

RISK OF EXTIRPATION OF STELLER SEA LIONS IN THE GULF OF ALASKA AND ALEUTIAN ISLANDS: A POPULATION VIABILITY ANALYSIS BASED ON ALTERNATIVE HYPOTHESES FOR WHY SEA LIONS DECLINED IN WESTERN ALASKA

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ABSTRACT

We estimated the risk that the Steller sea lion will be extirpated in western Alaska using a population viability analysis (PVA) that combined simulations with statistically fitted models of historical population dynamics. Our analysis considered the roles that density-dependent and density-independent factors may have played in the past, and how they might influence future population dynamics. It also established functional relationships between population size, population growth rate and the risk of extinction under alternative hypotheses about population regulation and environmental variability. These functional relationships can be used to develop recovery criteria and guide research and management decisions. Life table parameters (*e.g.*, birth and survival rates) operating during the population decline (1978–2002) were estimated by fitting simple age-structured models to time-series of pup and non-pup counts from 33 rookeries (subpopulations). The PVA was carried out by projecting all 33 subpopulations into the future using these estimated site-specific life tables (with associated uncertainties) and different assumptions about carrying capacities and the presence or absence of density-dependent population regulation. Results suggest that the overall predicted risk of extirpation of Steller sea lions as a species in western Alaska was low in the next 100 yr under all scenarios explored. However, most subpopulations of Steller sea lions had high probabilities of going extinct within the next 100 yr if trends observed during the 1990s were to continue. Two clusters of contiguous subpopulations occurring in the Unimak Pass area in the western Gulf of Alaska/eastern Aleutian Islands and the Seguam–Adak region in the central Aleutian Islands had relatively lower risks of extinction. Risks of extinction for a number of subpopulations in the Gulf of Alaska were reduced if the increases

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observed since the late 1990s continue into the future. The risks of subpopulations going extinct were small when density-dependent compensation in birth and survival rates was assumed, even when random stochasticity in these vital rates was introduced.

Key words: Steller sea lion, *Eumetopias jubatus*, population viability analysis, extinction risk, recovery criteria.

Population viability analysis (PVA) attempts to predict the probability of a species or population going extinct (or reaching some threshold number of individuals) in a specified period, usually through the use of a stochastic simulation model (Shaffer 1981, Gilpin and Soulé 1986, Reed *et al.* 2002). The complexity of PVA models ranges from diffusion models of total population size (*e.g.*, Dennis *et al.* 1991) to density-dependent, age-structured models of metapopulations that explicitly account for factors influencing birth, survival, and dispersal rates such as harvest, genetics, and habitat quality/quantity (*e.g.*, Lacy 1993). The degree of model complexity and the factors considered should reflect the biology of the study species and, importantly, the data that are available (Murphy *et al.* 1990, Stephens *et al.* 2002).

The Steller sea lion (*Eumetopias jubatus*) has experienced a dramatic decline in abundance during the past 25 yr, due in large part to the decline of breeding populations in western Alaska (Loughlin *et al.* 1992, Trites and Larkin 1996). As a result, the western "distinct population segment" (DPS, west of 144°W longitude) was classified as "endangered" under the United States Endangered Species Act (National Marine Fisheries Service 1997). The United States National Marine Fisheries Service has considered PVA to be an important tool for assessing the risk of extinction of the Steller sea lion and thereby guiding the management and recovery of the species (National Marine Fisheries Service 1992). Two previous PVAs examined the risk of extirpation of the Steller sea lion in western Alaska given the stochastic continuation of recent population trajectories (>10% chance of extirpation within 100 yr; York *et al.* 1996, Gerber and VanBlaricom 2001).

The utility of PVA has been questioned given that there are almost always large uncertainties involved in predicting the probability of a species going extinct (Taylor 1995, Ludwig 1999, Ellner *et al.* 2002). It is therefore extremely important that all significant sources of uncertainty be considered, quantified, and reported if a PVA is performed. Assessing the long-term viability of the Steller sea lion is particularly troubling because of the uncertainty regarding the specific factors that drove the population decline (National Research Council 2003). Several hypotheses have been proposed to explain the 80% decline, including anthropogenic mortality, predation by killer whales, and a reduction in the quantity, quality, and/or availability of prey as a result of fisheries or environmental change (Alverson 1992, DeMaster and Atkinson 2002, Springer *et al.* 2003, Trites and Donnelly 2003, Trites *et al.*, in press). However, it has been difficult to conclusively reject any of the hypotheses due to a lack of key data.

Bayesian statistical methods provide one useful approach to quantifying ecological uncertainty (Ellison 1996, Hilborn and Mangel 1997, Punt and Hilborn 1997, Wade 2000). PVAs can be conducted in a Bayesian framework by fitting a population model to data to estimate probability distributions for the parameters of the model (Wade 2002). The population can then be simulated forward in time by drawing random samples of parameter values from their joint probability distribution. Repeating the

simulations many times yields a probability that the population will go extinct or drop below some threshold in a specified time period.

The objective of our study was to conduct a PVA of the endangered Steller sea lion in the Gulf of Alaska and Aleutian Islands. Given the uncertainties discussed above, it is difficult to derive one distribution describing the probability of extirpation of this species in these regions. Thus, we explored three qualitatively distinct scenarios regarding the roles of density-independent and density-dependent factors in the historic decline and future population dynamics. For each scenario, a population model was fit to historical count data through a Bayesian framework. The population was then projected forward using the joint probability distribution for the parameters of that population model and additional assumptions about future dynamics. This provided a probability of extinction for that given model and set of assumptions. By examining the probabilities of extinction under three different scenarios, we sought to bound and thereby quantify the uncertainty associated with the risk of extirpation.

Our PVA is useful for assessing the appropriateness of the current “endangered” status of the western DPS, and for developing criteria for changing the listing status of Steller sea lion populations. Our study also demonstrates the usefulness of combining statistically fitted models of historical population dynamics with future simulations from those models for quantifying uncertainty about the past dynamics of a population with limited information (count data), and for quantifying uncertainty about the future dynamics of a population with even less information. It further shows how predicted risks of extinction are affected by alternative hypotheses regarding the nature of the mechanisms that drive the dynamics of a population.

METHODS

Our PVA of the Steller sea lion in western Alaska was comprised of two steps. First, a simulation model of sea lion subpopulations (*i.e.*, 33 individual rookeries) was fit to historical count data (pups and non-pups) using a Bayesian statistical framework to simulate the decline and estimate probability distributions of life table parameters that were consistent with the population trajectories (see *Decline Analysis* below). Second, these 33 subpopulations were simulated forward in time (beginning in 2002) by randomly selecting life history and other model parameters from their previously generated joint probability distribution (see *Future Simulations* below). The future simulations were strictly a simulation exercise (not a model-fitting exercise), and in some cases entailed several assumptions (outlined below) in addition to those of the decline analysis. The analyses of the historic decline and projected future dynamics were performed under three alternative scenarios (or hypotheses) about the roles of density-independent and density-dependent factors in the past and future dynamics of these subpopulations (Fig. 1).

All scenarios began by assuming that all subpopulations of Steller sea lions in western Alaska were at carrying capacity in 1978 with equilibrium survival and birth rates (see *Decline Analysis* below). The first two scenarios we considered (Scenarios I and II, Fig. 1) were similar to previous PVAs that have been done for the Steller sea lion in western Alaska (York *et al.* 1996, Gerber and VanBlaricom 2001). We assumed the historic decline and future dynamics were driven by unspecified density-independent factors (*e.g.*, direct anthropogenic mortality or killer whale predation) and estimated the probability of extinction if the estimated current birth and survival

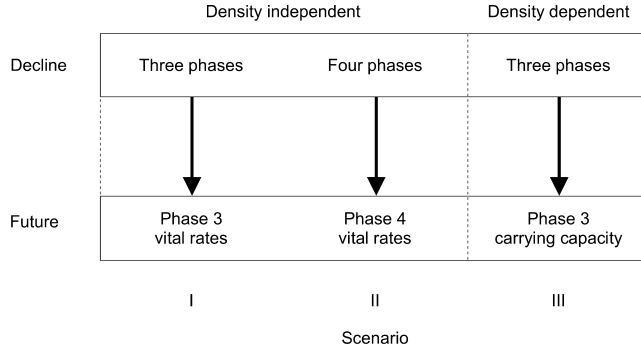


Figure 1. Modeled scenarios that represent alternative hypotheses about historical and future population dynamics. All scenarios began at carrying capacity in 1978 (Phase 1). Phases refer to periods of time that encapsulate similar historic population trends. The modeled dynamics of the decline recognized that sea lion numbers were once high (Phase 1), then declined rapidly (Phase 2) to low numbers (Phase 3), with a possible change in trends in the late 1990s (Phase 4). Future dynamics indicate the conditions applied to the modeled numbers of sea lions after 2002.

rates were to continue in the future. These two scenarios differed in the number of times the dynamics of sea lion populations were allowed to change during the historic decline (Fig. 1). We did not assume density dependence in Scenarios I and II.

