Measure Twice, Estimate Once: Pacific Salmon Population Viability Analysis for Highly Variable Populations

CHARLES M. PAULSEN*

16016 Southwest Boones Ferry Road, Suite 4, Lake Oswego, Oregon 97035, USA

RICHARD A. HINRICHSSEN

Hinrichsen Environmental Services, 4608 Union Bay Place NE, Seattle, Washington 98105-4027, USA

TIMOTHY R. FISHER

Fisher Fisheries, Ltd. 18403 South Clear Acres Drive, Oregon City, Oregon 97045, USA

Abstract.—Because many stocks of Pacific salmon *Oncorhynchus* spp. are listed under the U.S. Endangered Species Act (ESA), research has focused on predicting the future population dynamics for these low-abundance stocks. One method used to make predictions is known as population viability analysis. Pacific salmon populations exhibit much higher apparent variability than other ESA-listed vertebrates, and high variability increases the probability of extinction. If the high variability is primarily due to counting methods, it could be reduced in model predictions by using methods that correct for measurement error, sampling error, or both. Using data from British Columbia pink salmon *O. gorbuscha* and Snake River spring- or summer-run Chinook salmon *O. tshawytscha* and several modeling approaches (Ricker, Dennis, and state-space models), we compared repeated counts of the same population (e.g., spawner and fry, dam and redd counts). We applied the methods to the first half of the time series and compared the predictions with the last half of the time series. The results demonstrated that having counts of all life stages of a Pacific salmon population is no guarantee that variability will be markedly reduced. Measurement error is not the primary cause of high variability in empirical estimates of abundance or in predicted future abundance for the stocks analyzed. The very wide bounds on predicted abundance limit the utility of the model predictions for making management decisions. Furthermore, obtaining more accurate or complete measurements of population abundance is unlikely to reduce the wide error bounds in predictions of future abundances.

Over the past 15 years many stocks of Pacific salmon *Oncorhynchus* spp. have been listed as threatened or endangered under the U.S. Endangered Species Act (ESA) (NOAA Fisheries 2005). This has focused researchers' attention on a difficult problem: how best to predict the future course of population dynamics for listed stocks whose abundances are often greatly reduced from historic levels. One method used to make such predictions is known as population viability analysis (PVA). Several PVA methods have been used for modeling listed salmon populations, beginning with spawner–recruit (SR) models familiar to many fisheries biologists (e.g., Marmorek et al. 1998; Paulsen and Hinrichsen 2002). More recently, researchers, drawing on methods used for other ESA-listed vertebrate species (e.g., northern spotted owl *Strix occidentalis caurina*, loggerhead sea turtle *Caretta caretta*, snail kite *Rostrhamus sociabilis*, and

Bachman's sparrow *Aimophila aestivulus*; Morris et al. 2002), have employed diffusion approximation methods (e.g., Holmes 2004; Holmes and Semmens 2004). These methods have also been applied for long-term projections by management agencies at the evolutionarily significant unit (ESU) and population levels (NOAA 2000). Unlike spawner–recruit models diffusion approximation methods do not require information on the age of returning progeny (recruits) and, therefore, can be employed for stocks where the age-at-return data may be incomplete or missing. In the terminology of Dunham et al. (2006), the spawner–recruit methods are “matrix” models, while the simpler diffusion approximations are “scalar” methods. Matrix models may yield more accurate results in some circumstances at the cost of requiring data on age structure. The details differ among models, but in all cases one purpose for applying them is to predict future population numbers (including the likelihood of extinction) based on past trends in abundance.

In comparing diffusion approximation analyses for ESA-listed Pacific salmon with those for other species, researchers have noted that the Pacific salmon

* Corresponding author:
cpaulsen@paulsenenvironmentalresearch.com

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populations exhibit much higher apparent variability than other listed vertebrates (Hinrichsen 2001). This is crucial to the predictions arising from PVA since, all else being equal, high variability increases the probability of extinction, sometimes substantially. This occurs because modeled population trajectories can reach zero (i.e., become extinct), or fall below a quasi-extinction threshold, simply at random. Because this high variability appears to be unique to Pacific salmon populations (when compared with other ESA-listed vertebrates), much effort has recently been expended exploring methods to help understand and correct for high population variability (e.g., Holmes 2001; Staples et al. 2004). If the apparent high variability is primarily a problem with counting methods it could be reduced by correcting for measurement error, sampling error, or both, and other possible problems. Some researchers have questioned whether PVA methods are useful or meaningful (Ludwig 1999; Fieberg and Ellner 2000). However, no researcher to our knowledge has taken an empirical approach to this problem for Pacific salmon populations; i.e., comparing modeled population projections with empirical data on population abundance.

Because Pacific salmon have been culturally and economically important species to European settlers for over 100 years, substantial resources have been expended to estimate annual subadult and adult harvest, returns of adult spawners, and, less frequently, the number of emigrating juveniles (e.g., Marmorek and Peters 1998; Petrosky et al. 2001). While no counting method is entirely free of error methods commonly employed include relatively accurate weir or dam counts for many stocks (as opposed to counts of parr or smolts or harvest estimates). In a few cases repeated estimates of abundance are made for the same stock and life stage (e.g., counts at multiple dams and repeated spawning ground surveys). In this study, we take advantage of several of these repeated estimates of abundance to investigate whether high variability in Pacific salmon population abundance can be at least partially attributed to measurement error. If the variability is a consequence of measurement error, then better methods might be employed to count salmon, albeit at higher costs than at present. This, in turn, will reduce uncertainty and inaccuracies in the population predictions resulting from PVAs. If, on the other hand, measurement error is a small fraction of the overall variability, this will have important implications for predicted population dynamics for ESA-listed stocks of Pacific salmon. This occurs because high variability leads to high risk of extinction. Furthermore, high variability limits researchers' abilities to provide useful predictions of future population trajectories to fishery management and regulatory agencies.

We begin with some definitions of sampling and measurement error. We then present the data used in the analyses, giving particular attention to the accuracy of estimates of adult and redd (nest) abundance. Next, we outline the methods applied to the data to compare repeated counts of the same population (e.g., dam and redd counts), along with the PVA methods employed to correct for sampling and measurement error. We then estimate model parameters using the first 20 years of the data series data and compare the predictions with the last 18–24 years of empirical estimates. We conclude with a discussion of the implications of high variability for predicting the future population dynamics of listed stocks using PVA.

