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Application of diffusion approximation for risk assessments of sea turtle populations

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Abstract. Population viability analysis (PVA) to forecast extinction risk is a commonly used tool in decision- and policy-making processes of governments and conservation organizations. A drawback to PVA is the high degree of uncertainty in these forecasts due to both population stochasticity and parameter estimation uncertainty. With sparse or noisy data, extinction probabilities frequently have 95% confidence intervals ranging from 0 to 1. To make stochastic simulation results more interpretable, we present a new metric, susceptibility to quasi-extinction (SQE), to assess whether or not a population is *at risk* of declining to a prespecified level (quasi-extinction). Following standard methods for diffusion approximation of extinction risk, we use a parametric bootstrap to determine the 95% CI for the probability of quasi-extinction. SQE is the proportion of this parametric bootstrap that indicates a high (defined as $\geq$0.90) probability of quasi-extinction, resulting in a point estimate that integrates both parameter uncertainty and stochasticity in extinction forecasting. We demonstrate the application of the metric with sea turtle nest census data, which have a high degree of year-to-year variance and represent only a small fraction of the total population. Using population simulations, we found that for these types of data a critical SQE value of 0.40 corresponds to populations that have a true risk of quasi-extinction. The metric has an accuracy of >80%, which can be increased further by lowering the 0.40 threshold and trading off Type I error (considering a population to be "not at risk" when it actually is) and Type II error (considering a population to be "at risk" when it actually is not), giving managers a flexible and quantitative tool for assessments of population status.

Key words: diffusion approximation; endangered species; fisheries management; listing criterion; population viability; PVA; quasi-extinction risk; sea turtles; susceptibility to quasi-extinction.

Introduction

Assessment of the current status and possible future trajectories of endangered species is a critical step in the development of conservation and management policies (Beissinger and McCullough 2002, Morris and Doak 2002). Although each species or population requires consideration of its unique life history characteristics and the data that are available for assessment modeling, there is an advantage to using a standard method for assessment within a taxon (McClure et al. 2003). However, the choice of an assessment tool and appropriate modifications to it should include careful analysis of its performance in the face of uncertainty (Ludwig 1996, Ellner et al. 2002, Sæther and Engen 2002, Staples et al. 2005, Holmes et al. 2007). Does the model accurately identify population status? Is it robust under a range of uncertainty in parameters or environmental stochasticity? Is it appropriately precautionary? These questions are of critical importance to resource managers who may need to apply a method to multiple populations, often with poor data for model parameterization, and should be considered in assessment model development.

Population viability analysis (PVA), including extinction risk estimates using simple stochastic diffusion approximation, is a well-established body of theory (Beissinger and McCullough 2002, Morris and Doak 2002). However, practical applications have been hampered by the high uncertainty of the results (Ludwig 1996, Fieberg and Ellner 2000, Ellner et al. 2002, Sæther and Engen 2002, Staples et al. 2005, Holmes et al. 2007). Holmes et al. (2007) identify the "(0,1) criticism," describing the case in which the confidence intervals on extinction risk generated by stochastic simulation range from 0 to 1, or are bimodal at 0 and 1, for many of the models based on the sparse data sets available for endangered species. Suggestions for dealing with issues of uncertainty include the use of population prediction intervals, which are the smallest time intervals that include a decline to an extinction threshold (Sæther and Engen 2002), risk-based population monitoring that uses short time frames and quasi-extinction thresholds close to current population size (Staples et al. 2005), and the use of Bayesian decision theory to consider all possible parameter combinations not possible with

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frequentist approaches (Ludwig 1996). The determination of how to identify and communicate levels of risk is an ongoing problem for conservation biology and has limited the applicability of population viability management to status determinations of threatened and endangered species (Holmes et al. 2007).

Here we present a novel method for the application of diffusion approximation to risk assessment and status determination that circumvents the problem of large confidence intervals, which can arise with highly uncertain or variable abundance estimates. We use a bootstrapping approach to derive a single metric, the susceptibility to quasi-extinction (SQE), to assess if the *probability* of a population's risk of quasi-extinction is high enough to warrant a particular status listing. The metric incorporates the two types of uncertainty: error introduced by parameter estimation by diffusion approximation and the uncertainty due to the stochastic nature of a population's future trajectories. We use sea turtles as an example of the application of the method; however, it can be readily applied to any species for which census data are available. We use population simulations to validate the method and to determine a critical value for the metric, above which a population is likely to be at risk. This quantitative method to set thresholds for evaluation of a population's status should be useful for managers because it is straightforward to implement and fits well within the language of listing criteria for endangered species (IUCN 2001).

The objectives of our study were (1) to develop a new metric for quantifying quasi-extinction risk (SQE) that is based on the well-known diffusion approximation methods, but that incorporates multiple sources of uncertainty not traditionally parsed by diffusion methods; and (2) to implement this metric for endangered sea turtles to illustrate its application to long-lived vertebrates with high uncertainty in adult abundance estimates.

Methods

Case study: sea turtles

Sea turtles present unique problems for population assessment (Heppell et al. 2002). Six of the seven species of sea turtles worldwide are listed as either threatened or endangered by both the U.S. Endangered Species Act and the World Conservation Union (IUCN) Red List (IUCN 2001). These species continue to be taken as bycatch in many fisheries (NMFS 2001, Lewison et al. 2004) and are also actively harvested in many regions of the world (Koch et al. 2006). The life cycles of many populations include trans-oceanic migrations, thus requiring coordinated, multinational conservation efforts to protect and manage these populations (Heppell et al. 2002). The available data for many of these populations include only beach counts of nests or nesting females, which is a small and variable fraction of the whole population. These census data can be considered highly corrupt due to the high year-to-year variation in numbers of nesting females, numerous sources of observation error, and the fact that adult females represent only a small fraction of the population (<2%; Crowder et al. 1994, Lewison et al. 2004). Hence, there is a need for a metric that can accurately determine risk for populations with these types of data. Diffusion approximation techniques that explicitly account for data uncertainty can serve as an assessment tool for sea turtles and hold promise for application to listing decision reviews, recovery planning, and fisheries management.

In their criteria for listing a species as critically endangered, endangered, or "of concern," the IUCN calls for observed, estimated, inferred, or suspected population size reductions of 90%, 70%, or 50%, respectively, over the last 10 years or three generations, whichever is longer, up to a maximum of 100 years (IUCN 2001). Because some sea turtles do not reach sexual maturity for as much as 40 years, depending on species and population (Balazs and Chaloupka 2004), three generations can be quite long: time series of 35–100 years need to be considered and good historical abundance records do not generally exist over such time periods. Diffusion approximation models for population viability fall nicely into the language of the IUCN listing criteria (Holmes et al. 2007). However, before there can be practical applications of the models, methods for dealing with uncertainty in risk assessments must be clearly defined.

