The Reliability of Using Population Viability Analysis for Risk Classification of Species

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Abstract: *I examine whether or not it is appropriate to use extinction probabilities generated by population viability analyses, based on best estimates for model parameters, as criteria for listing species in Red Data Book categories as recently proposed by the World Conservation Union. Such extinction probabilities are influenced by how accurately model parameters are estimated and by how accurately the models depict actual population dynamics. I evaluate the effect of uncertainty in parameter estimation through simulations. Simulations based on Steller sea lions were used to evaluate bias and precision in estimates of probability of extinction and to consider the performance of two proposed classification schemes. Extinction time estimates were biased (because of violation of the assumption of stable age distribution) and underestimated the variability of probability of extinction for a given time (primarily because of uncertainty in parameter estimation). Bias and precision in extinction probabilities are important when these probabilities are used to compare the risk of extinction between species. Suggestions are given for population viability analysis techniques that incorporate parameter uncertainty. I conclude that testing classification schemes with simulations using quantitative performance objectives should precede adoption of quantitative listing criteria.*

Confiabilidad de el uso del análisis de Viabilidad Poblacional para claificacion de riesgo de especies

Resumen: *En el presente trabajo se examinó si es apropiado usar las probabilidades de extinción generadas por los análisis de viabilidad poblacional, basados en las mejores estimaciones para los parámetros del modelo, como criterios para el listado de especies en las categorías del Libro Rojo tal como fuera recientemente propuesto por la Unión Internacional para la Conservación de la Naturaleza. Las probabilidades de extinción están influenciadas por la exactitud con que son estimados los parámetros del modelo y por la exactitud con que el modelo describe la verdadera dinámica poblacional. En este estudio se evalúo el efecto de la incertidumbre en la estimación de los parámetros por medio de simulaciones. Se utilizaron simulaciones basadas en el león marino Steller para evaluar el sesgo y la precisión en las estimaciones de la probabilidad de extinción y para considerar el desempeño de dos esquemas de clasificación. Las estimaciones del tiempo de extinción estuvieron sesgadas (debido a la violación de la suposición de una distribución de edades estable) y se subestimaron la variabilidad de la probabilidad de extinción para un tiempo dado (debido principalmente a la incertidumbre en la estimación de los parámetros). El sesgo y la precisión en las probabilidades de extinción, son importantes cuando estas probabilidades son usadas para comparar el riesgo de extinción entre especies. Se sugieren técnicas de análisis de viabilidad poblacional que incorporan la incertidumbre en los parámetros. Concluyo que el análisis de los esquemas de clasificación con simulaciones usando objetivos de desempeño cuantitativos, debería preceder la adopción de criterios de listados cuantitativos.*

Introduction

The World Conservation Union (IUCN) is proposing to revise its scheme to classify species because new developments in conservation biology allow for the development of more objective and scientifically-based methods (Mace et al. 1992). Two schemes have been proposed (Table 1) (Mace & Lande 1991; Mace et al. 1992); their goal is to categorize species realistically based on their risk of extinction. Although the schemes offer qualitative and quantitative criteria, I address only a single quantitative criteria: the probability of extinction. The probability of a species going extinct, as estimated by a population viability analysis (PVA), is obviously of crucial importance and seems to offer a sound scientific basis upon which to make conservation decisions. But can we rely on PVA? How well does it really work? Before we use PVA as a method for categorizing species, we need to know how well we can estimate extinction probabilities and whether the categories, as defined by probabilities of extinction in the proposed classification schemes—critical, endangered, and vulnerable,—do justice to the risk facing various species. Ideally, biologists should be able to test the performance of the two schemes against a range of scenarios representing the range of species to be categorized, and I demonstrate the benefits of doing this through computer simulations. Through these simulations we can see what could happen when we apply the proposed schemes to an endangered species. Although I use only a single model, the analysis reveals imprecision and bias in estimates of extinction probabilities and differences in results between the two proposed categorization schemes.

Gilpin and Soulé (1986) created the process of PVA to provide a framework to integrate risk factors that contribute to the probability of extinction. PVA plays a valuable role in identifying major population risk factors within a species (Boyce 1992; Armbruster & Lande 1993; Haig et al. 1993). When we know little about important factors, such as adult survival rate, it is

Table 1.   Listing criteria for probability of extinction in a given time.

| Category[a] | Classification Scheme[b] | |
	Mace & Lande 1991	Mace et al. 1992
Critical	>50% in 5 years or 2 generations	>50% in 5 years or 2 generations
Endangered	>20% in 20 years or 10 generations	>20% in 20 years or 5 generations
Vulnerable	>10% in 100 years	>10% in 50 years or 10 generations

[a] Populations should be placed in a particular category if the probability of extinction matches one of the descriptions in the classification scheme.
[b] Number of years or number of generations, whichever is longer.

