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Implications of three viability models for the conservation status of the western population of Steller sea lions (*Eumetopias jubatus*)

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Abstract

Two distinct viability models are developed for Steller sea lions (*Eumetopias jubatus*) to evaluate the sensitivity of extinction risk to various levels of stochasticity, spatial scale and density dependence. These models include a metapopulation model, Analysis of the Likelihood of Extinction (ALEX; Possingham et al., 1992; Possingham, H., Davies, I.A., Noble, I. 1992. ALEX 2.2 Operation Manual. Department of Applied Mathematics, University of Adelaide, Adelaide, SA 5005; Australia.), and a model that incorporates both sampling and process error in estimating population parameters from timeseries data (Gerber and DeMaster, 1999; Gerber, L.R., DeMaster, D.P. 1999. An approach to endangered species act classification of long-lived vertebrates: a case study of north Pacific humpback whales. Conservation Biology 13 (5);1203–1214.). Results are compared with a third model that encompasses three different geographic scales (York et al., 1996; York, A.E., Merrick, R.L., Loughlin, T.R. 1996. An analysis of the Steller Sea lion metapopulation in Alaska. In: McCullough, D.R. (Ed.), Metapopulations and Wildlife Conservation. Island Press, Covelo, CA pp. 259–292). The combination of modeling approaches provides a basis for considering how model parameterization and the selection of classification criteria affect both model results and potential status determinations. Results from the models generally agree with regard to central tendency, 25th and 75th percentile times to extinction. For Steller sea lions, the distributions of time to extinction for each model were narrower than the range of extinction distributions between models. If this finding applies generally to listed species, it would suggest that more than one viability model should be considered when listing decisions are made. On a more applied basis, the results of our analysis provide a quantitative assessment of extinction risk of Steller sea lions in the context of its status pursuant to the US Endangered Species Act.

Keywords: Steller sea lions; Criteria; Endangered Species Act; Status; Population model; Population viability analyses (PVA)

1. Introduction

There has been much dissatisfaction among conservation biologists regarding the way decisions are made with respect to listing species as endangered or threatened under the United States Endangered Species Act of 1973 as amended (ESA; Tear et al., 1993; Wilcove et al., 1993; Easter-Pilcher, 1996). Listing criteria generally are more qualitative than quantitative, and often they are overtly arbitrary. There are several tools for quantifying endangerment (IUCN, 1994), but each approach has drawbacks and limitations. In addition, critical data often are lacking. In light of the broadly perceived lack of objectivity in making ESA conservation decisions, population viability analysis (PVA) offers an approach to making classification decisions less arbitrary and more grounded in scientific information by allowing explicit estimation of the likelihood that a population will persist for a particular time period (IUCN, 1994; Taylor 1995; Akcakaya et al., 2000). However, while several PVAs have been conducted, the application of results to conservation decisions has been limited (Ralls and Taylor, 1997; Beissinger and Westphal, 1998). Moreover, some have argued that PVA should not be used for management decisions, because model results are highly dependent upon estimated parameters (Boyce, 1992; Ludwig, 1999).

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In this paper we examine the degree to which population viability models for Steller sea lions (*Eumetopias jubatus*) influence ESA and IUCN classification decisions, given uncertainty in population parameters. Steller sea lions offer an interesting example to consider PVA and listing decisions. Among marine mammals for which reasonable population estimates are available, Steller sea lions are by far the most abundant species to be listed as "endangered" pursuant to both the ESA and the IUCN (Table 1). This suggests that the ESA status of Steller sea lions may be inconsistent with other listed mammals, at least in the context of population size. Since there is no single consensus PVA approach to the classification of species in peril, it is important to ask to what extent management decisions (such as listing or delisting) are dependent on arbitrary decisions about selection of a specific PVA (Mills et al., 1996) for Steller sea lions.

