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**Endangered Species Act Status of the Western Population of Steller Sea Lions
(*Eumetopias jubatus*) under the IUCN Classification Scheme**

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ABSTRACT

The World Conservation Union (IUCN) classification scheme is applied to the western population of Steller sea lions to determine the population's status pursuant to the U.S. Endangered Species Act (ESA). Analysis methods suggested by the IUCN, such as population viability analysis (PVA) and minimum viable population (MVP), are examined as tools for determining quantitative and objective risk classification criteria. To provide an informative estimate of the extinction distribution for Steller sea lions, three PVA models are considered, and results of each model are compared. Results of all three models meet the classification criteria for vulnerable. 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. Results of the MVP analysis are highly sensitive to assumptions about sex ratio (1:3 for adult sex ratio, 1:15 for breeding sex ratio) and the specified effective population size (500 or 5000). Regardless of the uncertainty in both PVA and MVP estimates, the Western population of Steller sea lions would be considered as endangered if the IUCN classification scheme was strictly followed because at least one of the five criteria has been met. The population would be considered as threatened under the ESA when none of the five criteria for endangered are met, but at least one of the criteria for vulnerable is met. Results are based upon the assertion that the IUCN categories of critically endangered and endangered are jointly comparable to the ESA category of endangered, and the IUCN category of vulnerable is comparable to the ESA category of threatened.

Key Phrases: IUCN classification scheme; ESA status of Steller sea lions; PVA and sensitivity to density dependence and stochasticity; MVP and ratio of actual to effective population size.

Key Words: Steller sea lions, criteria, endangered, IUCN, ESA

INTRODUCTION

Statement of Problem

The United States Endangered Species Act of 1973 as amended (ESA) provides two categories for the classification of species, however the Act provides no criteria for determining the appropriate category. Because current categories of species status may not reflect actual extinction risks, the need for revision of species classification scenarios has long been a priority of the World Conservation Union (IUCN) and has more recently become a priority among agencies in the US. Quantitative criteria that define extinction risks based on population viability analysis (PVA) and trends in abundance provide a systematic method for determining species status pursuant to the ESA and the Red Lists of the IUCN.

In an effort to establish quantitative and objective criteria to assign species to categories of threat, Mace and Lande (1991), for the IUCN, proposed a three-level system of classification. Categories are defined in terms of the probability of extinction within a specific time period: 1) Critical species have a 50% or greater probability of extinction within 5 years or 2 generations; 2) Endangered species have a 20% or greater probability of extinction within 20 years or 10 generations; 3) Vulnerable species have a 10% or greater probability of extinction within 100 years. The IUCN method of classification has been applied experimentally to a range of taxa; however the method needs further development for generalized application (Mace and Lande 1991, IUCN 1994). Mace (1994) suggests that this systematic method for evaluating the status of a species provides the necessary information for assessing extinction rates and for identifying regional and taxonomic biases in species classification.

Subsequently, major revisions have been put forth in regard to the system proposed by Mace and Lande (1991), including: 1) numerical criteria appropriate to all organisms and the introduction of non-threatened categories (Mace et al. 1992); 2) a more explicit structure clarifying the significance of the non-threatened categories (IUCN 1993); and 3) an emphasis on a precautionary application of the system (Mace and Stuart 1994). Recently, the IUCN Species Survival Commission has clarified previous proposals to establish quantitative criteria for classification within threatened categories in its final *IUCN Red List Categories* (1994). The threatened categories comprise part of a larger scheme, which includes, respectively:

1. Evaluated,
2. Adequate Data,
2. Lower Risk (conservation dependent, near threatened, least concern),
3. Threatened (critically endangered, endangered, vulnerable),
4. Extinct in the Wild,
5. Extinct.

It is possible to classify all taxa into one of these categories. For those species listed as critically endangered, endangered, or vulnerable under the threatened category, the scheme specifies a range of criteria; meeting any one of these criteria qualifies a taxon for listing at that level of threat. For each category, one of the five criteria is quantitative in nature, consistent with the Mace and Lande (1991) three-level system. Because data necessary to calculate extinction probabilities are scarce, more qualitative criteria are included under each category, including effective and actual population sizes, degree of population fragmentation, and population trends and fluctuations. The combination of these criteria is intended to address the variety of causative agents influencing a population's decline and to identify the

specific evidence and data required for classification of a species under each category of threat.

The adoption of a similar system in the US would make listing decisions more consistent for marine mammals as well as other taxa. However, sufficient data to allow reliable estimates of extinction risk are not available for all marine mammals, so a system allowing the use of additional criteria is necessary. Such a system could be based on some combination of population size and number, assumed to represent a specific level of extinction risk. Any system of criteria developed for use with the ESA should be rigorously tested against a variety of population and metapopulation models before implementation.

For threatened and endangered species, the ESA requires that Recovery Plans include specific criteria that determine when species should be removed from the list of endangered and threatened wildlife. As the first marine mammal to be removed from the list, the change in status of the gray whale (*Eschrichtius robustus*) has generated significant interest within governmental and nongovernmental organizations in applying the quantitative criteria specified by the IUCN to the management of marine mammal populations. Based on this interest, here we seek to classify the western population of Steller sea lions (*Eumetopias jubatus*) pursuant to the ESA in the context of the IUCN classification scheme.

Steller sea lion Distribution and Population Structure

Steller sea lions range from the Channel Islands, California, around the Pacific Rim to northern Japan, with most of the world population breeding between the central Gulf of Alaska and the western Aleutians (Loughlin et al. 1987). Two separate populations of Steller sea lions are currently recognized within U.S. waters: an eastern population, which includes animals east of Cape Suckling, Alaska (144 west longitude), and a western U.S. population, which includes animals at and west of Cape Suckling. This population structure was identified by Loughlin (1994) using the phylogeographic approach of Dizon et al. (1992) and the following categories: (1) Distributional data: geographic distribution continuous, yet a high degree of natal site fidelity and low (<10%) exchange rate of breeding animals between rookeries; (2) Population response data: substantial differences in population dynamics (York et al. in press); (3) Phenotypic data: unknown; and (4) Genotypic data: substantial differences in mitochondrial DNA (Bickham et al. 1996). The strongest evidence for population separation is based on genotypic studies of Bickham et al. (1996).

