Estimating risks in declining populations with poor data

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Census data on endangered species are often sparse, error-ridden, and confined to only a segment of the population. Estimating trends and extinction risks using this type of data presents numerous difficulties. In particular, the estimate of the variation in year-to-year transitions in population size (the ''process error'' caused by stochasticity in survivorship and fecundities) is confounded by the addition of high sampling error variation. In addition, the year-to-year variability in the segment of the population that is sampled may be quite different from the population variability that one is trying to estimate. The combined effect of severe sampling error and age- or stage-specific counts leads to severe biases in estimates of population-level parameters. I present an estimation method that circumvents the problem of age- or stage-specific counts and is markedly robust to severe sampling error. This method allows the estimation of environmental variation and population trends for extinction-risk analyses using corrupted census counts—a common type of data for endangered species that has hitherto been relatively unusable for these analyses.

One of the first questions a resource manager asks about threatened and endangered species is, "How bad is it?" At its most formal level, this question can be converted into a population viability analysis (PVA), complete with estimates of extinction risk and minimum viable-population sizes. But even if a detailed PVA is not done, the ability to summarize the trajectory of populations is crucial. Such a summary can be used to inform managers on how much improvement must be made in survival or reproduction to arrest a declining trend. It can be used to assign priorities among different populations with different trends and to quantify the short-term risks of waiting while managers or scientists seek more definitive information. One of the more practical methods for addressing these questions was presented by Dennis *et al.* (1), wherein they illustrate how treating a time series of population counts as a diffusion process can yield estimates of extinction risk. This diffusion approximation has since been used to estimate extinction risks for numerous species of conservation concern (1–4).

An oft-cited limitation of this method, however, is the sensitivity of its parameter estimates to sampling error (refs. 5 and 6 but also see ref. 7). Estimates of environmental variance (see refs. 1, 3, and 8) are usually small, and are much smaller than the severe sampling-error variance that plagues the data sets for many threatened and endangered species. Although improving the quality of data collection is an obvious recommendation, this is not possible for historical data. Furthermore, severe sampling error may be very difficult to remove because of a variety of logistical constraints. Finally, not only is sampling error severe in many cases, it often changes through time as methods are improved, personnel changes, or entirely new methods of sampling are adopted. A less commonly recognized limitation is that for many species, only particular age classes or life stages are amenable to census. For instance, spawners are counted for salmon, nesting or breeding adults are often counted for birds, mothers with cubs are counted for grizzly bears, and egg counts are used for many other species. Counts of only a subset of the population pose difficulties, because most risk analyses require

that the count at time $t + 1$ stems from the count at time t—an assumption that fails with many age- or stage-specific counts.

Here I use stochastic age-structured matrix models to generate data, to which I add high and erratic sampling errors. I then demonstrate the severe estimation errors that can occur when age- or stage-specific counts are used as a surrogate for population counts. Finally, building on the previous work of Dennis *et al.* (1), I develop an alternative, more robust method for estimating population parameters from highly corrupted age- or stage-specific counts.

The Method and Parameter Estimation of Dennis *et al*. The population dynamics model used by Dennis *et al.* (1) originates from the observation that at the population level, stochastic age-structured models with no density dependence behave as a stochastic, discrete time model with exponential growth or decline:

$$N_{t + \tau} = N_t \exp(\mu\tau + \varepsilon) \text{ where } \varepsilon \sim N(0, \sigma^2\tau). \qquad [1]$$

The probability distribution of population size at time $t + \tau$ is lognormal. The parameter μ determines the rate at which the median increases through time, whereas σ determines the rate of spread of the distribution, in other words, the variability of population size at time $t + \tau$. By a diffusion approximation, the long-term trends, extinction probabilities, and times to extinction are calculated easily (1).

When censuses are conducted yearly and there are no missing census points, the maximum likelihood estimates of μ and σ^2 are (equations 24 and 26 in ref. 1):

$$\hat{\mu}_{\text{tot}} = \text{mean}[\ln(N_{t + 1}/N_t)]$$

$$\hat{\sigma}^2_{\text{tot}} = \text{var}[\ln(N_{t + 1}/N_t)]. \qquad [2]$$

Note that $\hat{\mu}_{\text{tot}}$ and $\hat{\sigma}^2_{\text{tot}}$ refer to the parameters that are estimated from the true population size with no sampling error.