In using diffusion approximation for extinction risk estimates, Holmes (2001) advocates the use of running sums to reduce some the variability in parameter estimation to improve performance of the model as a method of producing a more meaningful estimation of population size, which is critical to setting appropriate quasi-extinction thresholds (Holmes 2004). Here we estimate changes in the total numbers of adult females in a population of marine turtles over a given time period, based on annual observations of nests or nesting females. Because most sea turtles do not reproduce annually, we use what we know about remigration intervals to establish reasonable running sum lengths.

Breeding remigration intervals for adult female sea turtles vary among individuals and populations, probably depending on age and environmental conditions (Broderick et al. 2001, Rivalan et al. 2005, Saba et al. 2007). We have imperfect information on remigration intervals for most populations because these estimates are confounded by imperfect site fidelity of females and by mortality; most studies do not account for these effects. Despite these limitations, some generalizations can be made. One-year remigration intervals are rare, but two- and three-year intervals are much more common, usually followed by four-year intervals (Richardson et al. 1978, Van Buskirk and Crowder 1994, Hughes 1996, Reina et al. 2002, Hatase et al. 2004, Rivalan et al. 2005). Hence, we used running sums of two, three, or four years to span a likely range for most

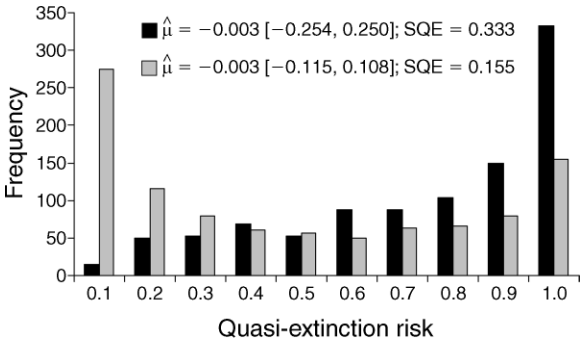

FIG. 1. Histogram of the results of the parametric bootstrap (N = 1000) for estimating quasi-extinction risk using the diffusion approximation method where estimated mean population growth rate, $\hat{\mu}$, and its variation, $\hat{\sigma}^2$, were estimated as in Dennis et al. (1991). Shown are the results for two simulated populations with the same mean values of $\hat{\mu}$ but different levels of variance, as indicated by the 95% confidence limits in square brackets. Population A is indicated by the black bars, population B by the gray bars. Susceptibility to quasi-extinction (SQE) is the proportion of the replicates from the bootstrap procedure that indicated a >0.90 probability of quasi-extinction.

sea turtles. Information on remigration intervals and how they vary among years and individuals is lacking for most nesting populations. We explore the consequences of using a running sum of two, three, or four years for simulated populations with underlying mean remigration intervals that range from two to four vs. a running sum that is consistent with the actual remigration interval characteristic of the population.

Diffusion approximation

We use diffusion approximation methods to estimate quasi-extinction risks (Dennis et al. 1991, Holmes 2001, Holmes and Fagan 2002, Morris and Doak 2002). This method uses time series of abundances to estimate mean population growth rate (μ) and the variance of this rate (σ^2). These parameters are estimated using simple linear regression (Dennis et al. 1991) and can be used to estimate PVA risk metrics, including mean time to extinction and probabilities of declining to a preset threshold (quasi-extinction). We present the details of our application of the equations in conjunction with a running sum in Appendix A.

Dealing with uncertainty in extinction estimates: defining "susceptibility to quasi-extinction"

The probability density function for hitting a quasi-extinction threshold, QET, is described by the inverse Gaussian distribution (Morris and Doak 2002):

$$g(t|\mu, \sigma^2, d) = \frac{d}{\sqrt{2\pi\sigma^2 t^3}} \exp\left[\frac{-(d+\mu t)^2}{2\sigma^2 t}\right] \qquad (1)$$

where $d = \log(n_0/\mathrm{QET})$ and n_0 is the current population size based on the running-sum transform of the data. For μ and σ^2 in Eq. 1, we used the parameter estimates $\hat{\mu}$ and $\hat{\sigma}^2$ and $\hat{\sigma}_p^2$. The variance estimate $\hat{\sigma}^2$ is the total variance and it includes both observation and process error. The estimate $\hat{\sigma}_p^2$ removes observation error and includes only process error (Holmes and Fagan 2002). To calculate the total probability of reaching an extinction threshold at any time T, Eq. 1 is integrated from $t = 0$ to $t = T$, resulting in the following cumulative distribution function:

$$G(T|\mu, \sigma^2, d) = \Phi\left(\frac{-d-\mu T}{\sqrt{\sigma^2 T}}\right) + \exp\left(\frac{-2\mu d}{\sigma^2}\right)\Phi\left(\frac{-d+\mu T}{\sqrt{\sigma^2 T}}\right) \qquad (2)$$

where $\Phi(z)$ is the standard normal cumulative distribution function. We used the parametric bootstrap estimation procedure from Morris and Doak (2002) to compute a range of quasi-extinction estimates by sampling from the estimated distribution of $\hat{\mu}$ land $\hat{\sigma}^2$ or $\hat{\sigma}_p^2$. We determined if the quasi-extinction threshold value was reached over a time period of $T = 3$ generations or 100 years, whichever value is smaller, which is consistent with the IUCN listing criteria (IUCN 2001).

Morris and Doak (2002) use the parametric bootstrap method to estimate 95% CI around quasi-extinction risks; however, a major drawback for this analysis is that for populations with growth rates that are close to zero (stable) or with high interannual variance, the estimated 95% CI for extinction probability often ranges from 0 to 1 when large values of T are used (Ludwig 1999, Feiberg and Ellner 2000). This is not informative for management purposes, yet there are ongoing needs for listing criteria that require the best available scientific input. We suggest a metric other than the mean and confidence intervals for extinction risks as a measure of the likelihood of quasi-extinction of the population. Instead, we calculate the proportion of replicates from the parametric bootstrap procedure that indicate a high (>0.90) *probability* of quasi-extinction.