Estimates of Steller sea lion abundance are based on actual counts of nonpups at 'trend sites,' a subset of the entire National Marine Fisheries Service survey area. This area contains most of the population and has been surveyed regularly since the early 1970's (see NMFS 1992). Correction factors developed from the 1989 rangewide survey include 1.331 to be multiplied by the nonpup count to estimate total nonpup abundance and 2.63 divided by nonpup counts to estimate the number of pups in the population (Loughlin et al. 1992). For the western population, application of these correction factors to the 1994 counts for the Gulf of Alaska, Aleutian Islands, and the Bering Sea resulted in an estimate of 33,600 nonpups and 9,600 pups, for a total abundance estimate of 43,200, representing a 64% decline since the 1960's (Loughlin et al. 1992). Using these correction factors and 1994 counts for the eastern population (Southeast Alaska, California, and Oregon) resulted in an estimate of

18,600 nonpups and 5,300 pups, for a total abundance estimate of 23,900 Steller sea lions in the Eastern population, representing a 36% decline since the 1960's (NMFS 1995).

Current Status and Management Criteria

Steller sea lions were listed as threatened under the provisions of the ESA in December of 1990 (55 FR 49204). The Steller Sea Lion Recovery Plan (NMFS 1992) specified that development of quantitative criteria for changing status under the ESA is essential in effectively managing Steller sea lions. Reclassification and delisting were proposed in the plan to be based on a benchmark figure of 90,000 animals older than pups counted at trend sites in the Kenai-Kiska area, the trend site count of animals in the mid 1970's (NMFS 1992).

The Recovery Team suggested that the species should be listed as endangered when trend counts become less than 17 percent of this benchmark value (15,300 animals); if trend counts exceed 17 but less than 40 percent (>15,300 animals; <36,000 animals), the species should be listed as threatened (NMFS 1992). This approach was developed to address the problem of a rapidly declining population; the team believed that if the population was declining rapidly and NMFS waited until the threshold was crossed there might not be sufficient time for management actions to reverse the problem. However, the Recovery Team identified three situations where the population should be classified as endangered, if trend counts were between 17 and 25 percent of the benchmark (>15,300 animals; <22,500 animals) and either (NMFS 1992);

- 1) The Kenai-Kiska nonpup trend count declines by at least 10 percent over 3 or more consecutive survey years,

2) The overall Pup Production Index (as defined in Recovery Plan, count data combined in 2 year blocks) in the Kenai-Kiska area declines by 10 percent over the count in the previous 2-year block.

3) The number of animals declines

by at least 10 percent over a three-year period since 1989 in three or more of the six other regions (Russia, western Aleutians, eastern Gulf of Alaska, southeast Alaska, British Columbia, and California-Oregon-Washington).

Delisting was recommended to occur when the trend count is greater than 40 percent of the benchmark (>36,000), or when the number of animals is stable or increasing in at least three of the six regions (NMFS 1992). Because these standards were perceived as having an uncertain quantitative basis, they were not accepted by NMFS. To date, no explicit criteria have been used in establishing the species status. The classification system proposed by Mace and Lande (1991) has not been formally applied to Steller sea lion status determination.

The Recovery Plan suggested that quantitative measures such as PVA or trend analysis would provide a robust estimation of the likelihood of extinction. York and Merrick (1993) subsequently described a PVA predicting extinction of the western population in one hundred years based on the 1985-1994 population trend, and York et al. (1996) developed three spatially distinct metapopulation models to investigate the population's persistence under a range of population structures and characteristics. These predictions 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 reclassification of the species; specifically that the western population be listed as endangered, while the eastern population remain threatened (69 FR 192). This status determination was finalized in May 1997.

Population viability analysis (PVA) and minimum viable population (MVP)

PVA is a process to evaluate population data to estimate the likelihood that a population will persist for a particular time period. Both intrinsic factors, such as population dynamics and characteristics, and extrinsic factors, such as environmental effects, determine extinction risks. The related concept of minimum viable population (MVP) includes an estimate of the minimum number of organisms of a particular species needed for that species to exist for some particular time (Boyce 1992). PVA embraces MVP, but PVA does not seek to estimate the absolute minimum population necessary for persistence. A variety of approaches defining viable populations have been adopted in recent years, illustrating that there is no clear definition of the concept (Gilpin and Soulé 1986, Soulé 1987, Shaffer 1981, Mace and Lande 1991).

Boyce (1992) envisions PVA as an integral part of any species management plan, not as a tool to estimate extinction probabilities, but as a forum to implement an adaptive resource management plan (eg; PVA's are useful in prioritizing management actions). PVA allows scientists and managers to test the sensitivity of a species' persistence to changes in life history parameters and to better define optimal objectives for recovery. Incorporating assumptions from life table analysis may provide insight to understanding the causes of population declines (Crouse et al. 1987, York 1994). However, while several PVA's have been conducted, the application of results to conservation decisions has been limited. With the exceptions of the grizzly bear (*Ursus arctos horribilis*), the northern spotted owl (*Strix occidentalis caurina*), the Snake river chinook salmon (*Oncorhynchus tshawytscha*), and the Steller sea lion (*Eumetopias jubatus*), most PVA's remain unpublished and have not been applied to conservation decisions (Boyce 1992, Shaffer 1983, Emlen 1995, Taylor et al. 1995).

Several caveats are necessary in regard to conducting PVA's. PVA has come under an increasing amount of scrutiny in recent years as a result of a difficulty in model parameterization (Mills et al. 1996), a lack of standardization between models (Lindenmayer et al 1995), and a lack of reliability for risk classification of a species (Taylor 1994). Lindenmayer et al. (1995) found three computer "package" programs to be structurally different and variable in the way stochasticity and density dependence were incorporated. Mills et al. (1996) reported that model functions were difficult to accurately parameterize and that that density dependence was incorporated differently in four package PVA programs.

