	20,284	7,044	226	3.92
1975	12,651	501,913	483,837	78.0	11,489	16,757	9,787	163	3.03
1976	7,754	613,450	439,852	136.1	9,491	23,284	7,061	223	5.18
1977	13,536	557,681	571,807	83.6	13,188	16,797	9,672	0	2.94
1978	11,637	724,986	439,852	100.3	9,514	23,009	7,100	148	3.43
1979	14,792	557,681	351,882	61.7	13,032	36,045	11,697	459	4.14
1980	14,830	446,145	582,011	69.5	18,569	15,399	10,662	0	3.02
1981	13,292	417,989	394,074	61.2	3,554	26,025	12,673	2,750	3.39
1982	24,727	235,926	539,212	31.3	7,681	22,955	37,811	81	2.77
1983	18,011	280,788	377,115	36.5	13,391	40,561	5,773	0	3.32
1984	24,007	359,327	384,181	31.0	21,312	5,773	4,140	0	1.30
1985	26,174	415,819	269,091	26.3	650	14,761	1,263	0	0.64
1986	21,551	470,909	212,073	31.7	15,301	18,105	911	0	1.59
1987	24,961	727,927	58,209	31.5	13,052	8,195	1,148	77	0.90
1988	20,663	710,149	316,693	49.7	5,919	10,790	3,328	50	0.99
1989	24,469	401,531	316,693	29.8	10,790	7,918	2,147	76	0.86
1990	9,100	401,531	281,505	75.3	4,485	5,107	3,288	132	1.46
1991	16,975	356,916	263,911	36.7	2,893	7,823	5,705	73	0.97
1992	18,959	334,609	285,904	32.8	4,431	13,572	3,166	453	1.14
1993	7,207	362,493	235,321	83.2	7,688	7,531	19,613		
1994	7,366	298,360	408,183	96.1	4,266	46,659			
1995	7,831	517,528	372,994	113.9	26,428				
1996	7,471	472,914	416,100	119.3					
1997	8,563								
1998	9,198								
1999	10,817								
2000	19,578								

[a] To the mouth of the Columbia River.

$$p(R_i \,|\, \alpha, \beta) = \frac{1}{\sqrt{2\pi\sigma^2}} \frac{1}{\log_e(R_i)} \times \exp\left\{\frac{[\log_e(R_i) - \log_e(\hat{R}_i)]^{-2}}{2\sigma^2}\right\}, \quad (5)$$

we calculated a likelihood value for each Ricker (α, β) pair using equation (1) and each Beverton–Holt (p, c) pair using equation (3) and the observed R:

$$L\left(\alpha \,\middle|\, \beta, R_i\right) = \frac{1}{\sqrt{2\pi\sigma^2}} \frac{1}{(R_i)} \times \exp\left\{-\frac{[\log_e(R_i) - \log_e(\hat{R}_i)]^{2}}{2\sigma^2}\right\}, \quad (6)$$

where i = the data point in the adult return or smolt recruit data set. The closed-form solution was used to estimate the parameter σ as follows:

$$\sigma = \sqrt{\frac{\sum [\log_e(R) - \log_e(\hat{R})]^2}{n}}. \qquad (7)$$

The asymptotic properties of the negative log-likelihood ratio of the parameter values to the best-fit parameter value converge to a chi-square distribution (Hilborn and Mangel 1997). This was used in determining the confidence intervals of the parameter values via nonlinear maximum likelihood techniques (Hilborn and Mangel 1997).

Decline in productivity.—We followed Schaller et al. (1999) and introduced a class effect variable, τ, to examine differences in productivity between the two time periods; τ is equal to 0 for the years before the completion of Lower Granite Dam and 1 thereafter. The null hypothesis for linear versions of the Ricker curve,

$$\log_e\left(\frac{R}{S}\right) = \alpha + \beta_1 S + \beta_2 \tau + \beta_3 S\tau + \varepsilon, \qquad (8)$$

and the Beverton–Holt curve,

$$\frac{S}{R} = \alpha + \beta_1 S + \beta_2 \tau + \beta_3 S\tau + \varepsilon, \qquad (9)$$

was that $\beta_1 = \beta_2 = \beta_3 = 0$.

Under the alternative hypothesis, we tested whether the interaction term ($\beta_{3)}$ was significantly different from zero in both models ($P < 0.05$).

Sample importance resampling.—Sample importance resampling (SIR) techniques (Rubin 1987) were used to generate distributions around the management parameters. We projected the adult returns from the juvenile data using 2.7, 3.6, and 6.4% smolt SARs (average postdam, average predam, and maximum observed, respectively; Table 1). We ran simulations that picked 100,000 pairs of randomly selected values of α and β for the Ricker curve and p and c for the Beverton–Holt curve. We computed S_{MSY} based on these projected numbers and compared them with the result of using a 20% SAR (Ward 2000). The uniform distribution for the parameter choices used in the SIR were α (or p) $\sim U[0, 30]$ returns per spawner and β (or c) $\sim U[0, 500{,}000]$ adult returns.

We calculated a likelihood of S_{MSY} for each (α, β) or (p, c) pair from the products of the likelihoods, that is,

$$L(S_{\mathrm{MSY}} \mid \alpha, \beta, R_i) = \prod_{i=1}^{n} \frac{1}{\sqrt{2\pi\sigma^2}} \frac{1}{(R_i)} \times \exp\left\{-\frac{[\log_e(R_i) - \log_e(\hat{R}_i)]^2}{2\sigma^2}\right\}, \qquad (10)$$

where n = the number of data points in the escapement–adult return or escapement–smolt recruit database. These likelihood values were accumulated in increments of 1,000 between 0 and 500,000 (500 bins of S_{MSY} values) over the 100,000 randomly selected pairs.

