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Cross Validation of Quasi-extinction Risks from Real Time Series:

An Examination of Diffusion
Approximation Methods

July 2005

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Cross Validation of Quasi-extinction Risks from Real Time Series:

An Examination of Diffusion
Approximation Methods

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Executive Summary

Population viability analysis (PVA) has quickly become a widespread component of conservation planning for at-risk species. However, the quantitative utility of the PVA toolkit remains a strongly contested issue, with recent efforts turning from pure simulation studies to include direct assessments of the predictability of the dynamics of real populations.

To explore further the efficacy of such extinction risk modeling, we employed a cross-validation approach with long-term population censuses from 271 time series representing 46 taxa, most of which were of past or present conservation concern (including 7 populations that actually went extinct). We used diffusion-approximation methods to estimate quasi-extinction risks for each population via two parameter-estimation techniques: the classical Dennis approach and the recently developed Dennis-Holmes approach. The latter technique can partition process error (environmental stochasticity) from nonprocess error (such as observation error).

We found that quasi-extinction modeling that accounted for nonprocess error via the Dennis-Holmes approach more accurately matched realized population minima evident in the time series. Overall diffusion modeling correctly predicted the fraction of populations crossing quasi-extinction thresholds (>0 individuals). We also found little degradation of the predictability of quasi-extinction risks with lengthening prediction time horizons—from 10 to 30 year horizons. At the same time, we found relatively low predictive ability for complete extinction events. With the exception of sockeye salmon, these events appeared to be due to declines that were well outside the normal distribution of year-to-year growth rates (i.e., some anomalous event). For PVAs based on diffusion approximations, these results highlight both shortcomings (such as an absence of case-by-case certainty and the unpredictability of extinction) and successes (the ability to describe well the behavior of a collection of populations and species).

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Introduction

An estimated 1,100–11,500 extinctions occur each year from a multitude of causes, most of which can be traced back to human impacts (Cox 1997). This loss of biodiversity has been called an “extinction crisis” (Soulé 1986), and in response to this crisis ecology has seen a surge of interest in the characterization of population vulnerability. However, biologists trying to develop ways to estimate extinction risks have encountered several logistical roadblocks. Most notably, we have precious few studies that provide long-term data detailing fluctuations in total population counts (Lawton 1996). Most population censuses have been conducted over a relatively short period (e.g., Orell 1989, Pistorius et al. 2000) or have been conducted only intermittently (e.g., Pierson and Turner 1998, Robertson and Jarvis 2000). As a consequence, long-term censuses of complete populations are relatively rare, meaning that conservation biologists must often use relatively short-term data to forecast population fates over longer time spans. Such forecasting has proved challenging because of the difficulties inherent in the accurate estimation of parameters underlying the dynamics of biological populations (Ludwig 1996, Ludwig 1999, Fieberg and Ellner 2000, Holmes 2001, Ellner et al. 2002).

Despite these difficulties, population viability analyses (PVAs) have now become a standard tool in conservation biology, with goals ranging from providing detailed guidance on management actions (Crouse et al. 1987) to simply characterizing the degree or nature of risk faced by populations (Morris et al. 1999, Fagan et al. 2001). Obtaining sufficiently detailed field data to parameterize models of population viability involves a challenging amount of work. Consequently, but unfortunately, for most species and situations, we lack the data required for all but the crudest PVAs. Indeed, it is telling that a recent synthesis found only 21 data sets (19 species) with sufficient data for full PVA assessments (Brook et al. 2000). These data sets, which contained substantial detail on population size- or age-structure, life history, and demography, are far more characteristic of focused efforts by academic researchers than of the cash-strapped monitoring efforts by governmental wildlife agencies and nongovernmental organizations upon which so much modern conservation action depends. Though helpful when available, such detailed demography and basic population biology data are often lacking for species of conservation concern. As a result, any full assessment of the utility of PVAs must examine their performance when faced with less detailed information.

Though still uncommon, long-term studies providing a continuous record of censuses, population counts, or estimates of population size occur more frequently than do in-depth demographic studies. Diffusion approximations (DAs) (e.g., Dennis et al. 1991, Holmes 2001) are one set of techniques that researchers have developed to estimate population vulnerability and extinction risk from limited data. The key to such approaches is the assumption of a simple stochastic exponential growth model and the estimation of the population growth rate and its variability from the year-to-year (or census-to-census) transitions in population size associated with such a model. These parameters, in combination with the most recent known population size, are then used to calculate the probability that a population will decline to extinction within a specified time frame. These models can also be used to discern additional information as well

(Dennis et al. 1991), including profiles of quasi-extinction risk. Such profiles define the probability that a population will decline to each of a series of population sizes, of which extinction, or $N_t=1$, is but one of many potential values of interest (hence, “quasi-extinction”).

Diffusion-approximation models provide a tool for estimating quasi-extinction risk, although such models may be constructed and parameterized in a variety of ways (Dennis et al. 1991, Lande et al. 1998, Engen and Saether 2000, Holmes 2001). One method of assessing the accuracy of DA models is to evaluate their performance in quantifying risk in real populations, as Ludwig (1999), Brook et al. (2000), and Ellner et al. (2002) have done. The general approach taken is a cross-validation analysis in which the first portion of a time series is used for estimating parameters, then the predictions of those parameterized models are evaluated by comparing them to the realized dynamics evident in the remaining portion of the time series. Brook et al. (2000) outlined the utility of applying cross-validation techniques to issues of extinction risk. They concluded that the good agreement between model predictions and realized dynamics evident in the evaluation portion of their time series was a strong endorsement of PVAs as a conservation tool. Ellner et al. (2002) criticized this conclusion, arguing that the results of Brook et al. (2000) fell far short of “predictive accuracy” and instead merely demonstrated an absence of bias in ensemble—rather than species-level—estimates of probabilities of quasi-extinction.

Although one could take issue with Brook et al. (2000) for the inclusion of populations of relatively abundant species such as white-tailed deer (*Odocoileus virginianus*) and domestic sheep (*Ovis aries*) that are very well-studied ecologically but of much less interest from an extinction-risk perspective (Coulson et al. 2001), we find other details of their approach to be problematic. For example, the small size of their data set forced Brook et al. (2000) to combine evaluations of the performance of population viability models over different time frames within the same analysis. Specifically, by examining model performance on the basis of “halves” of time series, Brook et al. (2000) combined extinction risk evaluations spanning only 6 years of data with evaluations spanning 28 years of data. Using half the data to parameterize and the other half to evaluate without regard for differences in time span (and hence variability) represented by those halved data sets complicates overall assessments of model performance. In addition, their method cannot be applied to species with nonoverlapping generations or other complicated life histories; these require a different approach (see Holmes 2001). A third and perhaps most important issue is that the analysis of Brook et al. (2000) involved only one species that actually went extinct. This limitation introduces a potential bias in that the dynamics of populations going extinct may differ from those that decline but do not go extinct. Despite these difficulties, Brook et al. (2000) provided a significant introduction to the issue of assessing the utility of extinction risk models via real data. Using data sets involving fewer species, Ludwig (1996) and Fieberg and Ellner (2000) have also conducted explorations of the utility of extinction risk modeling. These papers contrast with the optimistic conclusions of Brook et al. (2000), arguing that observation error and other uncertainties that plague real data make determinations of extinction risks rather futile exercises. In response to such criticisms, Brook et al. (2002) argue that despite its quantitative weaknesses, PVA remains a useful tool for conservation that is superior to alternative, often ill-formed resource management approaches that neglect potentially valuable data.

In this technical memorandum, we seek to contribute to a resolution of these PVA conflicts in six ways: 1) by using a substantially larger data set of populations, including several that have gone extinct; 2) by placing a greater emphasis on species that are of conservation interest; 3) by using a “sliding window” approach that standardizes the length of time series used in cross validation (instead of halving sets of varying lengths); 4) by contrasting two alternative approaches for parameter estimation (one of which can be used on species with nonoverlapping cohorts); 5) by restricting ourselves to the kinds of data (i.e., time series of counts) that are more typically available from monitoring programs; and 6) by studying the performance of DA techniques for data with high sampling error.

Methods

We conducted extensive literature searches to identify 49 time series of population censuses (representing 43 taxa) containing at least 21 years (20 transitions) of data (Appendix A). Gaps in the sequence of censuses were permissible. For this data set, we included only time series resulting from the application of standardized census techniques that provided an estimate of total size for wild populations. Six of these time series were from populations that were monitored as they actually went extinct. For populations monitored to extinction, we relaxed our restriction on time series length; the shortest such series we found involved an extinction in its 14th year of monitoring. Seven of these 49 time series were also included in the analysis of Brook et al. (2000).

An additional 222 time series (including one extinction) for four salmon species (Chinook, coho, steelhead, and sockeye) were collected from databases maintained by the National Marine Fisheries Service and the Pacific States Marine Fisheries Commission (Appendix B). Many of these time series involved species and stocks of conservation concern (Kareiva et al. 2000). These time series differ from the nonsalmon time series in a number of ways. First, salmon life history is characterized by long delays between birth and reproduction, combined with semelparity by most adults. These traits mean that counts of spawners in one year have no direct relationship with counts the next year. Second, the life history of salmon leads to striking boom-bust cycles in spawner count numbers—cycles that would be reflected to a much lesser degree in a total population count representing an integration of many age classes. Thus the variability in the censused class, spawners, is higher than that in the total population, and spawner variability does not directly reflect the underlying environmental variability affecting the total population's trajectory. Third, salmon data are also plagued by unusually high observation error due not only to human variability, but also to variability in climate and run-timing that affect census accuracy (Hilborn et al. 1999, Dunham et al. 2001). For these reasons, the salmon time series include error structures considerably different than those present in the nonsalmon time series of Appendix A. We have therefore analyzed the two groups separately in order to contrast the accuracy of PVA predictions for data sets with high and low error.

Observation error and cycles linked to age structure or other factors constitute types of “nonprocess” error. Historically, the need to disentangle such nonprocess errors from process errors (i.e, variability extrinsic to the population, such as environmental stochasticity) has represented a major stumbling block to conservation risk assessment and other areas of ecology (e.g., Carpenter et al. 1994, Ludwig 1996, Fieberg and Ellner 2000). To cope with highly corrupted data, Holmes (2001) developed a method to facilitate partitioning of the different error types from population time series. We compare this new method with more traditional DA approaches in our analyses, exploring their relative performance in data sets both with and without substantial nonprocess errors.