Taylor (1994) reported that uncertainty in parameter estimates obscures robust predictions of extinction probability distributions. Because the range of extinction times increases with increasing uncertainty, changing PVA techniques affects the choice of classification criteria. Thus classification criteria based on PVA are inherently based on assumptions about uncertain life history parameters. Further, requiring quantitative data for management decisions places the burden of proof on scientists in a manner detrimental to the species of concern.

The IUCN criteria focus on population trends and broad habitat conditions, emphasizing that PVA should identify appropriate kinds of data for assigning status to species, though much additional effort would be needed to develop comprehensive models and collect necessary field data. While Mace and Lande define quantitative criteria for IUCN species classification, Boyce (1992) points out that definitions of criteria for viability, persistence, and extinction are arbitrary. In short, PVA does not include management criteria, but provides one form of input into risk classification of species. The same can be said regarding MVP estimates.

Use of the MVP concept for risk classification of species offers one approach to addressing the potential problems affecting small populations. MVP has been used as a threshold number for defining endangered status for southern sea otters

(*Enhydra lutris*) and may contribute to status determination of Steller sea lions under the IUCN classification scheme (Ralls et al. 1983, Ralls et al. 1996). The "50/500" rule, initially advanced by Franklin (1980) and Frankel and Soulé (1981), prescribes a short-term minimum effective population size (N_e) of 50 to prevent an unacceptable rate of inbreeding and a long-term N_e of 500 to maintain overall genetic variability. Franklin (1980) reported that a genetically effective population size of 500 is satisfactory because at this population level the loss of genetic variation caused by inbreeding and random genetic drift is balanced by gains of mutation. In 1981, Frankel and Soulé reported that the number of individuals in a population that are required to achieve a genetically effective population size may be several times greater than 500. More recently, Lande (1994) reported that an effective population size of about 5000, rather than the Franklin number of 500, is necessary to maintain normal levels of genetic variance under a balance between mutation and random genetic drift. Mutational variance is the change in genetic variance from one generation to the next due to mutation, and adaptive genetic variance describes the change in genetic variance due to adaptation. Thus, the difference between the two N_e estimates results from Lande's (1994) assumption that adaptive genetic variance is an order of magnitude lower than mutational variance, whereas Franklin assumed equality.

N_e has both a genetic and a demographic definition. N_e (demographic) is the minimum size of an ideal population with an even sex ratio and stable age distribution that has the same net change in abundance over a year as the actual population size (Caughley 1994). N_e (genetic) may be defined by analogy with N_e (demographic) as the minimum ideal population of breeding individuals produced each generation by random union of an equal number of male and female gametes randomly drawn from the previous generation. It is the average number of individuals in a population that actually contribute genes to succeeding generations

(Caughley 1994). Unless otherwise stated, we refer to N_e in the context of a genetic effective population size. Generally, this number is lower than the total number of mature individuals in the population (N_a) or the total number of individuals in the population (N), being reduced by the following factors: (a) a higher proportion of one sex may reproduce; (b) some individuals will pass on more genes by having more offspring in a lifetime than others; and c) any severe past reduction in population size may result in the random loss of particular genotypes.

To translate N_e to the actual population size (N_a), Soulé (1980) suggested that in general the N_e/N_a ratio is approximately 25-33% with short and long term N_e 's of 150-200 and 1500-2000. While the MVP values resulting from such translations of the 50/500 rule generally fall within an order of magnitude of each other, ideally estimates should be determined on a population-specific basis.

METHODS AND RESULTS

STELLER SEA LION STATUS UNDER THE IUCN CLASSIFICATION SCHEME

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. The ESA defines the following categories of threat;

The term "endangered species" means any species which is in danger of extinction throughout all or a significant portion of its range...the term "threatened species" means any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range (Endangered Species Act of 1973, Section 3)

The question now becomes, how do the IUCN criteria relate to the ESA categories of threat? In practice, because the ESA categories are ambiguous, status determinations are generally applied unevenly among taxa. Further, while the ESA specifies two categories of threat (threatened and endangered) the IUCN establishes three categories (vulnerable, endangered and critically endangered). The IUCN category of critically endangered is intended for extreme emergency cases where a species has a high probability of extinction within the immediate future (i.e., a few years), while the IUCN category of endangered implies a high probability of extinction within a few decades. In light of this and given the above definitions, Lande (personal communication) suggests that the IUCN category of endangered and critically endangered may be jointly comparable to the ESA category of endangered. Thus a species in which one of the IUCN endangered or critically

endangered criterion are met is in our scenario endangered pursuant to the ESA. According to Lande, the IUCN definition of vulnerable is comparable to the ESA category of threatened.

Other interpretations of the relationship between the IUCN and ESA categories of threat are possible, and could be considered. For example, one might equate the IUCN category of endangered and vulnerable as jointly comparable with the ESA category of threatened. In the context of these assumptions about the relationship between the ESA and IUCN categories of threat, the IUCN classification scheme can then be used as a starting point for developing objective criteria for classification of species pursuant to the ESA (see Table 1). Below we describe the methods used to apply analytical tools specified in the IUCN framework to Steller sea lions.

POPULATION VIABILITY ANALYSIS

To attain an informative estimate of the extinction probability distribution for Steller sea lions, three PVA models are considered, and results of each model are compared. Two structurally distinct population viability analysis (PVA) models are developed to evaluate 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 1992), which provides an example of a computer package program; and a demographic model which incorporates the effect of environmental stochasticity on life history parameters according to Eberhardt's (1977) theory of life history responses to density dependence. These models are compared to a metapopulation model which encompasses three different geographic scales (York et al. 1996). In the following discussion we summarize the methods and results for each model.

Model #1: Demographic Model

Methods

The discrete growth rate of a population (λ) is a function of many factors, and variation in λ may be produced in several ways. Here, while λ itself is considered to be independent of density (Figure 1a), variability in λ increases with density (Figure 1b). In the demographic model, λ becomes more variable as the population approaches K as a result of increased variability of elements of the Leslie matrix (independent variables) impacting λ (dependent variable). The Leslie matrix represents age specific fecundity and survival rates; when multiplied by the age vector, the Leslie matrix transforms the age vector of one time period to the age vector of the next time period (Leslie 1945). As a general rule, as stochasticity in λ increases, the expected growth rate is the geometric average of the per time step

growth rates. Since geometric means are lower than arithmetic means for any heterogeneous set of numbers, with an arithmetic mean of 1, the geometric mean must be below 1.0 and the expected growth is an exponential decline.