Using Age- or Stage-Specific Counts as Surrogates for Population Level Counts. When only age- or stage-specific data are available, one option is to assume that these data have the same statistical properties as total population counts and simply to use them in lieu of population counts. For example, the estimates $\hat{\mu}_{\text{age}}$ and $\hat{\sigma}^2_{\text{age}}$ could be calculated by using A_t in place of N_t in Eq. **2**, where A_t is the age- or stage-specific count at time t. However, unless the variability among ages is similar and correlated, the variability measured in one age class will differ from the variability at the population level (which is what we are trying to estimate). Another option is to transform the data by using a running sum to obtain a count that more closely approximates the total population,

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Bias with No Sampling Error
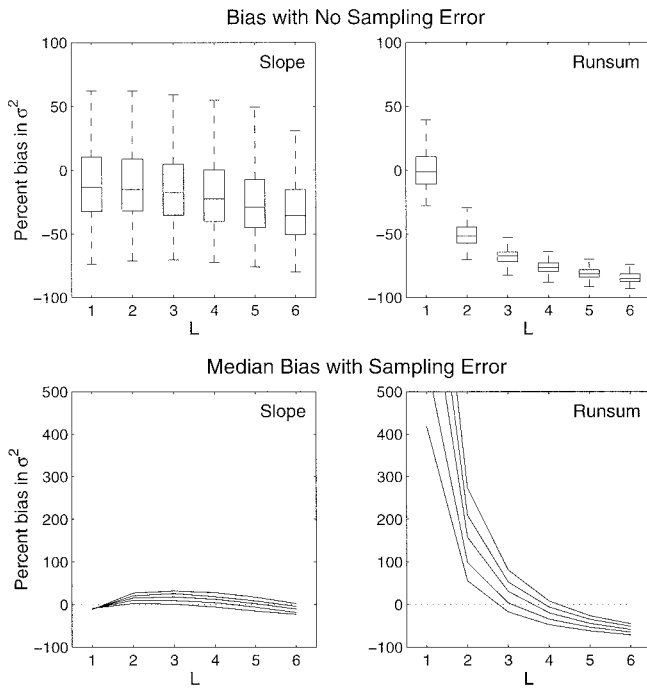
Median Bias with Sampling Error

Fig. 1. Effect of L, the number of counts added together, on the biases in the estimates of $\hat{\sigma}^2_{\text{tot}}$ with the slope (*Left*) and running sum (*Right*) methods. The data are from 500 100-year realizations of the stochastic exponential growth model (Eq. **1**) with $\mu = -0.05$ and $\sigma^2 = 0.05$. The results are relatively insensitive to the level of μ ($\mu < 0$) or σ^2. The median bias and variability in the parameter estimates when no sampling error is present are shown (*Upper*). The median biases when sampling error is 2, 4, 6, 8, or $10 \times \sigma^2$ are shown (*Lower*).

$$R_t = \sum_{i=1}^{L} w_i A_{t-i}, \qquad [3]$$

where L is the number of counts added together to give the running sum count at time t and w_i is the weight given to each count. The optimal transformation would use survivorship and fecundity information to calculate a proper w_i and L. However, in the examples presented here, I assume that survivorship and fecundity information is limited, and the best weighting cannot be determined. Instead, I use a uniform weighting of $w_i = 1$ for all i. L is determined by using basic knowledge of the species' generation time. One approach is to use the running sums directly as a surrogate for population counts:

$$\hat{\mu}_{\text{run}} = \text{mean}[\ln(R_{t+1}/R_t)]$$
$$\hat{\sigma}^2_{\text{run}} = \text{var}[\ln(R_{t+1}/R_t)]. \qquad [4]$$

Unfortunately, this straightforward method suffers from bias problems. When sampling error is absent, it gives variance estimates that are highly underestimated (Fig. 1 *Upper Right*), because the running sum transformation filters out variance. When sampling error is present, it can highly overestimate the variance (Fig. 1 *Lower Right*).

An Alternative Approach. To circumvent these bias problems, I developed an alternative estimation method, the slope method. This method was motivated by the observation that in a stochastic exponential process, the mean and variance of $\ln(N_{t+\tau}/N_t)$ are linear functions of τ with slopes of μ and σ^2. Because population counts through time are highly correlated,

— Total Population
- ■ - Running sum with no sampling error
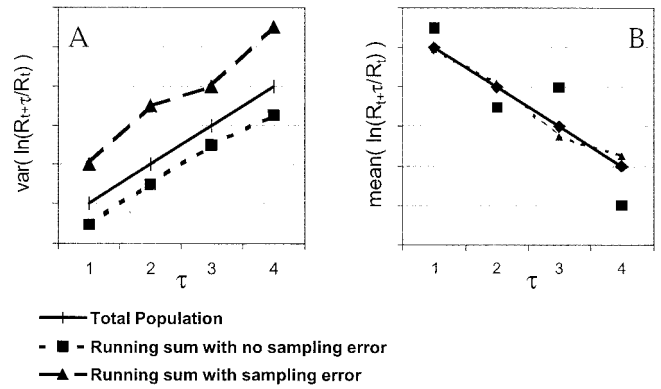-▲- Running sum with sampling error

Fig. 2. Illustration of the slope method for estimating the variance and mean of $\ln(N_{t+1}/N_t)$ from $\ln(R_{t+\tau}/R_t)$, where N_t is the total uncorrupted population count and R_t is a running sum of age- or stage-specific counts. The slope of $\text{var}[\ln(R_{t+\tau}/R_t)]$ vs. τ is an estimate of σ^2. The slope of $\text{mean}[\ln(R_{t+\tau}/R_t)]$ vs. τ is an estimate of μ (in this case $\mu < 0$). The effect of sampling error on the $\text{var}[\ln(R_{t+\tau}/R_t)]$ vs. τ line is to raise the line while keeping the slope (used to estimate σ^2) approximately the same (*A*). The effect of sampling error on the $\text{mean}[\ln(R_{t+\tau}/R_t)]$ versus τ line is to increase the variance of the data around the line (*B*).