To consider the implications of PVA for determining the status of Steller sea lions, two structurally distinct PVA models are developed in order to compare the sensitivity of extinction distributions to various levels of stochasticity, spatial scale and density dependence. These include a metapopulation model, Analysis of the Likelihood of Extinction (ALEX; Possingham et al., 1992) and a model that incorporates both sampling and process error in estimating population parameters from timeseries (see Gerber and DeMaster, 1999, for methods as applied to North Pacific humpback whales). Results from these models are compared with an existing metapopulation model that encompasses three different geographic scales (York et al., 1996). Thus, we compare outcomes of five models: (1) the ALEX simulation package; (2) methods developed by Gerber and DeMaster, 3) a spatially local population dynamics model developed by York et al., (3) a metapopulation model developed by York et al.; and (4) an aggregate model developed by York et al. based on entire survey areas. We focus on comparison of the models as applied to the western population of Steller sea lions, in the context of IUCN and ESA classification criteria. This combination of modeling approaches allows us to consider how model parameterization affects model results and how the selection of classification criteria may influence status determinations.

2. Steller sea lion distribution, population structure, status and management criteria

Steller sea lions range from southern California around the Pacific Rim to northern Japan, with most of the world population occuring between the central Gulf of Alaska and the western Aleutian Islands (Loughlin et al., 1987). Two separate populations of Steller sea lions are currently recognized within USA waters: an eastern population, that includes animals east of Cape Suckling, Alaska (144° west longitude), and a western USA population, that includes animals at and west of Cape Suckling. Hereinafter we focus exclusively on the western population of Steller sea lions. This population, that currently includes 39,500 animals (Hill et al., 1997), has declined in numbers by approximately 64% since the 1970s (Loughlin et al., 1992, Figs. 1 and 2).

Steller sea lions were listed as a threatened species under the provisions of the ESA in December of 1990 (55 FR 49204). The Steller Sea Lion Recovery Plan [National Marine Fisheries Service (NMFS) 1992] suggested that reclassification should only occur when the species recovered to 90,000 adult and juvenile animals at trend sites in the Kenai–Kiska area, or roughly the estimated abundance in the mid-1970s. Similarly, the species should be listed as endangered when trend counts become less than 17% of this benchmark value (15,300 animals); if trend counts exceed 17% but are less than 40% (>15,300 animals; <36,000 animals), the species should be listed as threatened (NMFS 1992). Delisting was recommended to occur when the trend count is greater than 40% of the benchmark (>36,000), or when the number of animals is stable or increasing in at least three of the six survey regions (NMFS, 1992). Because these standards were perceived as arbitrary, they were not accepted by NMFS. To date, no explicit criteria have been used in establishing the species' status.

The Recovery Plan (NMFS, 1992) for the species reports that quantitative measures such as PVA or trend analysis would provide a robust estimation of the likelihood of extinction. York et al. (1996) developed three spatially distinct metapopulation models to investigate the population's persistence assuming a range of population structures and characteristics. These predictions, the IUCN's classification of Stellers as endangered, and other information about population trends from 1990 to 1993 influenced NMFS to reevaluate the status of the species (NMFS, 1995). In October 1995, the NMFS proposed that the western population be listed as endangered, while the eastern population remain threatened (69 FR 192). This status determination was approved and finalized in May 1997. In the following section we summarize the methods and results of two distinct models applied to the western stock of Steller sea lions, and we compare our results with those of York et al. (1996).

3. Model description

3.1. Model No.1: ALEX

To provide a comparison with a generic PVA program, a number of package programs, including

Table 1
Classification of the western population of Steller sea lions under the IUCN classification scheme