Thus, the effect of environmental variability on the population growth rate is modeled by associating a random variable with survival and fecundity rates. The magnitude and density of variability were modeled based on Eberhardt's (1977) theory that juvenile survival, age at first reproduction, adult reproductive rate, and adult survival *respond sequentially to density dependence*. Variability in each of these life history parameters increases to different degrees as density increases, causing λ to be more variable at higher densities (see Figure 1). TRUE BASIC programming language was used in this modeling effort.

York's (1994) life table describes vital rates when the population is stable ($\lambda=1.0$); perturbing this life table revealed that a 20% reduction in juvenile survival is a consistent explanation for the current decline rate. Thus, to yield a growth rate that actually describes the current population growth rate ($\lambda=0.95$), the York (1994) Leslie matrix was altered by setting juvenile survival to 80% of the stable life table value (thus the mean λ value in Figure 1 is 0.95).

With mean λ set at of 0.95, variability was then incorporated into specific elements of the matrix, allowing life history parameters to change at different levels of density according to Eberhardts (1977) theory. Carrying capacity (K) was specified based on historical abundance levels. Juvenile survival, age at first reproduction, adult reproductive rate and adult survival were subject to random variability sequentially as the population approached K. Thus, both the magnitude and frequency of random variation was greatest for juvenile survival and smallest for adult survival. Random variability in the adult survival rate only came into play when the population was within 20% of K (above or below), otherwise it remained

constant. Juvenile survival, on the other hand, became stochastic when the population was within 80% of K .

The degree of random variability in the model was constrained by an assumed maximum annual rate of increase of 12%, and a corresponding maximum rate of decrease for each run. This rate corresponds to the average maximum known growth rate for pinnipeds (Barlow et al. 1995).

Variability in growth rate due to sampling error was incorporated as the coefficient of variation (CV) of the abundance estimate of the starting population size. For each iteration, a starting population size was randomly drawn within the bounds of the known variance of the abundance estimate. Based on a CV of .6 (Sease et al. 1994), the starting population sizes for each age class included a term for random variability with bounds equivalent to 6% on either side of the abundance estimate for that age class with an approximate 95% confidence interval. For example, the first age-class was estimated to include 4,200 animals; thus the model randomly selects a starting population size between 3,696 and 4,704. Random selection of starting population sizes occurred independently for each age-class for each iteration. We will refer to the mean starting population size vector as the constant age vector; and the variable starting population size vector as the stochastic age vector.

Elements of the matrix were independently perturbed for 1000 runs and multiplied by the constant age vector. For each run, the stable age distribution was reached when the fraction of the population in each age category remained constant (at this point, the population grows exponentially). Thus, λ was estimated by N_{t+1}/N_t . Extinction was projected by multiplying each λ by the sum of the stochastic age vector for each time step. We recorded time to extinction as the number of timesteps required before the population reached an extinction threshold of 10. Of course, when the stochastic demographic parameters yielded a positive λ

value, the population did not go extinct. Times to extinction were then saved as an array, sorted, and graphically displayed as a cumulative probability of extinction in 100 years (see Figure 2).

Results

The cumulative probability of extinction distribution represents the proportion out of 1,000 runs that the population went extinct at any particular year until the population had a 100% probability of extinction in 250 years (see Figure 2). Of 1,000 runs, the median time to extinction is 86 years. This represents the time at which 50% of the simulations resulted in extinction. Until 45 years there is a zero probability of extinction; however the extinction curve increases steeply to reach a 67% probability of extinction in 100 years. The first and third quartile times to extinction were 65 and 125 years, respectively, representing the times at which 25% and 75% of the simulations resulted in extinction.

Model #2: Analysis of the Likelihood of Extinction

Methods

To provide a comparison to a generic PVA program, a number of package programs, including RAMAS (Ferson et al. 1988), VORTEX (Lacy et al. 1995), NEMESIS (Gilpin 1993), NMIN (Lerczak et al. 1995), 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).

The species data contain basic life-history data, including age structure, and birth and death rates. Based on York et al. (1994), a .22, .15, and .14 probability of death for newborns (0-1), juveniles (1-4) and adults (4-30), respectively and a .3 probability of an adult female (age 8 to 30) giving birth to one female offspring annually were assumed.

Population subunits within the metapopulation were defined based on groupings of rookeries corresponding to NMFS survey areas in the Central Gulf of Alaska, Central Aleutian Islands, Western Gulf of Alaska and Eastern Aleutian Islands (CGOA, CAI, WGOA, EAI). Phylogeographic information and a cluster analysis indicated that adjoining rookeries had common trends in these areas (York et al. 1996, Loughlin et al. 1994). Steller sea lions are not known to migrate, however a small degree of migration may occur between subpopulations. Here we assumed a

zero probability of migration. Because the effect of migration between subpopulations increases persistence time, our results may be biased toward a shorter time to extinction. Simulations assumed a population extinction threshold of 20 individuals for each of the 4 subpopulations. The proportion of the initial population which is currently extant was also specified. These proportions include .25, .31, .22, and .09 for the CGOA, CAI, WGOA and EAI, respectively.

Subpopulation patch areas were determined using Computer Aided Mapping and Resource Inventory System (CAMRIS; Ecological Consulting, Inc., Portland, Oregon). Based on home range estimates for 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). Polygons were overlaid on these specific areas for each subpopulation; terrestrial habitat was excluded from this measurement. Square kilometer determinations were recorded.

To calculate the minimum living area, the area of each patch was divided by the carrying capacity of the female portion of the population. Similarly, the minimum breeding area was calculated by dividing the area of each patch by the number of breeding females (the number of breeding females at carrying capacity multiplied by the probability that an adult female breeds multiplied by the proportion of adult females in the entire population). Three different assumptions about K were considered; 1) historical population levels (defined as "historical K"), 2) $.66 * K$, and 3) $.33 * K$ (see Table 2).