We demonstrate the application of this metric with two simulated populations (methodology for population simulations will be described) with the same value of $\hat{\mu} = -0.003$ but different levels of variance around $\hat{\mu}$: 95% CI of $\hat{\mu}$ for population A= (–0.254, 0.250) and for population B = (–0.115, 0.188); see Fig. 1. The parametric bootstrap for both of these populations estimated a 95% CI of 0 to 1 for quasi-extinction risk in three generations. These results are common to quasi-extinction risk estimates using diffusion approximation (Ludwig 1996, Fieberg and Ellner 2000, Ellner et al. 2002, Holmes et al. 2007). For population A, with the higher level of variance, 33.3% of the bootstrap replicates indicate a ≥0.90 probability of quasi-extinction, whereas population B, with lower variance, shows only 15.5% of replicates meeting this criterion, suggesting that population A is at somewhat greater risk of quasi-extinction than population B. We use the phrase "susceptibility to

quasi-extinction" (SQE) to describe this metric. Our choice of ≥ 0.90 to quantify the idea of "high probability of quasi-extinction" was arbitrary and different values could certainly be used. With the validation method described below, the results would be qualitatively the same regardless of the selection of this value. We explore the usefulness and accuracy of SQE as a means of comparing relative risks in populations (Morris and Doak 2002). For this metric to be useful, we need to establish a critical value above which SQE would be considered cause for concern, and below which it would not. We use population simulations both to establish the critical value and to test its accuracy.

Population simulations

Defining the critical value.—We established the critical value of the susceptibility to quasi-extinction (SQE) index by generating time series of nesting female abundances using stochastic population simulations (Appendix B; Fig. 2). We generated 500 "populations" and projected them for 30 years. The resulting time series of observed nesting females were used to compute $\hat{\mu}$ and $\hat{\sigma}^2$ or $\hat{\sigma}_p^2$ values by applying both the Dennis et al. (1991) and Holmes (2001) techniques. The SQE values were determined for each population at quasi-extinction thresholds of 50%, 70%, and 90% reductions from current population size. For the time horizon (T in Eq. 2) of the quasi-extinction risk, we followed the criteria guidelines provided by IUCN of three generations up to 100 years. The IUCN defines generation time as age at maturity plus one-half of reproductive longevity and it was calculated as $\alpha + \log(0.5)/\log(S_A)$, where α is age at maturity and S_A is mean adult survival.

To determine the "actual" extinction risk, each population was projected from the end of the 30-year time series for T years. The starting population size for each of these simulations was based on the number of adult females at the end of the 30-year time series, and we ran the model 1000 times for each population to assess quasi-extinction risk. We used quasi-extinction threshold (QET) values of 50%, 70%, and 90% reductions of starting population sizes and considered the proportion of the 1000 simulations that the populations fell below QET as the "actual" quasi-extinction risk.

There are two types of error that can be made in classifying populations as at risk or not at risk of quasi-extinction: (1) that a population is considered to be not at risk when in fact it is, and (2) that a population is considered at risk when in fact it is not. We refer to the first as a Type I error and the second as a Type II error. We compared the "actual" quasi-extinction risk with the SQE metric for these 500 populations to find the critical value for SQE that minimized both types of errors. If the "actual" extinction risk analysis indicated that >50% of the 1000 simulations crossed the QET, the population was considered at risk; otherwise it was considered not at risk. At each critical value, if the SQE for a population was greater than the critical value, it was considered at risk, otherwise not at risk. Spearman rank correlations (r_S) were calculated between actual extinction risk and diffusion approximation parameters and SQE (Zar [1999]; cor.test command in S-PLUS version 6.2; Insightful Corporation 2003).

Testing the critical value.—We then created an additional 300 simulated "populations" to test the accuracy of the critical value (Fig. 2) for different time series lengths and for different running-sum lengths. To test different time series lengths, we created a set of assessment "windows" for each of these populations by projecting them for time series of 15, 20, 25, and 30 years with new demographic parameters drawn from the set mean and variance of each parameter for that population at each time step from distributions centered at the mean (Appendix B: Table B1). This produced 1200 simulated time series (300 populations at four time series lengths). "Actual" quasi-extinction risks were established for each population at each time series length as described previously. We compare these "actual" results with those estimated from diffusion approximation using the same time series and the methods of both Dennis et al. (1991) and Holmes (2001).

To explore how (1) the choice of running-sum length influences the accuracy of the diffusion approximation analysis, and (2) whether or not the results are more accurate if a running sum that approximates actual remigration intervals is used, we divided the 300 simulated populations into three groups representing different mean remigration intervals of 2, 3, and 4 years. We delineated the groups with half-year intervals around the mean, such that remigration intervals between 1.5 and 2.49 would be considered in the 2-year group, and so forth. We applied 2-, 3-, and 4-year running sums to the time series of observed nesting adult females for each population in each of these three groups. For each of these different running sums, the current population size, n_0, changes, because this value is based on the running sum of the transformed data. We expect a running sum that is reflective of the remigration interval to result in higher accuracy than one that is not, as this would more closely approximate true numbers of adult females in the population.

Results

We applied both the Dennis et al. (1991) and the Holmes (2001) method to compute $\hat{\mu}$ and $\hat{\sigma}^2$ or $\hat{\sigma}_p^2$ for 800 simulated populations (Fig. 2), with sampling error incorporated as variance in the proportion of nesting females observed. A linear regression between estimates of process error (stochasticity), $\hat{\sigma}_p^2$, for the Holmes (2001) method and the total error, $\hat{\sigma}^2$, for the Dennis method resulted in a slope of 0.23, indicating that $\hat{\sigma}_p^2$ was generally lower than $\hat{\sigma}^2$ for the same population after time series length = 30 years (all 800 populations; Fig. 3). However, the confidence intervals of the estimate of $\hat{\sigma}_p^2$ for the Holmes (2001) method were wider than the