Criterion	Rank[a]
Critically endangered	
A. Population reduction in the form of either:	
1. An observed, estimated, or inferred reduction of at least 80% over the last 10 years or 3 generations;[b]	N
2. A reduction of at least 80%, projected or suspected to be met within the next 10 years or 3 generations;	
B. Extent of occurrence estimated to be less than 100 km^2 or area of occupancy estimated to be less than 10 km^2, and estimates indicating any 2 of the following:	
1. Severely fragmented or known to exist at only a single location.	
2. Continuing decline, observed, inferred or projected, in extent of occurrence, area of occupancy, area or quality of habitat, number of locations or subpopulations, number of mature individuals.	N
3. Extreme fluctuations in area of occurrence, area of occupancy, number of locations or subpopulations, number of mature individuals.	
C. Population estimated to number less than 250 mature individuals and either:	
1. An estimated continuing decline of at least 25% within 3 years or 1 generation, whichever is longer or,	N
2. A continuing decline, observed, projected or inferred, in numbers of mature individuals and population structure in the form of either severely fragmented (i.e. all subpopulations contain less than 20 mature individuals), or all individuals are in a single subpopulation.	
D. Population estimated to number less than 50 mature individuals	N
E. Quantitative analysis showing the probability of extinction in the wild is at least 50% within 10 years or 3 generations, whichever is longer.	N
Endangered	
A. Population reduction in the form of either of the following:	
1. An observed, estimated, inferred or suspected reduction of at least 50% over the last 10 years or 3 generations, whichever is the longer.	Y[c]
2. A reduction of at least 50%, projected or suspected to be met within the next 10 years or 3 generations, whichever is the longer.	
B. Extent of occurrence estimated to be less than 5000 km^2 or area of occupancy estimated to be less than 500 km^2, and estimates indicating any 2 of the following:	
1. Severely fragmented or known to exist at no more than 5 locations.	N
2. Continuing decline, observed, inferred or projected, in extent of occurrence, area of occupancy, area or quality of habitat, number of locations or subpopulations, number of mature individuals.	
3. Extreme fluctuations in area of occurrence, area of occupancy, number of locations or subpopulations, number of mature individuals.	
C. Population estimated to number less than 2500 mature individuals and either:	
1. An estimated continuing decline of at least 20% within 5 years or 2 generations, whichever is longer or,	N
2. A continuing decline, observed, projected or inferred, in numbers of mature individuals and population structure in the form of either severely fragmented (i.e. all subpopulations contain less than 250 mature individuals), or all individuals are in a single subpopulation.	
D. Population estimated to number less than 250 mature individuals.	N
E. Quantitative analysis showing the probability of extinction in the wild is at least 20% within 20 years or 5 generations, whichever is longer.	N
Vulnerable	
A. Population reduction in the form of either of the following:	
1. An observed, estimated, inferred or suspected reduction of at least 20% over the last 10 years or 3 generations, whichever is the longer.	Y[c]
2. A reduction of at least 20%, projected or suspected to be met within the next 10 years or 3 generations, whichever is the longer.	
B. Extent of occurrence estimated to be less than 20,000 km^2 or area of occupancy estimated to be less than 2000 km^2, and estimates indicating any 2 of the following:	
1. Severely fragmented or known to exist at no more than 10 locations.	N
2. Continuing decline, observed, inferred or projected, in extent of occurrence, area of occupancy, area or quality of habitat, number of locations or subpopulations, number of mature individuals.	
3. Extreme fluctuations in area of occurrence, area of occupancy, number of locations or subpopulations, number of mature individuals.	
C. Population estimated to number less than 10,000 mature individuals and either:	
1. An estimated continuing decline of at least 10% within 10 years or 3 generations, whichever is longer or,	N
2. A continuing decline, observed, projected or inferred, in numbers of mature individuals and population structure in the form of either a) severely fragmented (i.e. all subpopulations contain less than 1000 mature individuals), or all individuals are in a single subpopulation.	
D. Population very small or restricted in the form of either of the following:	
1. Population estimated to number less than 1000 mature individuals.	N

(*continued on next page*)

Table 1 (*continued*)

Criterion	Rank[a]
2. Population is characterized by an acute restriction in its area of occupancy (typically less than 100 km^2) or in the number of locations (typically less than 5). Such a taxon would thus be prone to human and stochastic events.	
E. Quantitative analysis showing the probability of extinction in the wild is at least 10% within 100 years or 5 generations, whichever is longer.	Y

[a] "Y" indicates the criterion is met, "N" indicates that it is not met.

[b] Generation time is assumed to be approximately 8.5 years for Steller sea lions, based on the average age of reproductively active females.

[c] The western North Pacific population of Steller sea lions declined by approximately 67% between 1985 and 1994 (NMFS, 1995). Assuming a generation length of 8.5 years, 3 generations are equivalent to 25.5 years. During past 24 years, (1970–1994), the population declined by approximately 77%.