To calculate the number of breeding females, it was assumed that 50% of the population is female, thus only $1/2 K$ was considered. This was done for each of the four subpopulations. For example, derivations for the Central Gulf of Alaska result in the following estimates:

$$\begin{aligned}
\text{Number of Breeding Females} &= (1/2)K * P(\text{adult females breeds}) * \% \text{ adult females} \\
&= 17575 * 0.87 * 0.31 \\
&= 4739.97
\end{aligned}
\tag{1}$$

$$\begin{aligned}
\text{Minimum Breeding area} &= \text{patch size calculated using CAMRIS } (1/2) / \text{Number of} \\
&\text{breeding females} \\
&= 320,200 \text{ km}^2 (1/2) / 4739.97 \\
&= 34 \text{ km}^2
\end{aligned}
\tag{2}$$

The catastrophe parameter field allows for incorporation of the frequency, effect and spatial scale of catastrophes. The extent to which the catastrophe may impact both population size and population biomass, the probability of catastrophe, and the scale of the catastrophe must be specified in the model. To test the response of population persistence to various levels of stochasticity, a range of scenarios were considered in this effort. Natural catastrophes, such as the epizootic which recently struck North Sea phocid seals, and human induced catastrophes may have influenced the Alaskan Steller sea lion population during 1985-89 (York et al. 1996). Because little information is available regarding the type, timing and magnitude of catastrophes influencing pinnipeds, considering multiple scenarios provided an estimate of the sensitivity of the population's persistence to various levels of catastrophes.

Under each of the three carrying capacities, two types of catastrophes were considered; a 'general catastrophe,' representing the significantly increased rate of decline between 1985 and 1990, and an El Niño catastrophe. El Niño is a suite of anomalous oceanographic conditions occurring periodically on a global scale. In the

North Pacific, El Niño often is associated with reduced upwelling, changes in sea level, and unusual storm patterns, often with a consequent reduction in water-column productivity (Ono and Trillmich 1991). Trillmich and Ono (1991) reported that El Niño events may also cause population-level declines of pinnipeds. Based on results reported in Trillmich and Ono (1991), it was assumed that El Niño may cause die-offs of up to 40% with a 3% probability of occurrence per year. For environmental stochasticity, two scenarios were considered (10% or 20% probability of occurrence per year) with variations in maximum possible impacts on both biomass and population (see Tables 3, 4 and 5).

This preliminary analysis provided insight into what parameters are most significant in assessing the persistence of the Steller sea lion. However, empirical evidence is not available to evaluate which of these scenarios is most probable. Thus, as a basis for comparison to the other two models, a secondary set of simulations was conducted using the same assumptions used in the demographic model described above and the York et al. (1996) model. To be consistent with these models, juvenile survival was reduced by 20%. Similarly, stochasticity was specified as a 25% probability of catastrophe occurring resulting in a 15% population reduction, and a historical K was assumed.

Results

As each level of stochasticity and carrying capacity has an associated extinction distribution, median times to extinction are summarized in Tables 3, 4 and 5 for simplification. Comparisons can be made between different assumed carrying capacities, between different probabilities of catastrophes, and between different life history assumptions. In all scenarios, the median time to extinction was longer for a 10% probability of catastrophe compared to a 20% probability of catastrophe. The median time to extinction also increased as the carrying capacity of the environment

increased. For example, at a 20% probability of occurrence allowing the catastrophe to impact 40% of the biomass and population, the median time to extinction was >100 years for historical K and 2/3 K and 88 years for 1/3 K.

The secondary simulation exercise provides the best basis for comparison with other models. This exercise resulted in a median time to extinction of 85 years, and a first and third quartile time to extinction of 77 and 92. ALEX output, including a cumulative probability of extinction distribution is summarized in Figure 3. This model seems to most accurately depict the state of the system under study. There is insufficient information to quantify a reduction of carrying capacity in the North Pacific ecosystem for Steller sea lions. This, combined with York's (1996) evidence that about 25% of the time the population declined by 15.6%, and evidence for a 20% reduction in juvenile survival, suggests that 85 years may be a robust estimate of extinction time for Steller sea lions. The critical assumption underlying this prediction is that the population will behave as it has since the mid-1970's.

Model #3: Multi-Scaled Metapopulation Model

York et al. (1996) developed three spatial models to predict the persistence of the Steller sea lion. This modeling effort provides an additional interesting comparison of the dependence of a model's conclusions on methods of analysis. Here the methods and results of each of these models are summarized (see York et al. 1996 for details).

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 (metapopulation model) and a Kenai-Kiska aggregate model (geographic scale). Dennis' (1991) stochastic model of exponential growth was applied to counts of adult female sea lions to project population growth. The distribution of future population size for 200 years was simulated 1,000 times for each rookery and cluster.

The number of animals remaining at each rookery or cluster was totaled 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 . Individual rookery extinctions were recorded in a similar fashion.

Rates of decline were estimated for each rookery in the local model. 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 the metapopulation model, 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 10 females were 99, 95 and 105 years. 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.

The rate of decline for the aggregate Kenai-Kiska model has varied over time; and the population was found to have declined at a significantly ($p < 0.001$) higher rate (15.6% per year, $SE = 1.8$) during 1985-1990. 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. The median time, first and third quartiles to reach 10 females were about 83, 80 and 86 years respectively.

Of the three models, the rookery model predicts the longest mean persistence time and the geographic model the shortest. All models are based on the assumption that the population will behave as it has since the mid-1970's. That is, there was no density dependent regulation incorporated into the models. Also, the

rate of increase was capped at .15 to constrain interannual variability to a biologically reasonable 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 picture of the population's probability of persistence.

MINIMUM VIABLE POPULATION OF STELLER SEA LIONS

For sea otters, Ralls et al. (1983) suggested a multiplier of 0.27 for converting the effective population size to the actual population size based on: 50% of population is immature, breeding sex ratio is 1 male to 5 females, and that variation in family size approaches a Poisson distribution. To develop a multiplier for Steller sea lions, a range of scenarios with different assumptions about sex ratio and variation in family size (offspring produced per female) were considered. Information about the percent of immature animals in each age class was incorporated into the N_e estimate. We assumed that each female contributes 2 pups in her lifetime. Because the ideal population remains constant in size over time, each female has to produce two living pups over her lifetime, one to replace herself and one to replace a male.