Table 2.   Age specific birth and survival rates based on York (1994).

| Age (years) | Leslie A | | Leslie B | |
	Survival	Fertility	Survival	Fertility
0	0.740	0.000	0.471	0.000
1	0.894	0.000	0.570	0.000
2	0.946	0.000	0.603	0.000
3	0.930	0.000	0.930	0.000
4	0.909	0.909	0.909	0.045
5	0.895	0.134	0.895	0.090
6	0.884	0.221	0.884	0.177
7	0.875	0.284	0.875	0.241
8	0.867	0.282	0.867	0.282
9	0.859	0.279	0.859	0.279
10	0.853	0.277	0.853	0.277
11	0.847	0.275	0.847	0.275
12–31	0.841	0.273	0.841	0.273

common practice to perform a sensitivity analysis spanning the possible range of values for adult survival rate (Ellis et al. 1993). Each estimate for adult survival rate produces a different distribution of extinction times. This approach can indicate how sensitive extinction times are to changes in adult survival rate, but it does not address the question of how to incorporate uncertainty in adult survival rate into a single distribution of extinction times. Usually, the PVA concludes with a distribution of extinction times based on the best estimates of parameters. The problem is that the risk factors that drive a PVA are much better known for some species than for others. Comparisons among species may therefore be misleading because the distribution of extinction times is based on a single set of parameter estimates and does not indicate the level of our ignorance concerning the species. If we are to use PVA as a common metric of risk among species, then we need to know how repeatable extinction-time estimates are within a species. This exercise follows the typical PVA protocol of using the best estimates for parameters to generate the distribution of extinction times. Although only a single species is considered, the exercise demonstrates the magnitude of the problem of the reliability of PVA extinction-probability estimates given the current PVA techniques.

Methods

Simulations are used to estimate precision and bias in estimated extinction times. I begin with a model with known parameters. This known model stochastically generates a known distribution of extinction times. Data sampled from the known model are used to estimate parameters for a PVA. This estimated model produces an estimated extinction-time distribution. Through repeated sampling of the known model, many data sets can be generated, and multiple estimated extinction dis-

tributions can be produced. These extinction distributions can then be used to assess bias and precision in the estimated extinction time distributions and to compare the performance of the proposed classification schemes.

The Known Model

To lend realism to the quantity and quality of data available for analysis, I based the known model on data used for risk assessment by the recovery team for Steller sea lions (*Eumatomias jubatus*) (National Marine Fisheries Service 1992). Data for this species are quite good. Counts of animals on all Alaskan breeding rookeries have been available since 1979 and for some rookeries date back to 1956. Counts are precise (coefficient of variation [CV] ≤ 0.05) and clearly document a dramatic decline that began in the eastern Aleutian Islands between 1960 and 1975. There are also data on age structure before and after the decline that can be used to estimate birth and survival rates (Calkins & Pitcher 1982; Calkins & Goodwin 1988). For most endangered species, fewer data of poorer quality are available. Any weaknesses revealed by these simulations will be magnified for the typical poorly-known species.

I chose two features of the collapse of Steller sea lion populations to incorporate in the model: the rate of decline and the spatial and temporal structure of the decline. In the known model, populations were governed by two Leslie matrices: Leslie *A*, which was zero growth (λ = 1), and Leslie *B*, which describes a decline (λ = 0.9). Lambda (λ) is the discrete rate of population growth and is the principal eigenvalue of the Leslie matrices. When the population is in stable age distribution, the dynamics are exponential growth:

$$N_{t+1} = \lambda N_t \qquad (1)$$

where N = population size, t = time, and λ = the discrete rate of population growth. The species is subdivided into populations that change from Leslie *A* to Leslie *B* at dates estimated from the data in the recovery plan. Environmental stochasticity is incorporated in first-year survival because survival of pups is known to vary with environmental conditions in many seals and sea lions (Trillmich & Ono 1991).

Thirty stochastic replicates of the known model were run. Each replicate produced a known extinction distribution. For each replicate, the following data were sampled for use in the estimated model: (1) estimates of abundance were recorded for the years when actual censuses occurred (Tables 5, 8, and 9 in National Marine Fisheries Service 1992; sampled from a lognormal distribution with mean = ln[abundance in known model], CV = 0.05), and (2) a random sample of females was taken from a single population before and after the start of population decline. These latter data

are used for estimation of birth and death rates. Details of this model are given in Appendix 1.