a running sum of those counts (if not too long) retains much of the lognormal properties of the component counts. Correspondingly, the mean and variance of $\ln(R_{t+\tau}/R_t)$ are approximately linear functions of μ and σ^2. With the slope method, the parameter estimates are

$$\hat{\mu}_{\text{slp}} = \text{slope of the reg. line of mean}[\ln(R_{t+\tau}/R_t)] \text{ vs. } \tau$$

$$\hat{\sigma}^2_{\text{slp}} = \text{slope of the reg. line of var}[\ln(R_{t+\tau}/R_t)] \text{ vs. } \tau. \qquad [5]$$

One of the strengths of the slope method is its robustness to extreme lognormal observation error, X_s, because $\ln(X_s \cdot N_{t+\tau}/X_s \cdot N_t) \sim N(\mu\tau, \sigma^2\tau + \text{constant})$ (see Figs. 1 and 2). The slope method underestimates $\hat{\sigma}^2_{\text{tot}}$ when sampling error is absent (Fig. 1 *Upper Left*), because of correlation between R_t and $R_{t+\tau}$ and serial correlation among $\ln(R_{t+\tau}/R_t)$, $\ln(R_{t+\tau+1}/R_{t+1})$, $\ln(R_{t+\tau+2}/R_{t+2})$, ... This bias, however, is much less than the bias with the running sum method—a negative 15% vs. a negative 75% bias ($L = 4$). With a very long time series, subsampling R_t to remove serial correlation might give better estimates, but with shorter data sets (20–50 years), the errors caused by removing data seem to be more severe than the bias caused by serial correlation.

The Errors Between the True and Estimated μ and σ_2. Estimates of μ and σ^2 include two different sources of error: (*i*) error caused by using a finite rather than an infinite time series and (*ii*) error caused by observation errors and counts that are not a representative sample of all ages. The first is the error between $\hat{\mu}_{\text{tot}}$, $\hat{\sigma}^2_{\text{tot}}$ and μ, σ^2. Dennis *et al.* (1) demonstrate how to calculate this type of error. The second type is the error between the true $\hat{\mu}_{\text{tot}}$ and $\hat{\sigma}^2_{\text{tot}}$ and values calculated from corrupted age or stage counts.

To explore this second type of error, I studied the behavior of time series generated from stochastic matrix models. One thousand simulated 20-year time series provided true population counts, N_t, and corresponding age- or stage-specific counts, which I later corrupted with sampling error. I then compared the true $\hat{\mu}_{\text{tot}}$ and $\hat{\sigma}^2_{\text{tot}}$, calculated by using N_t, with the estimates from the three methods using the corrupted counts. The stochastic matrix models I used were based on published age- or stage-structured matrix models for endangered Chinook salmon, sea turtles, and petrels. These species represent three very different life histories, but in each case, only a subset of age/stage classes

are countable. The magnitude of environmental variation added to the survivorship and fecundity parameters in the matrices was determined by direct data on fecundity variation or by fitting the model to reflect the variability observed in an available 20-year time series for each species (or a related species). To the age- or stage-specific counts, one of the following four types of sampling error was added. Note that the sampling error variance added was 5–20 times higher than the environmental variance.

(*i*) Unbiased error. The sampling error was drawn from the lognormal distribution, $\exp[N(\mu = 1.0, \sigma^2 = 0.5)]$. More than 50% of the corrupted counts were over 25% too high or 25% too low.

(*ii*) Unbiased but density-dependent error. Percentage-wise large errors were more common when counts were small. Sampling error was drawn from the lognormal distribution, $\exp[N(\mu = 1.0, \sigma^2 = y)]$, as follows: counts $< 100, y = 0.5 + (1 - \text{count}/100) \cdot 0.5$; counts $> 100, y = 0.5$.

(*iii*) Unbiased but erratic error. The accuracy of the counts was changed every 5 years. The sampling error was drawn from the lognormal distribution, $\exp[N(\mu = 1.0, \sigma^2 = y)]$, as follows: years 1–5, $y = 0.5$; years 6–10, $y = 1.0$; years 11–15, $y = 0.25$; and years 16–20, $y = 0.5$.

(*iv*) Biased and erratic error. Bias and accuracy of the counts changed every 5 years. The sampling error was drawn from the lognormal distribution, $\exp[N(\mu = x, \sigma^2 = y)]$, as follows: years 1–5, $(x, y) = (0.5, 0.5)$; years 6–10, $(x, y) = (1.0, 1.0)$; years 11–15 $(x, y) = (1.5, 0.25)$; and years 16–20 $(x, y) = (0.75, 0.5)$.