Following Brook et al. (2000), we analyzed the time series using a cross-validation approach. We parameterized our extinction risk models from one portion of a time series, the

estimation period, and then evaluated model performance over a subsequent portion, the evaluation period (Figure 1). We altered our methods of handling time series from those of Brook et al. (2000) in several key ways to increase standardization and internal consistency of our comparisons. Rather than halve each time series, we adopted a “sliding window” of 21 or 26 years for the nonsalmon and salmon species, respectively. The difference in window size arose because of the need to filter the time series with high error, as detailed below. The first 11 years (16 years for salmon) in each window was the estimation period and was used to estimate model parameters. We then used the remaining years in the window to evaluate model performance. Note that our approach means that the estimation and evaluation periods of each window were effectively independent, because the only connection between the two fractions was that the final population size during the estimation period became the initial population size during the evaluation period. Sliding windows in which the evaluation period had missing data were excluded from analysis, but windows with missing data in the estimation period were allowed since the parameterization methods could cope with missing census years. To limit disproportionate representation by long time series, we used at most 10 sliding windows (picked at random) from any time series. To increase the independence of windows within a time series, we separated the start years of adjacent windows by at least 5 years (Figure 1). For example, a 1960–1990 time series would be divided into 3 windows: 1960–1980, 1965–1985, 1970–1990.

Estimating Parameters from Time Series of Counts: The Dennis Method

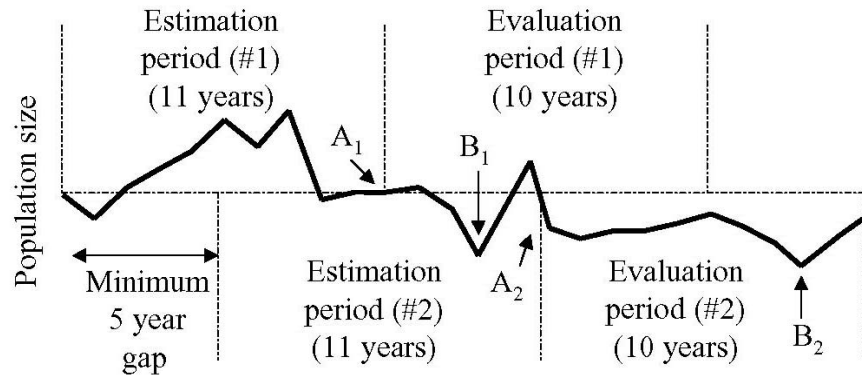
Dennis et al. (1991) present a diffusion approximation approach for estimating extinction risks using time-series data. Diffusion approximations of population data derive from work on stochastic age-structured models (see Tuljapurkar 1982 and Dennis et al. 1991). Theory demonstrates that in the absence of density-dependence, changes in the size of a structured population behave asymptotically according to a stochastic discrete time model:

$$N_{t+\omega} = N_t \exp(\mu \omega + \varepsilon_p), \tag{1}$$

where ε_p is Normal $(0, \sigma_p \sqrt{\omega})$

where N_t is the population size at time t , ω is the time gap between censuses ($\omega = 1$ for annual censuses), μ is the underlying mean year-to-year population growth rate, and σ_p is the standard deviation of the distribution of year-to-year fluctuations in growth rate, termed the process error. Equation 1 can be approximated by a diffusion process; the diffusion process can then be used to estimate the statistical properties of the stochastic trajectories (such as distributions of extinction times, probability of reaching population thresholds, etc.) as a function of μ and σ_p (Tuljapurkar 1982, Lande and Orzack 1988, Dennis et al. 1991). Dennis et al. (1991) discuss parameter estimation for the diffusion model and introduce a new estimation method that allows for missing years in the census time series used for parameterization. With the parameter estimates, a variety of extinction-related metrics can be calculated. One of these metrics, the probability that a population will reach a specified quasi-extinction threshold within a certain time frame, is widely used and forms the basis for our cross-validation analysis. Following prior usage, we refer to the combination of the Dennis et al. (1991) method for estimating parameters combined with DA for estimating risk metrics as the “Dennis method.”

A) Nonsalmon Time Series



B) Salmon Time Series

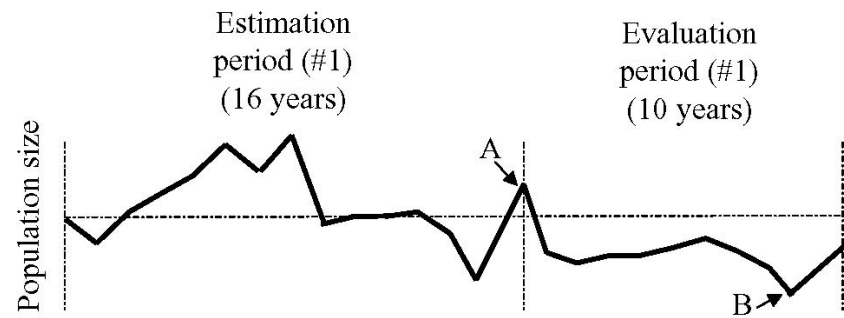


Figure 1. Schematic of a time series of population counts identifying data and population sizes utilized in cross-validation analyses. For nonsalmon time series (A), we used an “estimation period” and an “evaluation period” that were both 11 consecutive years in length (10 consecutive transitions). These two periods together form a “sliding window” that provides a snapshot of the population’s dynamics. Population size A_1 is the initial population size for the first evaluation period, whereas population size B_1 is the minimum population attained during the first evaluation period. In long time series, where it was possible to obtain more than one sliding window, windows were selected at random but always began at least 5 years later than its nearest neighbor (resulting in initial population size A_2 and attained minimum population size B_2). For salmon time series (B), we extended the estimation period to 16 years to accommodate the need to calculate running sums of population size.

Estimating Parameters Using Running Sums: The Dennis-Holmes Method

The Dennis method was developed for population processes of the form of Equation 1 where the true population numbers, N_t , are observed. However, in many cases the observed counts are corrupted to some degree by nonprocess error (such as observation error) and researchers record instead a corrupted count, O_t , of the form:

$$\begin{aligned}
 N_{t+\omega} &= N_t \exp(\mu\omega + \varepsilon_p), \\
 O_t &= \exp(\varepsilon_{np})N_t, \\
 \text{where } \varepsilon_p &\text{ is Normal}(0, \sigma_p \sqrt{\omega}) \\
 \text{and } \varepsilon_{np} &\text{ is } f(\mu_{np}, \sigma_{np})
 \end{aligned}
 \tag{2}$$

where N_t and O_t are the true and observed population numbers, respectively, and ε_p and ε_{np} are the process and nonprocess error respectively. The distribution of ε_{np} is unknown, and it has some unknown mean, μ_{np} , and variance, σ_{np}^2 .

One of the key differences between process and nonprocess error is that the nonprocess error does not feed back into the population process. Thus the variance due to nonprocess error does not grow with time. The most common example of nonprocess error is observation error in the counts themselves. However, other types of variability also act much like the model of Equation 2. For example, when the census includes only an age- or stage-specific subset of the population, the variance in this subset does not necessarily reflect the variance at the population level. Another example occurs when a clear relationship does not exist between the census count one year versus the next year, such as for insects with alternate-year cohorts or for sea-run salmon where the counts of returning adults in a given year are only weakly related to comparable counts the next year. A third common example of nonprocess error occurs when the population age structure has been perturbed, and the population is undergoing damped nonequilibrium cycles.

When nonprocess error is present at high levels within a time series, the Dennis method highly overestimates the process error variance, σ_p^2 (Holmes 2001). To circumvent these problems and generalize the DA approach for cases where nonprocess error is high, an alternative parameter estimation method (Holmes 2001, Holmes and Fagan 2002) was developed that separates process and nonprocess error. The method as presented in Holmes and Fagan (2002) involves an ad hoc running sum transformation of the data that is used to improve parameter estimation when working with the short time series (15–50 years) that are typical for real data. The appendix in Holmes and Fagan (2002) provides a more rigorous statistical discussion, without the transformation, for infinite time series. Tests of the running-sum method using simulated data (Holmes 2001, Hinrichsen 2002, Morris and Doak 2003, Holmes 2004) indicate that it can provide parameter estimates that are relatively unbiased even in the face of high sampling error and relatively short time series.

Here, we merely outline the method’s key features. The reader is referred to previous papers (Holmes 2001, Holmes and Fagan 2002, Holmes 2002) for more in-depth discussions. Central to the method is the translation of a time series of counts into a time series of running sums by adding together several consecutive counts to yield

$$R_t = \sum_{i=1}^L N_{t+i-1} \quad (3)$$

where L is the filter length, and should take values between 3 to 6. We used $L = 4$ for both salmon and nonsalmon time series. For consistency with established usage among salmon conservation biologists, we refer to the application of DA using this method as the “Dennis-Holmes method.” The calculations of the risk metrics are essentially those in Dennis et al. 1991, whereas the parameter estimation methods are those in Holmes and Fagan (2002).

Because they interfere with the calculation of the running sums, missing data (i.e., years with no census) require a different treatment in the Dennis-Holmes method than in the Dennis method. First, we eliminated from consideration all sliding windows in which data for 3 or more consecutive census years were missing. However, if one or two consecutive censuses were missing in the estimation period, the counts for those dates were linearly interpolated. This interpolation constitutes a standard step in the application of the Dennis-Holmes technique (Holmes and Fagan 2002). In contrast, sliding windows with missing data in the evaluation period were always excluded, because the missing data point could have been the population minimum for that window. In all cases, any analyses that compared the Dennis-Holmes and Dennis methods used identical sets of estimation and evaluation periods.