Methods

Measurement error.—Measurement error may occur in several forms, some of which are easier to correct (via improved counting methods) than others. The first and most obvious is simple miscounting (e.g., 10 redds are present in a spawning reach, but observers only locate 9 of them due to high turbidity). The second is that only part of the spawning population may be counted (sampling error), as is often the case for index population or index reach counts. Here, the problem is that some adults are spawning outside the index reach and the index reach contains a variable fraction of the total spawning population over spawning cycles. Both problems can be addressed by counting adult spawners at a weir below the spawning area or employing repeated redd counts over the entire spawning area. The third potential problem is that even complete counts of adult spawners do not enumerate the entire population (another case of sampling error): juvenile and adult fish at sea are obviously not counted at dams or weirs or during spawning surveys. For most Pacific salmon species, this problem does not admit to any straightforward solution.

Data.—We used several time series of adult spawning escapements and redd counts and one series of juvenile production to test the predictive capabilities of the SR and PVA models; we present these data in increasing order of their susceptibility to measurement error. The first is a series of adult spawning escapements for pink salmon *O. gorbuscha* and the resulting production of juveniles, which we used to investigate whether the apparent high variability of Pacific salmon populations is caused by measuring only one life stage (spawners) among several that are possible (e.g., fry, parr, smolts, subadults, and adults). The series is taken from Essington et al. (2000) and consists of weir counts of female pink salmon and the resulting fry production in Weaver Creek, British Columbia from 1965 to 1997 (Figure 1). Because all

FIGURE 1.—Weaver Creek pink salmon spawning females and fry produced (from data in Essington et al. 2000).

pink salmon spawning populations consist of a single age-class, the estimates of spawning females and fry constitute a near census of the population, even though spawning males are omitted from the counts.

The second time series consisted of counts of wild-origin spring–summer-run Chinook salmon *O. tshawytscha* listed as threatened under the ESA in 1992. Adults passing upstream were counted as they pass over Ice Harbor (ICH), Lower Monumental, Little Goose, and Lower Granite (LGR) dams on the Snake River on their spawning migration to the tributary subbasins of the lower Snake River basin (Figure 2; Appendix 1). Details on data sources and counting methods for these estimates are outlined in Appendix 2. Since ICH was constructed in 1962 there has been an almost continuous record of spring–summer-run Chinook salmon that ascended the fish ladders at each dam (Figure 3). Returning adults (ages 4 and 5) are separated from jacks (age 3) based on fish length as they are observed passing the fish counting window in each ladder. Some fish may not be counted due to passage via navigation locks, and others fall back below the dam, passing downstream via the turbines, spillways, or locks. However, the dam counts are believed to represent a near census of the population of adults returning to the Snake River basin above LGR. Since the late 1960s numerous spring–summer-run Chinook salmon hatchery programs have been established in the Snake River basin above LGR (Matthews and Waples 1991; Waples et al. 1991). However, dam

counts are maintained separately for both wild- and hatchery-origin Chinook salmon based on the presence of a complete adipose fin. (Virtually all hatchery-origin juveniles have their adipose fin clipped before release.) The wild proportion of the escapement was estimated by subtracting tributary harvest of hatchery adults and total hatchery returns of adults from the combined wild- and hatchery-origin dam count (Figure 4).

The third time series consisted of counts of redds for spring–summer-run Chinook salmon in the lower Snake River basin above LGR except for the Clearwater River basin, which was excluded from the ESA-listed population because the origin of the run is uncertain (Figure 4; Appendix 1). We used redds from a combination of ground and aerial counts in reaches that were counted consistently in each stream known to support spring–summer-run Chinook salmon spawning populations. Redd density (redds per kilometer) for the run-at-large is an aggregate of redds counted in 34 spawning areas (Figure 2). Details on data sources and counting methods for these estimates are outlined in Appendix 2.

The final time series consisted of recruits (adult progeny returning to the uppermost dam or the spawning grounds) produced from both adults at the uppermost dam and seven Snake River spring–summer-run Chinook salmon index stocks (Figure 2). The methods are reviewed in Schaller et al. (1999), and the source data for individual stocks and years are found in Beamesderfer et al. (1996). More details on

FIGURE 2.—Map of the study area showing the watershed accessible to Pacific salmon above Lower Granite Dam (dotted line), major rivers (solid lines), main-stem dams (“V” symbols), stocks used for redd densities (fish symbols), and major spawning areas (heavy lines).

the data sources and methods used for these estimates are outlined in Appendix 2.

As one moves from dam counts to redd densities to run reconstructions, more data and more assumptions are required. Furthermore, there is greater potential for measurement error when one must separate hatchery from wild fish at the dams, allow for the fact that redd counts cover index areas only, and extrapolate age at return (estimated from limited samples) to entire stocks.

Spawner–recruit model.—We first considered a Ricker model (Ricker 1954), which makes use of age-structured spawner data to construct a time series of recruits (progeny returning to spawn in the future) versus spawners. The Ricker model is of the form

$$R_t = S_t \exp(a - bS_t + w_t), \quad (1)$$

where R_t is recruits from the spawners in brood year t , S_t is spawners in year t , and w_t is uncorrelated errors with mean zero and constant variance σ^2 . Age-at-return estimates are required to attribute recruits to the spawning population that produced them (e.g., 4-

year-old recruits are the progeny of spawners from 4 years ago). We fitted this model in the usual way by applying ordinary least squares regression, that is,

$$\log_e(R_t/S_t) = a - bS_t + w_t, \quad (2)$$

where $t = 1, 2, \dots, T$ represents brood year (1962–1981). The residuals are a mixture of measurement error and process or environmental variation. In contrast to the models we consider next, this model is density dependent, so the spawning population declines as recruits per spawner increase.

All three models may also be estimated by means of bootstrapping or other methods that incorporate parameter uncertainty (Ellner and Fieberg 2003). Briefly, the bootstrapping consists of drawing repeatedly from the data (with replacement), estimating a set of parameters including the error term, and using the resulting parameter set to project future population numbers. This incorporates both parameter uncertainty and prediction uncertainty. For the populations analyzed here, these methods result in only a slight

FIGURE 3.—Counts of total (hatchery and wild) spring–summer-run Chinook salmon adults passing the four main-stem Snake River dams from the most downstream (Ice Harbor) to the most upstream (Lower Granite).

increase in the prediction intervals and so are not reported.