In our third scenario (Scenario III) we assumed that the historic decline was driven by reductions in carrying capacity (*e.g.*, as a result of a reduction in prey due to competition with fisheries or natural environmental change) with resultant density-dependent decreases in birth and survival rates. Under this scenario we assumed that density-dependent dynamics would regulate populations about their estimated current carrying capacities (*i.e.*, 1990s carrying capacities) in the future.

Basic Simulation Model

The basic population model was an age-structured, birth-pulse simulation of the female segment of a Steller sea lion subpopulation with a time-step of one year (Caswell 1989). Breeding sites (rookeries) in western Alaska (west of 144°W longitude) were assumed to be associated with single, unique subpopulations which were modeled individually so that:

$$N_{r,t,a} = \begin{cases} b_{r,t} \sum_{a=6}^{25} N_{r,t,a} & \text{if } a = 0 \\ N_{r,t-1,a-1} s_{r,t-1}^{juv} & \text{if } 1 \leq a \leq 5 \\ N_{r,t-1,a-1} s_{r,t-1}^{ad} & \text{if } 6 \leq a \leq 25 \end{cases} \quad (1)$$

where $N_{r,t,a}$ is the number of females of age a in subpopulation r in year t , b is annual birth rate (number of female pups per female), s^{juv} is the annual survival rate of juveniles, and s^{ad} is the annual survival rate of adults. The main assumptions of the basic simulation model were: (1) all female Steller sea lions mature sexually at 5 yr

of age and potentially give birth for the first time at 6 yr of age (Pitcher and Calkins 1981), (2) birth rate does not vary with age, (3) juvenile survival rate (applied prior to sexual maturity) and adult survival rate (applied after sexual maturity) do not vary with age, and (4) no females live longer than 25 yr (knife-edge survival senescence).

Density dependence was modeled in birth rate and juvenile survival rate for two purposes: (1) to initialize the simulation of the decline under all scenarios (specifically to calculate the stable age structure at carrying capacity), and (2) to allow for density-dependent population dynamics under Scenario III (Fig. 1). We assumed that both birth rate and juvenile survival rate were functions of the total number of non-pups (≥ 1 yr old; $N_{r,t}^{1+}$):

$$rate_{r,t} = rate^{\max} \left[1 - \left(\frac{N_{r,t}^{1+}}{N_r^*} \right)^z \right] \quad (2)$$

where *rate* refers to s^{juv} or b , $rate^{\max}$ refers to maximum juvenile survival or birth rate ($s^{juv \max}$ or b^{\max}), N_r^* is the theoretical number of non-pups at which both s^{juv} and b would equal 0, and z is a shape parameter (this parameterization of density dependence is similar to that of Breen *et al.* 2003). Equation 2 implies that the relationships between population size and juvenile survival rate (as a proportion of maximum juvenile survival rate) and between population size and birth rate (as a proportion of maximum birth rate) are identical. Because juvenile survival affects five age classes (Eq. 1), changes in juvenile survival account for a larger proportion of the density-dependent effect in our model than birth rate.

The number of non-pups at which both s^{juv} and b equal 0 (N_r^*) can be calculated as:

$$N_r^* = N_r^K \left[1 - \left(\frac{1 - s^{adK}}{s^{juv \max} b^{\max} s^{adK} (1 - s^{adK^{20}})} \right)^{1/6} \right]^{-1/z} \quad (3)$$

where N_r^K is the number of non-pups at carrying capacity in subpopulation r , and s^{adK} is the annual adult survival rate at carrying capacity (or normal adult survival rate). As z increases, N_r^* approaches N_r^K . Juvenile survival and birth rates at carrying capacity (s^{juvK} and b^K) were then calculated according to Equation 2 (substituting N_r^K for $N_{r,t}^{1+}$). The number of 1-yr-old animals at carrying capacity in subpopulation r (N_r^{1K}) was calculated from:

$$N_r^{1K} = N_r^K \left(\frac{1 - s^{juvK^4}}{1 - s^{juvK}} + \frac{s^{juvK^4} (1 - s^{adK^{21}})}{1 - s^{adK}} \right)^{-1} \quad (4)$$

Thus having calculated N_r^{1K} and s^{juvK} , and given s^{adK} , it was straightforward to determine the number of animals of other ages at carrying capacity.

Decline Analysis

The first part of our PVA involved fitting the simulation model to historical count data to simulate the decline. Each subpopulation was simulated from 1978 to 2002

under our three scenarios allowing for three or four sequential phases of population dynamics depending on the scenario (Fig. 1).

Subpopulations were assumed to begin at their carrying capacities and remain there through the end of Phase 1 under all scenarios, with equilibrium survival and birth rates (s^{juvK} , s^{adK} , and b^K). The numbers of non-pups at carrying capacity (N_r^K) were estimated parameters (N_r^K was allowed to vary among subpopulations). The parameter z was also estimated in Scenario III and we assumed that it did not vary among subpopulations and that its value ranged from 1.0 to 13.5 as suggested for marine mammals by Taylor and DeMaster (1993). Although our equation for density dependence (Eq. 2) is parameterized differently than that of Taylor and DeMaster (their eq. 3), the parameter z is equivalent. We determined through simulations that z values between 1.0 and 13.5 resulted in maximum net productivity at 50%–82% of carrying capacity in our population model, which is consistent with the range suggested by Taylor and DeMaster (1993).

Adult survival rate at carrying capacity and maximum birth and juvenile survival rates were fixed rather than estimated: $s^{adK} = s^{juv\max} = 0.915$ and $b^{\max} = 0.354$ for all subpopulations. These parameter values were chosen so that $s^{juvK} = 0.813$ and $b^K = 0.315$, which are consistent with a Steller sea lion life table developed by Calkins and Pitcher (1982) and York (1994) based on a collection of animals from the Gulf of Alaska in 1975–1978. The maximum birth and juvenile survival rates resulted in an annual rate of population increase of approximately 6%, which was consistent with the observed rates of increase of, initially small, Steller sea lion populations in southeast Alaska and British Columbia since the 1970s (Calkins *et al.* 1999, COSEWIC 2003).

Under Scenarios I and II, juvenile and adult survival and birth rates were allowed to change from their equilibrium values of Phase 1 in a density-independent manner in Phases 2, 3, and 4 (only Scenario II had a fourth phase; Fig. 1). We allowed for separate sets of vital rates for each subpopulation r in Phase y , denoted $\{s_{r,y}^{juv}, s_{r,y}^{ad}, b_{r,y}\}$ so that:

$$rate_{r,t} = \begin{cases} rate^K & \text{if } t < Y_{r,2} \\ rate_{r,y=2} & \text{if } Y_{r,2} \leq t < Y_{r,3} \\ rate_{r,y=3} & \text{if } Y_{r,3} \leq t < Y_{r,4} \\ rate_{r,y=4} & \text{if } Y_{r,4} \leq t \end{cases} \quad (5)$$

where *rate* represents s^{juv} , s^{ad} and b and $Y_{r,y}$ is the year that Phase y begins for subpopulation r . Changes in vital rates occurred immediately after a given breeding season and were “knife-edge” so that the same vital rates occurred throughout a given phase. Vital rates during each phase were estimated parameters, as were the years that each phase started.