Spring/Summer Chinook Salmon. The following is a modified Leslie matrix for Snake River spring/summer Chinook salmon (8) in which the spawner class is separate.

$$\begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \\ N_S \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0 & 0 & 0 & 19.11 \cdot 0.058 \cdot \varepsilon_1 \\ 0.8 \cdot \varepsilon_2 & 0 & 0 & 0 & 0 \\ 0 & 0.8 \cdot \varepsilon_3 & 0 & 0 & 0 \\ 0 & 0 & 0.815 \cdot 0.8 \cdot \varepsilon_4 & 0 & 0 \\ 0 & 0 & 0.185 \cdot 0.8 \cdot \varepsilon_4 & 1 & 0 \end{bmatrix}$$
$$\times \begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \\ N_S \end{bmatrix}_t. \qquad \textbf{[6]}$$

The ε_i terms represent environmental variability and were drawn from a multivariate lognormal distribution, $\exp[N(\mu = 0, \sigma^2 = 0.02)]$, with correlation 0.99 between the ε_is. All simulations were started with the age distribution: [8490 450 397 285 379]. This distribution is not the equilibrium age structure; it has a much higher number of 1- to 2-year-old fish. This distribution was chosen to illustrate the behavior of the parameter estimates when the age structure is far from equilibrium. In this case, the perturbed age structure creates a large pulse that travels through all of the time series.

For the running sum transformation, 5 consecutive spawner counts were added together,

$$R_t = \sum_{i=1}^{5} N_{s, t-i}, \qquad \textbf{[7]}$$

where $N_{s,t}$ is the spawner count at time t. The maximum spawner return age for this stock is 5, and a running sum of 5 counts is related to the number of total current and potential spawners in the population at time t.

Loggerhead Sea Turtles. Crowder *et al.* (9) estimated the following matrix for loggerhead sea turtles divided in the age classes; egg, and yr 1–7, yr 8–15, yr 16–32, and yr 32+ :

$$\begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \\ N_5 \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0 & 0 & 4.665 \cdot \varepsilon_1 & 61.896 \cdot \varepsilon_1 \\ 0.675 \cdot \varepsilon_2 & 0.703 \cdot \varepsilon_2 & 0 & 0 & 0 \\ 0 & 0.047 \cdot \varepsilon_3 & 0.657 \cdot \varepsilon_3 & 0 & 0 \\ 0 & 0 & 0.019 \cdot \varepsilon_4 & 0.682 \cdot \varepsilon_4 & 0 \\ 0 & 0 & 0 & 0.061 \cdot \varepsilon_5 & 0.809 \cdot \varepsilon_5 \end{bmatrix}$$
$$\times \begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \\ N_5 \end{bmatrix}_t. \qquad \textbf{[8]}$$

The environmental variance terms, ε_i, were drawn from the multivariate lognormal distribution, $\exp[N(\mu = 0, \sigma^2 = x_i)]$, where $x_1 = 0.5, x_2 = 0.01, x_3 = 0.01, x_4 = 0.01$, and $x_5 = 0.01$, and correlation of 0.99 between ε_is. These distributions were chosen to reflect the enormous variability in the annual number of nesting females (and hence, egg counts) that is a characteristic of many sea turtle populations (10, 11), and the observed variance patterns in a 26-year time series of egg counts of green turtles (*Chelonia mydas*) in Costa Rica (10). Unlike the salmon matrix, the sea turtle matrix does not tend to produce population cycles. This difference makes age- or stage-specific counts more robust as population estimators. However, high variability in one age class (in this case, the sampled egg class) relative to others also leads to biased parameter estimates.

Because sea turtle life spans are 30+ years, a biologically motivated running sum would include roughly 30 egg counts, weighted more toward recent egg counts. However, with a 20-year time series, the running sum cannot include more than ≈5–6 counts, while still leaving enough data points for estimation. For the example here, three egg counts were added together to produce each running sum.

Hawaiian Dark-Rumped Petrel. Breeding-colony censuses of this petrel include mainly birds aged 6–23 years. Juveniles comprise ≈50% of the population but most (70%) do not return to the colony and are not counted (12). Simons (12) estimated parameters for a 35 × 35 Leslie matrix for this endangered petrel by using juvenile survivorship (1–5 yr) = 0.8034 + ε_1, adult survivorship (6–35 yr) = 0.93 + ε_2, juvenile fecundity = 0, and adult fecundity = 0.294 + ε_3 (matrix not shown). The environmental variability terms, ε_i, were drawn from the multivariate lognormal distribution, $\exp[N(\mu = 0, \sigma^2 = x_i)]$, where $x_{1,2} = 0.01$ and $x_3 = 0.1$, with 0.99 correlation. The variance in adult fecundity reflects that observed by Simons. I did not have estimates of the variability in survivorships and chose moderately low levels. Simulations indicated that the results were not qualitatively sensitive to the level of variation in the survivorships.