Cross-validating Predicted Declines Against Observations

Our cross-validation analyses addressed whether the predicted probability of reaching a given threshold within the evaluation period matched the frequency of declines actually observed. This probability is similar to the probability of extinction (to 1 individual) except that we instead used a series of quasi-extinction thresholds (xN_0) where N_0 is the population size at the start of the evaluation period and x is a proportion from 0 to 1. Lande and Orzack (1988) and Dennis et al. (1991) give analytical solutions for the probability of crossing a quasi-extinction threshold before some time horizon t . However, these analytical solutions implicitly assume that the time series is observed continuously. For cross-validation purposes we had to adjust these analytical solutions, because the actual time series are only observed at discrete times—generally once a year (Holmes and Fagan 2002).

The Dennis method assumes that nonprocess error variability is minimal and attributes all variability to process error. In contrast, the Dennis-Holmes method assumes that some of the variability is nonprocess error, and partitions the variability between process and nonprocess error. These differences in the treatment of variability engender different predictions concerning the probability of observing quasi-extinction. To the extent that the nonprocess error in the data represents sampling error, the Dennis-Holmes method allows us to contrast the probability of observing quasi-extinction in our corrupted counts with the probability of true quasi-extinction (due to process error alone). When the observations are corrupted by sampling error, the

probability of observing quasi-extinction is greater than the probability of actual quasi-extinction.

Using the estimated probabilities of observing declines, denoted \hat{P}_D and \hat{P}_H (from the Dennis and Dennis-Holmes methods respectively), we compared curves describing the fraction of windows that actually crossed various quasi-extinction thresholds during the evaluation period versus the fraction expected to do so given the estimated probabilities. We calculated the expected fractions by summing the estimated probabilities for all evaluation periods divided by the number of periods, m :

$$\text{expected fraction} = \frac{1}{m} \sum_{i=1}^m \hat{P}_i \quad (4)$$

where \hat{P}_i is the \hat{P}_D or \hat{P}_H estimate for the i -th evaluation period.

Our study included three additional analyses addressing prominent issues in the study of extinction risk. For these comparative analyses, we used only the salmon data set because it had a sufficient number of long time series. First, we explored whether the accuracy of estimated quasi-extinction risks was influenced by the overall trend of the time series. We did this by examining separately those 62 salmon populations with overall declining trends and another 143 salmon populations best described as fluctuating. We characterized those time series with an estimated median rate of growth $1.05 > \exp(\hat{\mu}) > 0.95$ over the entire length of the time series as “fluctuating,” whereas “declining” time series were those with $\exp(\hat{\mu}) < 0.95$. Populations that were generally increasing ($\exp(\hat{\mu}) > 1.05$) were excluded.

Second, to explore how the predictability of quasi-extinction risks degraded over time, we examined whether the bias in the estimated probability of quasi-extinction increased as one projected over longer periods of time. It is well known that the confidence intervals around probability of extinction estimates widen as the projection period increases (Dennis et al. 1991, Fieberg and Ellner 2000). Our analysis looked instead at whether there was a change in the mean tendency to overestimate or underestimate declines. For this analysis, we selected those salmon time series for which 46-year windows were available. These windows were divided into a 16-year estimation period, as before, followed by a 30-year period for evaluation. We compared the predicted versus observed fraction of windows that reached quasi-extinction in the 10, 20, or 30 years after the prediction period. In this way, the same estimation period was used for comparing 10-, 20-, and 30-year evaluation periods.

Third, we expanded our analysis of estimation bias to examine the predictability of severe declines (defined as $\geq 95\%$) and extinctions. To do this, we examined the mean risk estimates for the subset of time series that experienced a severe decline or extinction during the evaluation period. Note that this analysis does not address the accuracy or precision of our probability estimates: that is something we cannot address without knowing the true underlying probabilities of decline (see Discussion section). Instead, this analysis addresses whether these severe events are unpredictable—whether because of the difficulties of estimating parameters for stochastic processes or simply because severe declines happen by chance.

Results

Unbiased Quasi-extinction Estimates

For the nonsalmon time series, with low nonprocess error, parameters estimated via either the Dennis or the Dennis-Holmes approach gave good estimates of the frequency with which thresholds of various magnitudes were observed during the evaluation period (Figure 2). However, for the data with high nonprocess error (the salmon data set) the Dennis method underestimates the frequency of small and moderate declines and overestimates the frequency of large decline (Figure 2). This is the pattern expected when process error is severely overestimated (Holmes and Fagan 2002), as we would expect the Dennis method to do when nonprocess is high. By separating the process and nonprocess error, the Dennis-Holmes method provided an improved match for this data set. The Dennis-Holmes predictions followed the shape of the observed curve more closely, although there was a slight (though uniformly present) underestimation of the observed risk of quasi-extinction. This pattern is suggestive of a slight underestimation of μ .

Analyses of the fluctuating and declining subsets of salmon stocks yielded similar results (Figure 3). In both types of time series, the Dennis method tended to underestimate the frequency of small and moderate declines and overestimate the frequency of large declines, whereas the Dennis-Holmes method more accurately captured the likelihood of both small and large declines. As the duration of the evaluation period was lengthened (Figure 4), we found no evidence that the bias in the predictability of quasi-extinction changed. Note that this is an analysis of bias only, it does not address the variability of the estimates, which theory indicates will increase with lengthened evaluation periods.

Severe Declines and Actual Extinction Events Had Low Predictability

When we examined those time series segments actually exhibiting severe declines during the evaluation period, we found that we would have predicted relatively few of them to experience such declines on the basis of their dynamics during the preceding estimation period. For the trajectories that experienced a 95% decline in the evaluation period, the mean estimated probability of such a decline was only 9% with the Dennis-Holmes method. With the Dennis method, mean probability was 23%, but this method overestimated risks for the salmon data (see Figure 2), from which came the vast majority of our data on severe declines. There was a close correspondence between the Dennis-Holmes estimated probability and the fraction of evaluation periods that actually experienced a 95% decline (also 9%). This suggests that in our data set, the majority of severe declines were low probability events that do occur in populations that are otherwise at low risk. In other words, if the true risk of 95% decline were 9%, we would expect (as we did) that 9% of evaluation periods would experience such decline. Supporting this

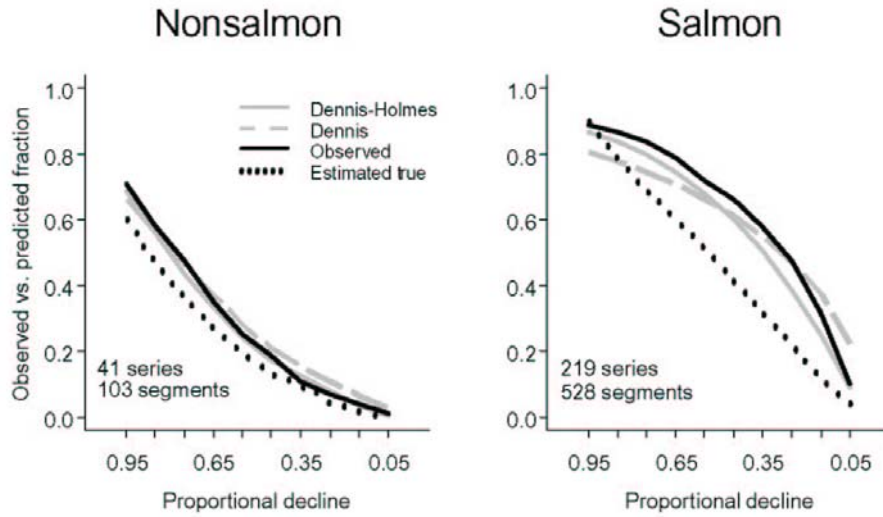


Figure 2. Observed and predicted fraction of trajectories that are observed to reach quasi-extinction thresholds. The evaluation periods were 10 years long for both data sets. The estimation periods were 11 years for the nonsalmon time series and 16 years long for the salmon time series.

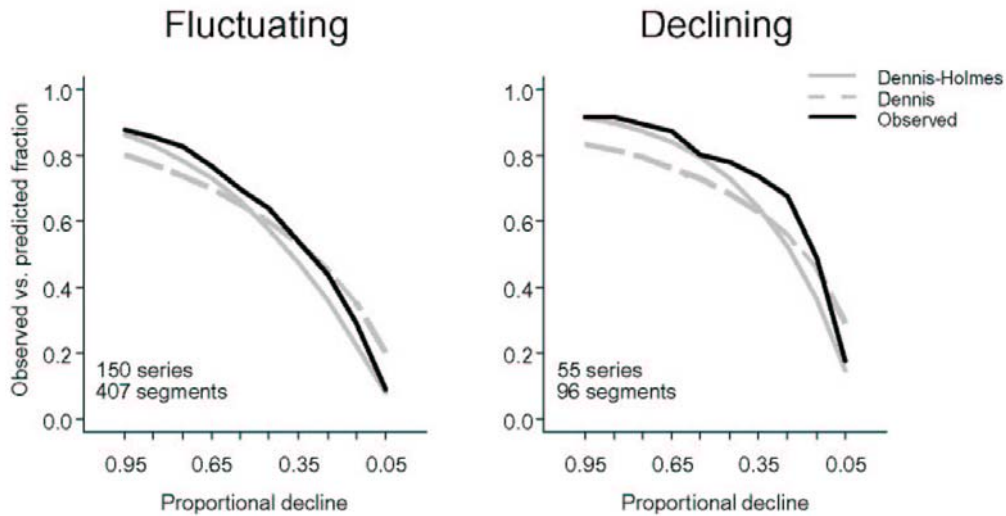


Figure 3. Observed and predicted fraction of trajectories that reach quasi-extinction thresholds for fluctuating versus declining time series from the salmon data set. Fluctuating time series were characterized as having an estimated median rate of growth ($\exp(\hat{\mu})$) between 1.05 and 0.95 over the entire length of the time series. Declining time series were characterized by an estimated median rate of growth of less than 0.95. Windows were 26 years long with a 16-year estimation period and 10-year evaluation period.