To determine a threshold population size for endangered for Steller sea lions based on MVP, we used a similar approach to that taken by Ralls et al. (1996) for Southern sea otters. However, we considered an N_e of 5,000 as the management objective, as suggested by Lande (1994), in addition to 500, as considered by Ralls et al. (1996). Next, the appropriate multiplier for translating N_e to N_a determined; and the reciprocal of the multiplier multiplied by N_e to establish the populations MVP (endangered threshold). The Ralls et al. (1996) approach in concept can thus be easily adapted for classifying Steller sea lions;

$$(1) \quad N_e = \frac{(N)(K) - 2}{K - 1 + (V_k/K)}$$

where N =total population size, K =mean number of successful gametes per parent, and V_k =variance of number of successful gametes per parent. Assuming that variation in family size follows a Poisson distribution and sex ratios for males to

females of 1:3 and 1:15, the variance in number of successful gametes per parent is estimated by;

$$(2) V_k = N_m/N (V_{k(m)}) + N_f/N (V_{k(f)}) + (N_m/N) (N_f/N) (K_m - K_f)^2$$

Where $V_{k(m)} = K_m(1-2/N)$ and $K_m = N_1/N_m$ with corresponding formulas for females. Assumptions about sex ratio should represent the effective numbers of males and females, based on mean and variance of lifetime fitness. Steller sea lion sex ratios at birth are close to parity but are roughly 1:3 for mature males to mature females and 1:15 for territorial males to adult females (Loughlin et al. 1987, Merrick et al. 1988). However, because the survival of breeding females is thought to be greater than that of males, the breeding sex ratio in a single year is likely more skewed than the correct value averaged over an individual's lifetime. Table 8 displays the sensitivity of the N_e estimate to the assumed sex ratio.

To combine the effects of percentage immature animals in the population and variations in breeding sex ratio with family size shown above on effective population size, an estimate of the percent immature animals is necessary. Applying the Barlow and Boveng (1991) generalized survivorship model to a life table developed by York (1994) resulted in estimates of percent immature animals (ages 1-4) of 52 and 49, respectively.

Based on this estimate, we assumed that N_e was half of 75, or 37.5% of N_a if a 1:3 sex ratio was assumed, and half of 23, or 11.5% of N_a if a 1:15 sex ratio was assumed. Table 10 displays the various MVP estimates under different sex ratio and target N_e assumptions. Given a target N_e of 500, MVP estimates were 1,300 and 4,400 for assumed sex ratios of 1:3 and 1:15. A target N_e of 5,000 increases MVP estimates by an order of magnitude to 13,300 and 43,500 for sex ratios of 1:3 and 1:15. For example, with a target N_e of 5,000, the minimum viable population size was

calculated as 5000 times the reciprocal of .115 (8.7) or 43,500 animals. These estimates represent the total number of individuals necessary for long term genetic viability under different assumptions about the relative importance of mutation and random genetic drift. It should be noted that within the community of conservation biologists, there is no consensus regarding the appropriate N_e to use in MVP estimates.

Based on this MVP analysis for Steller sea lions and a similar approaches used for risk classification of southern sea otters, a population should be considered endangered when it is less than the specified MVP (see Table 9).

Results

As the current population estimate for the Western population of Steller sea lions is 43,200 animals, our hypothetical criterion for endangered is met only when a sex ratio of 1:15 and an N_e of 5,000 was assumed. The Steller Sea Lion Recovery team suggested that the species be listed as endangered when trend counts become less than 17 percent of the 90,000 benchmark figure for delisting (15,300). Using correction factors produced by Loughlin et al. (1992) resulted in an estimate of 20,349 nonpups and 5,817 pups, for a total abundance of 26,167 sea lions as the benchmark for endangered. The estimated MVP's from our analysis (Table 10) differ from the Recovery Team recommendation and from the IUCN definition of an endangered status benchmark figure of 2,500 mature individuals (IUCN 1994).

SUMMARY OF RESULTS AND IMPLICATIONS FOR ESA CLASSIFICATION

Comparison of PVA approaches

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 Pasqual (in press) 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 PVA's, Gilpin (1993) contended that the best measure of a population's health is the distribution of times to extinction. Thus, three points on the extinction curve were compared for each of the three models: the median time to extinction, and the first and third quartile times to extinction (see Table 6). These distributions are illustrated as cumulative probability distributions, which climb from probability 0 to 1.0 against an abscissa of time, for both the ALEX and demographic model (see Figure 2 & 3 and see York et al. (1996) for corresponding figures).

Models varied in spatial structure, in whether density dependence was incorporated, and in the type and method of stochasticity incorporated (see Table 7). There were also substantial differences in how results were reported, making it difficult to make across the board comparisons. Within these constraints, if assumptions were standardized to the maximum extent possible, estimates of median time to extinction did not differ significantly. Median times to extinction were 86, 85, 83, and 99 years respectively for the demographic, ALEX and York et al. (1996) aggregate and cluster models. If the first and third quartile times to extinction were considered, however, results were not so similar, particularly when comparing the York et al. (1996) models with the demographic and ALEX models. In general, the probabilities of extinction for the York et al. (1996) models were smaller initially

but increases more rapidly than the other models. Clearly, the primary shortcoming of all approaches is the lack of data on density dependent mechanisms for Steller sea lions and the lack of data on the rate at which catastrophic events might occur.

Implications of PVA models for ESA classification

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. This represents a case study where the results of different models were surprisingly consistent. If one accepts the results of these models and the classification criteria suggested by the IUCN, PVA is a reliable tool for risk classification of Steller sea lions.

However, a number of caveats should be considered in interpreting these results. For Steller sea lions, and in general, it is not possible to define stochasticity in probabilistic terms nor to accurately predict how the growth rate of the population will change as the population size changes relative to K . Further, including the 25th and 75th percentile times to extinction reveals that the extinction distribution of each model is not as similar as suggested by the median time to extinction alone. This suggests that consideration of the distribution of times to extinction for more than one model provides a more pragmatic, albeit less precise, estimate of extinction probability.