Dennis model.—The Dennis model is density independent and does not make use of age-at-return data. Instead of modeling recruits per spawner as the

Ricker model does, it models spawners in a given year in terms of spawners from the previous year. The model was developed by Dennis et al. (1991) and is a stochastic, discrete-time model of exponential growth described by the equation

FIGURE 4.—Estimated wild spring–summer-run Chinook salmon adults that passed the uppermost Snake River dam and redds per river kilometer above Lower Granite Dam (excluding the Clearwater basin).

TABLE 1.—Descriptions of the three population viability analysis models used in the analyses of Pacific salmon.

Feature	Method		
	Ricker	Dennis	State-space
Age data required	Yes	No	No
Estimation method	Ordinary least squares	Ordinary least squares	Restricted maximum likelihood
Accounts for errors in population estimates	Not directly	No	Yes
Widely used in past	Yes (for Pacific salmon)	Yes (for other vertebrate species)	Less so
Ease of interpretation	High	Medium	Low
Use with missing data	Yes	Yes	No

$$S_t = S_{t-1} \exp(\mu + \eta_t), \quad (3)$$

where $t = 1, 2, \dots, T$, S_t represents population abundance at time t , and μ is the deterministic per-unit-abundance growth rate in population density. The error term, η_t , is included to model the stochastic deviations from long-term trend due to environmental effects. These errors are assumed to have a normal distribution with mean zero and variance Q . Letting $\alpha = \log_e(S_t)$, the growth process can be expressed as

$$\alpha_t = \alpha_{t-1} + \mu + \eta_t, \quad (4)$$

which represents a discrete-time random walk with drift process.

State-space models.—Because Pacific salmon may be counted with errors of the sort previously described we also used a model incorporating measurement error. The observed log abundance, y_t , is related to the true “state” through the equation

$$y_t = \alpha_t + \varepsilon_t, \quad (5)$$

where $\alpha_t = \log_e(S_t)$ is the true log abundance of spawners, and ε_t represents uncorrelated measurement errors (differences between actual and observed or estimated spawners) with mean zero and variance H .

Estimates of the state-space model parameters are obtained by means of the restricted maximum likelihood (REML) method. Although the method is only briefly summarized here, the details may be found in Staples et al. (2004). The REML method uses the fact that the second differences of the observed escape-ments follow a multivariate normal distribution that does not depend on μ (since the μ terms in each y cancel) and has a known covariance structure that depends on Q (environmental or process error variance) and H (measurement error variance). The likelihood function formed by this multivariate normal distribution is maximized to obtain the REML estimates of Q and H . The parameter μ is then estimated using a generalized least squares estimator of trend. The REML method was implemented using the R statistical package, and the likelihood function was maximized using the Boydén, Fletcher, Goldfarb, and

Shanno quasi-Newton method with box constraints (L-BFGS-B) of Byrd et al. (1995), which allowed Q and H to be constrained to be nonnegative (see Appendix 3 for R code to estimate the model).

Although the Ricker, Dennis, and state-space models are quite different, they all share an important feature: stationarity. That is, they all assume that the model parameters (a , b , μ , etc.) are constant over time, showing no shifts due to anthropogenic effects or climate regime shifts. Furthermore, they assume that residuals are uncorrelated with one another. Therefore, abrupt jumps in spawner abundance are not likely to occur in projections or predictions made with these models. Table 1 summarizes model features and data requirements.

Population prediction.—To determine how well the alternative population models project spawner abundance, we compared predicted spawner abundance with actual population abundance over a time span of more than 20 years. Starting with the estimated spawner abundances in 1981 and the parameter estimates derived from the 1962–1981 data we predicted the spawner trajectories for 1982–2004 and compared the predictions with the actual spawner observations over the same period. We did this for the Ricker, Dennis, and state-space models.

To test the Ricker model, we constructed predicted trajectories using equation (2) prospectively. We began the projections by setting S_{16} – S_{20} equal to the observed spawner abundances over 1977–1981, then used the Ricker equation to project spawner abundances over 1982–2004 (S_{21} – S_{44}) where S_{44} represented spawner abundance in 2004. The age structure (age at return) of the projected recruits was assumed to be constant over time and was set to the average observed age structure over 1962–1981. We constructed 10,000 spawner trajectories and used these to build envelopes that encompassed 90% of the predicted log spawner abundances (5th and 95th percentiles of the predicted distribution). To test how accurately the spawner–recruit model predicted spawners, we determined whether the prediction envelopes contained the actual spawner abundance observations over 1982–2004.

To use Dennis model for prediction, we set μ and Q equal to their ordinary least squares estimates. Prediction was accomplished by the Dennis model (equation 4) prospectively. We began the projections by setting α_{20} equal to the observed log spawner abundance in 1981, then used equation (4) to project the future log spawner abundances α_{21} – α_{44} , where α_{44} represented the log spawner abundance in 2004. Using this projection technique, we constructed 10,000 trajectories and used these to build envelopes that encompassed 90% of the predicted spawner abundances.

To use the state-space model for prediction, we set the state-space parameters equal to their REML estimates. Prediction was accomplished by means of the state-space model (equation 5) prospectively. As with the Dennis model, we began the projections by setting α_{20} equal to the observed log spawner abundance in 1981, then used equation (5) to project the actual log spawner abundances α_{21} – α_{44} . In contrast to the Dennis projections these projected log abundances were then perturbed by the estimated measurement error distributions to arrive at predictions of observed log spawner abundances. Because the measurement errors are assumed to be independent of one another, their variation does not propagate in the predictions. Using this projection technique, we constructed 10,000 trajectories and used these to build envelopes that encompassed 90% of the predicted spawner abundances.

Results

Having counts of all life stages of a Pacific salmon population is no guarantee that variability will be markedly reduced (Figure 1). The counts of female pink salmon spawners in Weaver Creek vary from less than 100 to over 2,000 during the 17 generations for which data are available. Similarly, estimates of fry production vary by a factor of about 40. The inability to count juveniles in freshwater or maturing fish at sea will reduce the accuracy of population size estimates, but having a census of an entire Pacific salmon population does not appear to reduce the interannual variation in population abundance.