Scenarios I and II were intended to simulate density-independent factors that may have caused the decline and to allow for two or three potentially different suites of factors to have caused the decline. The beginning of Phase 2 was limited to years between 1978 and 1985 inclusive. The lower bound (1978) was chosen so that the decline could start as early as the beginning of the time-series, while the upper bound (1985) was chosen based on the observation that the decline was underway by the mid-1980s. The beginning of Phase 3 was limited to years between 1988 and 1992 inclusive. The lower bound (1988) was chosen as a year when the suite of factors affecting Steller sea lions in Alaska may have changed. Perez and Loughlin (1991)

and Trites and Larkin (1992) reported that intentional and incidental kills of sea lions dropped off by 1988 (although some of this may have been due to the decreased number of animals rather than decreased mortality rates). Also, amendments were made to the Marine Mammal Protection Act in 1988 that prohibited intentional take and limited incidental take, and several management measures were implemented in 1990 (no-entry zones, trawl exclusion zones, *etc.*) (Loughlin 1998). The upper bound (1992) was chosen to allow an arbitrary amount of flexibility in fitting the beginning of Phase 3. Phase 4 of Scenario II was allowed to begin between the years 1996 and 2000. These years were chosen based on the observation that the rates of change in counts at some rookeries changed in the late 1990s (including increases at some previously declining rookeries).

Under Scenario III, carrying capacities were allowed to decrease from their estimated 1978 (or Phase 1) values in Phases 2 and 3 (Fig. 1). Thus, juvenile survival and birth rates were allowed to change in a density-dependent manner in Phases 2 and 3. We allowed for separate carrying capacities for each subpopulation r in Phase y so that:

$$N_{r,t}^K = \begin{cases} N_r^K & \text{if } t < Y_{r,2} \\ \beta_{r,2} N_r^K & \text{if } Y_{r,2} \leq t < Y_{r,3} \\ \beta_{r,3} N_r^K & \text{if } Y_{r,3} \leq t \end{cases} \quad (6)$$

where $\beta_{r,y}$ is the proportional decrease in carrying capacity, relative to Phase 1, for subpopulation r in Phase y . Decreases in carrying capacity were “knife-edge” so that the same carrying capacity occurred throughout a given phase. Both $\beta_{r,y}$ and $Y_{r,y}$ were estimated parameters. We used the same ranges of values for $Y_{r,y}$ in Scenario III as we did in Scenarios I and II for consistency.

We also allowed adult survival to decrease in a density-independent manner during Phase 2 in Scenario III so that:

$$s_{r,t}^{ad} = \begin{cases} s_{r,y=2}^{ad} & \text{if } Y_{r,2} \leq t < Y_{r,3} \\ s^{adK} & \text{otherwise} \end{cases} \quad (7)$$

where $s_{r,y=2}^{ad}$ was an estimated parameter. We allowed for this change in adult survival based on the results of Scenarios I and II, which suggested that there was some decrease in adult survival during Phase 2 for most subpopulations. However, the posterior probability distributions for adult survival in Phases 3 and 4 were very skewed toward, and almost always maximum at s^{adK} suggesting little evidence for decreased adult survival in Phases 3 and 4. This is consistent with direct and incidental mortality of sea lions declining in the late 1980s (see above), the most likely factors to affect the mortality of adults. Additionally, setting adult survival to its value at carrying capacity in Phase 3 of Scenario III made for a tighter relationship between current population sizes and the estimated current carrying capacities, which was our intended assumption for Scenario III.

Decline Parameter Estimation

Decline simulation parameters were estimated from ground counts of pups and from aerial, terrestrial, and offshore surveys of non-pups on 33 rookeries during

the breeding season (June–July) done by the National Marine Fisheries Service and the Alaska Department of Fish and Game during 1978–2002 (Appendix 1). We did not analyze existing counts of animals on non-breeding sites (haul-outs) during summer although these animals were accounted for in the model. The longest and most comprehensive series of count data come from rookeries, and are the best data available. Some of the sites we considered have non-breeding haul-out areas associated with them. When counts for a site were broken down by area (for the entire time series), we used only the counts from the area deemed to be a rookery. In cases where multiple counts were done at the same site in a single year, we used the average of these counts. We chose to begin the time-series in 1978 because survey methodology was mostly standardized by then and it was prior to the majority of the sea lion decline (Loughlin *et al.* 1992, Trites and Larkin 1996).

To estimate the parameters of the decline simulation model (and the uncertainty in those parameters), we fit the model to the count data using a Bayesian statistical framework (Gelman *et al.* 1995). We used uniform (or log-uniform) prior probability distributions for all parameters within which we attempted to include all realistic values (Table 1). We felt the ranges of the priors were sufficiently wide to not bias the posterior probability distributions (within the confines of our model structure assumptions). However, it is possible that prior distributions other than uniform and log-uniform would have produced different posteriors for parameters that were not updated much by the data. Nevertheless, the posterior probability distributions for predicted population size (*e.g.*, in 2002) were generally very different from their “priors” (the data were informative with respect to these quantities), so we do not think that different priors would have substantially changed the predictions of risk of extinction.

We assumed that the errors in the counts of Steller sea lions were log-normally distributed such that the likelihood function was:

$$\begin{aligned}
 l(\text{data} \mid \theta) &= \prod_{r=1}^{33} \prod_{t=1}^{T_r^{PC}} \frac{1}{\sigma^{PC} \sqrt{2\pi}} \exp \left(-\frac{[\log(PC_{r,t}) - \log(2N_{r,t,0})]^2}{2\sigma^{PC^2}} \right) \\
 &\times \prod_{r=1}^{33} \prod_{t=1}^{T_r^{NC}} \frac{1}{\sigma^{NC} \sqrt{2\pi}} \\
 &\times \exp \left(-\frac{\left[\log(NC_{r,t}) - \log \left(\alpha_r^{ad} \left[\phi_r^{juv} \sum_{a=1}^4 N_{r,t,a} + 2b_{r,t} \sum_{a=5}^{25} N_{r,t,a} \right] \right) \right]^2}{2\sigma^{NC^2}} \right)
 \end{aligned} \tag{8}$$

where

T_r^{PC} = number of years of pup counts at rookery r

T_r^{NC} = number of years of non-pup counts at rookery r

$PC_{r,t}$ = number of pups counted at rookery r in year t that pups were counted at rookery r

$NC_{r,t}$ = number of non-pups counted at rookery r in year t that non-pups were counted at rookery r

Table 1. Estimated parameters of the decline model. The total number of estimated parameters per subpopulation in Scenarios I–III were 11, 15, and 8, respectively, plus two common parameters under Scenarios I and II, and three common parameters under Scenario III.

| Parameter | Symbol | Prior probability distribution U() | Varied among subpopulations | Scenarios (Phases) |
|---|-----------------|------------------------------------|-----------------------------|----------------------------|
| Density-dependence shape parameter | z | 1, 13.5 | No | III |
| Number of non-pups at carrying capacity (1978) | N_r^K | 0, 35,000 ^a | Yes | All |
| Start of Phase 2 | $Y_{r,2}$ | 1978, 1985 | Yes | All |
| Start of Phase 3 | $Y_{r,3}$ | 1988, 1992 | Yes | All |
| Start of Phase 4 | $Y_{r,4}$ | 1996, 2000 | Yes | II |
| Juvenile survival rate Phase y | $S_{r,y}^{juv}$ | 0.010, 0.915 | Yes | I (2,3), II (2–4) |
| Adult survival rate Phase y | $S_{r,y}^{ad}$ | 0.010, 0.915 | Yes | I (2,3), II (2–4), III (2) |
| Birth rate Phase y | $b_{r,y}$ | 0.010, 0.354 | Yes | I (2,3), II (2–4) |
| Relative carrying capacity in Phase y | $\beta_{r,y}$ | 0.01, 1 | Yes | III (2,3) |
| SD of observation error in log pup counts | σ_{PC} | 0.01, 1 ^b | No | All |
| SD of observation error in log non-pup counts | σ_{NC} | 0.01, 1 ^b | No | All |
| Number of adults of both sexes hauled out on rookery r during the survey as a proportion of the number of adult females giving birth in subpopulation r | α_r^{ad} | 0.8, 2.0 ^b | Yes | All |
| Adjustment parameter, so that $\phi_r^{juv} \alpha_r^{ad}$ = the number of juveniles of both sexes hauled out on rookery r during the survey as a proportion of the number of juvenile females in subpopulation r | ϕ_r^{juv} | 0, 1 | Yes | All |