The posterior probability function was a rescaled likelihood in each S_{MSY} bin divided by all the likelihood values generated through the simulation, where i through n indicate the S_{MSY} bins:

$$P(S_{\mathrm{MSY}_i} \mid \alpha, \beta, R) = \frac{\sum L(S_{\mathrm{MSY}_i} \mid \alpha, \beta, R)}{\sum_{i=1}^{n} \sum L(S_{\mathrm{MSY}_i} \mid \alpha, \beta, R)}. \qquad (11)$$

Bayes' theorem (Casella and Berger 1990) was used to combine the information from the Ricker (vector R_1) and Beverton–Holt (vector R_2) models run on the projected adult return from smolt data. If the posterior probability $P(S_{\mathrm{MSY},I} \mid \alpha, \beta, R_1)$ from the Ricker model (equation 11) is redefined as the likelihood, $L(S_{\mathrm{MSY}(i)} \mid \alpha, \beta, R_1)$, and the posterior probability $P(S_{\mathrm{MSY}} \mid \alpha, \beta, R_2)$ from the Beverton–Holt model is redefined as the prior probability, $P(S_{\mathrm{MSY}} \mid R_2)$, then the new posterior probability of S_{MSY} using information from both models is

$$P(S_{\mathrm{MSY}_i} \mid \vec{R}_1, \vec{R}_2) = \frac{L(S_{\mathrm{MSY}_i} \mid \vec{R}_1) \times P(S_{\mathrm{MSY}_i} \mid \vec{R}_2)}{\sum_{i=1}^{n} L(S_{\mathrm{MSY}_i} \mid \vec{R}_1) \times P(S_{\mathrm{MSY}_i} \mid \vec{R}_2)}, \qquad (12)$$

where i refers to a specific value for the S_{MSY} in question and n is the range of S_{MSY} values examined.

Sensitivity analysis for hatchery fish spawning in the wild.—The number of hatchery fish that escaped the tribal and recreational fisheries and hatchery broodstock collection and that spawned naturally is unknown and varies by tributary. Although kelts (steelhead that spawn in multiple years) represent less than 2% of the steelhead population moving upstream (Dan Rawding, personal communication), we used the greatest observed percentage of kelts migrating downstream after spawning for the first time (Doug Hatch, Columbia

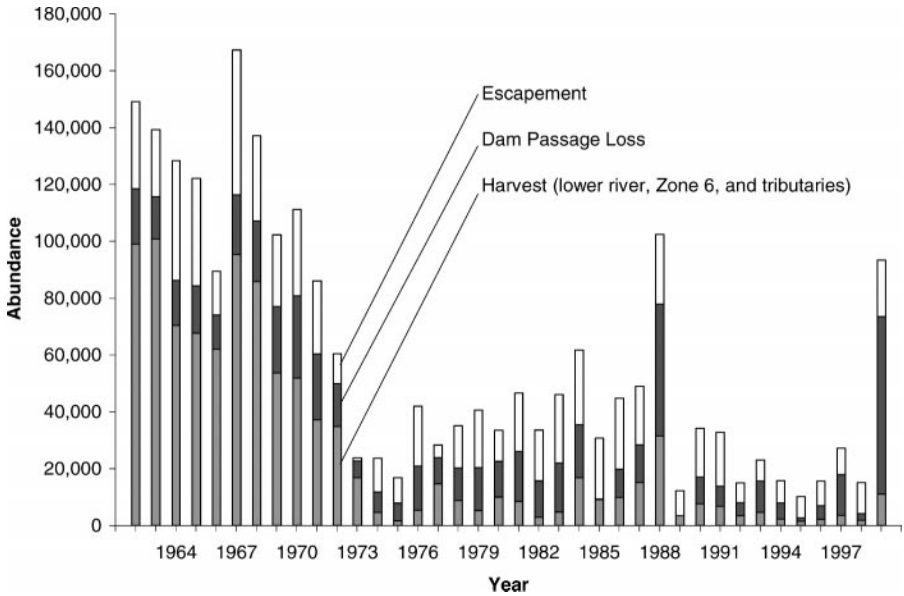

FIGURE 2.—Reconstructed abundance of wild Snake River steelhead at the mouth of the Columbia River, 1962–1999. Abundance consists of harvest, the dam passage loss of migrating adult spawners, and escapement (dam count less tributary harvest). Zone 6 is the stretch of the river between Bonneville and McNary dams. Data are from the Technical Advisory Committee, *U.S. v. Oregon*.

River Intertribal Fish Commission, personal communication) as our upper estimate of the percentage of hatchery fish spawning in the wild.

To estimate the effect of hatchery fish spawning in the wild on the escapement goals and model parameters, we increased the escapements in our database by multiples of 1–2.5, which would represent 0–60% of the spawning escapement's being hatchery fish. We ran two sensitivity analyses, one simulating a systematic bias and the other random year-to-year variation (error). In the former, we increased all of the spawning escapements in our database in 10% increments to simulate 10–60% hatchery spawners. In the latter, we adjusted each escapement in our time series independently within the range of 0–60% hatchery spawners and estimated a goal for the entire time series. We repeated this 100,000 times, and the mean and coefficient of variation (CV, defined as $\sigma/\bar{x}$) were generated for the overall goal and parameters depending on the model chosen.

Results

When the Dalles Dam on the main-stem Columbia River was completed in 1957, its reservoir inundated Celilo Falls and a major tribal dip-net fishery at that site. The loss of the tribal fishery plus the closure of the non-Indian commercial fisheries above Bonneville Dam contributed to the peak steelhead escapements in our data set shown in Table 1. Escapement estimates have since declined with the subsequent completion of the lower Snake River dams. It is interesting to note that before the completion of Lower Granite Dam in 1974, harvest rates of wild steelhead were high (Figure 2). After 1974, harvest rates dropped but adult dam passage mortalities increased (Figure 2).

Decline in Productivity, Survival, Maximum Production, and Capacity

The number of observed out-migrating smolts and returning adults from the postdam period was about half that from the period prior to the completion of Lower Granite Dam. The average number of observed out-migrating wild steelhead smolts declined from 1,470,308 to 845,343. The number of observed wild Snake River adult steelhead returning to the mouth of the Columbia River declined from 52,310 to 22,925. The Snake River escapement index declined from 36,524 to 16,434 (Table 2).

Higher average values of observed productivity in the postdam period (average adult returns and smolt recruitment per spawner were 2.37 and 63.13, respectively, compared with 2.28 and 46.59) were inversely related to lower escapement

TABLE 2.—Comparison of average observed wild Snake River steelhead smolt/spawner rates, smolt-to-adult survival rates, and adult return/spawner rates from the periods before and after the completion of lower Snake River dams.