The Estimated Model

The form of the estimated model was very similar to the known model because plots of population trajectories strongly indicated that populations that remained at constant levels later exponentially declined. Data sampled from the known model were used to estimate (1) the population growth rate for Leslie *B*, (2) the dates for the start of decline for each population, and (3) the age-specific birth and death rates for Leslie *A* and Leslie *B*. Details of the estimation procedure are given in Appendix 2. Parameters were estimated for each of the 30 replicates. For each replicate, 100 simulations were run to obtain the estimated extinction distribution (schematic in Fig. 1). Note that because PVAs always require parameter estimation, the known model is not considered a PVA. References to PVA results refer to the estimated model.

Results

Problems with both bias and precision in probabilities of extinction can be seen in Fig. 2. Differences between curves in the known model (Fig. 2A) arise from stochastic population dynamics. Differences between curves in the estimated model (Fig. 2B) arise from both stochastic population dynamics and sampling error, which leads to uncertainty in parameter estimation. Each of the distributions in Figure 2B would be the result of a PVA that used the best estimates for all parameters. For the sake of clarity, consider the probability of extinction in 100 years. Probabilities of extinction in 100 years were, for the known model, mean = 0.76, range from 0.64 to 0.82, and for the estimated model, mean = 0.50, range from 0.12 to 0.89. For this statistic, the median was very close to the mean, so statistics assuming a Gaussian distribution are appropriate. The mean probability of extinction in 100 years for the known model (0.76) is significantly greater than that from the estimated model (0.50) (Student's *t*: $p \ll 0.01$, df = 29). The negative bias in probability of extinction in 100 years in due to positive bias in estimates for λ (estimated mean = 0.908, Student's *t*: $p \ll 0.01$, df = 29, range 0.897 to 0.916 [known mean = 0.900]). Probability of extinction in 100 years was also more variable between models: variance in probability of extinction between estimated replicates (0.0514) was greater than variance between known replicates (0.0018) (*F*-test: $p \ll 0.01$, df = 29). The net result is that for any single PVA (Fig. 2B) the estimate of the probability of extinction in 100 years is likely to be low and could be within a large range (probabilities from 0.12 to 0.89). Generation times (required by the schemes, Table 1) estimated by the PVA
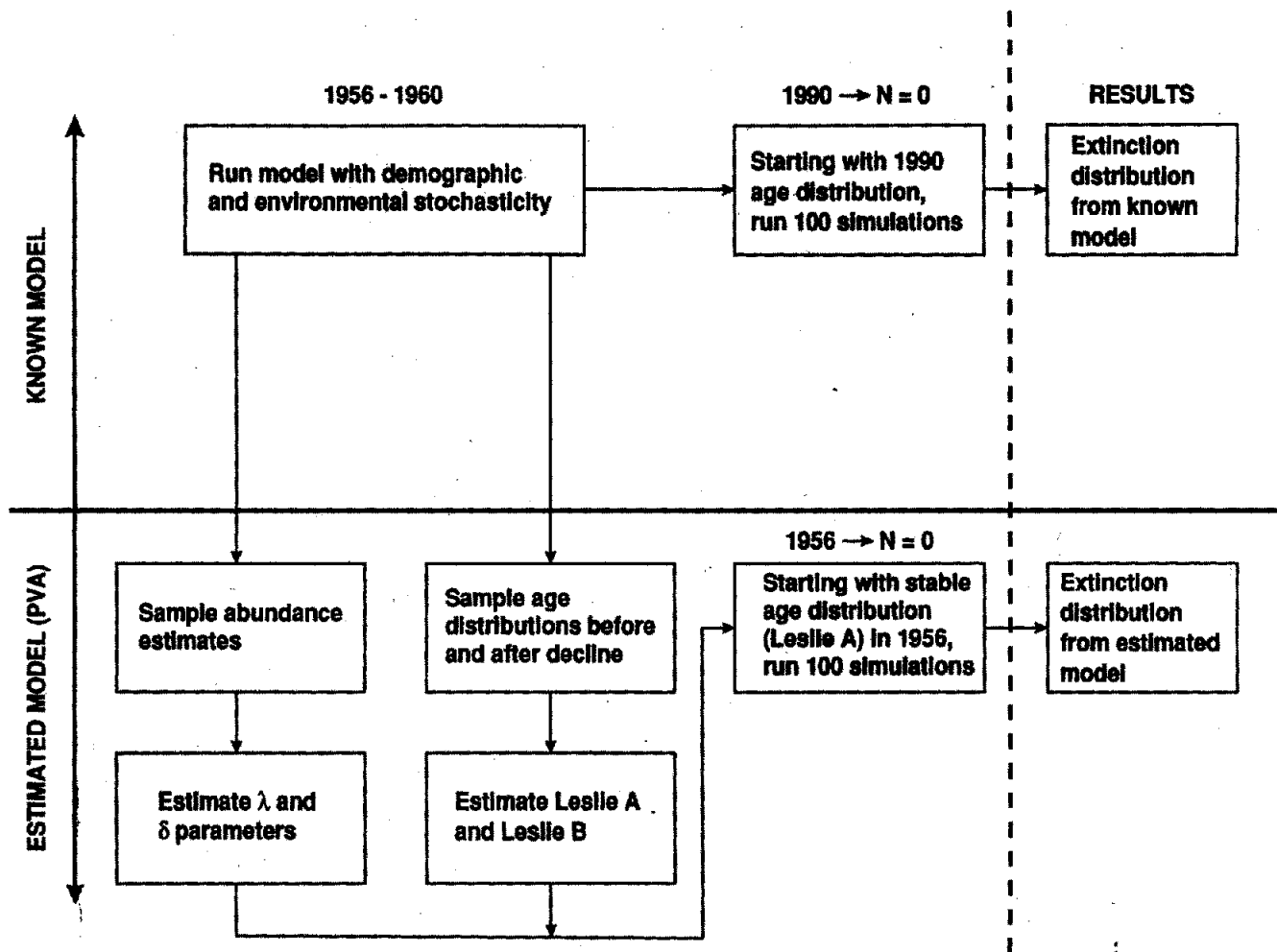
Figure 1. Schematic of a single replicate that is comprised of 100 simulations. Each replicate produces two extinction distributions, one for the known and one for the estimated model (Fig. 2A and 2B). Parameters are N = population size, λ = population growth rate, and δ = year of start of population decline (change from Leslie A to Leslie B).