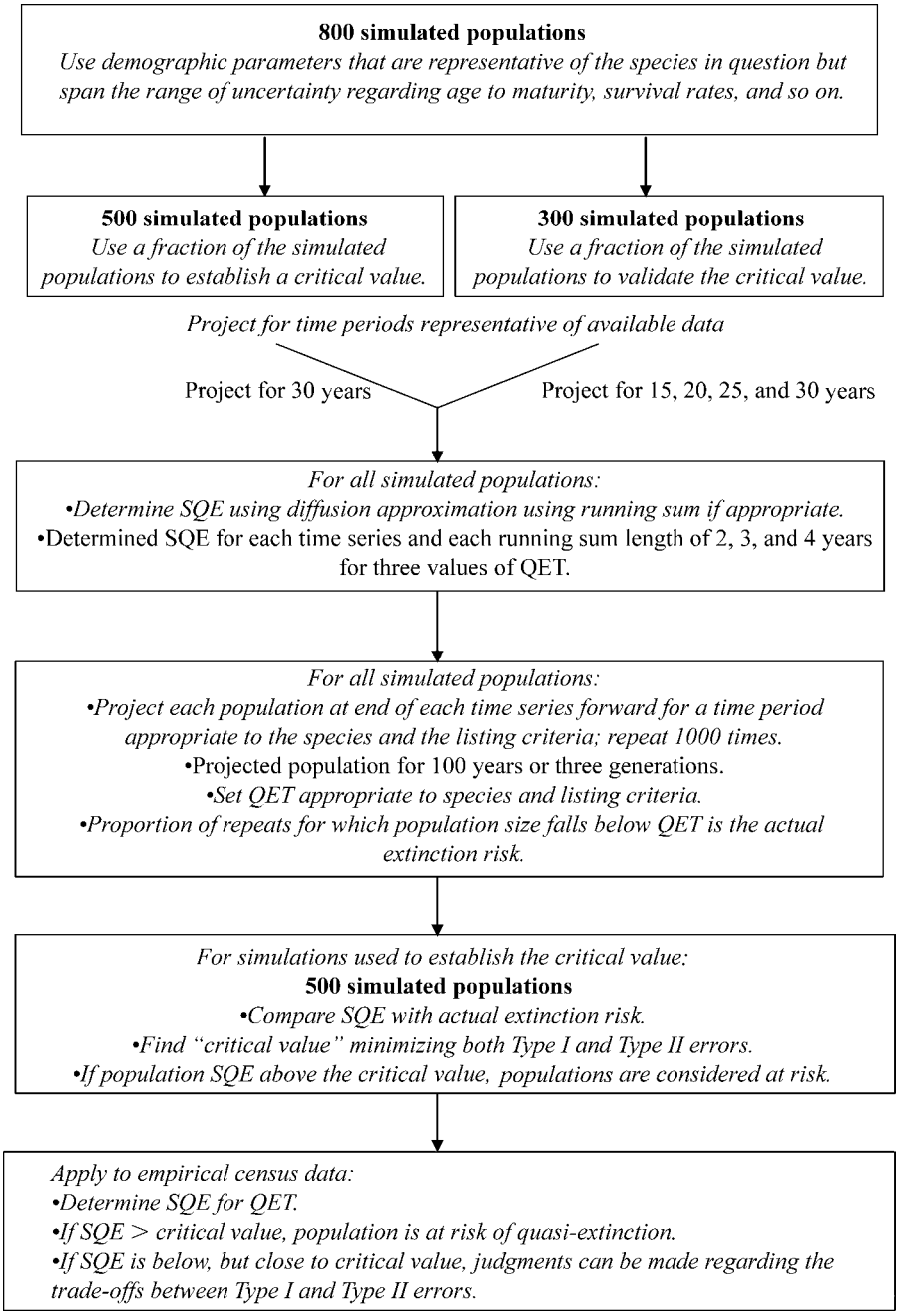

FIG. 2. Flow chart outlining the steps we followed to test and apply the susceptibility to quasi-extinction (SQE) metric. SQE is the proportion of replicates from the diffusion approximation that indicates a >90% chance of dropping below a predefined quasi-extinction threshold (QET). Italicized text indicates how the technique would be applied generally; additional text details the methods that we used for sea turtles. Values of QET = 50%, 70%, and 90% reductions in population size at the end of the time series were used. Type I error indicates finding a population to be at risk of quasi-extinction when it is not, whereas Type II error indicates finding a population to not be at risk of quasi-extinction when it is.

estimate of $\hat{\sigma}^2$ using the Dennis et al. (1991) method (from the 300 "populations" at different time series lengths; Fig. 4).

Susceptibility to quasi-extinction (SQE) is the proportion of the parametric bootstrap replicates that indicate a >90% chance of dropping below a predefined quasi-extinction threshold (QET). A linear regression of SQE resulting from the methods of calculating $\hat{\sigma}^2$ (Dennis et al. 1991) or $\hat{\sigma}_p^2$ (Holmes and Fagan 2002) resulted in a slope of 1.10, suggesting that the values were similar (time series length = 30 years; all 800 populations; QET = 50%; $R^2 = 0.83$; $P < 0.05$). SQE

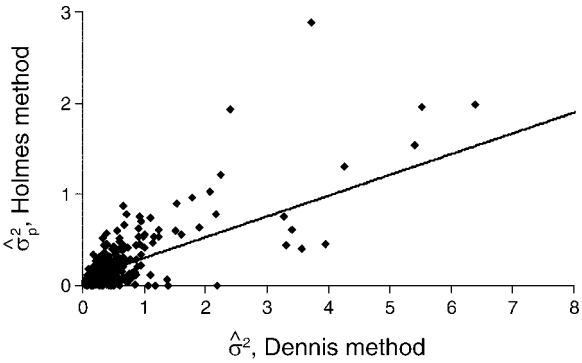

FIG. 3. Comparison of the mean value of $\hat{\sigma}^2$ from the Dennis et al. (1991) method vs. the process error, $\hat{\sigma}^2_p$, from the Holmes (2001) method for 500 simulated time series of observed nesting females. The solid line is a linear regression (slope = 0.23, $R^2 = 0.44$, $P < 0.05$).

incorporates both parameter uncertainty (variance of the estimate of $\hat{\sigma}^2$) and trajectory uncertainty ($\hat{\sigma}^2$). The Holmes method, based on a state–space model that decomposes the variance sources, gives less biased estimates of the true environmental variance, but at the cost of variance in the estimate of $\hat{\sigma}^2_p$. SQE combines these two variance costs, resulting in a high correlation between the SQE results of both methods.

The "actual" quasi-extinction risks resulting from the 500 simulated populations were highly correlated with the SQE value generated from diffusion approximation on the 30-year time series (Table 1). Approximately 95% of the actual quasi-extinction risks for the 500 model populations were either above 0.90 or below 0.10, allowing us to easily classify most populations' "actual risk." For the remaining 5% of the quasi-extinction risks, as noted in *Methods*, if the result indicated that >50% of the 1000 simulations for each model crossed the QET, it was considered at risk, and otherwise, not at risk.

Susceptibility to quasi-extinction (SQE) is based on parametric bootstrapping and must be assessed with a critical threshold probability value. In other words, the evaluation of risk to a population based on its current trajectory and variance requires a critical value for the proportion of replicates that have a high (>90%) probability of dropping below a QET. If this critical value is too high, there is a chance of Type I error, in which a population would be listed as "not at risk" when it actually has a high chance of dropping below a QET. On the other hand, if the critical value is set too low, there is a chance of Type II error, in which a population is assessed at a higher level of risk than it actually faces. To establish the critical value for SQE, we found the value that minimizes both Type I and Type II errors (Fig. 5). At each critical value, if the SQE for a population was greater than the critical value, it was assigned a value of "at risk"; otherwise, "not at risk." We found that a critical value between 0.35 and 0.45 was satisfactory for both methods and the three running sums (Figs. 5 and 6). This means that a species should be listed as "at risk" if 35–45% of bootstrapped replicates indicate a >90% probability of dropping below a predetermined QET. Based on our simulations, SQE with critical values correctly assessed quasi-extinction risk between 82% and 92% of the time (Fig. 7). Type I errors were less common than Type II errors and occurred with a frequency generally less than 10%. Decreasing the critical value for SQE could reduce the probability of underestimating risk if one is willing to increase the risk of Type II errors (Fig. 6).