^a There were no pup or non-pup counts at some rookeries in the late 1970s and early 1980s. In these cases we considered counts of non-pups done at these rookeries prior to 1978 and adjusted the upper bounds of the prior probability distributions of this parameter to approximate the upper bounds of the posterior probability distributions of this parameter for rookeries with similar counts in 1978 and 1979. Wooded, Akun, Ogchul, and Adugak islands each had counts of around 1,000–2,000 non-pups in the mid-1970s (Braham *et al.* 1980, Calkins and Pitcher 1982) so we chose 10,000 as the upper bound of the prior for the number of female non-pups at K . About 5,000 non-pups were counted at Ugamak Island in the mid-1970s (Braham *et al.* 1980) so we chose 17,500 as the upper bound of the prior.

^b Uniform on log scale.

- $N_{r,t,a}$ = predicted total number of females aged a in subpopulation r in year t that pups/non-pups were counted at rookery r
- $b_{r,t}$ = birth rate for subpopulation r in year t that non-pups were counted at rookery r (note that b is the proportion of females giving birth to female pups so $2b$ is the proportion of females giving birth assuming a 1:1 sex ratio at birth)
- σ^{PC} = SD of the observation error in the log of the pup counts (\cong CV of the error in untransformed counts)
- σ^{NC} = SD of the observation error in the log of the non-pup counts (\cong CV of the error in untransformed counts)
- α_r^{ad} = number of adults of both sexes hauled-out on rookery r during the survey as a proportion of the number of adult females giving birth in subpopulation r
- ϕ_r^{juv} = adjustment parameter, so that $\phi_r^{juv} \alpha_r^{ad}$ = the number of juveniles of both sexes hauled out on rookery r during the survey as a proportion of the number of juvenile females in subpopulation r .

The likelihood function (Eq. 8) had four parameters that were estimated in addition to the simulation model parameters. Two of these parameters, σ^{PC} and σ^{NC} , represented the variability of the count data around the deterministic trajectory of the population predicted by the simulation model. We assumed that this variability was due entirely to “observation” error. In some cases multiple counts have been done at the same site over several days to estimate daily variability. However, the error parameters in our model incorporate not only daily variability at a given site, but also variability in the scaling parameters (see below) among years. Thus, it was not possible to base this parameter solely on daily variability. The prior probability distributions for σ^{PC} and σ^{NC} were uniform on a log scale (Table 1; Gelman *et al.* 1995). We assumed that σ^{PC} and σ^{NC} did not differ among rookeries.

The other two estimated parameters of the likelihood function, α_r^{ad} and ϕ_r^{juv} , scaled the predicted number of female non-pups in the subpopulations to the number of non-pups observed on the corresponding rookeries. During the surveys, some non-pups (juveniles and adults) are at sea, while others are hauled-out at non-breeding sites. The sex ratio of non-pups is also uneven with fewer males than females (Calkins and Pitcher 1982, Trites and Larkin 1992). Thus, we had to adjust the number of female non-pups in subpopulations predicted by the model for direct comparison with the counts of non-pups on rookeries. Biologically it was more realistic to have different scaling parameters for juvenile and adult sea lions because the sex ratios and haul-out behavior of these groups differ. The scaling parameters were allowed to differ among subpopulations to account for the different sex and age compositions at each site. We scaled the number of adult non-pups relative to the number of adult females giving birth to ensure that the number of adults on the rookery was consistent with the number of females giving birth.

We limited α_r^{ad} to 0.8–2.0 (log-uniform prior), which assumed that the number of adults on land at the rookery during the surveys was at minimum 80% of the number of adult females giving birth that year (most adults on the rookery would be female, but some would be at sea), and at maximum 140% of the number of adult females in the population (twice the maximum percentage of adult females giving birth—given an adult sex ratio of approximately 2 females per 1 male (Trites and Larkin 1992), 140% is an appropriate maximum for a situation where most adults are hauled out on the rookery during the survey). We assumed ϕ_r^{juv} ranged from 0 to

1 (uniform prior), which assumed that anywhere from none to all of the juveniles in a subpopulation were on land at the rookery during the surveys (given the maximum value of 2 for α_r^{ad} and a 50:50 juvenile sex ratio).

Pups are very young at the time of the surveys and are confined to land. Thus, we assumed that ground surveys of pups on rookeries (divided by 2 assuming a 1:1 sex ratio) were unbiased estimates of the number of female pups in the respective subpopulations. A small number of pups are occasionally born on haul-outs, and may have introduced a small bias in modeled productivity.

Given the prior probability distributions for the parameters and the likelihood function, we estimated the joint posterior probability distribution of the parameters using a Markov chain Monte Carlo (MCMC) procedure (Gelman *et al.* 1995). We used uniform jumping distributions, but bounded them by the ranges of the respective prior probability distributions. We used "reflective" bounds so that random draws that fell beyond a given bound of the prior distribution were reflected back by a distance equal to the difference between the drawn value and the bound. For the integer parameters, $Y_{r,y}$, draws were reflected back by a distance equal to the difference between the drawn value and the bound, less one. Our reflective algorithm ensured that each random draw was used (which decreased computing time) and that the jumping distributions were still symmetrical; *i.e.*, $\Pr(\theta' | \theta) = \Pr(\theta | \theta')$. The widths of the jumping distributions were adjusted by 5% after each 750th cycle so that approximately 50% of the draws from the jumping distributions were accepted in each cycle. The widths of the jumping distributions were limited to 90% of the ranges of the respective prior probability distributions. The only exceptions were the widths of the jumping distributions for $Y_{r,y}$, which were fixed.

We assessed the convergence of the sample of the joint posterior from the MCMC procedure using the Bayesian Output Analysis package for R for Windows (Smith 2001). The Raftery and Lewis convergence diagnostics were computed for each parameter in an initial chain of 20,000 iterations and based on these results we re-ran the chain keeping every 750th iteration from 15,000,000 iterations not including a burn-in of 100,000 iterations. Geweke plots of the final sample (20,000 iterations) indicated that the outcome was consistent with convergence ($P > 0.05$) in the majority of each series of tests for each parameter. The Heidelberger and Welch stationarity and half-width tests failed rarely, and discards were not recommended for the majority of parameters. Despite these results being consistent with convergence, there was still substantial autocorrelation with some parameters (also indicated by the Raftery and Lewis dependence factors calculated for the median and 2.5th and 97.5th percentiles of the final sample). The dependence factors exceeded 5 for initial size and vital rates/relative carrying capacity in Phase 2 for several subpopulations including mainly Atkins, Ugamak, Akun, Adugak, Seguam, Kiska (Lief Cove), and Agattu (Gillon Point). Dependence factors also commonly exceeded 5 for many of the integer parameters. Thus, quantiles of the posterior distributions for these parameters should be interpreted with caution. Nevertheless, the suite of convergence tests suggests that convergence was obtained for most subpopulations excluding the integer parameters (*e.g.*, Marmot Island).

We also assessed the convergence of two of the quantities of primary interest predicted by the model: the number of female non-pups in each subpopulation in 2002 and the total number of females in each subpopulation and in western Alaska in 2102 (under all scenarios). The diagnostic tests provided strong evidence of convergence for the predicted number of female non-pups in each subpopulation in 2002 (dependence factors < 5 for all three quantiles; vast majority of Geweke tests

were consistent with convergence; no stationarity or half-width tests failed). The diagnostic tests were not informative with respect to convergence of the predicted numbers of animals in many individual subpopulations in 2102 under Scenarios I and II due to the large number of zeroes and the truncation in the distributions of predicted numbers. Nevertheless, there was strong evidence of convergence for many other subpopulations. There was strong evidence of convergence for the predicted number of females in each subpopulation in 2102 under Scenario III, except for the Akun subpopulation whose posterior had high autocorrelation. We believe this was a result of Akun having the lowest counts and having few counts from the early part of the time series. There was very strong evidence of convergence for the predicted total number of females in western Alaska in 2102 under all scenarios (dependence factors were around 1, and no tests failed).