(mean = 10.481, range 8.977 to 11.692) did not significantly differ from the known time (10.456).

Using the scheme of Mace and Lande (1991), all 30 replicates of the known model produced endangered classifications; 28 replicates of the estimated model produced endangered classifications and two produced vulnerable classifications. Using the scheme of Mace et al. (1992), all replicates of the known model produced vulnerable classifications; 28 replicates of the estimated model produced vulnerable classifications and two produced safe/low risk classifications.

Discussion

The results indicate that we are not ready to use PVAs, as they are currently done, to classify species. Although in this case most PVA replicates were classified in the

same category, for any given time the estimated probability of extinction varied widely. PVAs based on best estimates of parameters inadequately measure our true knowledge of the risk species face because uncertainty in parameter estimation is not incorporated into this measure of risk. The Steller sea lion simulations demonstrate that use of probabilities of extinction from a single PVA that used best estimates of unknown parameters may lead to widely differing results about species risk. For example, each of the distributions in Figure 2B represent possible PVA estimates of extinction times. These distributions are similar to what would be produced by commercial PVA packages. Differences are caused by small differences in sampling from the known model. Estimates of probability of extinction in 100 years vary dramatically, from 0.12 to 0.89. In order to understand how to improve PVA estimates, I will first review what caused the bias and precision problems in this example.
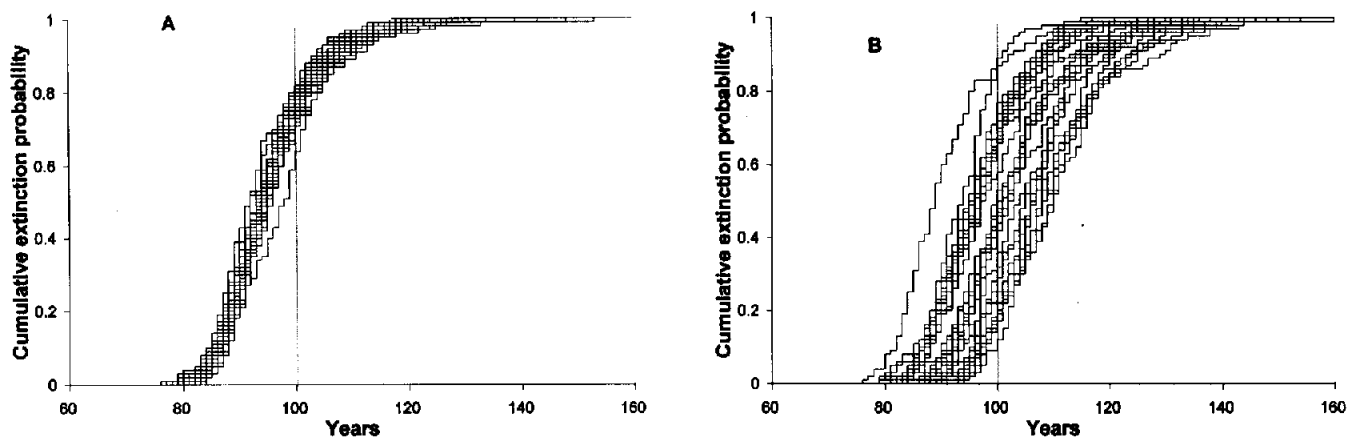
Figure 2. Cumulative extinction distributions for 30 replicates with 100 simulations per replicate of the known model (A) and the estimated model (B).