Although confidence intervals for $\hat{\sigma}^2$ decline with increasing times series lengths (Fig. 4), above 15 years, the length of the time series did not have a large impact on the accuracy of the diffusion approximation (Fig. 7). This result would suggest that SQE is robust to estimates of $\hat{\sigma}^2$. For the 15-year time series, quasi-extinction risk was correctly assigned more than 80% of the time. Although this level of accuracy was generally lower than it was for the longer time intervals, it would still be possible to apply these techniques to the shorter time intervals. Generally, a 4-year running sum resulted in higher accuracies than a 2-year running sum, with 3-yr being intermediate, consistent with the declining 95% CI for $\hat{\mu}$ and $\hat{\sigma}^2$ with increasing time series lengths, although this trend was not always the case (Fig. 7).

Accuracies were generally highest for QET = 50% reduction of current population size and declined from there for reductions of 70% and 90%. Contrary to our expectations, choice of running-sum length had little influence on the accuracy of diffusion approximation results (Fig. 8). The two diffusion approximation methods used here and the different running-sum lengths affected the estimates of $\hat{\sigma}^2$, and SQE was relatively insensitive to these estimates (Table 1). Hence these results, the similarity of SQE for the two diffusion approximation methods, and the insensitivity of SQE to running-sum length, are not surprising.

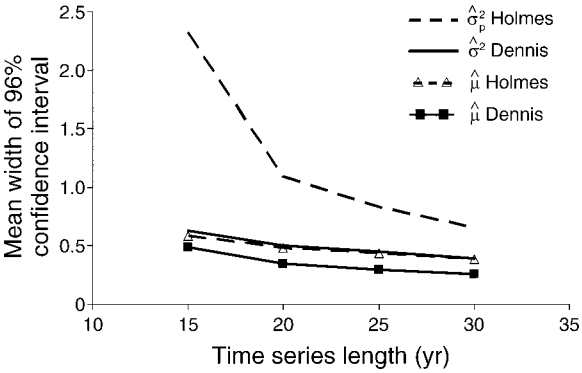

FIG. 4. The mean width of the 95% confidence intervals for parameters $\hat{\mu}$ and $\hat{\sigma}^2$ shown as a function of the length of the time series of simulated sea turtle nesting-beach data. The dashed line represents $\hat{\sigma}^2_p$ (process error) for the Holmes (2001) method; the solid line represents $\hat{\sigma}^2$ for the Dennis et al. (1991) method; the dashed line with open triangles represents $\hat{\mu}$ for the Holmes method; and the solid line with squares represents $\hat{\mu}$ for the Dennis method.

TABLE 1. Spearman rank coefficients (r_S) for various parameters and "actual" quasi-extinction risk as defined in *Methods: Population simulations.*

Parameter	r_S at "actual" quasi-extinction risk level		
	QET = 50%	QET = 70%	QET = 90%
Current population size	−0.790**	−0.776**	−0.694**
Estimated mean population growth rate, $\hat{\mu}$	−0.854**	−0.837**	−0.755**
Estimated variance of population growth rate, $\hat{\sigma}^2$	0.289**	0.266**	0.218**
SQE	0.863**	0.851**	0.777**

Notes: For susceptibility to quasi-extinction (SQE), the correlation coefficients represent the correlations at the same quasi-extinction threshold (QET) as the "actual" value: 50%, 70%, or 90% reductions from current population size (e.g., the correlation between the "actual" quasi-extinction risk at QET = 50% based on stochastic population simulations, and the SQE at QET = 50% is 0.863).

** Values are significant at $P < 0.005$.

APPLICATION OF THE METHOD

Estimates of extinction risk, as with any predictive models, are by nature uncertain. Extinction risk estimates are well-known to have very high uncertainty, because population dynamics are stochastic and because parameter estimates are uncertain (Holmes et al. 2007). The susceptibility to quasi-extinction (SQE) metric integrates both forms of uncertainty and allows scientists involved in listing decisions to formally balance the risk of Type I and Type II errors in management decisions. Under the IUCN listing criteria, when a population declines to 50% of the current population size over a three-generation time period, the population is given a listing of "concern"; a 70% reduction qualifies as "endangered" and a 90% reduction qualifies as "critically endangered," with some modification to these thresholds when mortality or habitat loss has not been addressed through conservation actions.

The methodology that we propose for marine turtles can be readily applied to nesting-beach data to ascertain listing status. Current population size should be estimated as the sum of the x most recent years, where x is the length of the running sum (i.e., 2, 3, or 4 years). Quasi-extinction values equal to 50%, 70%, and 90% of the estimated current population sizes can then be considered and SQE can be calculated using the methods presented here. Some assumptions regarding the time period being equal to three generations will need to be made, as there are imperfect data on age at maturity for most populations. If SQE is greater than 0.40, using diffusion approximation where $\hat{\mu}$ and $\hat{\sigma}^2$ are estimated as in Dennis et al. (1991) and a 3-year running sum, for any of the QET values, the nesting population would receive the most conservative listing. Based on our simulations, this results in a rate of Type I error of ~10%. Use of a lower critical value, 0.35 or 0.30, would lower this risk of Type I error but would result in much higher rates of Type II errors.

We demonstrate this method using three published data sets of leatherback nesting trends (Fig. 9): Parque Nacional Marine Las Baulas, Costa Rica (Tomillo et al. [2007]; data from 1988/1989–2003/2004; $N = 16$ years), St. Croix, U.S. Virgin Islands (Dutton et al. [2005]; data