RAMAS (Ferson et al., 1988), VORTEX (Lacy et al., 1995), NEMESIS (Gilpin, 1993), and ALEX (Possingham et al., 1992) were considered. Of these programs, ALEX was selected because it incorporates metapopulation dynamics, allowing relatively isolated population patches to have different growth rates and population sizes. Also, stochasticity may be incorporated by defining the probability of occurrence and maximum impact on population and biomass of different types of catastrophes. ALEX is based on a simple age structure of only three classes of individuals (newborn, juvenile, adult); there is no genetic component, and only one sex is counted (generally females). There are four primary parameter fields included in the model, including species data, catastrophe data, movement data and patch data (see Possingham et al., 1992 for description). In our view these features collectively suggest that ALEX is plausibly consistent with the known population biology of Steller sea lions. Later we describe the application of this model to Steller sea lions, focusing specifically on how we parameterized each of these four model components.

The species data contain basic life-history characteristics, including age composition and age-specific birth and death rates. Based on mortality estimates for females (York, 1994), we assumed a 0.22, 0.15, and 0.14 probability of death per year for newborns (0–1 years), juveniles (1–4 years) and adults (4–30 years), respectively, and a 0.3 probability of an adult female (age 8 to 30) giving birth to one female offspring per year. Population units within the metapopulation were defined

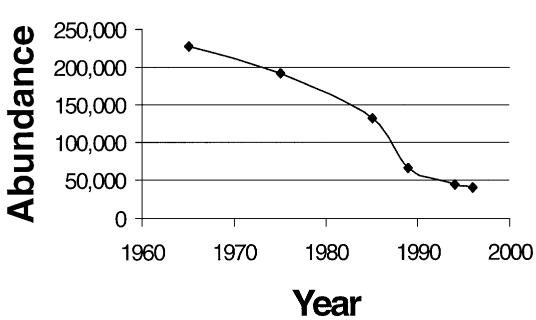

Fig. 1. Trends in total abundance of the western stock of Steller sea lions (data from NMFS, 1995).

based on groupings of rookeries in the Central Gulf of Alaska, Western Gulf of Alaska, Eastern Aleutian Islands, and Central Aleutian Islands (CGOA, WGOA, EAI and CAI and respectively, Fig. 2). Phylogeny and geographic information and a cluster analysis indicated that adjoining rookeries had common trends in these areas (Dizon et al. 1992; Louglin 1994; York et al. 1996). Steller sea lions are not known to migrate, and although a small degree of dispersal may occur between subpopulations, we assumed a zero probability of migration. Because the effect of migration between subpopulations may increase persistence time, our results may be biased toward a shorter time to extinction if undocumented migrations occur. A population extinction threshold of 10 individuals for each of the four subpopulations was assumed for each simulation.

The proportion of the initial population that currently exists was also specified (K). Estimates of carrying capacity were based on counts of adult and juvenile Steller sea lions in the Aleutian Islands and Gulf of Alaska in the late 1950s and early 1960s (Kenyon and Rice, 1961; Mathison and Lopp, 1963; Table 2, Fig. 2). Because coefficients of variation are not reported for these references, we consider this assumption for K to be highly tentative. It is possible that these estimates are biased high if carrying capacity has declined since this time. Current population sizes are 0.25, 0.22, 0.09 and 0.31 for the CGOA, WGOA, EAI and CAI, respectively.

The catastrophe parameter field allows for incorporation of the frequency, effect and spatial scale of catastrophes. Model parameters include the probability of catastrophe, the scale of the catastrophe, and the extent to which a catastrophe may impact population size and population biomass. Simulations were conducted using the same assumptions as York et al. (1996) and Gerber and DeMaster (1999) so that results are comparable. Thus, stochasticity was specified as a 25% probability of catastrophe occurring resulting in a 15% population reduction (corresponding to York et al.'s level of environmental disturbance).