Extinction distributions from PVAs are highly sensitive to λ. Positive bias in the estimated λ increases mean extinction time (Fig. 2B). Even small shifts in λ cause large changes in the probability of extinction in 100 years because the distributions have small ranges (known: mean = 47.133, CV = 0.194; estimated: mean = 49.7, CV = 0.192). Within 50 years therefore, the probability of extinction went from zero to one. This accounts for the relatively large range in percentage of extinction in 100 years for even the known model. A seemingly trivial bias in λ (<1%) has a dramatic effect on bias of the probability of extinction. Use of the slope of a regression to estimate λ assumes stable age distribution. The bias in λ occurred primarily because none of the populations had reached stable age distribution when λ was estimated. Not including variance in pup survival in the estimated model decreased percentage of extinction in 100 years by 1% and is therefore a minor contributor to the 36% difference in the mean percentage of extinction in 100 years between the known and estimated extinction distributions. Modelers should consider whether the assumption of stable age distribution is likely to be met and consider the consequences of violating this assumption.

The difference between the extinction distributions from the known and estimated models is not only in the bias in probability of extinction (indicated by the mean probability of extinction in 100 years) but is also in the precision of the probability of extinction (indicated by the range in probability of extinction in 100 years). The differences between the curves for the known model (Fig. 2A) are caused by demographic and environmental stochasticity. The greater "width" in the extinction curves for the estimated model (Fig. 2B) is due to uncertainty caused by parameter estimation. Thus, we have considered two types of uncertainty: uncertainty caused by the probabilistic nature of biology and uncer-

tainty caused by estimating parameters used in models to depict nature. It is the latter type that contributes most of the uncertainty in predicting extinction. We are, therefore, on shaky ground in estimating extinction from any single distribution in Fig. 2B, that is in basing our estimates on a single PVA.

Although current PVA techniques are inadequate to estimate probability of extinction for use as a common metric, incorporating uncertainty is not an insurmountable technical problem. Numerous techniques have been used to incorporate parameter uncertainty into models (Deriso et al. 1985; De la Mare 1989; Methot 1989; Hilborn & Walters 1992; Raftery et al. 1992; Wade 1994). It is beyond the scope of this paper to introduce techniques to incorporate uncertainty in parameter estimation into extinction probabilities. It is useful, however, to consider how changing PVA techniques affects the choice of classification criteria. In the spirit of understanding the implications of including uncertainty in parameter estimates into PVA, I use a very simple model as an example. For this hypothetical model, two pieces of information are available: a time series of abundance estimates (Fig. 3) and a range of estimates of variance in population growth rates taken from several different studies (0.05 ≤ CV ≤ 0.20). As more data are acquired, parameter estimates become more certain. In order to examine the effect of uncertainty, I will compare two scenarios: a well-known case with a 25-year time series available and a poorly-known case with only the last 5 years of abundance estimates available. Given the data, the probability of various growth rates is evaluated to obtain probability distributions for the two scenarios (Fig. 4). For details on how to calculate such distributions, see Raftery et al. (1992) and Wade (1994). For each scenario, 1000 simulations can be done as follows: (1) randomly choose a mean population growth rate from the appropriate distribution in
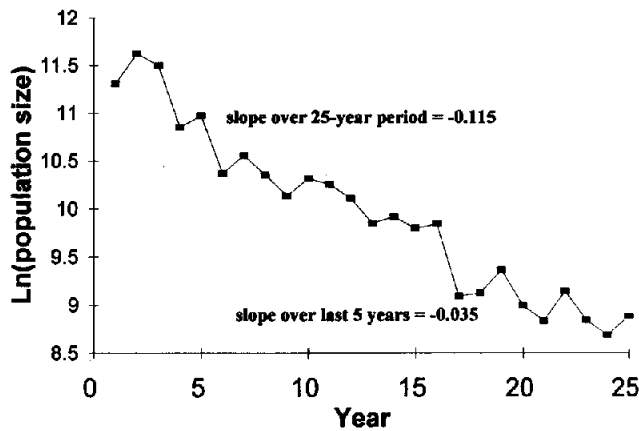
Figure 3. A randomly generated time series of abundance estimates. Parameters for the known model were λ = 0.9, CV for λ = 0.1, CV for abundance estimate = 0.2. The estimated λ for the 25-year period = 0.89 [ln(-0.115)], for the last five years = 0.97 [ln(-0.035)].