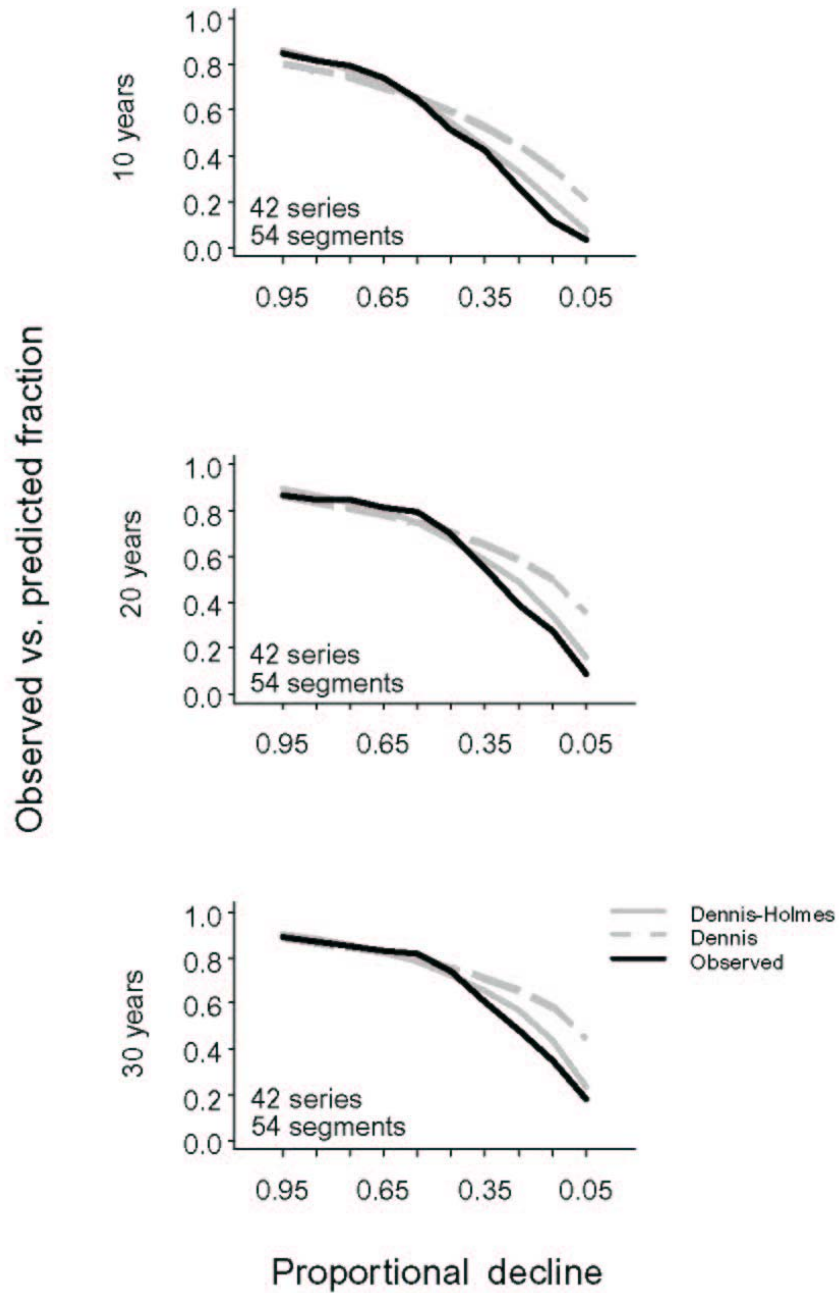


Figure 4. Change in the predictability of population declines as the duration of the evaluation periods was increased. Only those salmon time series with at least 46 years of data were used. For each plot, the same estimation periods were used but the evaluation period was extended from 10 to 20 to 30 years.

interpretation, we found that the yearly declines (the $\ln(N_{t+1}/N_t)$ ratios) of the trajectories which experienced a 95% decline did not have obvious outliers.

Seven of our time series captured actual extinction of a population (six nonsalmon populations plus Snake River sockeye). Like the estimates of severe decline, the estimated probabilities of extinction were very low for all species except sockeye salmon (Table 1). To examine whether the extinctions were outlier events, we examined the $\ln(N_{t+1}/N_t)$ ratios up to and including the extinction events. For all seven populations, the population dynamics were indicative of generally declining (or at least not increasing) populations (Figure 5). For six of the seven, the actual transitions to extinction were characterized by anomalously small $\ln(N_{t+1}/N_t)$ ratios (Figure 5). Since the estimated distribution of $\ln(N_{t+1}/N_t)$ is used to forecast declines, if the extinction event is anomalous, extinction itself will not be predicted based on the information in the estimation period.

Table 1. Estimated probabilities of observing a decline to one individual within the 10-year evaluation period for the populations that actually went extinct during the evaluation period.

Species	Probability of Observing Extinction (Dennis)	Probability of Observing Extinction (Dennis-Holmes)
African wild dogs (<i>Lycaon pictus</i>)	0.103	0
Middle spotted woodpecker (<i>Dendrocopos medius</i>)	0	0
Golden plover (<i>Pluvialis apricaria</i>)	0	0
Wood turtle (ALC) (<i>Clemmys insculpta</i>)	0	0
Wood turtle (BLC)	0	0
Snake River sockeye salmon (<i>Oncorhynchus nerka</i>)	0.33	0.095
Red-cockaded woodpecker (<i>Picoides borealis</i>)	0.002	0

Salmon and Nonsalmon Time Series Differ

Compared with the nonsalmon time series, salmon time series are substantially more variable and more likely to exhibit large percentage declines (Figure 2). The potential for precipitous declines underscores the extensive degree to which salmon data sets contain nonprocess error. The median nonprocess error variance for the salmon windows was 0.35 (with 75% of the estimates between 0.11 and 1.26), compared to a median nonprocess error variance of 0.006 for the nonsalmon windows with (75% of the estimates between 0.0008 and 0.15).

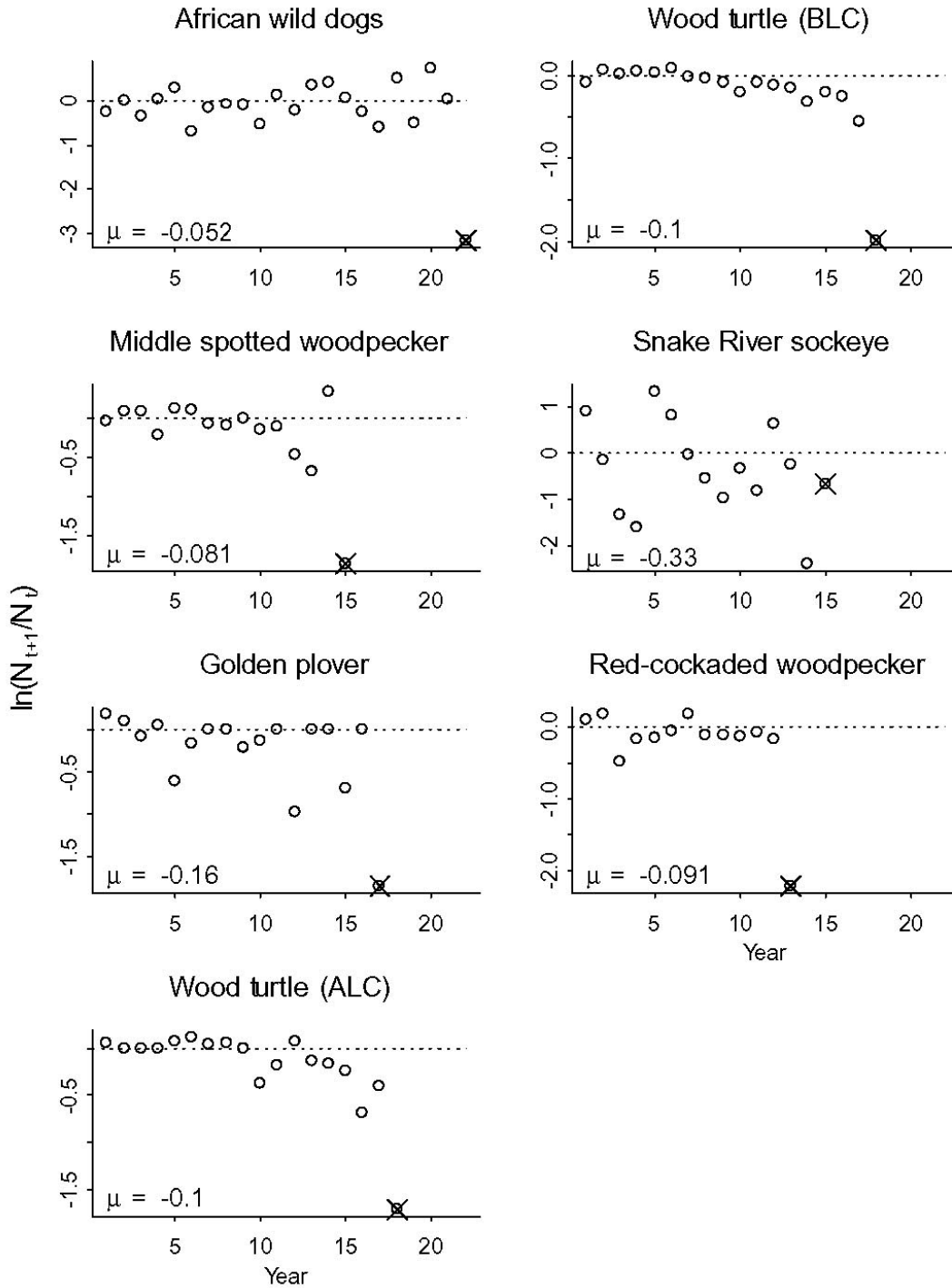


Figure 5. Distribution of $\ln(N_{t+1}/N_t)$ ratios for populations that went extinct. The crossed-through ratios denote the final declines that marked the extinction events. The parameter μ is the underlying mean year-to-year population growth rate from the diffusion approximation.

Discussion

Overall, our cross-validation analysis highlights several key results pertaining to the use of diffusion approximation methods for evaluating population vulnerability. Foremost, the relative matches between the diffusion approximation models and observed declines are a strong endorsement of this general approach to risk assessment. If diffusion approximations were poor descriptors of the underlying population processes, or if our conceptualization of process and nonprocess errors as drivers of population dynamics were inappropriate, this diffusion approximation with two parameters would not have allowed us to recapitulate the collection of population declines as closely as we did (Figure 2). From a practical perspective, this success is especially noteworthy in that we used only count data. This paucity of data, which contrasts strongly with the extensive life history and detailed demography needed for full population viability analyses like those conducted by Brook et al. (2000), is fairly typical of the data limitation facing many species of conservation concern. Consequently, being able to use such limited data to forecast the expected frequency of population declines for a collection of species suggests that diffusion approximation techniques can aid conservation planning at the multispecies/multipopulation level.