The relative fits of the models for each Scenario were examined using the maximum log-likelihoods obtained, along with Akaike's Information Criterion (AIC) and Bayes' Information Criterion (BIC).

Future Simulations

The second part of our PVA involved projecting each subpopulation forward in time (from the year 2002 to 2102) in a probabilistic manner using the simulation model and the samples from the joint posterior probability distributions generated in the simulation of the decline under the three scenarios (*i.e.*, 20,000 runs for each scenario; Fig. 1). In Scenarios I and II we assumed that the mean birth and survival rates for the next 100 yr were the same as those during Phases 3 and 4 of the respective analyses of the decline. Under these scenarios each subpopulation decreased or increased exponentially. For those subpopulations that increased rapidly in some simulations, we bounded their sizes at their estimated 1978 carrying capacities by implementing density dependence once their sizes exceeded these carrying capacities. The dynamics of all subpopulations after 2002 were subject to density-dependent regulation about their estimated Phase 3 carrying capacities under Scenario III.

Demographic stochasticity was added to the simulation model for the future simulations since this stochasticity can have a large effect on the probability of a small population going extinct. Demographic stochasticity in birth and survival rates was incorporated in an individual-based manner simulating a binomial distribution.

For the density-dependent scenario (III) we also explored the effect of additional stochasticity in birth and juvenile survival rates after 2002. In our analysis of the decline we treated all error as observation error. Thus, in Scenario III this error translates into uncertainty in carrying capacity, with density-dependent regulation resulting in subpopulations simply equilibrating to these estimated carrying capacities in the future. We were interested in how stochasticity in birth and juvenile survival rates due to environmental variation might affect the probabilities of extinction for subpopulations with small carrying capacities. Thus, we added this dynamic to the estimated model for some future simulations under Scenario III parting from strict projection from the posterior probability distribution.

Random future variations in birth and juvenile survival rates in Scenario III were modeled using random, logit-transformed normal deviates such that:

$$rate_{r,t} = \text{logit}^{-1}\{N(\text{logit}(\mu), B)\}rate^{\max} \quad (9)$$

where $\mu = 1 - (\frac{N_{r,t}^{1+}}{N_r^*})^z$ and B is the SD of $\text{logit}(\frac{rate_{r,t}}{rate_{\max}})$. B was assumed to be independent of μ meaning that the variance of $(\frac{rate_{r,t}}{rate_{\max}})$ can be approximated by $B^2\mu^2(1 - \mu)^2$

(Link and Doherty 2002). The same deviation (or proportional change) was applied to birth and juvenile survival rate in a given year, and we assumed no correlation in these deviations among years or among subpopulations. It seems reasonable that an environmental perturbation might affect birth and juvenile survival in the same way (at least qualitatively). If stochastic deviations in birth and juvenile survival rates were not correlated then our treatment of stochasticity would overestimate the effects of this variability on population growth rate.

We examined values of 0, 0.3, 0.6, and 0.9 for B , which corresponded to CVs in population growth rate of approximately 0, 1.5, 3.0, and 5.5%, respectively, and CVs in population size of 0, 5, 10, and 15%, respectively (determined through simulation). We confirmed that the CV of final population size in future simulations with $B = 0.9$, regressed on final population size in identical future simulations without additional stochasticity ($B = 0$), ranged from 15%–24% depending on population size (values $>15\%$ arose in small populations due to the additional effect of demographic stochasticity). We felt this was an appropriate maximum to examine given the similarity to the estimated CVs in population size in the analysis of the decline.

While Scenario III explored compensation in population growth rates at small population sizes, we did not explore depensation. Little is known about the dynamics of extremely small sea lion populations. Evidence for depensation in otariid populations (sea lions and fur seals) is weak, but it may be a factor at very low population sizes (Gerber and Hilborn 2001). Our findings should be considered in this context. For example, a predicted total of <500 sea lions in western Alaska, distributed among several subpopulations, may experience difficulty recovering due to depensation.

RESULTS

Decline Analysis

Given the number of subpopulations (33), the number of parameters (8–15 parameters per subpopulation plus 2–3 common parameters) and the number of scenarios (3) it is difficult to present all of the results of the decline analysis. We have therefore shown only results for key parameters of one density-independent Scenario (II) and the density-dependent Scenario (III) (Table 2). The full results of the decline analysis are also shown for one of the 33 subpopulations (Marmot Island) in Fig. 2–4.

In general, our simulation models yielded good fits to all of the rookery count data sets under both the density-independent and density-dependent scenarios (Fig. 2). For some subpopulations, the added flexibility of a fourth phase in Scenario II allowed the model to describe the data better. For example, at Seal Rocks in the Gulf of Alaska where the ratio of non-pups to pups was high and the non-pup counts increased (since the mid-1990s), the four-phase model described the data much better than the three-phase model (not shown in Fig. 2). There were some instances where the model predicted unrealistic pup dynamics under the density-dependent scenario (Scenario III). The knife-edge decreases in carrying capacity combined with the large decreases necessary to simulate the observed changes in counts at some rookeries produced downward spikes in the predicted number of pups during the transitional years between phases (*e.g.*, Fig. 2, right panel: density-dependent fit of pup counts). The AIC values for Scenarios I, II, and III were 393, 557 and 322, respectively, while the BIC values were 4,380, 5,986, and 3,238, respectively. These criteria suggest that

Table 2. Continued.