Subpopulation patch areas were determined using Computer Aided Mapping and Resource Inventory System (CAMRIS; Ecological Consulting, Inc., Portland, OR, USA). Based on home range estimates for

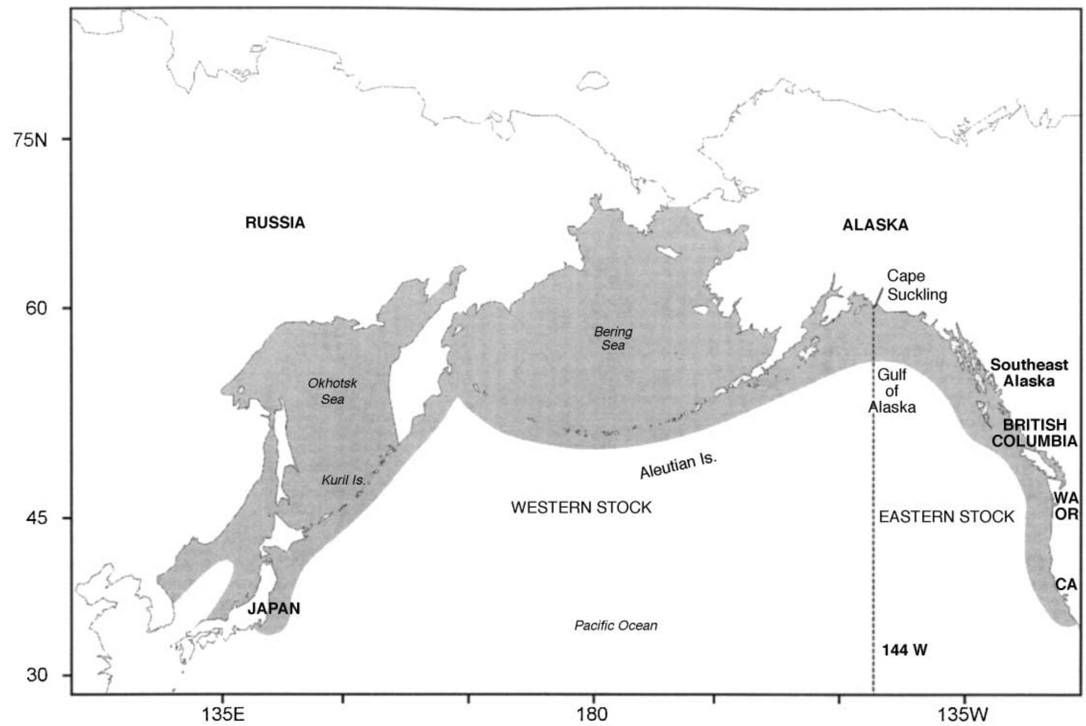

Fig. 2. The Steller sea lion is distributed around the North Pacific Ocean rim from Japan through the Kuril Islands and Okhotsk Sea, Aleutian Islands and central Bering Sea, southern coast of Alaska and south to the Channel Islands, California. The population is divided into Western and Eastern Stocks at 144° W longitude (from NMFS, 1992).

Table 2
Values for carrying capacity (K) considered in ALEX modeling effort[a]

	Assumed carrying capacity
Central Gulf of Alaska	35,150
Western Gulf of Alaska	24,320
Eastern Aleutian Islands	52,530
Central Aleutian Islands	28,115
Total	140,115

[a] Historical K is based on counts of adult and juvenile Steller sea lions in the Aleutian Islands and Gulf of Alaska in the late 1950s and early 1960s. Data from CGOA and WGOA are from Mathisen and Loop (1963); data from EAI and CAI are from Kenyon and Rice (1961). Coefficients of variation are not reported in these references, however Kenyon and Rice report that "an error of 6 to 10 percent" is inherent in the survey method used (photographs of animals taken during aerial surveys).

Steller sea lions (Merrick, 1996), it was assumed that sea lions forage within 300 km of shore during months other than the reproductive season, and that they generally occur shoreward of the 200 m depth contour (Kajimura and Loughlin, 1988). Patch area (km^2) was computed as polygon area less terrestrial habitat area.

As a relative measure of minimum living area for individual sea lions, the area of each patch was divided by the carrying capacity of the female portion of the population. Recognizing that habitat for sea lions is three-dimensional but that data about the vertical distribution of habitat is limited, we made the simplifying assumption of two-dimensional habitat as a relative measure of minimum living area. Similarly, the minimum breeding area was calculated by dividing the area of each patch by the number of breeding females (the number of mature females at carrying capacity multiplied by the probability that an adult female breeds multiplied by the proportion of adult females in the entire population). To calculate the minimum number of breeding females, it was assumed that at least 50% of the population is adult female, thus $0.5\times K$ was considered. We assumed this minimum estimate for percent breeding females because (1) Steller sea lions often forage as a group and do not have distinct territories, yet (2) during most of the year females are more common than males because males disperse away from islands after breeding while females remain. Thus, although local populations are always at least 50% female, because there are no distinct territories, we consider this value as a minimum estimate for percent breeding females. This was done for each of the four subpopulations. For example, applying this approach to the Central Gulf of Alaska results in the following estimates:

$$\begin{aligned} &\textit{Number of breeding females} = 0.5 \times \mathrm{K} \times \\ &\mathrm{P(adult\ female\ breeds)} \times \mathrm{P(adult\ females)} \\ &= 0.5 \times 35,150 \times 0.87 \times 0.31 \\ &= 4740 \end{aligned} \quad (1)$$

Minimum breeding area = patch size calculated using CAMRIS * (0.5) / number of breeding females

$$= 320,200\text{km}^2 \times 0.5/4740$$
$$= 34\text{km}^2 \qquad (2)$$

3.2. Model No. 2: Gerber and DeMaster approach to ESA classification

The second model differs from the ALEX in including less biological detail, and in being analytical, rather than simulated. Secondarily, it differs in being explicitly tied to ESA criteria. This model provides an alternate approach to the IUCN classification scheme for classifying Steller sea lions under the ESA. For the purpose of classifying a population's risk of extinction under the ESA, Gerber and DeMaster (1999) considered two attributes of population viability: (1) population size and (2) the population growth rate corresponding to the lowest 5% of the frequency distribution of likely growth rates ($\lambda_{.05}$). These attributes comprise both average tendencies to increase or decrease and variability about these tendencies due to intrinsic variability in population growth rates. To incorporate variability in growth rates Gerber and DeMaster extracted a maximum likelihood estimator of growth rate and confidence interval about that growth rate (using methods described in Dennis et al., 1991) on the assumption that the population changes can be approximated by a simple diffusion process with drift.

In the present study, we apply this approach to Steller sea lions, using abundance data for 1965–1997 (Fig. 1) to determine status under the ESA. In particular, we first ask whether there is a greater than 5% chance that the population will fall below a specified critical level (500) during the next 10 years (defined as the threshold level for endangerment). If the answer is yes, then the population should be listed as endangered. If the answer is no, we determine whether the population should be listed as threatened. To do this, we adopt a longer time horizon and ask if there is a greater than 5% chance of the population falling below 500 during a 35 year time period. If the answer is yes, then the population is categorized as threatened. If the answer is no (i.e. it is unlikely to fall below 500 during the next 35 years), then the species should be delisted altogether. The 0.05 probability specified in the criteria may be changed depending on what is considered an acceptable level of risk. Further, the selection of appropriate time periods should be approved by the policy-makers responsible for management. As our initial population size, we began with the most recent (1996) abundance estimate. While the Dennis et al. approach does not include observation error, we incorporated sampling error in the form of confidence limits. In lieu of simply taking the most recent estimate at face value, we decided to be more precautionary and use the lower bound of the 95% percent confidence interval about the last population estimate. The timeframes of 35 years and 10 years were not biological decisions, but rather were suggested by a panel of NMFS scientists as the longest timeframe over which the agency could reasonably engage in planning (Gerber and DeMaster, 1999).

4. Results

Median, first and third quartile time to extinction for all models are given in Fig. 3. To apply the Gerber and DeMaster approach to classifying species to Steller sea lions, we can use the recent abundance estimates reported by Hill et al. (1997) to determine the lower bound ($N_{\min}$) of the estimated 95% confidence interval for the best estimate of abundance. Using the Gerber and DeMaster approach, the probability that $N_{\min}$ will decline to an abundance level below the critical threshold in 10 years is greater than 0.05 if $\lambda_{(.05)}$ is $\leqslant$ 0.65. Thus, because $\lambda_{(.05)}$ from our analyses (0.83) was greater than the threshold level for endangered (0.65) but less than the threshold level for threatened (0.88), based on the criteria nested in our model, our results would be consistent with classification of Steller sea lions as threatened under the ESA. The Dennis model used in this approach can also be used to estimate median time to extinction, which was 62 years, with a first and third quartile time to extinction of 53 and 71.