Counts of adult spring–summer-run Chinook salmon at the lower Snake River dams (Figure 3) are both highly variable and highly correlated with each other (Spearman $r > 0.988$ among the four dams). The very high correlation among the counts, combined with the fact that the dam counts are a near census of the population of mature adults (see Methods and Appendix 1) strongly suggests that the high variability in the counts is not a consequence of measurement error, but is instead a feature of the actual population

dynamics of this stock. One consideration with these data is that processes that might produce measurement error (e.g., fallback of adults) could vary from year to year, but still be correlated across the four dams. Strong evidence exists from radio tagging studies that fallback over the dams and ladder reascension among spring–summer-run Chinook salmon (leading to inflation of adult Chinook salmon counts at the Snake River dams) is minimal and correlated with river flow. This results in a modest (2–11%) overcounting bias at the main-stem dams (Boggs et al. 2004). However, we found that correlation between dam counts at Lower Granite, which has a bias of no more than 2%, with Ice Harbor, which has a maximum bias of 11%, was extremely high (Spearman $r > 0.992$).

There also appears to be high variability over time in the wild portion of the adult return to the dams and associated redd densities in the 34 spawning areas (Figure 4). In addition, the redd counts, estimated independently from the dam counts, are highly correlated with the wild adult spawner estimate at the uppermost dam (Spearman $r = 0.946$). As one might expect, since the redd counts are an index of a subset of the adult spawning population, the correlation is not quite as strong as the correlations among the dam counts of adult spawners, but the correlation again suggests that the high variability in the abundance over time is a real phenomenon rather than an artifact of measurement error.

The results from the application of the three models (Ricker, Dennis, and state-space) to the estimates of wild adults at the uppermost dam and the seven index stocks are shown in Table 2. The stochastic growth rate, μ , for both the Dennis model and the state-space model are negative for all eight populations, indicating declining numbers of adult spawners for the 20-year period. Similarly, the Ricker a parameter is negative for all populations, suggesting that, on average, the stocks did not replace themselves. The state-space model is the only model that attempts to estimate both environmental variation (Q) and measurement error (H). In all eight cases measurement error is estimated to be substantially higher than environmental variation. For the counts of adult spawners at the dams, commonly accepted to be the most accurate of the time series we used, the state-space model suggests that measurement error of 0.18 is three times higher than environmental variation, which is estimated at 0.0596. The most extreme example of this is for the Poverty Flat index population where environmental variation is estimated to be zero with all the variation accounted for as measurement error (Table 2).

Figures 5–7 display model projections and actual abundance for an illustrative subset of the eight

TABLE 2.—Estimated parameters for the three population viability analysis models with data from 1962 to 1981.

Population	Model							
	Ricker			Dennis		State-space		
	<i>a</i>	<i>b</i>	σ^2	μ	σ^2	μ	<i>Q</i>	<i>H</i>
Wild adults at uppermost dam	−0.2146	$−4.48 \times 10^{-6}$	0.6631	−0.094	0.4009	−0.099	0.0596	0.1845
Index stocks								
Minam	0.5211	−0.0019	0.9977	−0.143	0.634	−0.137	0.0919	0.2387
Imnaha	0.6168	−0.0007	0.5767	−0.048	0.5055	−0.055	0.0853	0.2032
Poverty Flat	0.0412	−0.0006	0.5631	−0.138	0.2441	−0.148	0	0.1055
Johnson Creek	0.1339	−0.0014	0.7417	−0.099	0.377	−0.107	0.044	0.1621
Marsh Creek	−0.1915	−0.0006	1.3802	−0.077	0.8975	−0.122	0.1	0.3914
Sulphur Creek	0.0368	−0.0015	2.1915	−0.105	1.3107	−0.125	0.2131	0.521
Bear Valley–Elk Creek	−0.4608	−0.0001	0.8982	−0.126	0.6208	−0.148	0.0409	0.2753

populations: wild fish at the uppermost dam, Bear Valley, and Sulfur Creek. The numerical model results have several consequences for the model predictions. The Ricker model underpredicts the 2003 returns of wild adult spawners at the uppermost dam, with lower and upper bounds of 1,400 and 24,000 wild adults (Figure 5a). The Dennis model predictions have a lower 5% bound of 11 adults by 2003 and an upper 95% bound of approximately 90,000 adults, which is about 50% more wild adults than have returned to the Snake River basin since ICH was completed in 1962 (Figure 5b). The state-space model, on the other hand, predicts a steady decline in wild adult spawners such that predicted returns for 2003 are between 150 and 9,000 adults, while actual returns were approximately 35,000 (Figure 5c).

Model results for the Bear Valley–Elk Creek spring–summer-run Chinook salmon index population are broadly similar to those for wild adults at the uppermost dam. For the Ricker model (Figure 6a) the upper and lower bounds do bracket the actual values with the predicted upper bound always being below the maximum observed values from the early 1960s. The Dennis model (Figure 6b) predicts redd density of between 0 and 40 redds/km, with the upper bound more than twice the observed maximum redd density of 18 redds/km in 1963. The state-space model again underpredicts observed redd density with the upper bound being too low by a factor of 10 (Figure 6c).

Application of the models to the Sulfur Creek spring–summer-run Chinook salmon index population shows the Ricker model's upper bounds are much higher than any observed values (Figure 7a). Very wide upper and lower bounds are apparent for the Dennis model (Figure 7b), the upper bound ($>1,000$ redds/km) being more than 30 times the maximum observed (28 redds/km in 1966). The state-space model again underpredicts recent redd density (Figure 7c).

Discussion

Measurement error, in both the commonsense use (e.g., five fish were counted when 10 were present) and in the more technical senses defined earlier, can be problematic for measuring Pacific salmon populations. However, the results suggest that it is not the primary cause of high variability in estimates of Pacific salmon population abundance. The result contradicts findings for other species where estimates of environmental variance are usually small compared with sampling error variance (Holmes 2001). This genuinely high variability, in turn, limits the utility of these types of models to predict the future. Furthermore, the results suggest that more accurate or complete measurements of population abundance are unlikely to reduce the variation in abundance estimates. High variation in abundance, in turn, results in very wide bounds on model predictions of future abundance.