Figure 4; (2) randomly choose a CV for growth rate from the uniform distribution from 0.05 to 0.20; (3) for each year within a simulation, choose an annual growth rate from the distribution described by the mean and CV just chosen; (4) project the population until less than one individual remains.

The resulting extinction distributions differ dramatically, reflecting our greater knowledge about the well-known case (Fig. 5). The known distribution (mean λ = 0.9, CV = 0.1) is shown to highlight the effect of including uncertainty in parameter estimates, although in practice scientists will never know the true-parameters or resulting distribution. The most obvious effect is that the range of possible extinction times is increased with increasing uncertainty. This appears visually as a flattening of the cumulative extinction probability curve. Our
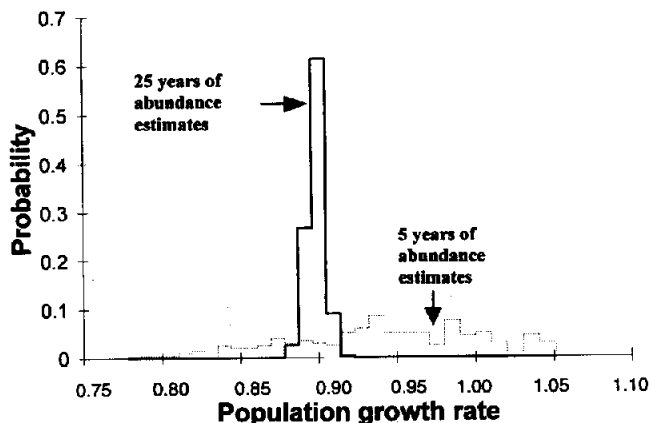

Figure 4. The probability of various population growth rates (λ), given the data in Figure 3.
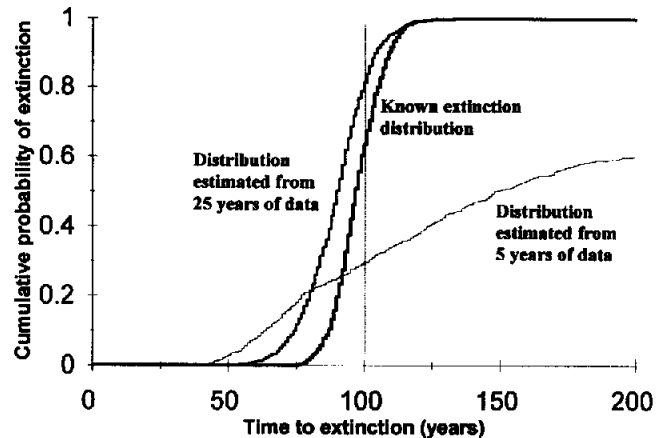

Figure 5. Cumulative extinction probability curves for a known model and two models that incorporate uncertainty in parameter estimation. Both estimated models use a uniform distribution for CV of λ (0.05 $\leq$ CV $\leq$ 0.20). Growth rates are chosen from the distribution in Figure 4 appropriate for the number of years of available data. The distribution for the poorly known case includes some probability of positive exponential growth (λ > 1), which results in infinite extinction times.

ignorance about the species means that we may under- or overestimate extinction times. Decisions need to be made despite uncertainty. In order to err on the side of species conservation, decisions should be based on criteria chosen to yield conservative decisions. Current criteria are based on a probability of extinction in a given time—for example a 20% chance in 100 years. Figure 5 shows that at 100 years the curve that includes the most uncertainty underestimates the probability of extinction. The best guarantee of a conservative criterion would be to choose a low probability of extinction. For example, if our classification criterion read "the year in which a population has a 5% chance of extinction is less than 100 years," we would have a good chance of making a conservative classification decision. Note that, using this criterion, the time to extinction increases as precision increases. For example, the time to reach a 5% chance of extinction increases from 56 to 70 years as the case goes from poorly to well known. Thus, this criterion provides an impetus to improve our knowledge of the population.