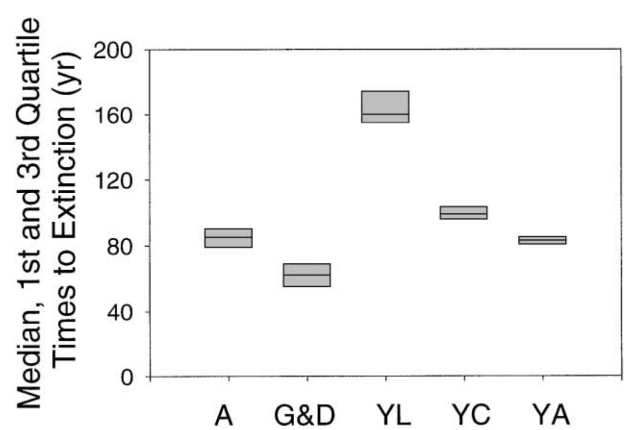

Fig. 3. Median, first and third quartile times to extinction, where A = ALEX; G&D = Gerber and DeMaster; YL = York-local; YC = York-cluster; YA = York-aggregate. Boxes represent within model variability, whereas differences between boxes show among-model variability. Average pairwise differences between the 1st, 2nd, and 3rd quartiles within models was 10 years while the average pairwise difference among models was 43.3 years. The average maximum difference in estimates of times to extinction was 15.0 years within models (third quartile minus first quartile) and 37.7 years among models.

5. Discussion

5.1. Comparison to York et al. (1996) multi-scaled metapopulation model

York et al. (1996) developed three models that consider different spatial scales to predict the persistence of the Steller sea lion. Scales for spatial models corresponded to Hanski and Gilpin's (1991) definition of a metapopulation; including a rookery model (local scale), a cluster of rookeries model (cluster or metapopulation model) and an aggregate model based on survey areas from Kenai to Kiska, Alaska (geographic scale, see York et al., 1996). York et al. used the Dennis et al. (1991) stochastic diffusion approximation for density-independent population growth, applied to counts of adult female sea lions at each of the scales to project populations. The distribution of future population size for 200 years was simulated 1000 times for each rookery and cluster. The number of animals remaining at each rookery or cluster was totalled to estimate the annual Kenai–Kiska population and the rookery totals were summed within each year to derive the distribution of total population size at time t. York et al. (1996) recorded individual rookery extinctions in a similar fashion. In the current analyses we consider the distributions for the local, cluster and the aggregate models reported in York et al. (1996) as a basis for comparison with our models.

For the York et al. rookery model, the results indicate that the median estimated time to reach a specified extinction threshold of 10 was 160 years. The first and third quartile times to extinction were 153 and 179 years, respectively. This relatively high probability of overall persistence was due to a positive growth rate at five small rookeries. Consequently, the rookery model predicts that some or all of these sites could persist beyond 100 years, regardless of extinction of other rookeries. For York et al.'s cluster of rookeries, a cluster analysis was used to determine spatial population structure. The estimated rates of decline among the clusters of rookeries varied over both space and time. The median, first and third quartile times to reach the threshold population level of 10 females were 99, 95 and 105 years, respectively. The relatively high persistence of the population in the cluster model was due to the positive growth rates in the Western Gulf of Alaska cluster. Finally, for the aggregate model, York et al. (1996) note that the observed rate of decline has varied over time. The population was found to have declined at a significantly higher rate (15.6% per year, S.E. = 1.8, $P < 0.001$) during 1985–1990 (as compared with prior to 1985 or after 1990). York et al.'s population projections were then based on the assumption that about 25% of the time the population was declining at 15.6%; this increased rate of decline was considered to reflect catastrophic stochasticity. They report that the median time, first and third quartiles to reach 10 females were about 83, 80 and 86 years, respectively.

Of the three spatial analyses following York et al., the rookery model results in the longest mean persistence time and the geographic model the shortest. All models were based on the assumption that fundamental vital parameters of the population will behave as they have since the mid-1970s. That is, there was no density dependent regulation incorporated into the models. Also, the rate of increase was capped at 0.15 to constrain interannual variability to a biologically reasonably level. York et al. (1996) suggested that the choice of model has only a marginal effect on results, and that taken together, the models provide a reasonable range of the population's probability of persistence.