Therefore, fishery managers should treat the predictions made by PVA models with caution. For the stocks analyzed here the predictions are either misleading (as with the state-space predictions for the wild spring–summer-run Chinook salmon adults at the uppermost dam) or are so broad as to be useless. For example, for the Sulfur Creek index population the Dennis model predicts that the stock will either decrease to zero or increase to levels many times higher than have ever been observed. At least on the face of it, one does not really need a model to make this conclusion. The state-space model often underpredicted returns, attributing what appears to be real (environmental) variation to measurement error. Furthermore, although the Ricker model, using additional data on age at return of adult spawners, performed somewhat better than the Dennis or state-space models, its predictions were also very broad. These results occurred despite our having used 20 years of data to calibrate the models—substantially more than is available for many ESA-listed stocks of Pacific salmon

5a.—Ricker model

5b.—Dennis model

5c.—State-space model

FIGURE 5.—Number of wild spring–summer-run Chinook salmon spawners that passed the uppermost Snake River dam, as estimated by the (a) Ricker, (b) Dennis, and (c) state-space models. The lines represent the observed values and the 5th and 95th percentiles of the model estimates.

6a.—Ricker model

6b.—Dennis model

6c.—State-space model

FIGURE 6.—Model results for the Bear Valley–Elk Creek index stock. Panel (a) shows the number of wild spring–summer-run Chinook salmon spawners as estimated by the Ricker model; panels (b) and (c) show the number of redds per kilometer as estimated by the Dennis and state-space models, respectively. The lines represent the observed values and the 5th and 95th percentiles of the model estimates.

7a.—Ricker model

7b.—Dennis model

7c.— State-space model

FIGURE 7.—Model results for the Sulfur Creek index stock (see Figure 6 for additional details).

(NOAA BRT 2003). Predictions using dam count data were not systematically tighter than those using redds or recruits per spawner despite the fact that dam counts have fewer potential sources of measurement error. These problems can also occur with healthy stocks: application of the Dennis and state-space models to spring Chinook salmon in the John Day basin, Oregon, resulted in very broad projections for the Dennis model and misattribution of variance to measurement error for the state space model.

What can be done to address these problems? First, we do not believe that state-space estimation techniques (or any other techniques known to us) applied to PVA are very useful for determining the extent of measurement error in time series of Pacific salmon abundance. If one needs to know precisely how many fish return to spawn (for example, as a means of detecting the effects of management actions on survival rates), then one must make more precise and accurate measurements rather than concocting more sophisticated (and more complicated) models. The trade-off, of course, is that more accurate methods (e.g., enumeration of adult spawners at weirs, repeated redd counts of entire spawning areas, using mark-recapture techniques) are more costly than less accurate methods, such as walking or flying an index area once to count redds.

Second, we strongly suspect that the high variability in the abundance of Pacific salmon populations will almost always preclude making accurate long-term predictions of abundance. We can think of only one exception. If one can both establish a strong correlation between abundance and some other factors (e.g., ocean conditions; Zabel et al. 2006) and accurately predict the values of those factors into the future, then it may be possible to make accurate long-term predictions. However, predicting changes in climate or other environmental covariates over several decades is, at best, very difficult. While harvest and other anthropogenic factors (e.g., dams, tributary habitat degradation) are obvious problems for the stocks analyzed here and for many other Pacific salmon stocks, changes in anthropogenic factors are unlikely to be the sole cause of either the general decline of ESA-listed stocks through the mid-1990s or the recent (post-2000) increases in adult spawner abundance. Application of much more complex models (e.g., Marmorek and Peters 1998), which explicitly incorporate harvest, hydrosystem, climate, and other effects, have very broad bounds on their population projections. Adding model complexity seems unlikely to reduce uncertainty in projections of abundance.

Rather than trying to predict future spawner abundance, it may be more useful to emphasize the development of data and analytical methods to assess

the effects of human actions (beneficial or otherwise) on salmon life stage survival and productivity. Recent analyses on this topic for these stocks have demonstrated that this is possible (e.g., Paulsen and Fisher 2005; Williams et al. 2005). Given that most human actions—with the significant exception of marine harvest—occur in freshwater environments, their effects are at least potentially monitorable using well-established technologies. These include use of passive integrated transponder (PIT) tags to estimate survival rates, operating juvenile migrant traps to estimate changes in juvenile production, and weirs to make accurate estimates of spawner abundance. This approach is preferable to making untenable predictions about the future trajectories of highly variable salmon stocks.

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Appendix 1: Chinook Salmon Data Used for Model Analyses

TABLE A.1.—Adult spring–summer–run Chinook salmon counted at the four Snake River main-stem dams, estimated wild adults at the uppermost dam, redds per kilometer above Lower Granite dam (excluding the Clearwater basin), age-3 to age-5 returns and recruits to the uppermost dam (no count data were available for Little Goose dam from 1982 to 1990).