Both the Dennis and Dennis-Holmes parameterization methods are useful for predicting risk of decline to quasi-extinction levels, but for different kinds of species and data sets. The Dennis method performed well for time series with low nonprocess error; whereas for time series with high nonprocess error, it tended to underestimate the probability that small declines will be observed and overestimate the probability of large declines. This is the expected pattern if process error variance is overestimated for these data sets and suggests that indeed, because the Dennis method combines nonprocess error and process error variance together, it overestimates the process error variance when nonprocess error is high. In contrast, the Dennis-Holmes method, which separates process and nonprocess error variance, yielded close estimates of the observed declines for the salmon data — but with a tendency toward slight underestimation. Close fits were also observed for the collection of nonsalmon time series with relatively low nonprocess error. It should be noted that our analyses cross-validated the probability of observing a decline. The Dennis-Holmes method makes a distinction between declines due to process error alone versus due to both process error and nonprocess error. To the extent that the nonprocess error represents some type of observation error, this is the distinction between the probability of observing quasi-extinction and the probability of actual quasi-extinction. The Dennis method does not make such a distinction since all variability is attributed to process error. When observation error is high, the difference between the actual versus observed declines is significant (Figure 2, dotted versus solid black lines).

Choosing between the different DA parameterization methods requires some judgment about the level of nonprocess error in the data. In those cases featuring relatively little nonprocess error (e.g., the nonsalmon time series in Appendix A), the Dennis-Holmes method yielded decline curves that closely matched the observed declines across species. However, this is an indication of a lack of bias and it does not address the level of variability in the estimates.

In fact, the Dennis-Holmes parameterization method trades an improvement in bias problems for an increase in the variability of the parameter estimates. Simulations indicate that when the nonprocess error variance is less than the process error variance, the Dennis et al. (1991) parameterization methods will provide tighter—although slightly biased—estimates. But when nonprocess error is high, the biases become severe and trading lack of bias for increased variability is warranted. See Holmes (2002) for a discussion on selecting parameterization methods for a particular population using sensitivity analyses based on age-structured models.

Our analyses looked primarily at whether our probability estimates were biased. It would have been interesting and compelling to examine the precision of the estimated probabilities, \hat{P} , directly using our data set (i.e., to look at the relationship between the estimated and true risks). Unfortunately, this is not possible unless the underlying true parameters of each time series are known (i.e., the true P) or unless it is known that the collection of time series all have very similar, albeit unknown, underlying parameters (i.e., similar P s). Likewise, it is uninformative to look for a relationship between specific estimated risk levels and the frequency of actual declines (i.e., were declines more likely when the estimated risks were higher), even though this appears to be a very natural analysis to do. To do such an analysis in a meaningful way, the true distribution of P (probability of decline) must be known. To see this, suppose that most of our populations have similar true probabilities of decline (we do not know if this is or is not the case), then the observed frequency of decline would be similar (i.e., would be approximately the true P) regardless of the estimated \hat{P} and regardless of the precision of the \hat{P} estimates. Although we could not examine precision with our data set, there is ample evidence that estimates of the probability of extinction (or quasi-extinction) tend to be highly uncertain with wide confidence intervals, particularly when the true probability is intermediate. This has been shown with simulations (Ludwig 1999, Fieberg and Ellner 2000, Ellner et al. 2002) and with calculations of the posterior probability distributions for risk metrics from real data (Holmes 2004).

However, the lack of bias that we observed in DA quasi-extinction probabilities suggests a way to circumvent the uncertainty problem. Rather than trying to attack the variability problem directly, the lack of bias suggests that we can use diffusion approximations to accurately estimate risk within groups rather than on a case-by-case basis. For example, say in a collection of 10 populations, we calculate that the mean probability of 90% decline in 10 years is 0.2. This estimate of the mean probability can be quite precise, since the variability of the mean is $1/\sqrt{10}$ less variable than the individual estimates. This analysis indicates that we should expect 2 of the 10 populations to experience a severe decline in 10 years, although we cannot determine which two. This type of analysis also emphasizes that although mean risk within the collection is low, the probability is high that a few of the populations will experience severe declines.

In contrast to the successes predicting proportional declines, the diffusion approximation model appeared to do poorly at predicting complete extinction events. Examining the population trajectories that experienced complete extinction (zero individuals), we found that both parameterization techniques (Dennis and Dennis-Holmes) appeared to do a distinctly poor job of signaling the real vulnerability of the populations (Table 1). Typically, the extinction-bound species, though declining, were expected to have a less than 1% risk of experiencing the pronounced drops they actually registered. In a collection of 271 time series with a 1% risk of

extinction, we would expect approximately 3 extinctions rather than the 7 in our dataset. This might be explained by arguing that extinctions attract attention and thus were more likely to be documented. However, in six of the seven extinctions, the final extinction event, as reflected in the final N_{t+1}/N_t ratio, was of unusual magnitude (Figure 5) and was outside the normal distribution of year-to-year variability. The one exception was sockeye salmon. For this species, the N_{t+1}/N_t ratio associated with the final extinction event was within the prior range of year-to-year variability. This suggests some kind of anomalous final collapse. Though disconcerting from the perspective of population prediction, such sudden, catastrophic events do mirror our conceptual understanding of the extinction process (Simberloff 1986, Simberloff 1988, Caughley 1994). Given this concept of extinction due to unpredictable catastrophic events, Coulson et al. (2001) have suggested that risk analyses should be used to predict decline to quasi-extinction levels that represent critical population sizes rather than decline to extinction, per se.

For severe declines (95%) rather than complete extinction per se, we found that the N_t to N_{t+1} ratios leading up to and immediately preceding the decline were well within the expected distributions and that the frequency of 95% declines in the data (9%) matched the expected probability from the DA model (also 9%). These observations suggest that the DA model was appropriately modeling the probability of severe decline. However, this did not translate into predictability of severe declines on a case-by-case basis. The mean probability of 95% decline for the windows that experienced a 95% decline was only 9%. These results emphasize that the very nature of stochastic processes means that the future is unpredictable and that severe declines will occur due to chance even when the probability of such events is low. Obviously severe declines will be more common for those populations with higher underlying risks, but if the vast majority of populations are at relatively low risk of severe decline, the majority of severe declines will be observed to come from populations with low risk and thus appear unpredictable. This emphasizes the point that for populations experiencing stochastic growth and decline, low estimated risks, no matter how precise, are not a guarantee that severe declines will not occur—indeed they most certainly will occur for some fraction of populations. Predicting the fraction of populations that will experience a severe decline is possible; determining exactly which populations will experience such severe declines will not generally be possible—except in the case of populations undergoing rapid and drastic declines or populations with very low year-to-year variability.

Overall, the results presented here highlight both successes and shortcomings of PVAs based on diffusion approximations. Clearly, the lack of predictive certainty that these models afford on a case-by-case basis could be construed as a limitation of extinction risk modeling. However, there are lessons to learn from the general patterns that emerge from multipopulation and multispecies analyses for conservation planning (see also Fagan et al. 2001). In the present case, it is worth emphasizing the advantages of being able to describe well the behavior of a collection of populations and species. Conservation biology is increasingly adopting a multipopulation, multispecies perspective, a view that is necessitated both by the increasing numbers of species of conservation concern and by the general need to act quickly to halt or reverse population declines. Often such action must take place in the absence of solid information on each component species, and from a practical perspective, broad brush multispecies conservation efforts may trade off case-by-case certainty for time. Although the knowledge that we will guess right “on average” may provide little solace when particular species or populations fail to persist, we must keep in mind that real population trajectories are

stochastic and by their very nature unpredictable regardless of the sophistication and accuracy of one's models. Taking a multipopulation approach may be the only viable means to achieve predictive power.

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Appendix A

Table A-1. Summary of nonsalmon population time series used in cross-validation analyses.

Species	Type of organism	Location of study population	Number of transitions	Unit of census	References	Minimum population size	Maximum population size
<i>Connochaetes taurinus</i> (Wildebeest)	Mammal	Ngorongoro Crater, Tanzania	21	Total population	Runyoro et al. 1995	6,250	18,500
<i>Ovibos moschatus</i> (Musk ox)	Mammal	Nunivak Island, Alaska	24	Total population	Spencer and Lensink 1970	31	714
<i>Ursus arctos horribilis</i> (Grizzly bear)	Mammal	Yellowstone National Park	28	Adult females	Foley 1994	33	57
<i>Cervus elaphus</i> (Red deer)	Mammal	Isle of Rum, UK	21	Females	Milner-Gulland et al. 2000	34	105
<i>Cervus elaphus</i> (Red deer)	Mammal	Isle of Rum, UK	21	Females	Milner-Gulland et al. 2000	34	61
<i>Canis lupus</i> (Wolves)	Mammal	Isle Royale National Park, Michigan	24	Total population	Peterson et al. 1998	12	50
<i>Panthera leo</i> (Lion)	Mammal	Ngorongoro Crater, Tanzania	22	Total population	Packer et al. 1999	50	109
<i>Telespiza cantans</i> (Laysan finch)	Bird	Laysan Island, Hawaii	24	Total population	Dennis et al. 1991	5,500	20,750
<i>Grus Americana</i> (Whooping crane)	Bird	Aransas, Texas	51	Total population	Dennis et al. 1991	16	145
<i>Parus major</i> (Great tit)	Bird	Wytham Wood, UK	30	Total population	Saether et al. 1998	119	340
<i>Zosterops lateralis chlorocephala</i> (Heron Island silvereye)	Bird	Great Barrier Reef, Australia	25	Total population	Brook and Kikkawa 1998	225	445

Table A-1. Summary of nonsalmon population time series used in cross-validation analyses. Continued.