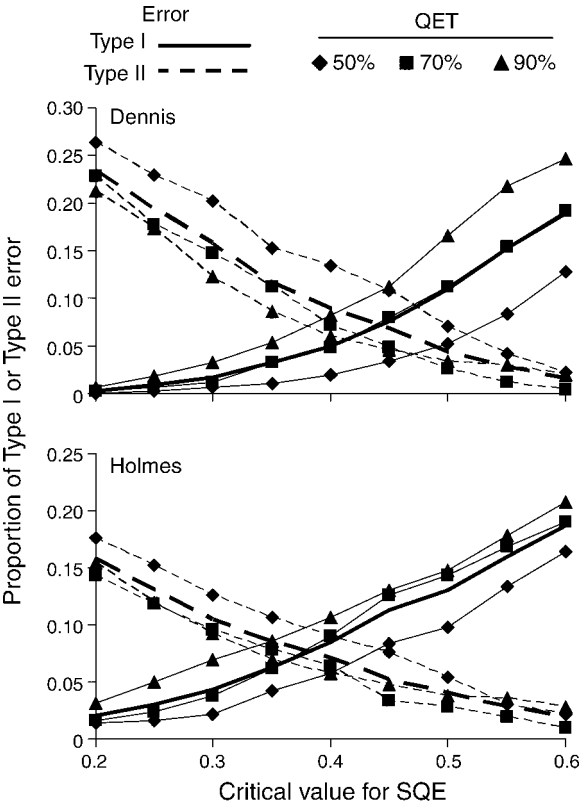

FIG. 5. The occurrence of both Type I error (failing to give an "at risk" assessment when a population is likely to drop below QET) and Type II error (giving an "at risk" assessment when a population is not likely to drop below QET) for simulated population assessments based on susceptibility to quasi-extinction (SQE). The top panel shows the results for the Dennis et al. (1991) method; the bottom panel shows results for the Holmes (2001) method. In both panels, heavy solid black lines represent the mean of the Type I error for all values of quasi-extinction thresholds (QET); lighter solid lines with different symbols show Type I error for QET = 50%, 70%, and 90%. The heavy dashed line is the mean of the Type II error for all values of QET; lighter dashed lines with different symbols show Type II error for QET = 50%, 70%, and 90%.

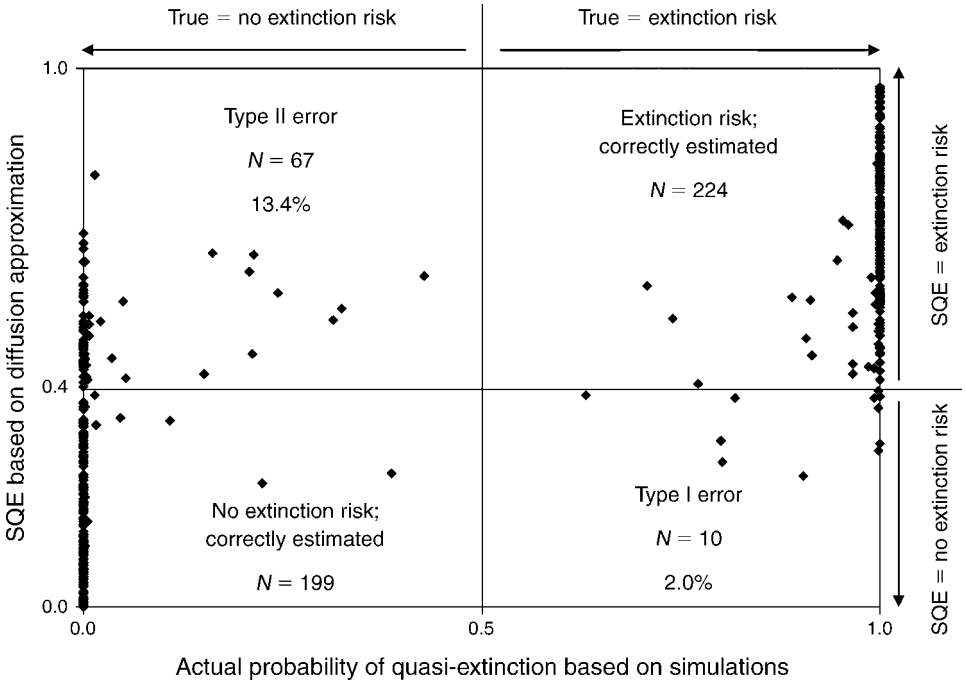

FIG. 6. Illustration of the method used to determine a critical susceptibility to quasi-extinction (SQE) value for evaluation of risk to sea turtle nesting-beach data. The plot compares the "actual" quasi-extinction risk evaluated by stochastic population simulations with the SQE risk metric for 500 simulated populations using $\hat{\mu}$ and $\hat{\sigma}^2$ from the Dennis et al. (1991) method and a quasi-extinction threshold (QET) of 50% of the starting population size. For "actual" quasi-extinction risk, the population was considered at risk if >50% of the simulations crossed the QET (vertical solid line). Shown here are the results of considering 0.40 as the critical value for SQE (horizontal solid line); see *Results* for details. In this example, extinction risk was correctly assigned as either risk or no risk for 84.6% of the populations.

from 1982–2001; $N = 20$ years), and KwaZulu-Natal, South Africa (Hughes [1996]; data from 1963–1994; $N = 32$ years). We used the mean value of age to sexual maturity of 14 years (Zug and Parham 1996), a 3-year running sum, and an adult survival rate of 0.90 to estimate a generation time of 21 years or a three-generation time period equal to 63 years. The SQEs for each of these populations were estimated using the diffusion approximation method, where the $\hat{\mu}$ and $\hat{\sigma}^2$ values were estimated as in Dennis et al. (1991).

Given the approach just outlined, the Costa Rica nesting beach, with $\hat{\mu} = 0.185$, $\hat{\sigma}^2 = 0.055$, and SQE > 0.95 at all quasi-extinction threshold values, would be listed as critically endangered (Table 2). The other two nesting beaches had SQE = 0 and would receive no listing (Table 2).

DISCUSSION

We present a new metric, the susceptibility to quasi-extinction (SQE), which is the proportion of a parametric bootstrap that indicates a high (defined as >90%) probability of quasi-extinction. Population simulations determined that SQE $\geq$ 0.40 (when $\geq$40% of the bootstrap samples indicated a probability of quasi-extinction $\geq$0.90) corresponded to populations that are at high risk of quasi-extinction. This approach yields more meaningful results than point estimates with large (often 0 to 1) confidence intervals that are typical of extinction risks. Instead, SQE considers the weight of the evidence by assessing the distribution of the quasi-extinction probabilities in the bootstrapped data and classifies populations as at risk or not at risk. Through population simulations we show that the classification is accurate more than 80% of the time for sea turtle nest census data, and that this rate of accuracy is easily increased by trading off Type I and Type II errors.