Year	Total adults by dam				Wild adults at uppermost dam	Redds/km	Returns			Age 4–5 recruits
	Ice Harbor	Lower Monumental	Little Goose	Lower Granite			Age 3	Age 4	Age 5	
1962	64,252				64,252	9.57	3,969	29,436	34,816	60,810
1963	47,653				47,653	8.45	8,704	17,401	30,252	49,890
1964	44,699				43,746	9.42	4,246	26,427	17,319	52,697
1965	21,894				21,089	5.56	4,320	12,044	9,044	63,682
1966	54,518				52,264	8.72	6,789	28,006	24,258	36,209
1967	57,724				56,143	8.93	6,543	23,339	32,804	48,543
1968	63,021				57,125	8.18	6,296	30,574	26,551	38,973
1969	76,907	68,274			64,089	5.91	4,790	41,965	22,123	24,239
1970	61,289	58,881	54,402		45,734	6.33	2,836	24,017	21,717	23,495
1971	52,397	47,800	43,168		38,308	5.80	4,500	26,116	12,192	9,632
1972	68,541	62,150	57,102		38,073	7.20	1,519	15,646	22,427	18,743
1973	70,384	71,326	63,711		38,788	7.92	746	15,461	23,327	56,498
1974	27,738	26,197	23,060		18,344	3.70	562	9,566	8,778	6,790
1975	27,344	27,713	23,676	23,722	17,776	3.97	152	3,847	13,929	4,290
1976	27,719	25,480	24,065	22,885	14,483	2.48	1,230	8,697	5,785	8,938
1977	51,898	44,990	45,187	43,913	29,128	3.48	899	19,082	10,046	11,384
1978	59,253	55,344	54,424	52,362	40,978	8.28	15	3,562	37,416	14,077
1979	10,259	8,825	9,980	9,467	5,287	1.49	401	2,025	3,228	5,692
1980	10,628	8,101	8,333	8,148	5,882	0.76	442	3,868	2,265	7,703
1981	18,908	17,295	16,724	16,441	10,680	2.00	606	6,169	5,070	11,236
1982	18,506	19,089		16,577	10,648	1.41	628	6,077	5,215	10,352
1983	16,510	16,639		13,412	9,400	1.87	253	1,965	8,000	15,568
1984	13,624	14,393		11,940	7,428	1.62	421	3,927	3,727	4,449
1985	35,360	31,657		30,145	7,941	2.27	298	5,046	3,776	5,667
1986	45,021	43,570		37,730	9,579	2.26	555	5,098	6,190	7,935
1987	37,835	36,714		34,726	9,738	3.25	184	5,715	5,254	6,278
1988	40,778	39,716		35,640	10,388	3.92	200	1,687	9,853	15,832
1989	18,829	19,656		16,124	5,328	1.17	371	2,786	2,762	3,085
1990	26,142	25,342		22,408	6,558	1.47	80	4,045	2,881	873
1991	14,874	12,868	10,563	10,432	5,173	1.26	286	1,517	3,890	1,310
1992	29,394	26,793	24,372	24,405	11,575	1.81	346	6,704	4,761	5,386
1993	31,513	31,475	30,400	28,924	9,953	3.01	109	1,696	9,128	11,999
1994	4,340	4,513	4,006	3,915	1,599	0.59	13	332	1,389	2,861
1995	2,257	2,533	2,098	1,799	1,088	0.29	109	621	541	
1996	9,250	9,107	8,379	6,814	3,274	0.76	215	2,784	689	
1997	50,594	47,632	47,246	44,564	7,263	1.72	136	4,957	2,602	
1998	17,907	14,888	14,810	14,208	8,002	1.65	198	1,295	7,042	
1999	14,602	7,296	6,718	6,556	2,688	0.91	398	1,866	1,566	
2000	43,048	40,200	38,628	37,755	7,333	2.12				
2001	186,443	200,074	190,752	185,693	28,951	4.64				
2002	111,814	100,048	98,086	97,184	37,696	5.49				
2003	98,912	89,321	83,357	87,031	34,699	5.40				

Appendix 2: Data Sources

Snake River Spring–Summer-Run Chinook Salmon Dam Counts

Chinook salmon are counted at the four main-stem Snake River dams as they ascend the river to spawn (USACE 2005). The fish are counted by trained observers at viewing windows in the fish ladders daily from April 1 to October 31 (0400–2000 hours) and recorded on video from April 1 to December 15 (0000–2400 hours; counting methods, dates, and times varied until 2002; USACE 2003). Chinook salmon are assigned to a run (spring, summer, or fall) based on dates that vary by dam (e.g., at Lower Granite Dam, spring = March 1–June 17, summer = June 18–August

17, and fall = August 18–December 15). Adult Chinook salmon (ages 4–5) are identified at the dams as those fish that are greater than 560 mm total length (Columbia River DART 2005). The dam counts are the total numbers of adult spring and summer Chinook salmon (wild- and hatchery-origin adults combined; Table 3 A.1).

Snake River Wild Spring–Summer-Run Chinook Salmon Escapement and Recruits

The estimated escapement of wild-origin adult spring–summer-run Chinook salmon above the uppermost dam on the Snake River was obtained from three

TABLE A.2.—Snake River spring–summer-run Chinook salmon index stocks: estimated spawners, recruits, and redds per kilometer.

Brood year	Minam			Imnaha			Poverty Flat			Johnson		
	Adult spawners	Total recruits	Redds per km	Adult spawners	Total recruits	Redds per km	Adult spawners	Total recruits	Redds per km	Adult spawners	Total recruits	Redds per km
1962	902	572	9.0	1,136	759	15.1	2,291	1,756	41.6	562	635	63.0
1963	512	350	4.8	528	1,489	8.1	1,546	1,040	33.3	466	436	56.8
1964	652	439	7.7	1,147	1,035	15.2	1,385	893	24.6	664	422	66.2
1965	601	660	6.7	863	1,335	11.5	511	1,473	16.1	134	619	24.8
1966	550	581	6.4	939	937	13.6	1,279	775	23.3	202	380	23.5
1967	212	624	2.5	1,007	2,274	13.1	1,017	747	20.8	637	565	61.1
1968	410	496	5.1	1,149	2,446	14.7	401	1,075	11.8	235	789	27.1
1969	627	505	8.2	1,399	1,333	18.4	904	477	15.9	593	325	58.3
1970	616	488	8.1	849	1,169	10.7	774	356	13.7	253	308	27.8
1971	406	169	5.3	1,588	423	22.3	469	276	8.1	411	166	39.1
1972	611	294	6.9	1,600	536	20.5	717	143	11.8	533	74	47.0
1973	461	698	5.6	2,507	2,373	31.7	884	645	14.0	652	434	57.9
1974	380	179	3.2	1,335	211	16.9	224	101	3.5	261	80	22.8
1975	299	41	2.8	718	208	9.1	284	55	4.6	173	23	14.7
1976	281	48	2.2	612	335	7.7	184	254	5.0	161	123	14.5
1977	165	71	1.0	689	532	8.7	290	234	4.4	198	112	17.3
1978	730	164	5.8	2,001	530	25.3	293	386	4.3	284	175	24.1
1979	40	50	0.6	238	558	3.2	76	162	1.5	66	39	7.7
1980	43	220	0.4	183	520	2.4	163	324	2.7	55	136	5.1
1981	50	538	0.6	453	615	6.0	187	367	3.0	102	158	9.6
1982	104	195	0.9	590	476	7.9	192	264	2.8	93	136	7.9
1983	103	492	0.9	435	593	5.8	337	1,118	5.0	152	391	13.5
1984	101	160	1.0	557	141	7.2	220	229	3.8	36	113	3.6
1985	625	189	4.9	699	111	8.8	341	262	5.6	178	94	16.0
1986	357	179	2.9	479	122	3.6	233	744	4.0	129	208	11.3
1987	569	58	4.8	448	52	3.1	554	430	8.4	175	106	15.4
1988	493	116	4.4	606	351	4.0	844	943	12.5	332	442	29.3
1989	197	54	1.7	203	118	1.3	261	285	4.2	103	90	9.0
1990	331	18	3.1	173	49	1.6	572	69	8.4	141	17	12.0
1991	189	21	2.3	251	39	2.0	538	92	8.5	151	29	13.7
1992	102	229	3.7	363	191	3.9	578	201	8.5	180	140	16.2
1993	267	208	3.7	1,178	151	8.8	866	456	12.8	357	253	30.3
1994	22	72	1.0	115	54	2.0	209	97	3.1	50	31	4.3
1995	97		1.1	81		1.3	81		1.3	20		1.9
1996	219		2.7	135		2.4	135		2.4	49		4.9
1997	474		4.7	363		5.3	363		5.3	236		20.1
1998	159		3.0	396		6.0	396		6.0	119		10.2
1999	282		3.6	153		2.6	153		2.6	49		4.9
2000			4.9			5.1			5.1			5.3
2001			11.4			12.6			12.6			37.8
2002			21.3			10.7			10.7			39.3
2003			15.2			12.5			12.5			66.6
2004			9.7			9.2			9.2			37.8