Species	Type of organism	Location of study population	Number of transitions	Unit of census	References	Minimum population size	Maximum population size
<i>Dendroica kirtlandii</i> (Kirtland's warbler)	Bird	Northern half of Michigan's lower peninsula	22	Singing males	Dennis et al. 1991, Solomon 1998	168	762
<i>Milvus milvus</i> (Red kite)	Bird	Wales	29	Total population	Davis and Newton 1981	24	98
<i>Rostrhamus sociabilis</i> (Snail kite)	Bird	Wetlands in central and southern Florida	25	Total population	Bennetts et al. 1999	30	780
<i>Somateria mollissima</i> (Eider)	Bird	Wadden Sea Coast, Germany	33	Breeding pairs	Becker 1991	40	283
<i>Tympanuchus cupido attwateri</i> (Attwater's prairie chicken)	Bird	Coastal Prairie, Louisiana and Texas	29	Total population	Peterson and Silvy 1996	65	8,730
<i>Ciconia ciconia</i> (White stork)	Bird	Baden-Wurttemberg, Germany	38	Breeding pairs	Newton 1998, Bairlein 1991	16	163
<i>Ciconia ciconia</i> (White stork)	Bird	Oldenburg/NW Germany	60	Breeders	Bairlein 1991	17	274
<i>Fulmarus glacialisoides</i> (Antarctic fulmar)	Bird	Pointe Geologie Archipelago, Adele Land, in Antarctic zone	25	Total population	Jouventin and Weimerskirch 1991	9	50
<i>Sterna dougallii</i> (Roseate terns)	Bird	main colonies in Ireland, Britain, and France	34	Breeding pairs	Cabot 1996	467	3,304
<i>Rana temporaria</i> (European frog)	Amphibian	Bern, Switzerland	27	Spawn clumps	Meyer et al. 1998	382	1,187
<i>Cyprinodon diabolis</i> (Devils Hole pupfish)	Fish	Devils Hole, Nevada	24	Total population	Andersen and Deacon 2001	127	313
<i>Euphydryas editha bayensis</i> (Jasper Ridge checkerspot)	Butterfly	Jasper Ridge, California	26	Females	Nicholls et al. 1996	18	2,000

Table A-1. Summary of nonsalmon population time series used in cross-validation analyses. Continued.

Species	Type of organism	Location of study population	Number of transitions	Unit of census	References	Minimum population size	Maximum population size
<i>Euphydryas editha bayensis</i> (Jasper Ridge checkerspot)	Butterfly	Jasper Ridge, California	26	Females	Nicholls et al. 1996	40	7,227
<i>Ischnura elegans</i> (Blue-tailed damselfly)	Odonate	Woodwalton Fen, Cambridgeshire, UK	26	Male territories	Moore 1991	7	45
<i>Sympetrum striolatum</i> (Common darter)	Odonate	Woodwalton Fen, Cambridgeshire, UK	26	Male territories	Moore 1991	2	19
<i>Coenagrion puella</i> (Azure damselfly)	Odonate	Woodwalton Fen, Cambridgeshire, UK	25	Male territories	Moore 1991	1	204
<i>Lestes sponsa</i> (Emerald damselfly)	Odonate	Woodwalton Fen, Cambridgeshire, UK	24	Male territories	Moore 1991	1	188
<i>Rissa tridactyla</i> (Kittiwake)	Bird	North Shields, Tyne and Wear, UK	33	Nests with eggs	Coulson and Thomas 1985	4	104
<i>Amazona vittata</i> (Puerto Rican parrot)	Bird	Puerto Rico	20	Total population	Dennis et al. 1991, Christian et al. 1996	14	137
<i>Copsychus sechellarum</i> (Seychelles magpie robin)	Bird	Fregate Is, Seychelles	21	Total population	Komdeur 1996	12	70
<i>Eschrichtium robustus</i> (California gray whale)	Mammal	California	23	Total population	Gerber et al. 1999	2,894	26,635
<i>Callorhinus ursinus</i> (Northern fur seal)	Mammal	St. George Island, Alaska	43	Pups	York et al. 2000, York 1985, York and Hartley 1981	20,775	115,250
<i>Callorhinus ursinus</i> (Northern fur seal)	Mammal	St. Paul Island, Alaska	43	Pups	York et al. 2000, York 1985, York and Hartley 1981	165,941	461,000
<i>Callorhinus ursinus</i> (Northern fur seal)	Mammal	San Miguel Island, California	24	Pups	York et al. 2000, York 1985, York and Hartley 1981	200	2,705
<i>Zalophus californianus</i> (California sea lion)	Mammal	California	20	Pups	York et al. 2000, York 1985, York and Hartley 1981	11,485	36,017
<i>Parus atricapillus</i> (Black-capped chickadee)	Bird	Litchfield and Morris, Connecticut	23	Winter population	Loery and Nichols 1985	85	328

Table A-1. Summary of nonsalmon population time series used in cross-validation analyses. Continued.

Species	Type of organism	Location of study population	Number of transitions	Unit of census	References	Minimum population size	Maximum population size
<i>Monachus shauinslandi</i> (Hawaiian monk seal)	Mammal	Hawaiian Islands minus Midway	20	Total population (almost)	Gilmartin and Eberhardt 1995, Ragen and Lavigne 1997	392	917
<i>Accipiter nisus</i> (Northern sparrowhawk)	Bird	Germany	22	Total population	Zollinger and Müskens 1994	2	83
<i>Himantopus mexicanus knudseni</i> (Hawaiian stilt)	Bird	Hawaiian Islands minus Kauai--Niihau	22	Total population (almost)	Reed and Oring 1993	320	1,100
<i>Grus japonensis</i> (Red-crowned crane)	Bird	Hokkaido, Japan	35	Total population	Masatomi 1987	33	365
<i>Loxodonta africana</i> (African elephant)	Mammal	Addo National Park, South Africa	68	Total population	Whitehouse and Hall-Martin 2000	10	280
<i>Melospiza melodia</i> (Song sparrow)	Bird	Mandarte Island, British Columbia	20	Territorial females	Ludwig 1999	4	71
<i>Lycaon pictus</i> (African wild dog)	Mammal	Serengeti Plains, Tanzania	19	Adults + yearlings	Ginsberg et al. 1995	0	77
<i>Dendrocopos medius</i> (Middle spotted woodpecker)	Bird	Southern Sweden	14	Adults	Pettersson 1985	0	25
<i>Pluvialis apricaria</i> (Golden plover)	Bird	Kerloch, NE Scotland	17	Total population	Parr 1992	0	114
<i>Clemmys insculpta</i> (Wood turtle)	Reptile	South-central Connecticut	19	Total population	Garber and Burger 1995	0	51
<i>Clemmys insculpta</i> (Wood turtle)	Reptile	South-central Connecticut	19	Total population	Garber and Burger 1995	0	58
<i>Picoides borealis</i> (Red-cockaded woodpecker)	Bird	Tall Timbers Research Station, Florida	14	Adults	Baker 1983	0	39

Appendix B

Table B-1. Summary of salmon population time series used in cross-validation analyses. StreamNet (2002) refers to the StreamNet identification numbers as of summer 2002.

Species	Evolutionarily significant unit	Stock	StreamNet # or reference	Type of count^a	Length in years
Chinook	California	Merced River (Fall)	61115	tlc	42
Chinook	California	Tuolumne River (Fall)	61116	tlc	50
Chinook	California	Stanislaus River (Fall)	61117	tlc	50
Chinook	California	Cosumnes River (Fall)	61121	tlc	36
Chinook	California	American River (Fall)	61122	tlc	54
Chinook	California	Feather River (Fall)	61123	tlc	44
Chinook	California	Yuba River (Fall)	61129	tlc	44
Chinook	California	Butte Creek (Spring)	61131	tlc	37
Chinook	California	Deer Creek (Fall)	61136	tlc	43
Chinook	California	Mill Creek (Fall)	61137	tlc	47
Chinook	California	Battle Creek (Fall)	90010	tlc	53
Chinook	California	San Joaquin River (Fall)	61118	tlc	42
Chinook	Lower Columbia River	Big Creek (Fall)	57497	rpm	29
Chinook	Lower Columbia River	Clackamas River (Spring)	50312	tlc	52
Chinook	Lower Columbia River	Clackamas River (Fall)	50990	rpm	28
Chinook	Lower Columbia River	Clackamas River N Fork (Fall)	50010	tlc	35
Chinook	Lower Columbia River	Clatskanie River (Fall)	50982	peak	51
Chinook	Lower Columbia River	Cowlitz River (Fall)(tule)	105030	tlc	34
Chinook	Lower Columbia River	Elochoman River (Fall)(tule)	103050	tlc	34
Chinook	Lower Columbia River	Gnat Creek (Fall)	50007	peak	35
Chinook	Lower Columbia River	Kalama River (Fall)(tule)	110050	tlc	34

Table B-1. Summary of salmon population time series used in cross-validation analyses. StreamNet (2002) refers to the StreamNet identification numbers as of summer 2002. Continued.