I have demonstrated that incorporating uncertainty in parameter estimation is important, and other work indicates that it should be technically feasible. Uncertainty in model choice, however, may require more than a technical fix to PVAs. The variance in extinction estimates would have been much greater had I given the 30 data sets to different modelers. The structure of a PVA depends on many decisions made by the modeler based

on her or his understanding of the population. What is the appropriate level of complexity? Is a density-dependent model or an exponential model warranted? At their root these questions concern the philosophy of conservation: Should models contain built-in conservatism? Should model choice reflect the cost of making mistakes in model choice? I chose here to address uncertainty in parameter estimation that can be approached with standard scientific methods. This alone was enough to answer the question of whether or not we are ready to use PVA to classify species. A full answer to how well we can estimate extinction probabilities requires conservation biologists to come to some consensus on model choice, which is both a technical and philosophical problem.

My second objective was to assess whether the proposed classification schemes did justice to the risk presented to species. This simulation exercise demonstrated not only that the two schemes perform quite differently but that the criteria for the scheme of Mace et al. (1992), which categorized two replicates as safe/low risk, may be insufficiently conservative (that is, not accurately represent the real risk to the species). Certainly using a suite of models representative of the species to be categorized would provide further insights into the performance of the schemes. Comparison of different schemes would be greatly facilitated by the use of quantitative objectives. For example, given a model with an actual probability of extinction that classifies it as endangered, simulations will not be classified as vulnerable with a probability of more than 5% nor as critical with a probability of more than 10%. Such an approach using quantitative management objectives has been nicely demonstrated in the revised management plan developed for the International Whaling Commission for the commercial harvest of whales (Donovan 1989). With quantitative objectives, not only could scheme performance be compared, but schemes could be refined to give better performance.

A final comment on including quantitative criteria in classification schemes in an attempt to make such schemes "more objective and scientifically-based" concerns the burden of proof (Belsky 1984). Numerous species, such as the Steller sea lion, could qualify for Red Data Book listing only under quantitative criteria—extinction probability or trends in abundance. Gathering data for such quantitative estimates is costly. Requiring a given probability of extinction (or trend) as criteria for listing could, unless defined very carefully, put the burden of proof on scientists in a manner detrimental to the species of concern. Being forthright about uncertainty in estimating extinction probabilities will require conservation biologists to communicate clearly to managers and policy makers why uncertainty is a necessary part of managing small populations and why uncertainty must be directly addressed in laws and regulations that manage small populations.

Literature Cited

Armbruster, P., and R. Lande. 1993. A population viability analysis for African elephant (*Loxodonta africana*): How big should reserves be? Conservation Biology 7:602–610.

Barlow J., and P. Boveng. 1991. Modeling age-specific mortality for marine mammal populations. Marine Mammal Science 7:50–65.

Belsky, M. H. 1984. Environmental policy law in the 1980s: Shifting the burden of proof. Ecology Law Quarterly 12:1–88.

Boyce, M. S. 1992. Population viability analysis. Annual Review of Ecology and Systematics 23:481–506.

Calkins, D. G., and E. Goodwin. 1988. Investigation of the declining sea lion population in the Gulf of Alaska. Alaska Department of Fish and Game, Anchorage.

Calkins, D. G., and K. W. Pitcher. 1982. Population assessment, ecology and trophic relationships of Steller sea lions in the Gulf of Alaska. Pages 447–546 in Environmental assessment of the Alaskan continental shelf. U.S. Departments of Commerce and Interior, Washington, D.C.

De la Mare, W. K. 1989. The model used in the Hitter and Fitter programs. Report International Whaling Commission 39:150–151.

Donovan, G. P., editor. 1989. The comprehensive assessment of whale stocks: the early years. The International Whaling Commission, Cambridge, England.

Deriso, R. B., T. J. Quinn, and P. R. Neal. 1985. Catch-age analysis with auxiliary information. Canadian Journal of Fisheries and Aquatic Sciences 42(4):815–824.

Ellis S., S. Leatherwood, M. Bruford, Z. Kaiya, and J. Seal. 1993. Baiji (*Lipotes vexillifer* population and habitat viability assessment—preliminary report. Species 20:25–29.

Gilpin, M. E., and M. E. Soulé. 1986. Minimum viable populations: The processes of species extinctions. Pages 13–34 in M. E. Soulé, editor. Conservation biology: The science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts.

Haig, S. M., J. R. Belthoff, and D. H. Allen. 1993. Population viability analysis for a small population of Red-cockaded Woodpeckers and an evaluation of enhancement strategies. Conservation Biology 7:289–301.

Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York.

Mace, G. M., and R. Lande. 1991. Assessing extinction threats: Toward a reevaluation of IUCN threatened species categories. Conservation Biology 5:148–157.