Period, averages, and change	Average spawning escapement	Average smolts per spawner	Average number of smolts produced	Average smolt-to-adult survival	Average number of adults returning[a]	Average adult returns per spawner	Average harvest rate (%)	Average interdam passage loss	Average interdam passage loss rate (%)
1962–1968	39,722	47.87	1,603,367	0.043		2.65	62.6	17,278	21.1
1962–1972	36,725	44.37	1,450,726	0.033		2.02	58.0	19,233	26.2
1962–1974	33,124	47.52	1,356,831	0.031		2.17	56.0	17,287	27.8
Predam average	36,524	46.59	1,470,308	0.036	52,310	2.28	58.9	17,933	25.0
1969–1996	17,876	60.65	879,486	0.025		2.22	27.5	12,620	36.0
1973–1996	15,608	64.39	828,800	0.028		2.47	23.7	10,948	36.1
1975–1996	15,816	64.35	827,744	0.028		2.42	21.8	11,344	36.1
Postdam average	16,434	63.13	845,343	0.027	22,925	2.37	24.3	11,637	36.1
Overall average	22,245	58.10	1,024,262	0.030		2.31	34.5	13,552	33.0
Change between pre- and postdam periods (%)	45.0	135.5	57.5	76.2	43.8	104.0	41.3	64.9	144.3

[a] To the mouth of the Columbia River.

density after the completion of the lower Snake River dams (Table 2). Similarly, the postdam Ricker and Beverton–Holt spawner recruit functions using both the adult return and smolt recruit data sets also show lower estimates of S_{MSY} coincident with higher productivity (Table 3), along with less contrast in the data (Hilborn and Walters 1992). The Beverton–Holt curve did not fit the data as well and therefore a comparison between the two time periods was not possible. The modeled differences are apparent regardless of which dam was used to determine the cutoff year: 1968, when Lower Monumental Dam was completed; 1972, when Little Goose Dam was completed; or 1975, when Lower Granite Dam completed. The differences in the modeled productivity estimated by the Ricker curve were statistically significant (Table 4).

Unlike productivity, the decline in the average observed smolt-to-adult survival rate from 0.036 to 0.027 after the completion of Lower Granite Dam (Table 2) cannot be explained by habitat carrying capacity and spawner density dependence. This suggests that there was a decline in survival during or after the downstream migration life stage since the completion of Lower Granite Dam. The results were the same regardless of which reference point was used to define the pre- and postdam data sets.

The interaction term between spawning escapement and time period was statistically significant between the periods before and after the completion of Lower Granite Dam (Table 4) regardless of the model (Ricker or Beverton–Holt) and data set (adult return or juvenile recruitment). This difference precludes us from combining the data from the two time periods into a single data set. We thus used the predam juvenile and adult data for most of our analysis.

Uncertainty in Parameters

Return-per-escapement values were highly variable for the observed escapement values. The correlation coefficients from the least-squares fits were better with smolt data ($r^2 = 0.8$ for the Beverton–Holt curve and 0.73 for the Ricker curve) than with the adult data. Both the Ricker and Beverton–Holt curves fit the adult data poorly ($r^2 < 0.1$). To work around the noisy data, we decided to use an approach involving simulations and the SIR algorithm to estimate the uncertainty in our management estimates.

The spawner–adult return data had a wider range of parameter estimates than the spawner–smolt recruit data because the spawner–adult return relationship included the smolt-to-adult life stage and the inherent variability in natural mortality for this life stage, which the spawner–smolt recruit data did not have. The likelihood profiles (Figure 3) for the adult return data set illustrate the uncertainty in the productivity (p and α) and capacity (S_{max}; c and β) parameters. We could estimate the upper and lower bounds of the 95% confidence intervals only for the Ricker α parameter, namely, 1.32 and 4.53 adult returns per spawner. We could estimate a lower 95% confidence interval for the Ricker β and Beverton–Holt p and c parameters (25,000 adult spawners, 1.35 adult returns per spawner, and

TABLE 3.—Comparison of pre- and postdam estimates of productivity, carrying capacity, number of spawners associated with maximum recruitment (S_{max}), and number of spawners associated with maximum sustainable yield (S_{MSY}) from various models using adult return and smolt recruit data for wild Snake River steelhead.

Data source and model	Time period[a]	Productivity	Carrying capacity[c]	S_{max}[d]	S_{MSY}
		Predam period			
Adult					
Ricker	1962–1968	5.8		44,113	29,408
	1962–1972	2.2		122,795	44,184
	1962–1974	2.9		69,511	31,686
Beverton–Holt	1962–1968	9.9	118,014		25,588
	1962–1972	2.8	147,000		35,330
	1962–1974	4.3	97,000		24,218
Smolt					
Ricker	1962–1968	144.1		32,982	32,371
	1962–1972	103.1		40,015	38,987
	1962–1974	94.0		43,791	42,560
Beverton–Holt	1962–1968	[b]	[b]		
	1962–1972	[b]	[b]		
	1962–1974	144.2	41,460		150,369
		Postdam period			
Adult					
Ricker	1969–1993	6.5		14,840	10,288
	1973–1993	7.8		12,592	9,227
	1975–1993	7.6		12,725	9,276
Beverton–Holt	1969–1993	[b]	[b]		
	1973–1993	[b]	[b]		
	1975–1993	[b]	[b]		
Smolt					
Ricker	1969–1996	131.7		19,923	19,520
	1973–1996	181.4		13,464	13,265
	1975–1996	187.2		13,153	12,965
Beverton–Holt	1969–1996	642.7	15,571		35,783
	1973–1996	[b]	[b]		
	1975–1996	[b]	[b]		

[a] Time periods are characterized as follows: 1962–1968 = pre–Little Goose Dam; 1969–1993 = post–Little Goose Dam; 1962–1972 = pre–Dworshak Dam; 1973–1993 = post–Dworshak Dam; 1962–1974 = pre–Lower Granite Dam; and 1975–1993 = post–Lower Granite Dam.
[b] Beverton–Holt curve did not fit properly.
[c] Parameter c in the Beverton–Holt model.
[d] Parameter β in the Ricker model.

40,000 adult spawners, respectively) but not the upper 95% confidence interval.

The curves through the spawner–juvenile recruit data had a better fit, as is evident from the likelihood profiles (Figure 4). The 95% confidence interval for the productivity estimates was 32–69 smolts per spawner for the Ricker curve and 33–174 smolts per spawner for the Beverton–Holt curve. The 95% confidence interval for β was 33,000–113,000 adult spawners. For the Beverton–Holt curve, the range of maximum carrying capacity in terms of juveniles was 835,000–2.87 million smolts. Assuming a 5% SAR, this translates to 42,000–143,500 spawners as the maximum spawning potential.