The breeding-bird counts were transformed by

$$R_t = \sum_{i=1}^{L=5} N_{\text{breeding}, t-i}. \qquad \textbf{[9]}$$

$L = 5$ was chosen as follows: the breeding bird count at time t contributes age-1 birds in year t, age-2 birds in year $t + 1$, age-3 birds in year $t + 2$, etc. Because petrels begin breeding on average at age 5, breeding-bird counts ($t - 4$ to t) contribute to the current total population size. With information on adult fecundity and juvenile survivorship, a better weighting could be
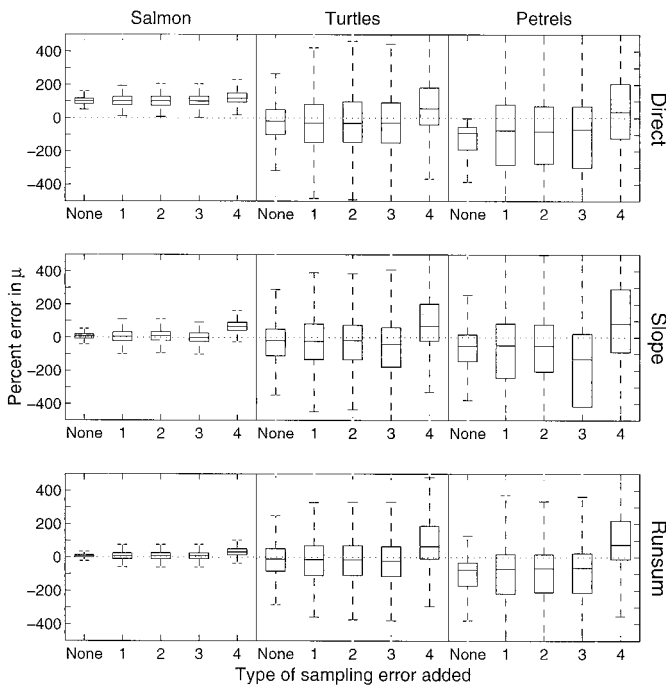
Fig. 3. Effect of severe sampling error on estimates of $\hat{\mu}_{tot}$ by directly using age or stage counts as surrogates for population counts (Direct), by using the slope method (Slope), or by using the running sum method (Runsum). In the boxplots, the middle line indicates the median; the box encloses 75% of the data; and the whiskers indicate the range of the entire data. The four types of sampling error are unbiased lognormal error (1), unbiased lognormal error with variance that depends on the count size (2), unbiased lognormal error with variance that changes every 5 years (3), and biased lognormal error with variance and bias that change every 5 years (4).

Fig. 4. Effect of severe sampling error on estimates of $\hat{\sigma}^2_{tot}$. Note that the scale (*Top*) is much larger, because of larger errors associated with the direct method. See Fig. 3 for a description of the boxplots and sampling-error types. Directly using age- or stage-specific counts leads to large biases in the estimate of $\hat{\sigma}^2_{tot}$, and sampling error greatly exacerbates the problem. The slope method allows significantly fewer biased estimates in the face of severe sampling error.

determined. I assume that such information is unavailable, as it often is, and I used a uniform weighting instead.

Results

For each time series, $\hat{\mu}_{tot}$ and $\hat{\sigma}^2_{tot}$ were calculated from the true total population count by using Eq. **2**. Estimates of $\hat{\mu}_{tot}$ and $\hat{\sigma}^2_{tot}$ then were calculated by using the uncorrupted and corrupted age- or stage-specific counts: $\hat{\mu}_{age}$ and $\hat{\sigma}^2_{age}$ with Eq. **2** directly from the corrupted counts, $\hat{\mu}_{run}$ and $\hat{\sigma}^2_{run}$ with Eq. **4** from the running sums, and $\hat{\mu}_{slp}$ and $\hat{\sigma}^2_{slp}$ with Eq. **5**. The percent differences between the estimated and true $\hat{\mu}_{tot}$ and $\hat{\sigma}^2_{tot}$ then were calculated. Two risk metrics, the mean rate of population growth [$\lambda = \exp(\hat{\mu} + \hat{\sigma}^2)$] and the probability of a 90% decline within a given time horizon (1), were calculated by using the estimated and true $\hat{\mu}_{tot}$ and $\hat{\sigma}^2_{tot}$. The probability of extinction could not be calculated because this requires an estimate of total population size, which is impossible to derive purely from age- or stage-specific counts with little other information.