Because nest census data for sea turtles can be considered highly corrupt due to the high interannual variation caused by remigration intervals, numerous sources of observation error, and the fact that adult females represent a very small fraction of the total population (<2%; Crowder et al. 1994, Lewison et al. 2004), the accuracy of SQE in classifying risk in these populations suggests that this method can be useful for a variety of species and life histories. In terms of its ability to accurately assign quasi-extinction risk, SQE estimated using the diffusion approximation method where the $\hat{\mu}$ and $\hat{\sigma}^2$ or $\hat{\sigma}_p^2$ values were estimated as in the Dennis et al. (1991) or Holmes (2001) diffusion approximation models performed equally well for sea turtle nest census data and the time periods considered here. Because they are computationally simpler, the Dennis et al. (1991) methods for estimating trend and variance may be more tractable for management purposes. However, because

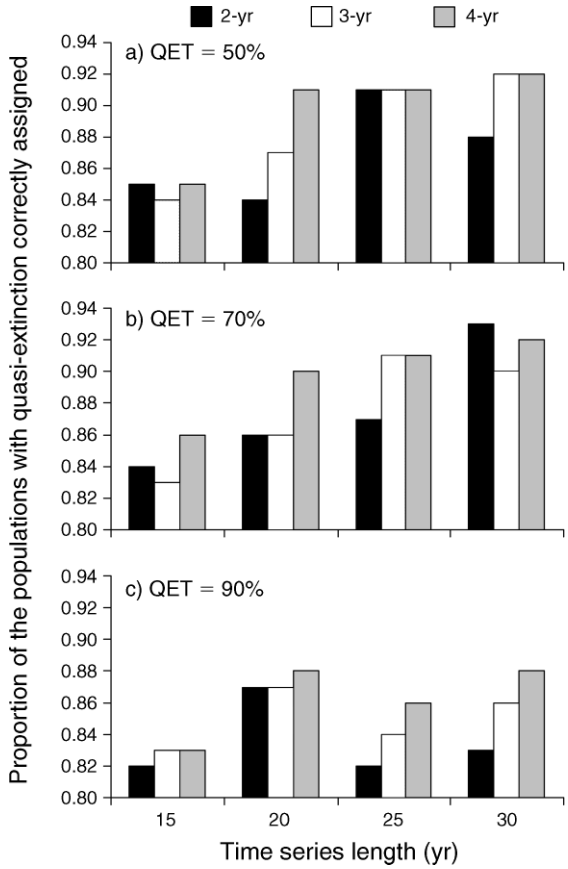

FIG. 7. The proportion of the 300 simulated populations with quasi-extinction risk correctly assigned for the three different running sums following Dennis et al. (1991) for calculations of $\hat{\mu}$ and $\hat{\sigma}^2$. Black bars represent a 2-yr running sum (critical value = 0.45), open bars represent a 3-yr running sum (critical value = 4.0), and gray bars represent a 4-yr running sum (critical value = 0.375). The three panels show values of quasi-extinction thresholds (QET) of (a) 50%, (b) 70%, and (c) 90% of current population size.

the variance estimates for the Dennis et al. (1991) method are biased, these estimates will not improve with increased data collection. The less biased variance estimates of Holmes (2001) will improve with increased time series lengths. Hence, for other species with more complete census counts (i.e., counts that include multiple life stages and individuals that have equal interannual resighting probabilities) and longer time series of data, the Holmes (2001) method is likely to perform better than the Dennis et al. (1991) method.

Longer time series are always desirable. Accuracy for the correct classification of a population (high vs. low risk of quasi-extinction) based on SQE increased for time series greater than 20 years, although SQE for the15-year time series still correctly assigned risk vs. no risk more than 80% of the time. We found the highest degree of accuracy with 3- and 4-year running sums, even when actual remigration interval was ~2 years. This is probably because increasing running-sum length decreases interannual variability and, hence, the variance around $\hat{\mu}$.

The language of the IUCN listing criteria poses the question that *if current conditions continue*, what is the likelihood of a population reaching a quasi-extinction threshold? As indicated in Appendix B, we incorporated a large amount of stochasticity into the population models; however, they are all driven by the exponential growth model in which population growth is density independent and the mean value of the demographic parameters remained the same through the entire time period, making the inherent assumption that current conditions remain the same. The SQE, in combination with the critical value above which the population is considered at risk, resulted in quasi-extinction risk assessments that were in close agreement with the

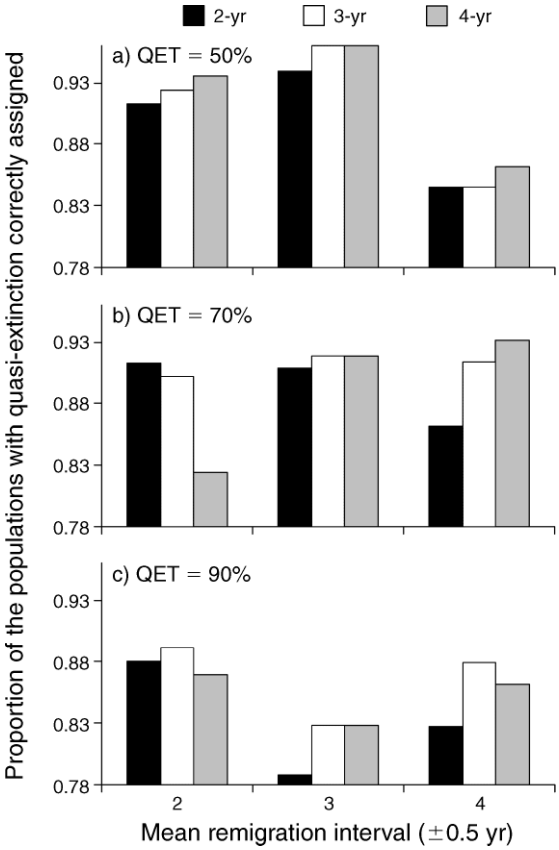

FIG. 8. Comparison of results of using a running sum descriptive of that known for the population vs. using a general running sum. Shown here are results using the Dennis et al. (1991) method of calculating diffusion approximation parameters. The *x*-axis is the true mean remigration interval for the populations, ±0.5. Three different running sums were then applied to each set of populations. Black bars represent a 2-yr running sum (critical value = 0.45), open bars represent a 3-yr running sum (critical value = 4.0), and gray bars represent a 4-yr running sum (critical value = 0.375). The three panels show values of quasi-extinction thresholds (QET) of (a) 50%, (b) 70%, and (c) 90% of current population size.

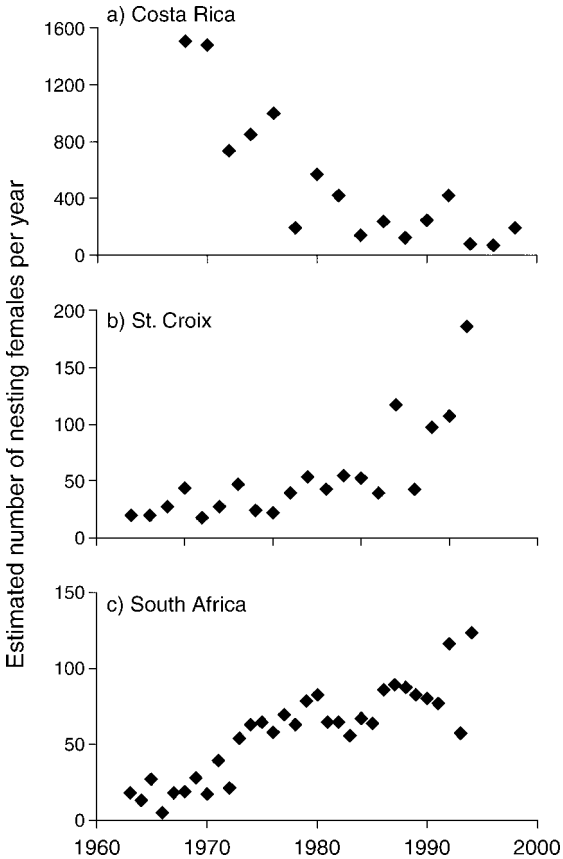

FIG. 9. Leatherback turtle nesting data for three leatherback nesting beaches in (a) Parque Nacional Marino Las Baulas, Costa Rica (Tomillo et al. 2007; data from 1988/1989–2003/2004, $N = 16$ years); (b) St. Croix, U.S. Virgin Islands (Dutton et al. 2005; data from 1982–2001, $N = 20$ years); and (c) KwaZulu-Natal, South Africa (Hughes 1996; data from 1963–1994, $N = 32$ years).