Simulation Results

The simulations indicate very different estimates based on the model choice. We derived goals using the predam juvenile data with the current SAR (2.7%) and compared them with the results of using the average SAR observed during the predam period (3.6%) and the maximum observed SAR in the Snake River (6.4%). These estimates were compared with a baseline optimum seen on the Keogh River in British Columbia (20%; Ward 2000). When the adult return data were used, S_{MSY} was estimated to be 28,000 (CV = 0.18) for the Ricker curve and 13,000 (CV = 0.21) for the Beverton–Holt curve. When the smolt recruit data were used with a 3.6% SAR, S_{MSY} was estimated

TABLE 4.—Results of analysis of variance comparing adult returns and juvenile recruitment with an escapement index before and after the completion of Lower Granite Dam (the dam completion variable = 0 before the completion of the dam and 1 thereafter). Ricker and Beverton–Holt curves were used to model productivity.

Source of variation	df	Sum of squares	Mean square	*F*	*P*
Adult returns–escapement (Ricker curve)					
Spawning escapement index	1	1.5292	1.5292	4.7013	0.039
Dam completion	1	0.589	0.589	1.811	0.190
Interaction	1	1.8053	1.8053	5.5503	0.026
Residuals	27	8.7821	0.3253		
Adult returns–escapement (Beverton–Holt curve)					
Spawning escapement index	1	0.6832	0.6832	4.3999	0.045
Dam completion	1	0.2055	0.2055	1.3237	0.260
Interaction	1	0.663	0.663	4.2698	0.049
Residuals	27	4.1922	0.1553		
Juvenile recruitment–escapement (Ricker curve)					
Spawning escapement index	1	3429.2	3429.2	49.7466	<0.001
Dam completion	1	416.5	416.5	6.0418	0.020
Interaction	1	1747.5	1747.5	25.3504	<0.001
Residuals	31	2136.9	68.9		
Juvenile recruitment–escapement (Beverton–Holt curve)					
Spawning escapement index	1	0.014497	0.014497	3.9099	0.057
Dam completion	1	0.013371	0.013371	3.6062	0.067
Interaction	1	0.021151	0.021151	5.7045	0.023
Residuals	31	0.114941	0.003708		

to be 23,000 (CV = 0.10) and 15,000 (CV = 0.27) for the Ricker and Beverton–Holt curves, respectively (Figure 5). The adult data fit was extremely poor for both the Beverton–Holt and the Ricker curves ($r^2 < 0.1$ for both models), and we dismiss those two management estimates (Figures 3, 5). The stock–recruit model fit the juvenile data best ($r^2 = 0.8$ for the Beverton–Holt curve and 0.73 for the Ricker curve). We used the juvenile data with average SAR to determine the optimal management parameters. We reconciled the two stock–recruit models using projected adult return data to come up with a joint management estimate (Figure 6) via Bayesian methods (equation 12). The com-

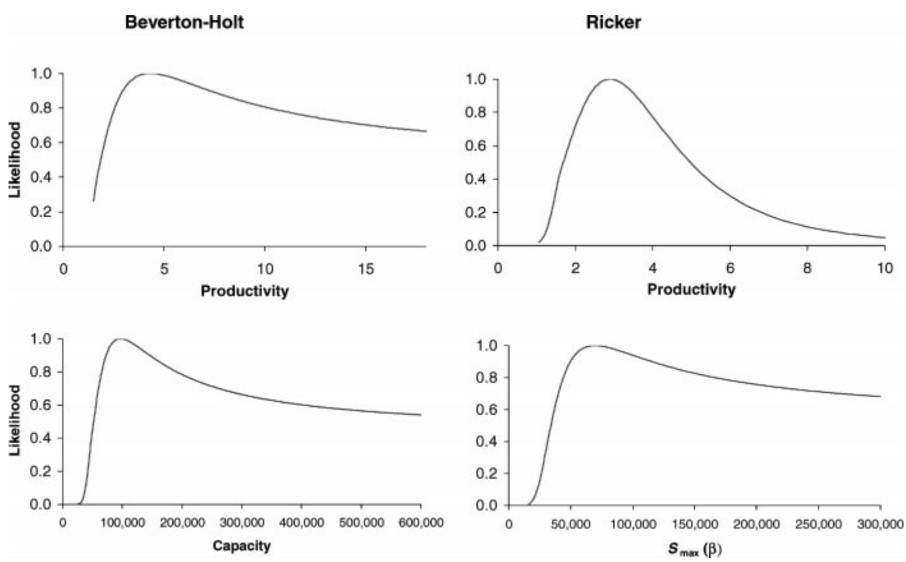

FIGURE 3.—Likelihood profiles for Beverton–Holt estimates of productivity and carrying capacity and Ricker estimates of productivity and the number of spawners associated with maximum recruitment (S_{max} or β) based on adult return data.

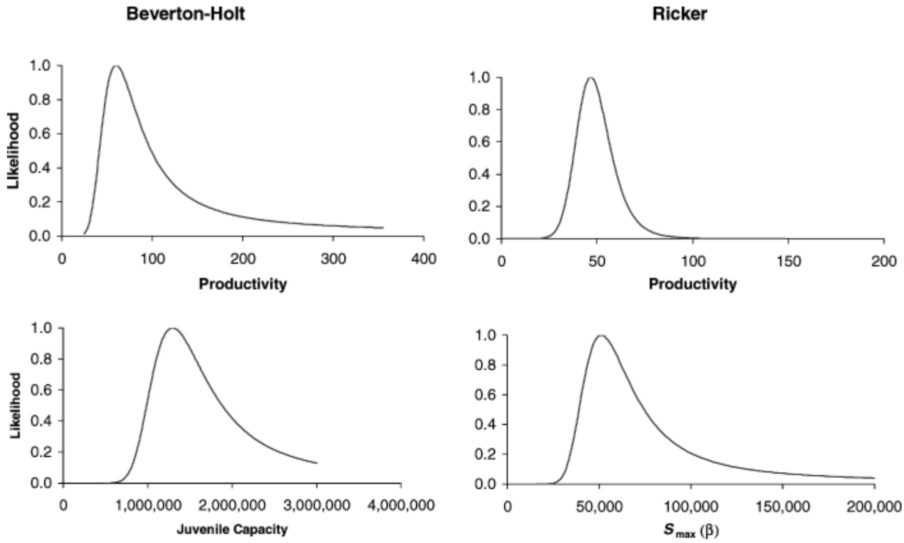

FIGURE 4.—Likelihood profiles for Beverton–Holt estimates of productivity and carrying capacity and Ricker estimates of productivity and the number of spawners associated with maximum recruitment (S_{max} or β) based on smolt recruit data.

bined posterior distributions were centered on 17,000 (CV = 0.08; Figure 6a), 21,000 (CV = 0.09; Figure 6b), 27,000 (CV = 0.12; Figure 6c), and 60,000 (CV = 0.11; Figure 6d) when we modeled the current 2.7% SAR, the predam 3.5% SAR, the maximum observed SAR (6.4%), and the 20% SAR rate observed on a pristine system (the Keogh River in British Columbia; Ward 2000), respectively.