Effect of Counts That Do Not Reflect the Population. The first complication I examined concerned simply the effect of age- or stage-specific counts (no sampling error) on parameter estimates. Figs. 3 and 4 (*Top*) show the difference between the true parameters and their estimates, $\hat{\mu}_{age}$ and $\hat{\sigma}^2_{age}$, calculated by using age- or stage-specific counts directly. In general, these specific counts were poor surrogates for population counts. The parameter $\hat{\sigma}^2_{age}$ was overestimated highly (1,000–7,000%). The parameter $\hat{\mu}_{age}$ was biased 100% upward for the salmon example (this bias was not present if the simulations were started with the age distribution at equilibrium). The bias in the parameter estimates had strong effects on the calculated risk metrics. The population
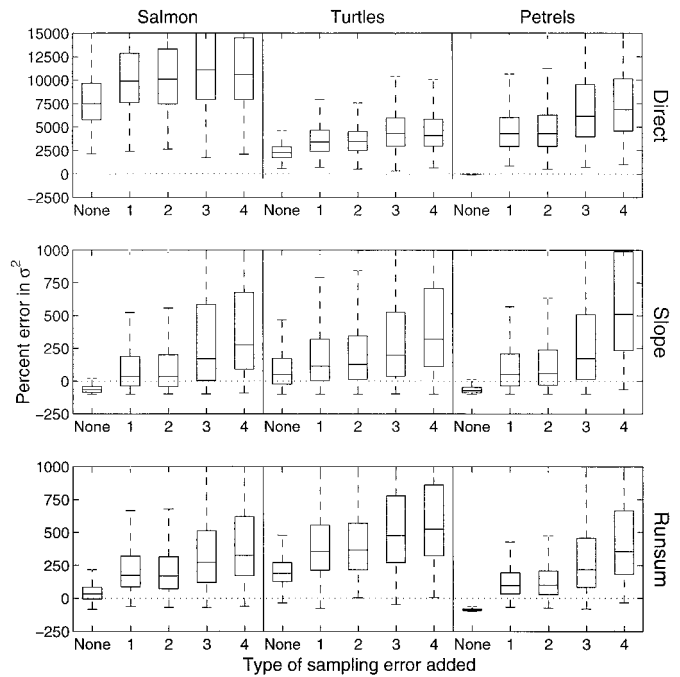
rate of decline was overestimated by a median of 150% for the salmon and 53% for sea turtles (Fig. 5). Although the estimate was good for the petrels, it became biased upward when sampling error was present (next section). Similarly, the estimates of probability of a 90% decline within a given time horizon were biased highly for salmon and sea turtles (similar to Fig. 6 *A–C*).

The true $\hat{\mu}_{tot}$ and $\hat{\sigma}^2_{tot}$ were much more accurately estimated by using the running sum and slope methods [compare Figs. 3 and 4 (*Top*) to Figs. 3 and 4 (*Middle* and *Bottom*)]. Note the scale in the lower panels (Fig. 4) is an order of magnitude smaller because of the smaller error with these methods. The bars marked "None" indicate the simulations with no sampling error. Both methods greatly improved the estimation of $\hat{\sigma}^2_{tot}$. The median bias of $\hat{\sigma}^2_{slp}$ was −45%, +51%, and −72% for salmon, sea turtles, and petrels. The median bias of $\hat{\sigma}^2_{run}$ was +41%, +190%, and −87%. Estimation of $\hat{\mu}_{tot}$ improved greatly for salmon; the new estimates were unbiased and tight but there was little improvement for the other species. The better estimates of $\hat{\sigma}^2_{tot}$ translated into significantly better risk estimates. The median overestimation of population growth rate ranged between 0.3% and 4% with low variability (Fig. 5). The estimates of probability of a 90% decline in a given time frame also improved and were relatively unbiased, although variable (similar to Fig. 6 *C* and *D*).

Effect of Severe Sampling Error. When age and stage counts were used as direct surrogates for population counts, high sampling error caused substantial overestimation of $\hat{\sigma}^2_{tot}$ (Fig. 4). The most extreme increase occurred for the petrels. In this case, $\hat{\sigma}^2_{age}$ gave an unbiased estimate when no sampling error was present but overestimated by a median 4,300–6,900% with sampling error added. The other two species showed smaller but still large overestimates. The corresponding estimates of population growth were highly biased (Fig. 5), and the estimates of the
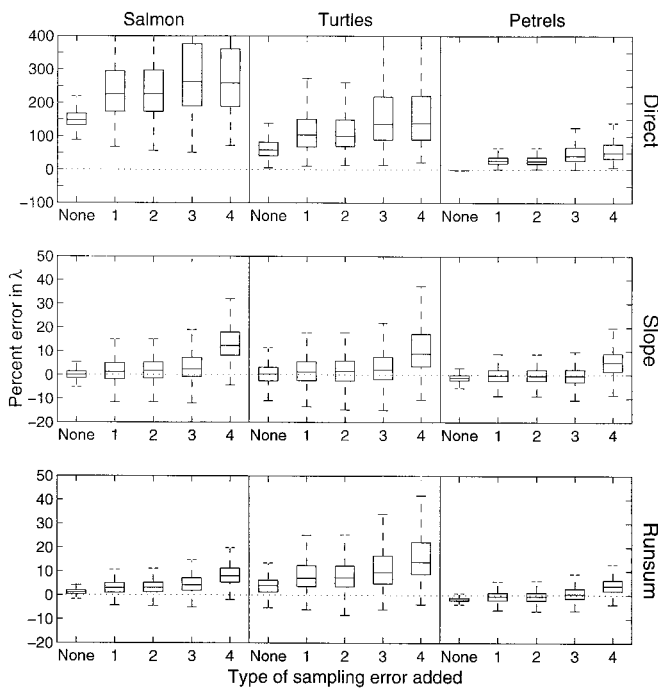
Fig. 5. Effect of severe sampling error on estimates of the mean rate of population decline, λ. Note that the scale (*Top*) is much larger, because of larger errors associated with the direct method. See Fig. 3 for a description of the boxplots and sampling-error types.