| Rookery | Scenario II | | | | Scenario III | | | |
|------------------------------|------------------------|---------------------|---------------------|---------------------|---------------------|---------------------|----------------------------|---------------------|
| | Juvenile survival rate | | Adult survival rate | | Birth rate | | Relative carrying capacity | |
| | Phase 2 | Phase 3 | Phase 4 | Phase 2 | Phase 3 | Phase 4 | Phase 2 | Phase 3 |
| Ogchul | 0.79 (0.47,0.91) | 0.79 (0.53,0.91) | 0.77 (0.25,0.91) | 0.70 (0.50,0.87) | 0.86 (0.73,0.91) | 0.83 (0.58,0.91) | 0.18 (0.06,0.34) | 0.25 (0.11,0.35) |
| Adugak | 0.57 (0.07,0.86) | 0.86 (0.70,0.91) | 0.71 (0.10,0.91) | 0.78 (0.55,0.89) | 0.87 (0.77,0.91) | 0.85 (0.66,0.91) | 0.25 (0.13,0.35) | 0.30 (0.18,0.35) |
| Yumaska | 0.67 (0.14,0.90) | 0.84 (0.62,0.91) | 0.81 (0.19,0.91) | 0.79 (0.42,0.91) | 0.86 (0.76,0.91) | 0.86 (0.63,0.91) | 0.28 (0.07,0.35) | 0.28 (0.16,0.35) |
| Seguam (Saddleridge) | 0.58 (0.09,0.87) | 0.86 (0.71,0.91) | 0.81 (0.20,0.91) | 0.66 (0.29,0.86) | 0.89 (0.80,0.91) | 0.87 (0.70,0.91) | 0.22 (0.03,0.35) | 0.24 (0.12,0.34) |
| Kasatochi | 0.81 (0.51,0.91) | 0.87 (0.68,0.91) | 0.85 (0.38,0.91) | 0.73 (0.52,0.89) | 0.89 (0.76,0.91) | 0.89 (0.76,0.91) | 0.29 (0.18,0.35) | 0.19 (0.09,0.31) |
| Adak (Cape Yakak/Lake Point) | 0.86 (0.62,0.91) | 0.89 (0.78,0.91) | 0.83 (0.34,0.91) | 0.76 (0.41,0.91) | 0.90 (0.84,0.91) | 0.88 (0.76,0.91) | 0.18 (0.09,0.34) | 0.30 (0.20,0.35) |
| Gramp Rock | 0.79 (0.44,0.91) | 0.86 (0.72,0.91) | 0.79 (0.17,0.91) | 0.81 (0.63,0.91) | 0.88 (0.79,0.91) | 0.87 (0.72,0.91) | 0.27 (0.16,0.35) | 0.25 (0.15,0.34) |
| Tag | 0.71 (0.16,0.90) | 0.85 (0.58,0.91) | 0.79 (0.19,0.91) | 0.82 (0.62,0.91) | 0.88 (0.77,0.91) | 0.85 (0.65,0.91) | 0.25 (0.13,0.35) | 0.22 (0.12,0.34) |
| Ulak | 0.78 (0.29,0.91) | 0.80 (0.60,0.91) | 0.65 (0.08,0.90) | 0.82 (0.59,0.91) | 0.88 (0.77,0.91) | 0.83 (0.62,0.91) | 0.25 (0.04,0.35) | 0.26 (0.15,0.35) |
| Amchirka (Column Rocks) | 0.75 (0.15,0.91) | 0.75 (0.23,0.91) | 0.60 (0.06,0.90) | 0.68 (0.19,0.87) | 0.87 (0.73,0.91) | 0.83 (0.57,0.91) | 0.21 (0.04,0.35) | 0.23 (0.09,0.34) |
| Ayugadak | 0.79 (0.40,0.91) | 0.81 (0.53,0.91) | 0.77 (0.15,0.91) | 0.79 (0.59,0.90) | 0.85 (0.72,0.91) | 0.86 (0.64,0.91) | 0.22 (0.10,0.34) | 0.24 (0.11,0.35) |
| Kiska (Lief Cove) | 0.74 (0.34,0.91) | 0.83 (0.59,0.91) | 0.48 (0.04,0.87) | 0.65 (0.43,0.81) | 0.87 (0.77,0.91) | 0.82 (0.58,0.91) | 0.25 (0.11,0.35) | 0.20 (0.09,0.34) |
| Kiska (Cape St. Stephen) | 0.67 (0.12,0.90) | 0.84 (0.57,0.91) | 0.66 (0.08,0.90) | 0.76 (0.55,0.88) | 0.84 (0.69,0.91) | 0.84 (0.62,0.91) | 0.26 (0.12,0.35) | 0.23 (0.11,0.35) |
| Buldir | 0.54 (0.06,0.85) | 0.84 (0.35,0.91) | 0.57 (0.05,0.89) | 0.74 (0.55,0.88) | 0.84 (0.69,0.91) | 0.78 (0.55,0.91) | 0.28 (0.14,0.35) | 0.23 (0.10,0.35) |
| Agattu (Cape Sabak) | 0.55 (0.05,0.90) | 0.83 (0.52,0.91) | 0.54 (0.06,0.88) | 0.85 (0.58,0.91) | 0.84 (0.70,0.91) | 0.80 (0.59,0.91) | 0.24 (0.12,0.34) | 0.26 (0.13,0.35) |
| Agattu (Gillon Point) | 0.87 (0.60,0.91) | 0.82 (0.59,0.91) | 0.63 (0.08,0.90) | 0.88 (0.79,0.91) | 0.85 (0.73,0.91) | 0.84 (0.66,0.91) | 0.29 (0.04,0.35) | 0.28 (0.16,0.35) |
| Attu (Cape Wrangell) | 0.78 (0.32,0.91) | 0.83 (0.56,0.91) | 0.76 (0.31,0.91) | 0.83 (0.54,0.91) | 0.85 (0.72,0.91) | 0.75 (0.54,0.90) | 0.25 (0.11,0.35) | 0.28 (0.16,0.35) |
| | | | | | | | 0.27 (0.11,0.35) | 0.11 (0.06,0.18) |

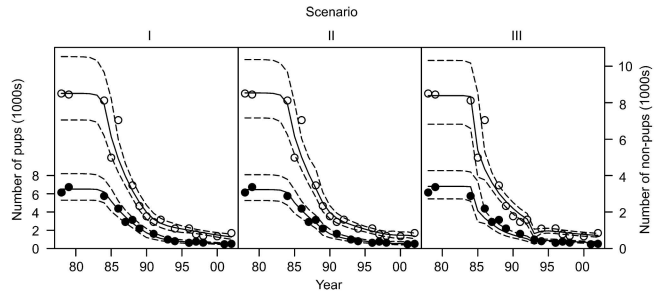


Figure 2. Observed counts of Steller sea lion pups (●) and non-pups (○) between 1978 and 2002 at Marmot Island (data points), and the numbers predicted by the decline simulation model (lines) under density-independent and density-dependent scenarios (see Fig. 1). Solid lines represent median predicted values and the dashed lines represent the 2.5th and 97.5th percentiles of predicted values.

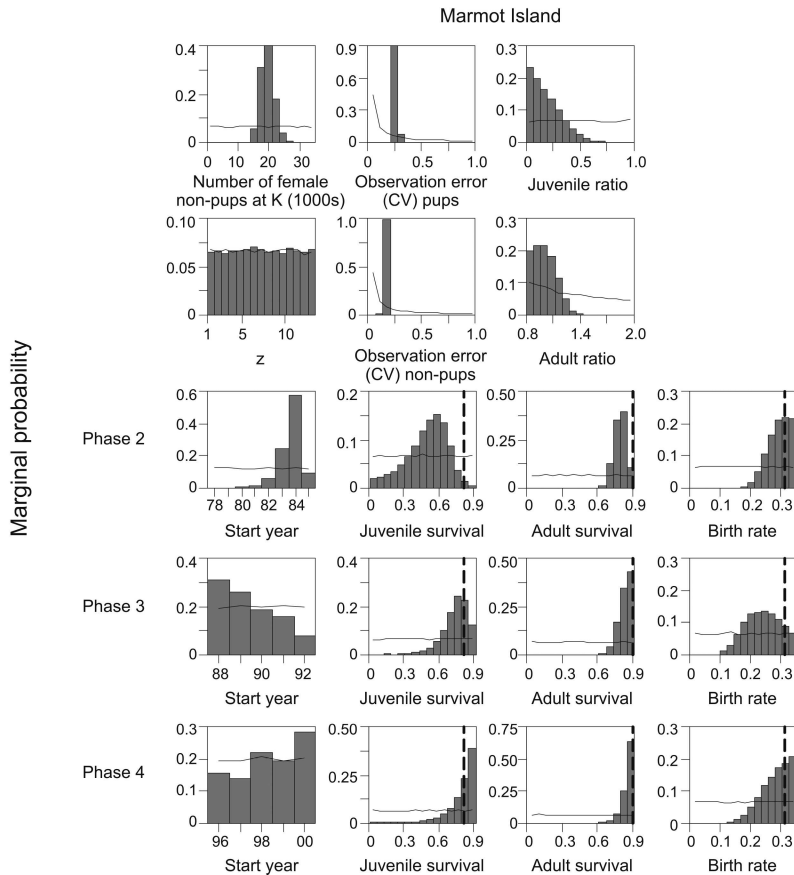


Figure 3. Marginal probability distributions for the parameters of the density-independent decline in the Marmot Island subpopulation (Scenario II). Solid lines represent prior probabilities and bars represent posterior probabilities. Vertical dashed lines indicate the assumed values of those parameters at carrying capacity.