It is important to note that if we have poor estimates of productivity and capacity (as shown in Figure 3), we will have a poor estimate of S_{MSY} for our target management parameter (Figure 5; adult data). However, by using Bayesian methods to reconcile the different data and model estimates (equation 12; Figure 6), we provide an alternative approach to obtaining target reference points for management when the data are noisy. This approach also takes into account current limitations in the overall productivity of the stock and suggests different estimates for management purposes based on improvements in overall SARs.

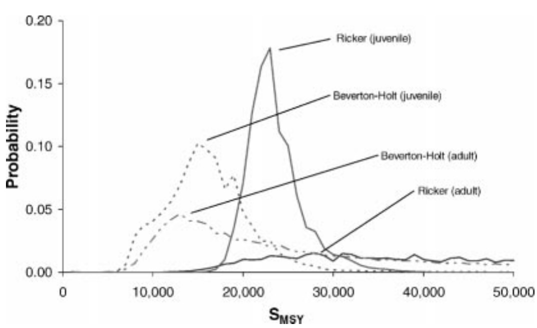

FIGURE 5.—Probability distribution of the spawning stock size corresponding to the maximum sustainable yield from Beverton–Holt and Ricker curves with (1) adult return data and (2) smolt recruit (juvenile) data and the assumption of a 3.6% smolt-to-adult survival rate.

Influence of Hatchery Fish Spawning in the Wild on the Goal

Figure 6 assumes that all the juvenile production comes from natural spawners. If our estimates of hatchery spawners in the wild are biased downward, then our estimates of steelhead productivity will be biased upward and our estimates of S_{MSY} will increase, giving us a CV of 0.07–0.12 depending on the model chosen (Table 5). The relationship between the straying rate and estimates of S_{MSY} can be seen (Table 6) when a systematic bias is modeled. At present, data on hatchery straying rates are not collected in a systematic manner. If we use a conservative estimate of 40%, our estimates of S_{MSY} from Figure 6 would be adjusted upward by approximately 26% for the Ricker model and 9% for the Beverton–Holt model (Table 6). If we run our SIR analysis assuming a 6.4% SAR and these straying estimates, our derived goal

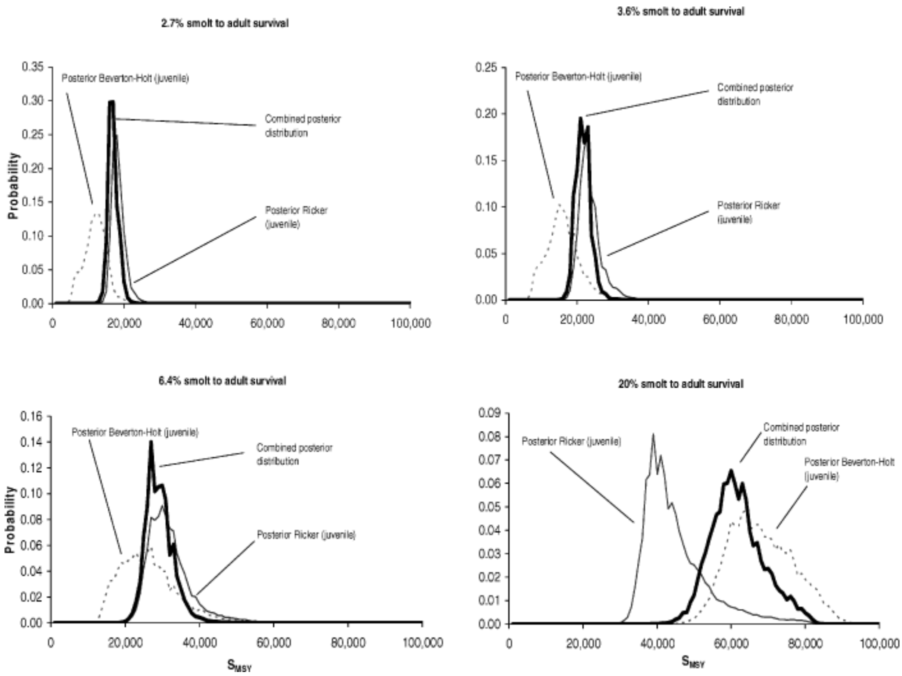

FIGURE 6.—Posterior probability distributions of the spawning stock size corresponding to the maximum sustainable yield (S_{MSY}) from Beverton–Holt and Ricker curves with smolt recruit data and four assumed smolt-to-adult survival rates. The combined posterior probability distributions were derived using Bayesian methods.

would be 36,000 (CV = 0.09) fish, a 33% increase in the derived goal shown in Figure 6c.

Discussion

Healthy stock complexes often have subpopulations that display a wide array of life history strategies (Hilborn et al. 2003). Hilborn and Walters (1992) demonstrated that aggregate management goals for numerous subpopulations are often biased downward. Hilborn et al. (2003) describe a healthy and resilient sockeye salmon *O. nerka* stock complex in Bristol Bay. However, the aquatic habitat in Bristol Bay is relatively pristine. The Snake River habitat, on the other hand, has been greatly modified by human development. This is especially true in the migration corridor, which has been transformed from a free-flowing river into a series of pools or reservoirs. Some of the steelhead subpopulations tolerate the new environment better than others. For example, A-run summer steelhead rebounded more than B-run fish when ocean conditions recently became favorable. Thus, managing for an aggregate goal ignores individual subpopulations that may exhibit some life history strategy that is threatened by flow modifications through the hydrosystem and other limiting fac-

TABLE 5.—Effect of random error in the estimated number of hatchery fish spawning in the wild on Ricker and Beverton–Holt estimates of productivity, capacity, and the spawning stocks associated with maximum sustainable yield (S_{MSY}) and maximum recruitment (S_{MSP}). Estimates were based on smolt recruit data and assume a 6.4% smolt-to-adult survival rate (SAR). Values in parentheses are coefficients of variation.