Fig. 6. Effect of parameter estimates on the probability of a 90% decline in a given time horizon for salmon (*Top*), sea turtles (*Middle*), and petrels (*Bottom*). On the *Left*, the parameters were calculated by using the direct method (Eq. **2**) from corrupted age- or stage-specific counts. On the *Right*, the parameters were estimated by using the slope method (Eq. **5**). The solid lines show the median absolute difference between the probability of a 90% decline calculated with the corrupted counts vs. that calculated with the true population counts. The dashed lines show the range of 75% of the differences.

probability of a 90% decline were highly biased and variable for all species, including petrels (Fig. 6 *A–C*).

In contrast, the running sum and slope methods filtered out much of the high sampling error. With the slope method, the median upward bias in the $\hat{\sigma}^2_{tot}$ estimate was 35–275%, 100–250%, and 50–500% for the salmon, sea turtles, and petrels (Fig. 4). With the running sum method, the median bias was 175–325%, 300–400%, and 100–300%. This bias compares to median upward biases of 2,500–11,000%, when the corrupted counts were used directly. The resulting estimates of mean population growth with the slope method were unbiased and the upper and lower quartiles of the estimates varied between 5% low and 5% high for all except the worst sampling error (Fig. 5). The probability of a 90% decline within a given time frame was relatively unbiased (Fig. 6 *D–F*) but was highly variable.

Difference Between the Running Sum and Slope Methods. Comparing Figs. 3 and 4, it would seem that using running sums as a direct surrogate for population counts often gives less variable and no more biased estimates than the slope method. The sea turtle example is the exception and points out one of the weaknesses of the running sum method. The running sum estimates, especially $\hat{\sigma}^2_{run}$, are sensitive to L, the number of counts added together to create a running sum count. This sensitivity can be demonstrated by using the simple stochastic exponential process (Eq. **1**). With no sampling error, the bias in the estimate of $\hat{\sigma}^2_{tot}$ increases from −50% to −80% as L increases from 2 to 6 (Fig. 1 *Upper*). For the slope method, in contrast, the bias increases from −10% to −30%. With sampling error, the sensitivity of the running sum estimates becomes severe, with the bias changing rapidly from +50–300% to −80% when L is changed from 2 to 6 (Fig. 1 *Lower*). In comparison, the slope method estimates are relatively insensitive to L and high sampling error. In practice, choosing the optimal L may be difficult, because basic life history information is not available, e.g., mean age of return to breeding sites, mean lifespan, maximum breeding age, etc. Thus, robust-
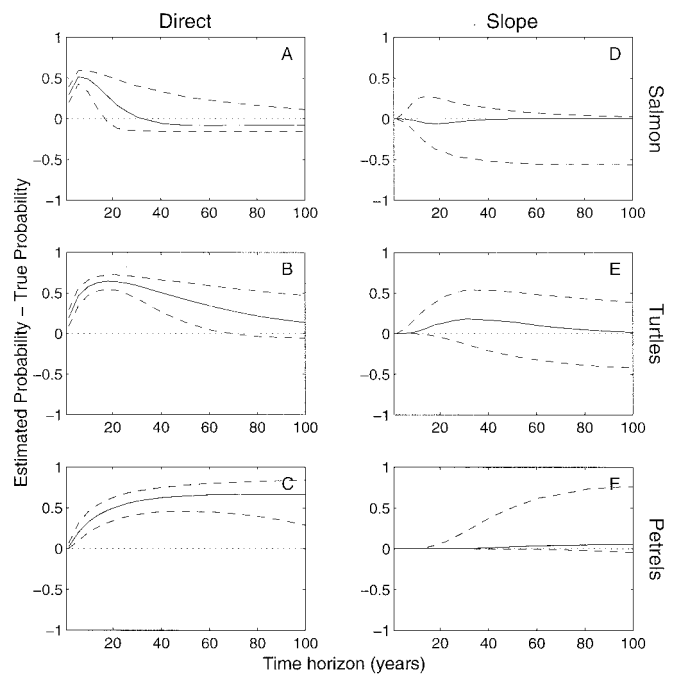
ness to poor choices for the running sum transformation is important.