Implications of MVP analysis for ESA classification

As we have seen, a status determination for Steller sea lions using the MVP approach is dependent upon assumptions about sex ratio and the assumed N_e . Until consensus is reached among conservation biologists about how to apply these "small population paradigm" theories to species management regimes, MVP

estimates cannot be "objectively" used as a risk classification criteria for any species. However, criteria may currently be presented in the context of assumptions used; thus it is left up to the manager to select the optimal strategy for status determination. A more detailed investigation of use of the appropriate N_e on a population-specific basis, and how to relate MVP to status determination, is necessary for effective application to classifying Steller sea lions under the ESA.

DISCUSSION

This represents a case study where the results of different PVA models are surprisingly consistent. Because different points on the extinction distribution represent different relative probabilities of extinction, benchmark figures for classification of species based on probability of extinction can be extremely subjective unless the full extinction distribution is considered. If one accepts the results of these models and the classification criteria suggested by the IUCN, PVA is a reliable tool for risk classification of Steller sea lions. Of course, this generality should be considered in the context of the underlying assumptions behind each model, and the subjective nature of the IUCN criteria. As uncertainty in data increases, the validity of PVA predictions, thus their potential for use in conservation decisions, decreases. In cases where data were limited, the IUCN classification system likely would not be flexible enough to result in a consistent status determination given three independent models. In such cases, PVA can be used for assessing the relative risk among species by parameterizing an identical model for different species and using Bayesian methods to quantify uncertainty in parameter estimates for each species (see Taylor et al. 1996). Results of this type of analysis would provide a quantitative and objective method of evaluating research and management priorities for threatened and endangered species in the face of scientific uncertainty.

For Steller sea lions, the various assumptions used to estimate N_e have significant implications for determining the status of the population. The Southern Sea Otter Recovery Team used a target N_e of 500, because it was thought to represent the minimum number necessary to preserve quantitative genetic variation in the short term (100 years) and because it was a criterion that had been suggested in published literature (Ralls 1996, personal communication). Frankel and Soulé (1981) reported 500 as "the minimum size for accommodation of continuing

evolution. At this size, the loss of genetic variation should be approximately balanced by the gain of mutation" (pg. 96). While more recent literature suggests that an N_e of 5,000 is necessary for long term genetic persistence, it has not been suggested in the literature that this be used as a criterion for classifying a species as endangered.

Because lack of genetic variability poses only long-term extinction risks for relatively small populations (Lande 1996 personal communication), use of MVP alone may not be an appropriate criterion for determining the status of the Steller sea lion. A temporary reduction below any MVP does not necessarily imply a high probability of extinction. However, while the current population size for Steller sea lions does not imply immediate peril, the population decline rate is significant. Further, a genetically-based MVP does not incorporate environmental, catastrophic, or demographic stochasticity, nor does it address population trends. These agents are likely more significant in driving population trends for species; particularly for pinnipeds which demonstrate extreme metapopulation dynamics due to their polygynous mating system (see York et al. 1996). Given the high level of site fidelity in breeding behavior of Steller sea lions, a population-level decline is likely magnified at the rookery-level.

Most conservation biologists would agree that classification criteria that do not incorporate uncertainty should be discouraged. With that in mind, there has been a clear preference in the published literature to abandon the concept of MVP and move toward PVA type of analyses. A related problem regarding the IUCN scheme is that it is not statistically rigorous, nor does it allow for consideration of the quality of the data on which a determination is made. Further analyses should be conducted to develop and refine analytical tools that incorporate uncertainty explicitly.

If the IUCN scheme were strictly applied to Steller sea lions, we would conclude that Steller sea lions should be considered as "endangered" pursuant to the ESA because *one* of the criteria for endangered (population trends, see Table 1) was met. This is based on the assumption that critically endangered and endangered classes under the IUCN classification scheme are equivalent to the endangered class under the ESA. However, other interpretations of the relationship between the IUCN and ESA categories of threat are possible, and could be considered. The key, as we see it, to applying the IUCN classification scheme is the use of multiple criteria, where data would typically be available to evaluate at least one of the criteria. Further, the classification of a population, based on one or more criteria being met, is a risk adverse approach. The potential for application of the IUCN scheme to other species is therefore substantial given the flexibility of the scheme in making status determinations with limited information. The primary shortcoming of the IUCN scheme at this point is the lack of sensitivity to uncertainty.

Acknowledgments

This research was supported by the North Pacific Universities Marine Mammal Research Consortium. D. DeMaster, P. Kareiva, T. Loughlin, R. Merrick and A. Trites provided thoughtful reviews of the manuscript.

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

Critically Endangered	
Criterion	Rank¹
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 ² ;	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 km² or area of occupancy estimated to be less than 10 km², and estimates indicating any 2 of the following:	
1. Severely fragmented or known to exist at only a single location.	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 250 mature individuals and either:	
1. An estimated continuing decline of at least 25% within 3 years or one 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 a) 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	
Criterion	Rank
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 ³
2. A reduction of at least 50%, projected or suspected to be met within the next ten years or three generations, whichever is the longer.	

¹"Y" indicates the criterion is met, "N" indicates that it is not met, "D" indicates data are insufficient to make determination.

² Generation time is assumed to be approximately 8.5 years for Steller sea lions, based on the average age of reproductively active females.

³ 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, three generations is equivalent to 25.5 years. During past 24 years, (1970 to 1994), the population declined by approximately 77%.

- B. Extent of occurrence estimated to be less than 5000 km² or area of occupancy estimated to be less than 500 km², and estimates indicating any 2 of the following:**
1. Severely fragmented or known to exist at no more than five 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 two 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 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

Criterion	Rank
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 ³
2. A reduction of at least 20%, projected or suspected to be met within the next ten years or three generations, whichever is the longer .	
B. Extent of occurrence estimated to be less than 20,000 km² or area of occupancy estimated to be less than 2000 km², and estimates indicating any 2 of the following:	
1. Severely fragmented or known to exist at no more than ten 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
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.