Model	Productivity	Capacity	S_{MSY}	S_{MSP}
No hatchery spawners				
Beverton–Holt	9.26	41,380	27,761	112,253
Ricker	5.48	49,999	32,504	85,008
Random proportion of hatchery spawners and 6.4% SAR				
Beverton–Holt	7.159 (0.23)	119,828 (0.08)	28,127 (0.12)	101,924 (0.04)
Ricker	4.035 (0.12)	67,384 (0.12)	37,555 (0.07)	92,662 (0.05)

TABLE 6.—Effect of systematic bias in estimates of hatchery fish spawning in the wild on Ricker and Beverton–Holt curve estimates of productivity, capacity, and the spawning stocks associated with maximum sustainable yield (S_{MSY}) and maximum recruitment (S_{MSP}). Estimates were based on smolt recruit data and assume a 6.4% smolt-to-adult survival rate.

Proportion hatchery spawners	Change in escapement estimate	Productivity	Capacity	S_{MSY}	S_{MSP}	Change in estimate S_{MSY}	Change in estimate S_{MSP}
			Ricker curve				
0.0	1.00	6.0	43,791	29,512	78,586		
0.1	1.10	5.5	47,732	31,132	81,545	0.05	0.04
0.2	1.20	5.0	52,549	32,935	84,722	0.12	0.08
0.3	1.30	4.5	59,117	35,100	88,349	0.19	0.12
0.4	1.40	3.9	67,000	37,280	91,744	0.26	0.17
0.5	1.50	3.3	78,824	39,769	95,123	0.35	0.21
0.6	1.60	2.7	96,340	41,914	96,929	0.42	0.23
			Beverton–Holt curve				
0.0	1.00	9.3	125,838	27,761	112,253		
0.1	1.10	8.5	125,838	28,359	111,031	0.02	−0.01
0.2	1.20	7.7	125,838	28,990	109,536	0.04	−0.02
0.3	1.30	6.9	125,838	29,700	107,499	0.07	−0.04
0.4	1.40	6.1	125,838	30,357	105,054	0.09	−0.06
0.5	1.50	5.1	125,837	31,018	101,386	0.12	−0.10
0.6	1.60	4.2	125,837	31,439	95,952	0.13	−0.15

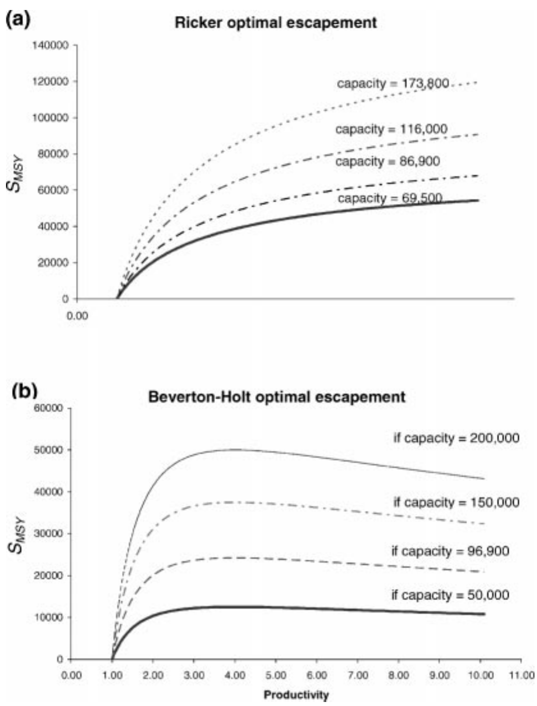

FIGURE 7.—Effect of different productivity and carrying capacity values on estimates of the spawning stock size corresponding to the maximum sustainable yield (S_{MSY}) from **(a)** Ricker and **(b)** Beverton–Holt curves.

tors. Unfortunately, real-time data on the various subpopulations are unavailable, and working with the aggregate population is the only management option at this time.

For rebuilding and management, both estimates of productivity and capacity (or S_{MSP}) are essential. Assuming a constant value for capacity, varying the estimates of productivity yields very different estimates of management goals such as S_{MSY} from the Ricker model (Figure 7a). The effect of productivity on S_{MSY}, given a fixed estimate of capacity, is not as sensitive in the Beverton–Holt model once replacement rates are greater than 4 (Figure 7b; Table 6). However, the productivity of wild Snake River summer steelhead has recently been near or below replacement levels (e.g., a total return of 0.97 adults at the mouth of the Columbia River for brood year 1991; Table 1). Given data with very low return-per-spawner ratios, the models will generate extremely low target management parameters and goals like S_{MSY}, which is a problem with using the postdam data sets (Figure 6a, b). While very low escapement goals are attainable, they do not contribute to rebuilding the population.

The inherent problems with derived escapement goals based on standard spawner-to-adult estimates will recur in fisheries management as long as we lump survival over different life cycle stages (Figures 5, 6). The juvenile data indicate that freshwater productivity is high (Figure 4). The bottleneck is clearly smolt-to-adult survival (Figure

6a, b). If SAR is improved over time, the overall recovery goal (S_{MSY}) for Snake River steelhead can be raised to 60,000 adults (Figure 6d). Management agencies reject low escapement goals, as they are inherently biased owing to a lack of contrast in the data (Hilborn and Walters 1992). But managing the fisheries for a higher goal derived from data with higher productivity will be an exercise in frustration unless the management agencies also take action to rectify the habitat and migration corridor problems that reduced capacity and productivity in the first place. The results from our analysis indicate that changes in freshwater spawning and rearing survival could not explain the overall decline in productivity for Snake River summer steelhead (Figure 4). Petrosky et al. (2001) and Wilson (2003) came to the same conclusion for Snake River spring and summer Chinook salmon. Thus, rebuilding efforts should closely examine the juvenile-to-adult survival rates (Figures 6, 7).

Escapement goals need to be designed to mesh with efforts to improve productivity, capacity, and maximum production. Suppose productivity is between 2 and 4 recruits per spawner and we use the Beverton–Holt curve as our management model. If the management agencies have the objective of increasing observed carrying capacity through specific habitat-enhancing activities, realistic escapement goals could be set and upgraded to the next higher contour level corresponding to the target capacity (Figure 6b or Figure 7b [or to the right side of the contour in Figure 7b if productivity is improved]), which would rebuild the population over the long term. Migration corridor activities would most likely involve improvement in spring and summer flows and instream passage through the dams (Marmorek et al. 1998). As one option identified in the biological opinion for the federal hydrosystem, the dams could be removed completely, but the practical reality of this is debatable. Supplementation may also provide a boost in natural production for these stocks (Phillips et al. 2000), but they will not be sustainable without increases in overall productivity (Sharma et al. 2005).