Species	Evolutionarily significant unit	Stock	StreamNet # or reference	Type of count^a	Length in years
Chinook	Lower Columbia River	Klickitat River (Fall)(tule)	131030	tlc	33
Chinook	Lower Columbia River	Lewis River (Fall)(bright)	113030	tlc	34
Chinook	Lower Columbia River	Lewis River E Fork (Fall)(tule)	113040	tlc	34
Chinook	Lower Columbia River	Plympton Creek (Fall)	50005	peak	35
Chinook	Lower Columbia River	Washougal River (Fall)(tule)	116050	tlc	34
Chinook	Lower Columbia River	White Salmon River (Fall)(tule)	128050	tlc	33
Chinook	Lower Columbia River	Wind River (Fall)(tule)	121002	tlc	34
Chinook	Lower Columbia River	Youngs River (Fall)	50276	peak	51
Chinook	Middle Columbia River (Spring)	American River (Spring)	61466	rpm	30
Chinook	Middle Columbia River (Spring)	Beaver Creek (Spring)	50178	rpm	31
Chinook	Middle Columbia River (Spring)	Bull Run Creek (Spring)	52055	rpm	37
Chinook	Middle Columbia River (Spring)	Clear Creek (Spring)	52054	rpm	40
Chinook	Middle Columbia River (Spring)	Granite Creek (Spring)	52053	rpm	40
Chinook	Middle Columbia River (Spring)	John Day River (Spring)	50148	rpm	40
Chinook	Middle Columbia River (Spring)	John Day River M Fork (Spring)	50167	rpm	40
Chinook	Middle Columbia River (Spring)	John Day River N Fork (Spring)	50158	rpm	35
Chinook	Middle Columbia River (Spring)	Mill Creek (Spring)	50177	rpm	31
Chinook	Middle Columbia River (Spring)	Warm Springs River (Spring)	50175	rpm	31
Chinook	Middle Columbia River (Spring)	Wind River (Spring)	122050	tlc	28
Chinook	Upper Columbia River (Spring)	Chiwack River (Spring)	60044	redds	36
Chinook	Upper Columbia River (Spring)	Chiwawa River (Spring)	60057	rpm	37
Chinook	Upper Columbia River (Spring)	Entiat River (Spring)	NWFSC ^b	tlc	39
Chinook	Upper Columbia River (Spring)	Icicle Creek (Spring)	60063	rpm	31
Chinook	Upper Columbia River (Spring)	Icicle Creek (Spring)	143031	tlc	41
Chinook	Upper Columbia River (Spring)	Icicle Creek (Spring)	60827	peak	37
Chinook	Upper Columbia River (Spring)	Little Wenatchee River (Spring)	60059	rpm	39
Chinook	Upper Columbia River (Spring)	Little Wenatchee River (Spring)	60826	peak	34
Chinook	Upper Columbia River (Spring)	Lost River (Spring)	60046	rpm	36

Table B-1. Summary of salmon population time series used in cross-validation analyses. StreamNet (2002) refers to the StreamNet identification numbers as of summer 2002. Continued.

Species	Evolutionarily significant unit	Stock	StreamNet # or reference	Type of count^a	Length in years
Chinook	Upper Columbia River (Spring)	Methow River (Spring)	NWFSC ^b	tlc	39
Chinook	Upper Columbia River (Spring)	Nason Creek (Spring)	60061	rpm	39
Chinook	Upper Columbia River (Spring)	Twisp River (Spring)	60048	rpm	36
Chinook	Upper Columbia River (Spring)	Wenatchee River (Spring)	NWFSC ^b	tlc	39
Chinook	Upper Columbia River (Spring)	White River (Spring)	60058	redds	39
Chinook	Upper Columbia River (Spring)	White River (Spring)	60825	peak	37
Chinook	Upper Columbia River (Summer/Fall)	Hanford Reach (Fall)	M 1998 ^c	tlc	34
Chinook	Upper Columbia River (Summer/Fall)	Methow River (Summer)	60042	rpm	41
Chinook	Upper Columbia River (Summer/Fall)	Okanogan River (Summer)	60040	rpm	37
Chinook	Upper Columbia River (Summer/Fall)	Similkameen River (Summer)	60041	rpm	40
Chinook	Upper Columbia River (Summer/Fall)	Wenatchee River (Summer)	60055	rpm	41
Chinook	Snake River (Spring/Summer)	Alturas Lake Ck (Spring)	41012	rpm	48
Chinook	Snake River (Spring/Summer)	Bear Creek	B 1998 ^d	tlc	34
Chinook	Snake River (Spring/Summer)	Bear Creek (Clearwater) (Spring)	41068	rpm	29
Chinook	Snake River (Spring/Summer)	Bear Valley Creek (Spring)	41028	rpm	48
Chinook	Snake River (Spring/Summer)	Beaver Creek (Spring)	41036	rpm	46
Chinook	Snake River (Spring/Summer)	Big Creek (Spring)	41044	rpm	40
Chinook	Snake River (Spring/Summer)	Big Creek Upper	41045	rpm	43
Chinook	Snake River (Spring/Summer)	Big Sheep Creek (Spring)	50121	rpm	34
Chinook	Snake River (Spring/Summer)	Brushy Fork (Spring)	41078	rpm	28
Chinook	Snake River (Spring/Summer)	Camas Creek (Spring)	41048	rpm	46
Chinook	Snake River (Spring/Summer)	Cape Horn Creek (Spring)	41033	rpm	46
Chinook	Snake River (Spring/Summer)	Catherine Creek (Spring)	54594	rpm	41
Chinook	Snake River (Spring/Summer)	Catherine Creek N Fork (Spring)	57510	rpm	31
Chinook	Snake River (Spring/Summer)	Catherine Creek S Fork (Spring)	57511	rpm	31
Chinook	Snake River (Spring/Summer)	Crooked Fork (Spring)	41076	rpm	31
Chinook	Snake River (Spring/Summer)	Elk Creek (Spring)	41030	rpm	48
Chinook	Snake River (Spring/Summer)	Grande Ronde River (Spring)	57512	redds	38

Table B-1. Summary of salmon population time series used in cross-validation analyses. StreamNet (2002) refers to the StreamNet identification numbers as of summer 2002. Continued.

Species	Evolutionarily significant unit	Stock	StreamNet # or reference	Type of count^a	Length in years
Chinook	Snake River (Spring/Summer)	Hayden Creek (Summer)	41024	rpm	27
Chinook	Snake River (Spring/Summer)	Herd Creek (Summer)	41018	rpm	29
Chinook	Snake River (Spring/Summer)	Imnaha River (Spring)	B 1998 ^d	tlc	47
Chinook	Snake River (Spring/Summer)	Imnaha River (Spring)	50124	rpm	49
Chinook	Snake River (Spring/Summer)	Johnson Creek (Summer)	B 1998 ^d	tlc	43
Chinook	Snake River (Spring/Summer)	Johnson Creek (Summer)	41060	rpm	46
Chinook	Snake River (Spring/Summer)	Knapp Creek (Spring)	41035	rpm	46
Chinook	Snake River (Spring/Summer)	Lake Creek (Summer)	41059	rpm	46
Chinook	Snake River (Spring/Summer)	Lemhi River (Spring)	41023	rpm	43
Chinook	Snake River (Spring/Summer)	Lookingglass Creek (Spring)	57513	rpm	41
Chinook	Snake River (Spring/Summer)	Loon Creek (Summer)	41038	rpm	43
Chinook	Snake River (Spring/Summer)	Lostine Creek (Spring)	57514	rpm	34
Chinook	Snake River (Spring/Summer)	Lower Salmon River	NWFSC ^b	rpm	43
Chinook	Snake River (Spring/Summer)	Lower Valley Creek	NWFSC ^b	redds	43
Chinook	Snake River (Spring/Summer)	Marsh Creek (Spring)	B 1998 ^d	tlc	43
Chinook	Snake River (Spring/Summer)	Marsh Creek (Spring)	41031	rpm	44
Chinook	Snake River (Spring/Summer)	Minam River (Spring)	B 1998 ^d	tlc	36
Chinook	Snake River (Spring/Summer)	Minam River Upper (Spring)	50074	rpm	34
Chinook	Snake River (Spring/Summer)	Minam River Lower (Spring)	50097	rpm	41
Chinook	Snake River (Spring/Summer)	Moose Creek (Spring)	41071	rpm	28
Chinook	Snake River (Spring/Summer)	Newsome Creek (Spring)	41088	rpm	26
Chinook	Snake River (Spring/Summer)	Poverty Creek	B 1998 ^d	tlc	43
Chinook	Snake River (Spring/Summer)	Red River (Spring)	41084	rpm	26
Chinook	Snake River (Spring/Summer)	Salmon River E Fork (Spring)	41015	rpm	32
Chinook	Snake River (Spring/Summer)	Salmon River E Fork (Summer)	41016	rpm	43
Chinook	Snake River (Spring/Summer)	Salmon River S Fork (Summer)	41056	rpm	43
Chinook	Snake River (Spring/Summer)	Salmon River Upper (Spring)	41001	rpm	43
Chinook	Snake River (Spring/Summer)	Salmon River Upper (Summer)	41002	rpm	41

Table B-1. Summary of salmon population time series used in cross-validation analyses. StreamNet (2002) refers to the StreamNet identification numbers as of summer 2002. Continued.

Species	Evolutionarily significant unit	Stock	StreamNet # or reference	Type of count^a	Length in years
Chinook	Snake River (Spring/Summer)	Secesh River (Summer)	41058	rpm	43
Chinook	Snake River (Spring/Summer)	Selway River (Spring)	41062	rpm	31
Chinook	Snake River (Spring/Summer)	Sulphur Ck (Spring)	B 1998 ^d	tlc	48
Chinook	Snake River (Spring/Summer)	Sulphur Creek (Spring)	41026	rpm	48
Chinook	Snake River (Spring/Summer)	Valley Ck Upper (Spring)	41008	rpm	43
Chinook	Snake River (Spring/Summer)	Valley Ck Upper (Summer)	41009	rpm	46
Chinook	Snake River (Spring/Summer)	Wallowa Creek (Spring)	50119	rpm	35
Chinook	Snake River (Spring/Summer)	Wenaha River S Fork (Spring)	50120	rpm	35
Chinook	Snake River (Spring/Summer)	White Cap Creek (Spring)	41066	rpm	28
Chinook	Snake River (Spring/Summer)	Yankee Fork (Summer)	41005	rpm	38
Chinook	Snake River (Spring/Summer)	Yankee W Fork (Summer)	NWFSC ^b	rpm	38
Chinook	Snake River (Spring/Summer)	Yankee W Fork (Spring)	41006	rpm	38
Chinook	Snake River Basin (Fall)	Snake River Basin	P 1999 ^e	tlc	33
Chinook	Upper Willamette River	McKenzie River above Leaburg Dam	ODFW ^f	tlc	29
Chinook	Upper Willamette River	McKenzie River (Spring)	57319	redds	29
Chinook	Upper Willamette River	Molalla River (Fall)	50999	rpm	28
Chinook	Upper Willamette River	Santiam River S (Fall)	50017	rpm	28
Chinook	Upper Willamette River	Santiam River N (Fall)	50019	rpm	26
Chinook	Upper Willamette River	Willamette River (Fall)	50987	rpm	28
Chinook	Oregon Coast	Bear Creek (Chetco) (Fall)	50568	peak	35
Chinook	Oregon Coast	Buck Creek (Alsea) (Fall)	52076	peak	46
Chinook	Oregon Coast	Clear Creek (Fall)	50445	peak	51
Chinook	Oregon Coast	Coquille River S Fork (Fall)	50541	peak	40
Chinook	Oregon Coast	Coquille River N Fork (Fall)	50549	peak	47
Chinook	Oregon Coast	Coquille River E Fork (Fall)	53494	peak	38
Chinook	Oregon Coast	Coquille River M Fork (Fall)	53498	peak	37
Chinook	Oregon Coast	Cronin Creek (Newhalem) (Fall)	50412	peak	26
Chinook	Oregon Coast	Deep Creek (Chetco) (Fall)	50569	peak	39

Table B-1. Summary of salmon population time series used in cross-validation analyses. StreamNet (2002) refers to the StreamNet identification numbers as of summer 2002. Continued.