sources. (The uppermost dam changed during the period of interest as new projects were added; it was Ice Harbor in 1961–1968, Lower Monumental in 1969, Little Goose in 1970–1974, and Lower Granite from 1975 on; see www.cbr.washington.edu/crisp/hydro/.) Escapement for the years 1962–1978 was obtained from Petrosky et al. (2001; Table 1, column entitled “Upper Dam Wild”) Escapement for the years 1979–2001 was obtained from S. Kiefer, Idaho Department of Fish and Game (IDFG), Boise. Petrosky et al. (2001) used dam counts to derive wild spring–summer-run Chinook salmon spawner estimates for the years 1962–1999. Estimated escapement for the years 2002–2003 was obtained from S. Kiefer. The wild component was

estimated by subtracting the tributary harvest of hatchery fish and the total run size from the combined wild and hatchery dam count before 2000 (see Petrosky et al. 2001) and estimated from analysis of fin-ray growth patterns from fish sampled at Lower Granite Dam thereafter (see Kiefer et al. 2004 for the general methods used). The methods used were identical to those used for the figure in NOAA BRT (2003). Although the methods used in NOAA BRT (2003) were not specified, we assume that they are similar to those used in Petrosky et al. (2001) since the wild adult escapement estimates are very similar in years in which data are available from both sources (1979–1999).

Age-4–5 adult recruits from wild adults at the

TABLE A.2.—Extended.

Brood year	Bear Valley–Elk			Marsh			Sulphur		
	Adult spawners	Total recruits	Redds per km	Adult spawners	Total recruits	Redds per km	Adult spawners	Total recruits	Redds per km
1962	1,574	1,885	23.8	604	1,255	9.7	409	869	10.3
1963	1,936	1,337	29.2	651	675	10.6	611	594	18.5
1964	1,716	1,568	26.2	1,259	691	20.2	179	887	6.5
1965	838	1,527	13.2	686	783	12.4	101	780	4.2
1966	1,851	618	27.7	724	561	11.6	845	471	28.6
1967	1,439	682	22.7	1,099	558	18.6	724	451	27.0
1968	1,820	1,625	27.7	830	1,013	13.3	725	587	28.6
1969	1,198	384	18.5	390	329	8.0	731	200	27.8
1970	1,123	781	16.7	829	467	16.3	508	347	18.8
1971	476	257	7.4	490	87	10.1	331	88	11.7
1972	761	155	11.3	555	80	11.2	425	28	14.3
1973	1,371	1,001	20.0	934	609	18.6	477	418	15.7
1974	420	216	6.2	382	92	7.5	181	94	6.1
1975	698	52	10.1	358	17	7.2	305	15	10.1
1976	217	77	3.6	76	56	1.7	75	25	2.8
1977	385	145	5.6	178	118	3.5	30	38	1.0
1978	711	174	10.3	491	70	9.7	394	47	12.9
1979	215	112	3.1	83	73	1.7	90	8	3.0
1980	42	260	0.6	16	178	0.3	12	44	0.4
1981	151	248	2.2	115	199	2.3	43	300	1.4
1982	83	413	1.3	71	228	1.4	17	150	0.6
1983	171	1,210	2.5	60	484	1.2	49	615	1.6
1984	137	89	2.1	100	60	2.1	0		0.0
1985	295	146	4.2	196	86	3.9	62	116	2.0
1986	224	229	3.4	171	102	3.8	385	252	13.1
1987	456	153	6.6	268	56	5.6	67	42	2.2
1988	1,109	715	16.1	395	274	8.1	607	261	20.0
1989	91	75	1.3	80	25	1.6	43	17	1.6
1990	185	18	2.7	101	4	2.1	170	4	3.6
1991	181	18	2.6	72	5	1.5	213	7	4.8
1992	173	138	2.6	114	61	2.4	21	36	0.0
1993	709	502	10.2	216	226	4.7	263	164	7.3
1994	33	43	0.5	9	3	0.2	0	0	0.0
1995	16		0.1	0		0.0	4		0.2
1996	56		0.5	18		0.4	23		0.8
1997	225		2.0	110		2.3	43		0.4
1998	372		3.4	164		3.4	140		4.4
1999	72		0.7	0		0.0	0		0.0
2000			2.8			1.3			0.4
2001			6.4			7.3			0.4
2002			10.1			7.0			9.9
2003			11.3			12.6			8.5
2004			2.9			1.0			1.4

uppermost dam were calculated from Petrosky et al. 2001; Table 4. A.1). The seven Snake River spring–summer-run Chinook salmon index stocks used in this analysis are thought to have the most complete and accurate counts and to have minimal spawning by straying hatchery fish (Beamesderfer et al. 1997). Typically, the counts have been done in index areas, a subset of the entire spawning reach used by spring–summer-run Chinook salmon, and the index area counts are expanded to the entire spawning area based on the proportion of each spawning reach sampled (Schaller et al. 1999). They are expanded further from redds to spawners based on estimates of sex ratios and of prespawning mortality derived from recoveries of female carcasses with substantial numbers of unspawned eggs. This yields estimates of the total spawning population for each index stream and year. Ages of the spawners are based on body size and scale sample analysis on carcasses recovered during the surveys. After each group of recruits is assigned to its appropriate parent group (e.g., age-5 recruits in year t are the progeny of brood year $t - 5$), summing over age-classes for each brood yields the total recruits for a brood year.