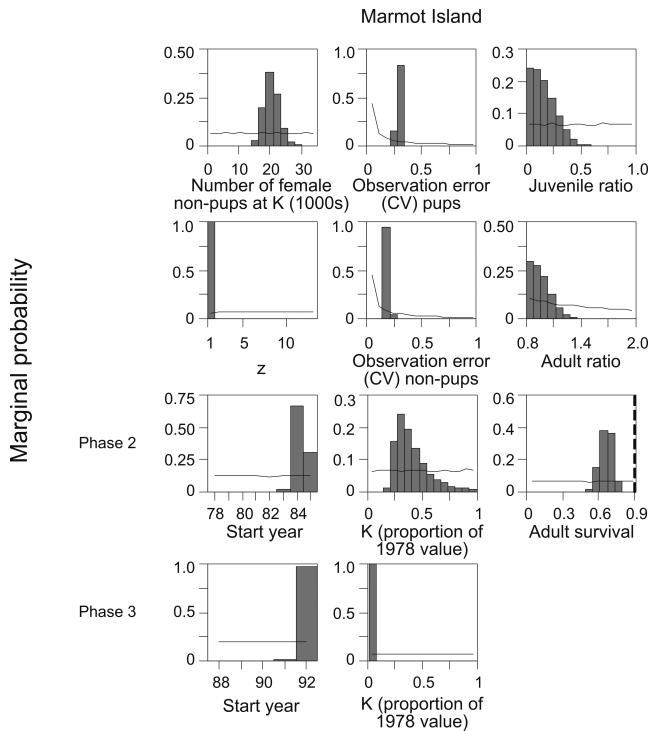


Figure 4. Marginal probability distributions for the parameters of the density-dependent decline in the Marmot Island subpopulation (Scenario III). Solid lines represent prior probabilities and bars represent posterior probabilities. Vertical dashed lines indicate the assumed values of those parameters at carrying capacity.

the evidence (lowest values) was strongest for the density-dependent model. However, our models were heavily parameterized so these model selection criteria indicate evidence for a more parsimonious model (the density-dependent model had the least number of parameters) rather than indicating that density-dependent dynamics *per se* described the data better.

The marginal posterior probability distributions for the parameters of the decline simulation model indicated that the count data were relatively informative with respect to some parameters, but completely uninformative with respect to others (Table 2, Fig. 3–4). For example, posteriors for the sizes of subpopulations in 1978 were relatively narrow (sizes were relatively well estimated) except for those rookeries where animals were not counted during the early part of the time-series.

The median years that the phases began varied among subpopulations as did the spread of the posterior probability distributions around these years. Often the probability distributions for the transitional years were similar between the density-dependent and density-independent scenarios, but not always. For example, when the aforementioned spikes in pup numbers occurred under the density-dependent scenario, the probabilities that those transitions were in years previous to pup counts were naturally low (*e.g.*, compare the probability that Phase 3 started in 1990 in

Fig. 3, 4). The timing parameters were not estimated well enough to discern a temporal geographic pattern to the decline (after 1978).

Under density-independent scenarios (I and II), the estimated specific changes in vital rates that drove the decline varied among subpopulations. The median predicted juvenile and adult survival rates tended to be lower in Phase 2 than in Phases 3 and 4 (Table 2). An exception to these patterns was several of the central and western Aleutian Islands where the median juvenile survival rates were lower in Phase 4 than in Phase 3, and in some cases even lower than in Phase 2. The median adult survival rates were higher than the median juvenile survival rates for the majority of subpopulations in all Phases (Table 2). The intervals of 95% posterior probability were almost always wider for juvenile survival than adult survival. The intervals of 95% posterior probability for birth rate were relatively wide in all phases, and no clear patterns were evident (Table 2). For Marmot Island, our analysis suggested that juvenile survival, and to a lesser extent adult survival, was probably reduced in the 1980s relative to its value at carrying capacity in 1978 (Fig. 3). Our analysis also suggests that juvenile and adult survival rates in this subpopulation likely increased during the 1990s, and that birth rate was potentially lower during the early to mid-1990s than during the 1980s or the late 1990s through 2002 (Fig. 3).

Under the density-dependent decline scenario (III), the intervals of 95% posterior probability were very wide for relative carrying capacity during Phase 2 (= 60% for 24 subpopulations, Table 2). There was a strong indication of a reduced carrying capacity during Phase 2 (relative to 1978) for some subpopulations (*e.g.*, Marmot Island, Fig. 4), but not for others (Table 2). For most subpopulations, the posteriors suggested that some decrease in adult survival rate occurred during Phase 2 (14 subpopulations had median values that were <80% of the assumed 1978 value, Table 2). However, the 95% intervals of posterior probability for 24 subpopulations contained an adult survival rate during Phase 2 that was = 90% of the 1978 value (Table 2). The 95% intervals of posterior probability for carrying capacities during Phase 3 were narrower than during Phase 2 for all but three subpopulations, and the median carrying capacities in Phase 3 were <50% of their assumed values in 1978 for all but two subpopulations (Table 2, Fig. 4). However, there were two groups of contiguous subpopulations (Chernabura–Akutan, Kasatochi–Gramp) that had the widest 95% intervals of posterior probability for carrying capacity in Phase 3, in some cases including a substantial probability that carrying capacity had not changed relative to 1978. For example, four of these subpopulations' intervals contained a Phase 3 carrying capacity that was >90% of its assumed 1978 value (Table 2).

The posteriors for the scaling parameters, α_r^{ad} and ϕ_r^{juv} , were similar between the density-independent and density-dependent scenarios (Fig. 3, 4). The 95% intervals of posterior probability for the CVs of observation error were approximately 21%–28% for pup counts and 14%–21% for non-pups (Fig. 3, 4). The estimated error in pup counts under the density-dependent scenario (III) was higher due to the sometimes unrealistic, predicted trajectories discussed above (26%–33%). The density-independent scenarios (I and II) naturally provided no information about z (the density dependence shape parameter), while z in the density-dependent scenario was estimated to be very close to the lower bound of the prior (*i.e.*, $z = 1$). The latter result reflects the fact that as z became lower, juvenile survival and birth rates were lower for a given population size relative to carrying capacity (Taylor and DeMaster 1993), and large decreases in juvenile survival and birth rates were necessary to drive the declines of some subpopulations.

Table 3. Median values (and 95% intervals) of probability for total number of female Steller sea lions in western Alaska in 2102 (pups and non-pups, all subpopulations) and the number of subpopulations with >0.05 and >0.50 probability of ≤ 50 females under each Scenario (Fig. 1).

| Scenario | Total number of females | Number of subpopulations with $>x$ probability of ≤ 50 females | |
|-------------------|-------------------------|--|------------|
| | | $x = 0.05$ | $x = 0.50$ |
| I | 18,731 (8,337, 38,079) | 30 | 21 |
| II | 18,457 (3,613, 47,125) | 33 | 28 |
| III ($B = 0$) | 27,421 (23,840, 34,167) | 0 | 0 |
| III ($B = 0.9$) | 20,681 (17,648, 25,964) | 0 | 0 |

Future Simulations

As expected, Scenarios I and II yielded the highest risk of extinction and the lowest probable number of Steller sea lions in western Alaska in 100 yr time (*i.e.*, in 2102, Table 3). The probability of there being <50 females in 2102 was >0.5 for 21 subpopulations under Scenario I and 28 under Scenario II (Table 3). The mean predicted sizes of subpopulations in 2102 varied within and between Scenarios I and II (Fig. 5). Under Scenario I, there were two groups of contiguous subpopulations whose mean sizes in 2102 were >500 females: Atkins to Akutan, and Seguam Island to Gramp Rock (Fig. 5). The majority of the rest of the subpopulations had mean sizes <100 females in 2102 under Scenario I. Under Scenario II, several of the mean sizes of the Atkins-Akutan subpopulation group decreased with two being <300 females (Fig. 5). Unlike Scenario I, mean sizes of >500 females occurred for subpopulations outside these two geographic clusterings under Scenario II, particularly in the Gulf of Alaska (*e.g.*, Marmot, Sugarloaf, Chirikof, Chowiet; Fig. 5).

Under Scenarios I and II, the main factors determining the size of a subpopulation in 2102 were the size of that subpopulation in 2002 and the rate of growth of that subpopulation in Phase 3 or 4, respectively, which was assumed to continue into the future (Fig. 6). Larger subpopulations with higher growth rates were more likely to be larger in 2102. Although the sizes and growth rates of the subpopulations varied, two groups of contiguous subpopulations under Scenario I had combinations of these factors that specified the largest sizes in 2102. Allowing for a change in population dynamics during the late 1990s in Scenario II increased the most likely population size in 2102 for many subpopulations in the Gulf of Alaska and Central Aleutian Islands because the rates of change in counts at many of these rookeries increased during the late 1990s.