"actual" risk determined by the stochastic population models. Hence, although SQE may not be predictive, as current conditions are not likely to continue, it is a useful and accurate metric for categorizing populations consistent with IUCN listing criteria.

We did not explore the effects of density dependence in our simulations. For sea turtles, density-dependent impacts on vital rates have been noted only rarely (Bjorndal et al. 2000, Chaloupka 2001), and many populations are depleted in comparison to historic levels (Jackson et al. 2001). Hence, it is unlikely that density-dependent processes are important factors in most sea turtle populations today. In addition, the simple stochastic exponential growth model has been demonstrated in other simulation studies to adequately approximate complex population processes (Sabo et al. 2004, Staples et al. 2005, Holmes et al. 2007). Sabo et al. (2004) found that diffusion approximation using density-independent models of population growth gave reasonably appropriate assessments of extinction risk for populations with density-dependent processes. It is therefore likely that our methods could be successfully applied to species for which density-dependent processes are important considerations, but additional simulation analysis is warranted if density-dependent compensation or depensation is likely to have a strong effect on population growth rate.

Comparison of SQE with other methods for estimating uncertainty in risk estimation

Other studies have acknowledged the difficulties of dealing with uncertainty in the application of population viability analysis to management decisions. Ludwig (1996) compared Bayesian and frequentist approaches to demonstrate that the point estimates from frequentist statistics do not consider the uncertainty in population parameters and processes and, hence, tend to underestimate risk of extinction. He proposed that the Bayesian method highlights risks of early collapse that are rare, but plausible, in light of the data that frequentist approaches cannot consider. Although we used a frequentist approach, this bias in underestimating extinction risk was circumvented by considering only the fraction of the bootstrapped risk estimates that had a high value and then ground-truthing the methodology with population simulations and establishing a critical value. Because the critical value minimized Type I and Type II errors, there is no bias in the direction of the uncertainty incorporated in our method.

Sæther and Engen (2002) suggest the use of population prediction intervals (PPI), which are the smallest time intervals that include a decline to a quasi-extinction threshold, as a means of bypassing the uncertainties

TABLE 2. Susceptibility to quasi-extinction values calculated for three leatherback turtle nesting beaches.

Nesting beach	n_0	$\hat{\mu}$	$\hat{\sigma}^2$	QET 50%	QET 70%	QET 90%
Costa Rica	335	−0.185 [−0.326, −0.0439]	0.055 [0.029, 0.141]	1.000	1.000	0.978
U.S. Virgin Islands	390	0.104 [0.016, 0.191]	0.029 [0.016, 0.175]	0.000	0.000	0.000
South Africa	297	0.056 [−0.003, 0.116]	0.025 [0.016, 0.045]	0.000	0.000	0.000

Notes: The nesting beaches are in Parque Nacional Marino Las Baulas, Costa Rica (Tomillo et al. 2007; data from 1988/1989–2003/2004, $N = 16$ years); St. Croix, U.S. Virgin Islands (Dutton et al. 2005; data from 1982–2001, $N = 20$ years); and KwaZulu-Natal, South Africa (Hughes 1996; data from 1963–1994, $N = 32$ years). Values at three quasi-extinction thresholds (QET) of 50%, 70%, and 90% reductions from current population size (n_0), as estimated from the sum of number of nesting females for the last three years of the time series are reported. Estimates of mean population growth rate $\hat{\mu}$ and its variance $\hat{\sigma}^2$ are given with the 95% confidence limits in brackets.

inherent in longer time frames. They propose that the important metric in the face of uncertain population parameters is time to extinction, rather than the probability of extinction occurring. Holmes et al. (2007) found that PPIs can complement quasi-extinction risk estimates with wide confidence intervals. Similar to SQE, PPIs incorporate uncertainty both from stochasticity and from parameter uncertainty to draw inference about an unobserved stochastic variable. In this case, rather than risk of extinction, the variable is time to extinction. The drawback to PPIs is that they only realistically apply to declining populations, which is typical of populations for which population viability assessments are made. However, many protected populations are increasing and it is useful to have a metric that can place the status of these populations into the same context as declining population, such as with SQE.

Similar to the approach of Sæther and Engen (2002), Staples et al. (2005) recommends the use of shorter time frames, plus quasi-extinction thresholds that are close to current population size, which minimizes uncertainty in risk assessments. They suggest monitoring how risk changes over time, because this warns of future declines more readily and rapidly than any statistical tests for trends. The approach of Staples et al. (2005) in conjunction with the SQE metric proposed here may be a useful tool in monitoring populations over time. Increases or declines in SQE detected from the incorporation of new data over time may highlight recoveries or collapses much earlier than would traditional trend analyses.

Our approach to uncertainty is unique, although it can complement other approaches. There is a need in conservation biology decision making for formal decision theory frameworks for extinction risk assessment whereby managers weigh the potential costs of making an incorrect decision (Holmes et al. 2007). Although the SQE metric is a point estimate that does not explicitly state confidence intervals, error and uncertainty are still inherent in it, shown as the possibility of making Type I or Type II errors. Through simulations, these errors can be quantified. The SQE metric allows managers to formally balance the trade-offs between the risk of making a Type I error (leading to species decline or extinction) against the cost of making a Type II error (unnecessarily curtailing human activities that may affect a population).

Based on our simulation studies with age-structured exponential growth models, diffusion approximation and the SQE metric is a promising assessment tool that can be applied to sea turtle nest count data and, with additional validation, expanded to other species. The SQE metric provides a quantitative method to index current population status and allows for comparisons between populations. With the modifications presented, it can provide results that are meaningful and easily interpreted for management decisions.

Acknowledgments

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APPENDIX A

Details of the diffusion approximation method (*Ecological Archives* A019-032-A1).

APPENDIX B

Population simulations (*Ecological Archives* A019-032-A2).