Regardless of the spawner–recruit model used, it is pointless to manage for unrealistically high escapement goals in the short term if the underlying causes of reduced productivity and maximum production (for the Ricker model) or capacity (for the Beverton–Holt model) are not rectified. Unless existing levels of productivity or capacity are improved, steelhead runs will continue to decline barring substantial increases in ocean survival rates. Early indications suggest some increase in ocean survival, but survival is a cyclical phenomenon. Since we have no control over ocean conditions, the management status quo (whereby only harvest rates are controlled) can only build the populations to a certain level. To rebuild the steelhead runs to more historic abundance levels, instream survival rates and/or the adult carrying capacity (maximum adult escapement levels) will have to be increased over time. Given that the freshwater habitats of the 25 Snake River steelhead subpopulations are in major wilderness areas (Hassemer et al. 1997), the practical reality is to focus on increasing the SAR through better passage facilities for both the downstream and upstream migrations of the steelhead run.

Acknowledgments

The Technical Advisory Committee for *U.S. v. Oregon,* including Cindy LeFleur (WDFW), Curt Melcher (ODFW), and Greg Mauser (IDFG), helped to locate the tributary harvest data and to edit the spawner–recruit database and run reconstruction methods. Enrique Patino (NMFS) provided a spreadsheet to summarize all of the tributary harvest so that it could be used to estimate a spawner index. Stuart Ellis (CRITFC), Pat Frazier (ODFW), and Tim Roth (USFWS) reviewed the documents. Charlie Petrosky (IDFG) also offered insights on interpreting the spawner–recruit data with respect to tributary harvest above Lower Granite Dam, the parr and smolt data, and the Dworshak Dam counts. Two anonymous reviewers suggested helpful additions to the analysis.

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Appendix follows

Appendix: Reconstruction of Returns by Age

TABLE A.1.—Snake River wild adult summer steelhead counts at the uppermost dam by age.

Escapement year	Index of wild steelhead at uppermost Snake River dam[a]	Index of tributary harvest of wild steelhead[b]	Escapement index	Wild returns by age				
				Age 3	Age 4	Age 5	Age 6	Age 7
1954								525
1955							22,726	372
1956						54,065	16,131	281
1957					30,623	38,374	12,190	303
1958				247	21,735	28,999	13,143	315
1959				175	16,425	31,267	13,652	231
1960				132	17,710	32,477	9,986	400
1961				143	18,395	23,756	17,337	294
1962	108,186	46,125	62,061	148	13,455	41,243	12,727	247
1963	76,788	34,370	42,418	108	23,360	30,277	10,698	246
1964	58,028	20,534	37,494	188	17,149	25,451	10,644	197
1965	62,566	27,203	35,363	138	14,415	25,322	8,513	128
1966	64,987	32,261	32,726	116	14,343	20,251	5,551	50
1967	47,536	31,503	16,033	116	11,470	13,206	2,176	61
1968	82,529	30,570	51,958	92	7,480	5,178	2,658	44
1969	60,584	25,758	34,827	60	2,933	6,323	1,888	108
1970	50,927	20,246	30,681	24	3,581	4,491	4,673	64
1971	50,670	14,811	35,859	29	2,544	11,117	2,770	80
1972	40,523	15,964	24,560	21	6,297	6,589	3,450	106
1973	26,426	9,361	17,065	51	3,732	8,208	4,582	87
1974	10,360	790	9,570	30	4,649	10,901	3,767	122
1975	12,652	2	12,651	37	6,174	8,962	5,300	89
1976	8,987	1,233	7,754	50	5,076	12,609	3,861	119
1977	22,245	8,709	13,536	41	7,142	9,184	5,146	0
1978	13,184	1,547	11,637	58	5,202	12,242	3,073	106
1979	16,424	1,632	14,792	42	6,934	15,599	8,352	261
1980	21,814	6,984	14,830	56	8,036	10,996	6,058	0
1981	17,932	4,641	13,292	0	2,537	14,787	5,451	670
1982	25,231	505	24,727	0	4,364	9,874	9,216	61
1983	18,378	368	18,011	0	5,760	9,887	4,366	0
1984	24,497	490	24,007	0	5,195	4,366	2,097	0
1985	26,708	534	26,174	0	492	7,475	744	0
1986	21,991	440	21,551	0	7,749	10,665	446	0
1987	25,470	509	24,961	0	7,689	4,011	376	39
1988	21,085	422	20,663	248	2,897	3,533	1,679	37
1989	24,968	499	24,469	0	3,533	3,993	1,601	42
1990	9,286	186	9,100	75	2,262	3,810	1,836	46
1991	17,321	346	16,975	18	2,158	4,367	1,972	54
1992	19,346	387	18,959	17	2,473	4,691	2,319	97
1993	7,354	147	7,207	20	2,657	5,516	4,197	
1994	7,516	150	7,366	21	3,124	9,984		
1995	7,991	160	7,831	25	5,655			
1996	7,623	152	7,471	46				
1997	8,738	175	8,563					
1998	9,386	188	9,198					
1999	11,038	221	10,817					
2000	19,978	400	19,578					

[a] IDFG (2001), Appendix A, Table 2. The 1967–1984 and 1997–2000 numbers were updated using data from Charlie Petrosky (IDFG, personal communication).

[b] Tributary harvest data for Idaho were provided by Greg Mauser (IDFG, personal communication); data for Washington were provided by Cindy LeFleur (WDFW, personal communication); and data for 1962–1973 for Oregon were provided by Curt Melcher (ODFW, personal communication). Additional data analysis and updates were provided by Enrique Patino and Charlie Petrosky (NMFS and IDFG, personal communication).

TABLE A.2.—Age composition (%) from wild summer steelhead samples collected at Lower Granite Dam.

	Age				
Year	3	4	5	6	7
1985	0	30	58	12	0
1986	0	12	50	38	0
1987	0	17	58	24	1
1988	0	27	47	26	0
1989	0	21	40	37	3
1990	0	5	47	47	1
1991	0	45	43	12	0
1992	1	40	55	4	0
1993	0	39	55	6	0
1994	1	47	47	5	0
Average	0	28	50	21	0

TABLE A.3.—Estimated interdam survival (conversion) rate from wild B-run steelhead dam counts and Zone 6 harvest. See text for additional information.