The decreased bias provided by the slope method comes with a cost. Its variance estimate, $\hat{\sigma}^2_{slp}$, is much more variable than the estimates from the direct or the running sum methods (Fig. 1 *Upper*). When sampling error, age-structure perturbations, or age-specific variability are high, the significantly reduced bias provided by the slope method will outweigh the increased variability in its variance estimate (Fig. 1 *Lower*). When the data do not suffer from such problems (e.g., the expected sampling error variance is less than the environmental variance), standard methods (1) or $\hat{\sigma}^2_{age}$ should give better parameter estimates. The slope method should be viewed as a complement to the methods introduced by Dennis *et al.* and specifically as a tool for data sets beset by high nonprocess error variance. Finally, note that the slope method has greater data needs. In its current form, the method does not allow missing data, and in addition, 15 to 20 years of data seem to be a minimum (for an L of 4). Using the method with only 10 years will result in severe underestimates of environmental variance. This problem rapidly dissipates as the time series' length increases to 20 years.

Discussion

Limited and error-riddled data are common for many species for which management decisions and status assessments must be made. Although improving sampling techniques is always warranted, certain constraints are often impossible to remove. Age- or stage-specific counts are one of these problems. Commonly, one segment of the population, often the juvenile segment, is unobservable. In addition, sampling error can be extreme or changing from year to year as methods and personnel change. In this paper, I introduce a slope method for estimating population parameters in the face of these two problems. The main advan-

tage of this method is that it allows estimates of rates and risks of population decline with a well established tool (diffusion approximations) by using age- or stage-specific censuses that are corrupted with sampling error. Previously, the parameters for simple count-based extinction analyses could not be estimated with this common type of data.

One of the interesting features of the slope method is its ability to separate environmental variance from sampling error variance by using the different statistical properties of each, even when the sampling error is severe, e.g., orders of magnitude greater than the environmental variance. Previous methods have used strategies that partition the two sources of variability when the magnitude of the sampling-error variance is known or the ratio to the environmental variance is known (13–16). However, it is uncommon in conservation settings that the magnitude of the sampling error, absolute or relative, is known. Our consequent inability to estimate environmental variance in the face of sampling error variance has been one of the greatest obstacles to the estimation of parameters for population extinction analyses. The slope method presents a different strategy, separating the environmental variance from much larger sampling-error variance, by observing that the variance of the ratio of logarithm counts separated by n years should be governed by the function (environmental variance·n + sampling-error variance).

Like any model, the application of a diffusion approximation can be abused, and its success depends on certain assumptions. It, or any other population viability analysis, is likely to encounter troubles if there are substantial environmental trends or if variability does not conform to some well behaved distribution like a lognormal distribution. Fortunately, both of these assumptions can be tested readily. More problematic is the question of density dependence. This possibility can be tested (17), although, should populations grow, they will obviously climb out of the region of no density dependence. Conversely, if populations continue to shrink to only a handful of individuals, they are likely to enter a region of density depensation (or Allee effects). An oft-mentioned concern is autocorrelation in the environmental variability. The behavior of stochastic exponential population processes with correlated environmental variability is discussed in refs. 1 and 18. In short, the same diffusion approximation is valid for correlated variance. The μ parameter is unaffected but the σ^2 estimate must be increased by the level of correlation. Methods for estimating σ^2 in short time series with correlated noise are covered in ref. 18. In its current form, the slope method assumes that the environmental noise is relatively uncorrelated and will underestimate σ^2 in time series with correlated noise. However, keep in mind that the slope method is used in situations where nonenvironmental variance is very high, in which case σ^2 will tend to be overestimated.

Even when all of the assumptions are met, one needs to be cautious when interpreting and using the risk metrics estimated by simple diffusion approximations. Probabilities of reaching a specific threshold (e.g., extinction) have been criticized harshly, because they tend to be biased and have large confidence intervals for short or error-ridden data sets (5, 6). In the examples here, the slope method removed much of the bias in the estimated probability of a 90% decline within a given time frame, but the estimates were highly variable for two of the three species. Success at estimating probabilities for one species, salmon, suggests that estimating probabilities of hitting thresholds (such as extinction) is not necessarily doomed. It may be possible to delineate regions of parameter space [μ, σ^2, time horizon, time-series length] where estimates of extinction probability are likely to be poor. Previously, this region would have included the entire parameter space for error-ridden data. The methods developed here considerably shrink the region of poor estimates.

On the other hand, the reliance on a risk metric with recalcitrant estimation problems is difficult to justify when an equally useful parameter, λ, the expected mean annual rate of population change, is readily available and is well estimated, even with very poor data. Without pretending to predict an extinction risk, λ itself provides some answers to the question, "How bad is it?" If λ is low, populations generally are at greater risk and will require larger improvements in survival or fecundity to mitigate the risk. In addition, the lower λ and the smaller the initial population size, the less time there is to "wait and learn more" before taking action. In addition, for threatened and endangered populations, a λ greater than 1 (headed toward recovery) is the legal imperative for management. This is not to argue that λ captures the same aspects of risk that probability of extinction does, or that probabilities of extinction should be abandoned. Small populations with λ greater than 1 but high environmental variability will still have high extinction risks. But until estimation methods are improved further, numerical estimates of the probability to hit a given threshold such as extinction will be dubious for many species (but not all). In those cases, where probability estimates are expected to be poor, I believe that λ is the more useful risk metric. It is certainly the most reliably estimated.

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