Y⁴

Table 2. Range of carrying capacities (K) considered in modeling effort. Historical K based on counts of adult and juvenile Steller sea lions at all sites in the late 1950's and early 1960's

	Historical K	.66 Historical K	.33 Historical K
Central Gulf	35,150	23,550	11,951
Western Gulf	24,320	16,294	8,268
Eastern Aleutians	52,530	35,195	17,860
Central Aleutians	28,115	23,550	9,559
Total	140,115	98,590	47,640

Table 3. ALEX PVA results (historical K assumed)

20% Probability of catastrophe occurring 10% Probability of catastrophe occurring

Maximum impact	Median time to Extinction	Maximum impact	Median time to Extinction
10%	>100 yr.	10%	>100 yr.
20%	>100 yr.	20%	>100 yr.
30%	>100 yr.	30%	>100 yr.
40%	>100 yr.	40%	>100 yr.
50%	94 yr.	50%	>100 yr.
60%	83 yr.	60%	>100 yr.
70%	66 yr.	70%	>100 yr.
80%	61 yr.	80%	>100 yr.
90%	59 yr.	90%	80 yr.
100%	48 yr.	100%	79 yr.

Table 4. ALEX PVA results. (.66 historical K assumed)

<u>20% Probability of catastrophe occurring</u>		<u>10% Probability of catastrophe occurring</u>	
<i>Maximum impact</i>	<i>Median time to Extinction</i>	<i>Maximum impact</i>	<i>Median time to Extinction</i>
10%	>100 yr.	10%	>100 yr.
20%	>100 yr.	20%	>100 yr.
30%	>100 yr.	30%	>100 yr.
40%	>100 yr.	40%	>100 yr.
50%	>100 yr.	50%	>100 yr.
60%	80 yr.	60%	>100 yr.
70%	65 yr.	70%	>100 yr.
80%	59 yr.	80%	>100 yr.
90%	46 yr.	90%	>100 yr.
100%	41 yr.	100%	90 yr.

Table 5. ALEX PVA results. (.33 historical K assumed)

<u>20% Probability of catastrophe occurring</u>		<u>10% Probability of catastrophe occurring</u>	
<i>Maximum impact</i>	<i>Median time to Extinction</i>	<i>Maximum impact</i>	<i>Median time to Extinction</i>
10%	>100 yr.	10%	>100 yr.
20%	>100 yr.	20%	>100 yr.
30%	92 yr.	30%	>100 yr.
40%	88 yr.	40%	>100 yr.
50%	73 yr.	50%	>100 yr.
60%	65 yr.	60%	>100 yr.
70%	60 yr.	70%	>100 yr.
80%	50 yr.	80%	>100 yr.
90%	40 yr.	90%	>100 yr.
100%	37 yr.	100%	71 yr.

Table 6. Median, first and third quartile times to extinction for 4 models

Model	First Quartile Time to Extinction	Median Time to Extinction	Third Quartile Time to Extinction
Demographic	65 years	86 years	125 years
ALEX (secondary model)	77 years	85 years	92 years
York et al. 1996 (cluster model)	95 years	99 years	105 years
York et al. 1996 (aggregate model)	80 years	83 years	86 years

Table 7. Description of all Models

Model	Median Time to Extinction	Type of Stochasticity	Spatial Scale	Density Dependence
Demographic	86 years	Environmental stochasticity Measurement error	Geographic	yes (limited)
ALEX	85 to >100 years (see Tables 3,4 &5)	Environmental stochasticity Catastrophic stochasticity Demographic stochasticity	Metapopulation	no
York et al. 1996	Rookery model: 160 years Aggregate Model: 83 years Cluster Model: 99 years	Environmental stochasticity Catastrophic stochasticity	Local Metapopulation Geographic	no

Table 8. Estimate of N_e for a Steller sea lion population of 100 breeding individuals

Assumed Sex Ratio	Number parents (N_a)	Number female parents (N_f)	$N_f \times$ average pups per female	Number pups (N_p)	Number male parents (N_m)	$N_m \times$ average pups per male	Number successful gametes (k)	Mean successful gametes per parent (K)	Variance successful gametes per parent (V_k)	Effective Population size (N_e)
1:3	100	75	75x2	150	25	25x6	300	3	5.6	75x0.5
1:15	100	94	94x2	188	6	6x31.33	376	3.76	51.28	23x0.5

Table 9. MVP estimates for Steller sea lions given different sex ratio and Ne assumptions

Target Ne	MVP Estimate (1:3 Sex Ratio)	MVP Estimate (1:15 Sex Ratio)
500	1,333	4,350
5000	13,333	43,500

Figure Legends

Figure 1(a) Parameterization of the per capita growth rate

Figure 1(b) Dependence of variation in λ on population size

Figure 2. Cumulative probability of extinction distribution for demographic model

Figure 3. Output data for secondary simulation effort from Analysis of the Likelihood of Extinction (ALEX) model

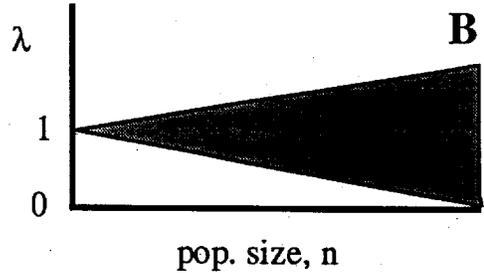
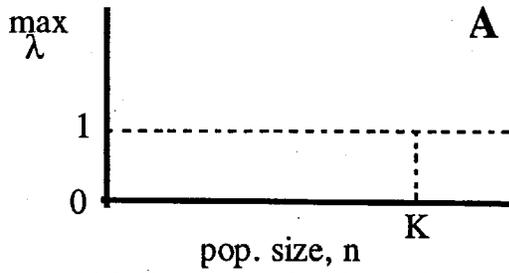


Figure 1(a). Parameterization of the per capita growth rate; (b) Dependence of variation in λ on population size

Figure 2. Cumulative probability of extinction distribution for demographic model