5.2. Model consistency and implications for population status

Developing a PVA requires not only decisions about what type of model structure represents the dynamics of the population, but also the choice of a meaningful model output to represent a population's persistence. Groom and Pascual (1997) suggested that reporting the mean or median time to extinction without the associated variance can hide information, especially if there is substantial uncertainty. To compare PVAs, Gilpin (1993) contended that the best measure of population viability is the distribution of times to extinction. Because the entire distribution for the York et al. model was not available, and the format for the output for the ALEX model is not consistent with that for the Gerber and DeMaster model (see Gerber, 1998), three points on the extinction curve were compared for each of the three models. We propose that consideration of three points on the extinction distribution accurately represented these distributions (Fig. 3).

Although the models vary in spatial structure, in whether density dependence is incorporated, and in the type and method of stochasticity used, estimates of median time to extinction do not differ drastically, with the exception of the York et al. rookery model (Fig. 3). Because the estimate of median extinction time for the rookery model is considered to be an outlier (York, personal communication), we decided to test how model comparisons changed when this model was eliminated. The timespan between individual estimates of time to extinction between models was substantially reduced when the rookery model was eliminated. In both cases (with and without the rookery model), the first and third quartile times to extinction did not deviate substantially from the median time to extinction (Fig. 3). This is a surprising result in light of the emphasis in recent literature on considering the full distribution of times to extinction. In all cases, the differences in time to extinction between models were much greater than that within a particular model (Fig. 3). For example, the average difference between all pairwise combinations of first, second, and third quartile times to extinction within each model was 10.0 years. The average difference between combinations among models was 43.3 years. The average maximum difference (third quartile minus first quartile) in estimates of times to extinction was 15.0 years within models and 37.7 years among models. This suggests that consideration of multiple viability analyses can be informative in estimating extinction risk. The primary shortcoming of all approaches is lack of data on general life history of the species that might allow for a particular model to be used based on the biology of the species, and a lack of data on the rate at which catastrophic events might occur and the consequences of such events.

5.3. Implications of PVA models for ESA and IUCN classification

These results may be useful in determining the ESA status of Steller sea lions. Table 1 identifies each of the IUCN criteria under the threatened category for critically endangered, endangered and vulnerable, and ranks Steller sea lions within each category. First, it should be noted that Steller sea lions meet IUCN criterion A for endangered, based on a population reduction of at least 50% over the last three generations. Focusing specifically on criterion E, which specifies different levels of extinction risk for each category, results of all three models meet the classification criteria for vulnerable as defined by the IUCN. Under no circumstances did the probability of extinction within 20 years exceed 20%, and all models indicated that within 100 years the species had at least a 10% probability of extinction (Table 1). For example, results of applications of the ALEX and York et al. (1996) models meet the classification criterion E, for vulnerable as defined by the IUCN (Mace and Lande, 1991). The Gerber and DeMaster (1999) model provides an alternate classification approach to that developed by the IUCN. Results from this analysis are consistent with a recommendation to classify the western population of Steller sea lions as threatened, pursuant to ESA. If we assume that the IUCN category of vulnerable is comparable to the ESA category of threatened, results of the Gerber and DeMaster model would be consistent with the results of the ALEX and York et al. (1996) models, where status was considered within the IUCN scheme. This comparison suggests that the IUCN's PVA criterion may be robust to the fact that uncertainty is not explicitly included in the scheme. Nonetheless, to formally develop a recommendation for the ESA status of Steller sea lions, model uncertainty should be incorporated into a single measure of extinction risk.

Our results should be no surprise to conservation biologists who are familiar with the paucity of data available for imperiled species. Because PVAs typically are based on limited data, they should be viewed as tools to compare relative risk among populations. For Steller sea lions, we found that results from three distinct viability models generally agree. But is this an artifact of the data available for Steller sea lions being uniquely unambiguous? In cases where species data are highly uncertain, model output is likely to be less precise, thereby limiting the potential use of such models in conservation decisions. For Steller sea lions, the distributions of time to extinction for each model were narrower than the range of extinction distributions between models. This suggests that distributions of times to extinction for more than one model should be considered in determining the conservation status for imperiled species.

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