Mace, G., N. Collar, J. Cooke, K. Gaston, J. Ginsberg, N. Leader Williams, M. Maunder, and E. J. Milner-Gulland. 1992. The devel-

opment of new criteria for listing species on the IUCN red list. Species 00:16–22.

Methot, R. D. 1989. Synthetic estimates of historical abundance and mortality for Northern Anchovy. American Fisheries Society Symposium 6:66–82.

National Marine Fisheries Service. 1992. Recovery plan for the Steller Sea Lion (*Eumatopias jubatus*). Prepared by the Steller Sea Lion Recovery Team for the National Marine Fisheries Service, Silver Springs, Maryland.

Raftery, A. E., G. H. Givens, and J. E. Zeh. 1992. Inference from deterministic population dynamics models about bowhead whale (*Balaena mysticetus*) replacement yield. Technical Report 232. University of Washington, Seattle.

Trillmich, F., and K. A. Ono, editors. 1991. Pinnipeds and El Niño: Responses to environmental stress. Springer-Verlag, Heidelberg, Germany.

Wade, P. 1994. Abundance and populations dynamics of two eastern Pacific dolphins, *Stenella attenuata* and *Stenella longirostris orientalis*. Ph.D. dissertation. University of California, San Diego.

York, A. E. 1994. The population dynamics of northern sea lions, 1975–1985. Marine Mammal Science 10:38–51.

Appendix 1.

The Known Model

Steller sea lion populations began declining in the center of the species' range some 30 years ago and have not yet shown decline in some areas (southeast Alaska). The model subdivided the species into the six Alaska populations delineated in the recovery plan: western Aleutian Islands (WAI), central Aleutian Islands (CAI), eastern Aleutian Islands (EAI), western Gulf of Alaska (WGA), central Gulf of Alaska (CGA), southeast Alaska (SEA) (National Marine Fisheries Service 1992). I estimated dates for the start of decline for populations (δ_{pop}) from census data (NMFS 1992), as follows:

$$\delta_{pop} = N_{first} + t \text{ and} \tag{2}$$

$$t = \frac{\log\left(\frac{N_{last}}{N_{first}}\right)}{\log \lambda}, \tag{3}$$

where t = years from N_{first} when λ becomes 0.9, N_{first} = population size from first census, N_{last} = population size from last census (1992), and λ = discrete rate of population growth (0.9).

Start of decline of south east population (δ_{SEA}) (1997) was estimated by regressing the δ_{pop} for other populations against their distance from EAI (the population with the earliest δ_{EAI}). Leslie *B* assumed a multiplicative decrease in survival rates for ages zero to three and a decrease in fertility from age five through eight, relative to Leslie *A* (Table 2). The model included variability in survival of the first age class (CV = 0.1). The variability in first-year survival necessitated an iterative solution such that the long term realized λ = 0.9.

I ran 30 replicates of the model. Each replicate started in stable age distribution for Leslie *A*. Simulations started in 1956, and abundances for each population were assumed to be the same as they were for N_{first}. There was no movement between populations. Simulations were Monte Carlo and changed δ_{pop} years after the first census from Leslie *A* to Leslie *B* for each population. For each replicate, data were sampled and the age distribution of populations in 1990 was saved. Starting from the same 1990 age-specific population vector, 100 trials were run of population trajectories to obtain a known extinction distribution.

Appendix 2

The Estimated Model

In 1976 and 1982, 120 females were sampled from CGA (δ_{CGA} = 1977, similar to actual data sampled), and age and pregnancy status were recorded. I estimated each population's δ_{pop} (except SEA) by regressing years when the population size was significantly less than the starting 1950s population against time. δ_{pop} was estimated as the year when the function would intersect N_{first}. For Leslie *B*, λ was estimated as the mean of regressed slopes for the populations. δ_{SEA} was estimated by regressing δ_{pop} for the other populations against their distance from EAI. Leslie *A* was estimated using the 1976 sample of CGA females and a program to estimate survival rates (Barlow & Boveng 1991). The likelihood of the decline being due to reductions in age-specific birth or death rates was investigated by comparing the expected age distribution in 1982 to the observed distribution using decreases in survival and birth rates for different combinations of ages. The change that generated the highest Kolmogorov-Smirnov probability was used to generate Leslie *B*. PVA simulations started in stable age distribution for the estimated Leslie *A* in 1956. For each replicate, 100 simulations were run to generate the estimated extinction distribution. The PVA model was a Monte Carlo simulation. No environmental variability was included because there are no data on variability in birth and death rates for Steller sea lions.