Species	Evolutionarily significant unit	Stock	StreamNet # or reference	Type of count^a	Length in years
Chinook	Oregon Coast	Dry Creek (Sixes) (Fall)	53505	peak	32
Chinook	Oregon Coast	Emily Creek (Chetco) (Fall)	53516	peak	28
Chinook	Oregon Coast	Grant Creek (Yaquina) (Fall)	52074	peak	44
Chinook	Oregon Coast	Humbug Creek (Newhalem) (Fall)	50414	peak	49
Chinook	Oregon Coast	Lake Creek (Siuslaw) (Fall)	52078	peak	46
Chinook	Oregon Coast	Middle Creek (Coquille) (Fall)	53492	peak	39
Chinook	Oregon Coast	Millicoma River W Fork (Coos) (Fall)	52080	peak	38
Chinook	Oregon Coast	Moon Creek (Nestucca) (Fall)	50452	peak	26
Chinook	Oregon Coast	Niagara Creek (Nestucca) (Fall)	50570	peak	52
Chinook	Oregon Coast	Siuslaw River N Fork (Fall)	50498	peak	47
Chinook	Oregon Coast	Sunshine Creek (Siletz) (Fall)	50572	peak	47
Chinook	Oregon Coast	Tillamook River (Fall)	50568	peak	47
Chinook	Oregon Coast	Salmon Creek (Coquille) (Fall)	52082	peak	42
Chinook	Oregon Coast	Umpqua River S (Fall)	66899	tlc	48
Chinook	Oregon Coast	Wilson River N Fork (Fall)	50445	peak	52
Chinook	Puget Sound	Cedar River (Summer)	60645	tlc	36
Chinook	Puget Sound	Green/Duwamish River	NWFSC ^b	unk	30
Chinook	Puget Sound	Hood Canal (Summer)/(Fall)	61992	tlc	32
Chinook	Puget Sound	Hood Canal SE	NWFSC ^b	unk	32
Chinook	Puget Sound	Nisqually River (Summer)	60677+61583	tlc	32
Chinook	Puget Sound	Nooksack River	60586	tlc	30
Chinook	Puget Sound	Puyallup River	60665	tlc	32
Chinook	Puget Sound	Samish River	NWFSC ^b	unk	32
Chinook	Puget Sound	Sauk River (Summer)	61470	tlc	26
Chinook	Puget Sound	Sauk River (Spring)	61471	tlc	33
Chinook	Puget Sound	Skagit River Lower (Fall)	61475	tlc	26
Chinook	Puget Sound	Skagit River (Spring)	NWFSC ^b	unk	31
Chinook	Puget Sound	Skagit River (Spring) HMU	NWFSC ^b	unk	33

Table B-1. Summary of salmon population time series used in cross-validation analyses. StreamNet (2002) refers to the StreamNet identification numbers as of summer 2002. Continued.

Species	Evolutionarily significant unit	Stock	StreamNet # or reference	Type of count^a	Length in years
Chinook	Puget Sound	Skagit River S Fork	60606	tlc	32
Chinook	Puget Sound	Skagit River Upper (Summer)	61474	tlc	26
Chinook	Puget Sound	Skokomish River	60689	tlc	32
Chinook	Puget Sound	Snohomish River	60638	tlc	30
Chinook	Puget Sound	Sound South	NWFSC ^b	unk	28
Chinook	Puget Sound	Stillaguamish River	60611	tlc	30
Chinook	Puget Sound	Suiattle River (Spring)	NWFSC ^b	unk	33
Chinook	Puget Sound	White River (Spring)	NWFSC ^b	unk	30
Chinook	Puget Sound	White River	60674	dc	44
Steelhead	Lower Columbia River	Clackamas River (Summer) (N Fork Dam)	50316	dc	28
Steelhead	Lower Columbia River	Clackamas River (Winter) (N Fork Dam)	50320	dc	42
Steelhead	Middle Columbia River	Bear Creek (John Day)	57526	rpm	39
Steelhead	Middle Columbia River	Beech Creek (John Day)	57530	rpm	33
Steelhead	Middle Columbia River	Beech Creek E Fork (John Day)	57531	rpm	33
Steelhead	Middle Columbia River	Big Wall Creek (John Day)	57533	rpm	32
Steelhead	Middle Columbia River	Camp Creek (John Day)	54587	rpm	32
Steelhead	Middle Columbia River	Canyon Creek (John Day)	57536	rpm	26
Steelhead	Middle Columbia River	Cottonwood Creek (John Day)	54597	rpm	38
Steelhead	Middle Columbia River	Deep Creek (John Day)	57538	rpm	26
Steelhead	Middle Columbia River	Deer Creek (John Day)	50094	rpm	26
Steelhead	Middle Columbia River	Fields Creek (John Day)	54598	rpm	40
Steelhead	Middle Columbia River	Kahler Creek (John Day)	54599	rpm	34
Steelhead	Middle Columbia River	McClellan Creek (John Day)	50104	rpm	33
Steelhead	Middle Columbia River	Murderers Creek (John Day)	50106	rpm	38
Steelhead	Middle Columbia River	Parrish Creek (John Day)	50109	rpm	38
Steelhead	Middle Columbia River	Riley Creek (John Day)	50111	rpm	39
Steelhead	Middle Columbia River	Tex Creek (John Day)	50114	rpm	34
Steelhead	Middle Columbia River	Umtilla River (Summer)	50515+57508	dc	30

Table B-1. Summary of salmon population time series used in cross-validation analyses. StreamNet (2002) refers to the StreamNet identification numbers as of summer 2002. Continued.

Species	Evolutionarily significant unit	Stock	StreamNet # or reference	Type of count^a	Length in years
Steelhead	Middle Columbia River	Wind Creek (John Day)	50118	rpm	29
Steelhead	Upper Columbia River	Wenatchee River and Tribs	180072	tlc	33
Steelhead	Snake River	Camp Creek (Imnaha)	54589	rpm	33
Steelhead	Snake River	Crow Creek (Grande Ronde)	54575	rpm	33
Steelhead	Snake River	Devils Run Creek (Grande Ronde)	54567	rpm	33
Steelhead	Snake River	Elk Creek (Grande Ronde)	54569	rpm	34
Steelhead	Snake River	Five Points Creek (Grande Ronde)	50023	rpm	33
Steelhead	Snake River	Fly Creek (Grande Ronde)	50026	rpm	33
Steelhead	Snake River	McCoy Creek (Grande Ronde)	50025	rpm	35
Steelhead	Snake River	Meadow Creek (Grande Ronde)	50024	rpm	35
Steelhead	Snake River	Peavine Creek (Grande Ronde)	54565	rpm	30
Steelhead	Snake River	Phillips Creek (Grande Ronde)	50022	rpm	32
Steelhead	Snake River	Prairie Creek (Grande Ronde)	54564	rpm	33
Steelhead	Snake River	Swamp Creek (Grande Ronde)	54573	rpm	34
Steelhead	Snake River	Wallowa River (Grande Ronde)	54572	rpm	32
Steelhead	Upper Willamette River	McKenzie River (Summer)	54595	dc	28
Steelhead	Upper Willamette River	Santiam River N Late (Winter)	51005	dc	27
Steelhead	Upper Willamette River	Santiam River S (Summer) (Foster Dam)	50902	dc	28
Steelhead	Upper Willamette River	Santiam River S (Winter) (Foster Dam)	51004	dc	31
Steelhead	Upper Willamette River	Willamette River (Winter) (Will Falls Dam)	50305	dc	50
Steelhead	Upper Willamette River	Willamette River (Summer) (Will Falls Dam)	50945	dc	30
Steelhead	Klamath Mountains Province	Rogue River (Summer)	51222	dc	57
Steelhead	Klamath Mountains Province	Rogue River (Winter)	51223	dc	57
Steelhead	Oregon Coast	Umpqua River N (Summer)	50512	dc	53
Steelhead	Oregon Coast	Umpqua River N (Winter)	50513	dc	54

Table B-1. Summary of salmon population time series used in cross-validation analyses. StreamNet (2002) refers to the StreamNet identification numbers as of summer 2002. Continued.

Species	Evolutionarily significant unit	Stock	StreamNet # or reference	Type of count^a	Length in years
Steelhead	Puget Sound	Baker River (Skagit) (Winter)	60896	dc	55
Steelhead	Puget Sound	White River (Puyallup) (Winter)	60900	dc	51
Chum	Columbia River	Grays River W Fork	WDFW ^g	peak	32
Chum	Columbia River	Grays River	WDFW	peak	32
Chum	Columbia River	Hardy Creek	WDFW	peak	33
Chum	Columbia River	Crazy J	WDFW	peak	32
Chum	Columbia River	Hamilton	WDFW	peak	32
Chum	Columbia River	Hamilton Springs	WDFW	peak	33
Sockeye	Snake River	Snake River mainstem	FPC ^h	dc	16

^a Type: dc = dam count, peak = one time peak count of spawners or carcasses, redds = redd count along an index reach, rpm = redds per mile, tlc = total live count (an estimate of the total number of spawners), unk = unknown.

^b Northwest Fisheries Science Center

^c Marmorek and Peters 1998

^d Beamesderfer et al. 1998

^e Peters et al. 1999

^f Oregon Dept. of Fish and Wildlife

^g Washington Dept. of Fish and Wildlife

^h Fish Passage Center (2002)

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