Run year	Bonneville Dam count	Zone 6 harvest	Harvest rate (%)	Zone 6 escapement	Lower Granite Dam count	Zone 6 escapement to Lower Granite Dam conversion rate (%)	Wild B-run at Columbia River mouth
1985	12,987	4,030	31.0	8,957	8,858	98.9	13,252
1986	9,984	2,670	26.7	7,314	5,264	72.0	10,188
1987	13,994	5,211	37.2	8,783	5,377	61.2	14,280
1988	17,739	4,160	23.5	13,579	4,758	35.0	18,101
1989	12,356	4,330	35.0	8,026	8,016	99.9	12,608
1990	8,815	1,899	21.5	6,916	4,483	64.8	8,995
1991	6,206	1,859	30.0	4,347	3,180	73.1	6,333
1992	12,714	3,348	26.3	9,366	5,772	61.6	12,973
1993	4,381	836	19.1	3,545	1,440	40.6	4,470
1994	5,152	958	18.6	4,194	2,444	58.3	5,257
1995	1,847	344	18.6	1,503	1,290	85.8	1,885
1996	3,912	1,354	34.6	2,558	1,644	64.3	3,992
1997	3,913	558	14.3	3,355	1,327	39.5	3,993
1998	3,415	533	15.6	2,882	2,371	82.3	3,485
1999	4,145	470	11.3	3,675	890	24.2	4,229
2000	8,418	1,200	14.3	7,218	2,849	39.5	8,590

TABLE A.4.—Reconstruction of Snake River wild summer steelhead returns by age at the Columbia River mouth.

Escapement year	Number of dams between Bonneville (1938) and Lower Granite (1976)	Conversion rate between Bonneville Dam and Upper Snake River dams (%)	Zone 6 harvest rate (%)	Zones 1–5 harvest rate (%)	Wild returns by age
					Age 3
1954					
1955					
1956					
1957					
1958	2	86.0	3.3	38.1	514
1959	2	86.0	0.7	44.5	340
1960	2	86.0	1.2	43.4	318
1961	3	79.8	1.1	39.1	293
1962	3	79.8	0.3	35.2	278
1963	3	79.8	6.9	43.9	204
1964	3	79.8	6.0	34.9	382
1965	3	79.8	8.3	27.1	313
1966	3	79.8	2.3	31.8	233
1967	3	79.8	13.8	28.3	254
1968	4	74.0	9.3	34.2	196
1969	5	68.6	10.5	18.9	138
1970	6	63.6	12.2	18.4	54
1971	6	63.6	13.9	14.0	54
1972	6	63.6	16.3	17.9	39
1973	6	63.6	17.9	16.6	96
1974	6	63.6	10.2	6.6	65
1975	7	59.0	9.7	0.0	80
1976	7	59.0	10.1	0.0	93
1977	7	59.0	19.7	1.9	77
1978	7	59.0	19.5	1.4	106
1979	7	59.0	7.9	1.1	77
1980	7	59.0	7.9	1.5	105
1981	7	59.0	6.3	2.0	0
1982	7	59.0	5.8	1.6	0
1983	7	59.0	8.6	1.3	0
1984	7	59.0	25.4	1.7	0
1985	7	98.9	26.7	1.5	0
1986	7	72.0	19.4	2.0	0
1987	7	61.2	28.6	1.6	0
1988	7	35.0	29.5	1.3	421
1989	7	99.9	23.0	1.7	0
1990	7	64.8	20.3	2.0	230
1991	7	73.1	17.8	2.0	36
1992	7	61.6	19.0	2.0	23
1993	7	40.6	17.8	2.0	36
1994	7	58.3	11.7	2.0	62
1995	7	85.8	11.3	2.0	34
1996	7	64.3	11.4	2.0	213
1997	7	39.5	10.8	2.0	
1998	7	82.3	9.2	2.0	
1999	7	24.2	9.9	2.0	
2000	7	39.5	5.7	2.0	

TABLE A.4.—Extended.

Escapement year	Wild returns by age				Total returns
	Age 4	Age 5	Age 6	Age 7	
1954				1,094	1,094
1955			47,357	723	48,081
1956		112,661	31,332	676	144,669
1957	63,812	74,538	29,263	622	168,235
1958	42,219	69,615	26,956	592	139,896
1959	39,431	64,126	25,633	434	129,964
1960	36,322	60,980	18,783	812	117,214
1961	34,540	44,683	35,150	665	115,330
1962	25,309	83,619	28,816	496	138,518
1963	47,363	68,551	21,481	540	138,138
1964	38,828	51,103	23,367	417	114,097
1965	28,945	55,590	18,078	293	103,219
1966	31,487	43,005	12,698	115	87,539
1967	24,359	30,208	4,997	115	59,933
1968	17,110	11,889	4,981	82	34,258
1969	6,734	11,850	3,545	203	22,470
1970	6,712	8,432	8,811	138	24,147
1971	4,776	20,960	5,957	170	31,918
1972	11,872	14,170	7,376	197	33,654
1973	8,026	17,547	8,526	163	34,358
1974	9,939	20,284	7,044	226	37,557
1975	11,489	16,757	9,787	163	38,276
1976	9,491	23,284	7,061	223	40,151
1977	13,188	16,797	9,672	0	39,733
1978	9,514	23,009	7,100	148	39,877
1979	13,032	36,045	11,697	459	61,310
1980	18,569	15,399	10,662	0	44,734
1981	3,554	26,025	12,673	2,750	45,002
1982	7,681	22,955	37,811	81	68,529
1983	13,391	40,561	5,773	0	59,725
1984	21,312	5,773	4,140	0	31,225
1985	650	14,761	1,263	0	16,674
1986	15,301	18,105	911	0	34,316
1987	13,052	8,195	1,148	77	22,472
1988	5,919	10,790	3,328	50	20,507
1989	10,790	7,918	2,147	76	20,930
1990	4,485	5,107	3,288	132	13,241
1991	2,893	7,823	5,705	73	16,530
1992	4,431	13,572	3,166	453	21,645
1993	7,688	7,531	19,613		34,867
1994	4,266	46,659			
1995	26,428				
1996					
1997					
1998					
1999					
2000					