Snake River Basin Redds per Kilometer

Redd counts of spring–summer-run Chinook salmon spawning above Lower Granite Dam were obtained from Oregon Department of Fish and Wildlife (ODFW) spawning survey reports from 1962 to 2003 (generally available as photocopies from the Grande Ronde Watershed District Office; ODFW 2004), tribal fisheries departments from about 1990 to 2003 (Nez Perce and Shoshone-Bannock Tribes; most contained in Lutch et al. 2003; 2003 counts and transect details

for 1990–2002 from various tribal reports), and IDFG from 1962 to 2003 (IDFG 2005). Chinook salmon redds were counted either from fixed-wing aircraft or helicopters or by surveyors on foot in established river segments (transects). Most transects are counted multiple times over the course of a spawning season, and most surveys identified the total new redds counted during each survey; however, some only identified peak redds over all the surveys in a season.

We used total or peak redds (if the total was not reported) counted from transects that were consistently counted for approximately the last 10 years of the data set (except in cases of limited visibility or restricted access, e.g. forest fires) from 1962 to 2003. We excluded transects that were dropped from long-term monitoring before 2003 or not surveyed for more than about three consecutive years. If multiple surveys were available for a transect (i.e., IDFG and the tribal fisheries departments count many streams independently, and some streams are counted both by air and on foot), we used the more consistently conducted survey (i.e., that with the more consistent starting and ending points and counting in most or all years). The length of streams surveyed (km) was obtained from multiple sources, depending on the starting and ending points. If the survey started at a stream mouth that appears on the 1:100,000-scale U.S. Geological Survey (USGS) topographic maps, we used the river kilometers from the Pacific Northwest River Reach File database (StreamNet 2005). If the starting or ending points were described in some other way, we used stream length measured from 1:24,000 scale USGS topographic maps in electronic format (iGage Mapping Corp. 2005).

Appendix 3: Restricted Maximum Likelihood Model Code

(Available online at DOI:10.1577/T05-300.1.s1)

```
#R-code program to handle REML method
#Author: Richard A. Hinrichsen

#Read in the data
#Example data format:
#Year, Minam, Imnaha, Poverty, Johnson, Bear, Marsh, Sulfur, Upper_dam
#1962,8.9438,15.0745,41.4791,62.8522,14.7774,9.7160,10.3113,64252
#..

redds1.dat<-read.table("Index_stocks.csv",header=T,sep=",")
redds.dat<-redds1.dat[1:20,]

#Likelihood function based on second differences
#of log observations
lf<-function(y,Q,H)
{
  J<-diff(y,differences=2)
```

```

T<-length(y)
SIGW<-make.toep(T,Q,H)
U<-matrix(0,nrow=T-2,ncol=T-1)
for(ii in 1:(T-2)){
  U[ii,(ii:(ii+1))]<-c(-1,1)
}
SIGJ<-U%*%SIGW%*%t(U)
res<- -.5*log(2*pi*det(SIGJ))-.5*t(J)%*%solve(SIGJ)%*%J
return(res)
}

#Function to be maximized using optim()
fn<-function(par,y)
{
  Q<-par[1]
  H<-par[2]
  return(lf(y,Q,H))
}

#Returns the Toeplitz matrix SIGW
#needed for likelihood function lf()
make.toep<-function(T,Q,H)
{
  SIGW<-diag(Q+2*H,T-1)
  for(ii in 1:(T-2))
  {
    SIGW[ii,ii+1]<--H
    SIGW[ii+1,ii]<--H
  }
  return(SIGW)
}

#The function that produces the REML estimates
reml<- function(y)
{
  #begin by estimating Q and H from method
  #of moments
  T<-length(y)
  W<-diff(y)
  myacf<-acf(W,plot=F,type="covariance",lag=1)
  H<--myacf$acf[2]
  if(H<0)H<-.001
  Q<-myacf$acf[1]-2.*H
  par<-c(Q,H)
  res<-optim(par=par,fn=fn,
            gr=NULL,
            method="L-BFGS-B",
            lower=0,
            upper=Inf,
            hessian=T,
            control=list(fnscale=-1,trace=1,maxit=5000),
            y=y)
  Q<-res$par[1]
  H<-res$par[2]
  V<-make.toep(T,Q,H)
  VINV<-solve(V)
  E<-matrix(1,ncol=1,nrow=T-1)
  Varmu<-1./t(E)%*%VINV%*%E)
  mu<-Varmu*t(E)%*%VINV%*%W)
  sum.mat<-matrix(NA,nrow=3,ncol=2)
  sum.mat[1,1]<-mu
  sum.mat[2:3,1]<-c(Q,H)
  sum.mat[1,2]<-sqrt(Varmu)

```

```

varmat<--solve(res$hessian)
sum.mat[2:3,2]<-sqrt(diag(varmat))
dimnames(sum.mat)<-list(c("MU","Q","H"),c("Value","Std.Error"))
return(list(res=res,mu=mu,Varmu=Varmu,sum.mat=sum.mat))
}

#Table estimates, including SEs.
#Use SEs with caution because of
#boundary conditions (variances constrained to be nonnegative)
make.all.tables<-function()
{
  mynames<-names(redds.dat)
  n<-dim(redds.dat)[2]
  myappend<-F
  for(ii in 2:n){
    print(mynames[ii])
    y<-log(redds.dat[,ii])
    iii<-!is.na(y)
    y<-y[iii]
    res<-reml(y)$sum.mat
    write(file="reddtable2.csv",x=mynames[ii],append=myappend)
    myappend<-T
    write.table(file="reddtable2.csv",x=res,append=myappend,col.names
               =NA,sep=",")
  }
  return(NULL)
}

```