Although most subpopulations had a high probability of extinction within 100 yr under Scenarios I and II, the risk of extirpation of the Steller sea lion in western Alaska was low overall (Table 3). For example, there was <0.025 posterior probability of $<8,300$ females total under Scenario I and $<3,600$ females under Scenario II. Despite the median predicted total number of females being similar between Scenarios I and II, lower numbers had higher posterior probabilities under Scenario II because the posterior probability distribution was wider under Scenario II than under Scenario I (Table 3). Similarly, the probability of extinction for individual subpopulations was sometimes higher under Scenario II than under Scenario I even when the median

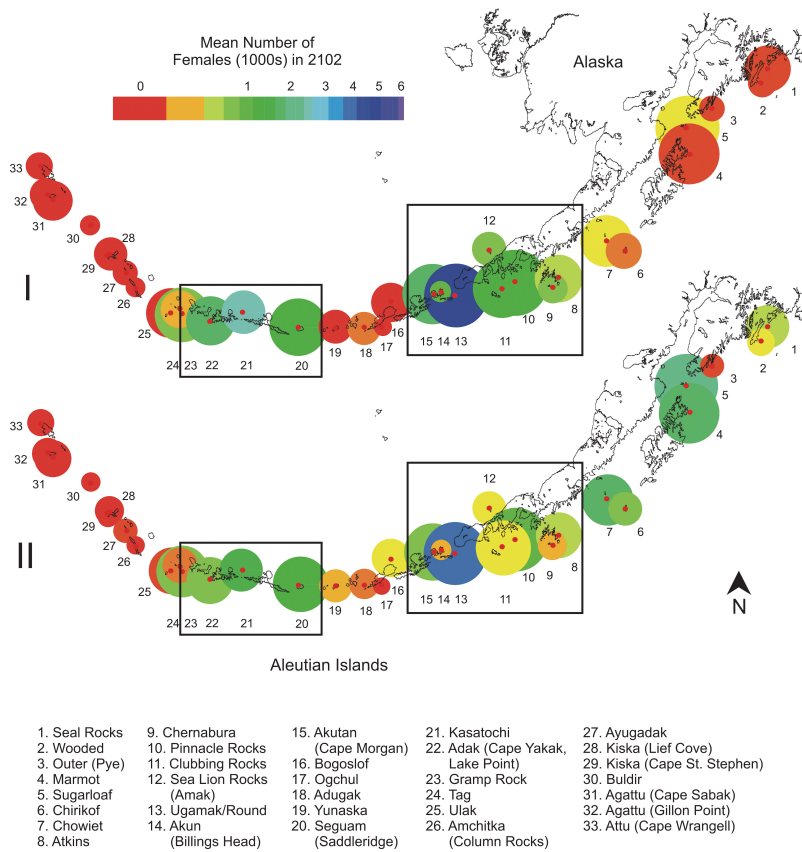


Figure 5. Mean predicted number of female Steller sea lions for each subpopulation in western Alaska under Scenarios I and II. The primary difference between the two panels is that Scenario I considered three phases of population changes, while Scenario II considered four phases by splitting the third phase into two periods. The colors of the circles reflect the predicted mean numbers of females in 2102. The areas of the circles are proportional to the mean predicted numbers of females in 2002. The boxes denote the Seguam/Adak region in the central Aleutian Islands (left box) and the Unimak Pass area in the western Gulf of Alaska/eastern Aleutian Islands.

predicted size did not change. This is likely an artifact of model parameterization and fitting given that Scenario II had an extra phase and thus more parameters for the same number of data points, which likely increased parameter correlation and reduced the precision of parameter estimates resulting in broader posterior probability distributions.

Under Scenario III with no future environmental variability there was no risk of extinction for Steller sea lion subpopulations in western Alaska since the subpopulations were simply regulated about their new carrying capacities (Table 3). Even when our maximum level of stochasticity was applied there was still <0.05 probability of <50 females in 2102 for all subpopulations under this scenario. The majority of the spread in the posterior probability distributions for total population size under Scenario III was a result of uncertainty in the estimated carrying capacities. The

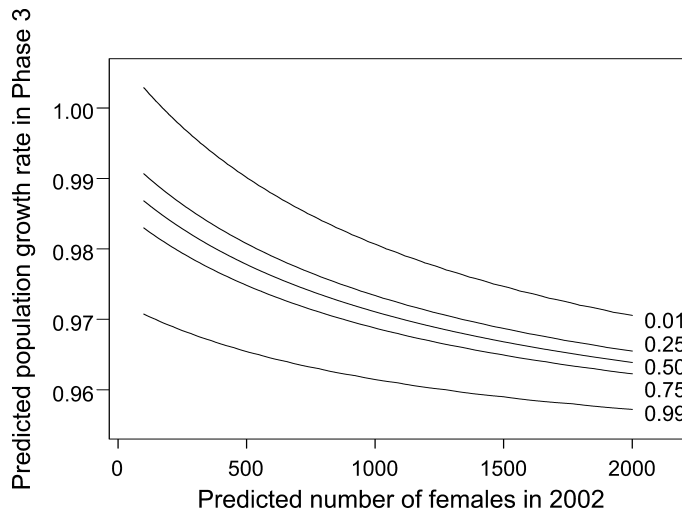


Figure 6. Contour plot showing the probability of fewer than 50 females being alive by 2102 in any given subpopulation (under Scenario I) as a function of the number of females in 2002 and population growth rate in Phase 3. The prediction surface was generated using the results of a logistic regression of the outcomes of each of the 20,000 PVA runs for each subpopulation. Independent variables were the predicted population size in 2002, the predicted population growth rate in Phase 3, and the interaction between these two variables.

addition of stochasticity due to environmental variation slightly increased the CVs of the posterior probability distributions (Table 3). Stochasticity decreased the median predicted number of females in individual subpopulations and in the overall total population in 2102 (Table 3). This decrease occurred because the distribution of overall population growth rates became skewed downward as stochasticity in vital rates increased. We had effectively limited the maximum potential rate of increase of populations to $\sim 6\%$ per year but did not set a minimum growth rate. Also, random stochasticity in a rate decreases the long-term expectation of that rate due to the multiplicative nature of population growth (Lande 2002). Unfortunately, it is not simple to calculate and account for this bias in our implementation of stochasticity (Eq. 9). With the density-dependent regulation in Scenario III these effects actually reduced the equilibrium population size, rather than decreasing the long-term population growth rate.

DISCUSSION

Estimation of Vital Rates from Count Data

When estimating parameters by fitting models to data, it is important that the complexity of the models and the number of parameters be appropriate for the data in hand and the objectives of the study. Simple models are more tractable and can have the same or better predictive accuracy as complex models (Stephens *et al.* 2002). In our decline analysis we attempted to estimate the parameters of a relatively simple, age-structured population model from counts of Steller sea lion pups and non-pups at breeding sites. Two difficulties with this technique reduced the precision of our

parameter estimates: (1) there were a lack of counts for each modeled component of the population (*i.e.*, separate counts of juveniles and adults), and (2) the counts represented only part of the population (*i.e.*, some of the animals were at sea or at non-breeding sites when the counts were made). Nevertheless, we found that relative changes in birth and survival rates over time in our model could be estimated from the two time series of counts.

The best data on the dynamics of a Steller sea lion population during the decline come from the Gulf of Alaska in the vicinity of Marmot Island (Rookery #4 in Fig. 5). York (1994) and Holmes and York (2003) used age-structured models to determine the changes in birth and survival rates that would have been necessary to drive the observed decline in counts and observed changes in age-structure determined from samples of animals and medium-format aerial photographs from this area. Their studies concluded that reduced juvenile survival was the likely mechanism driving the decline through the 1980s, but that a decreased birth rate might be responsible for the decline through the 1990s. Our analysis of the decline, which used only counts of pups and non-pups, also suggested that a decrease in juvenile survival was likely the main cause of the early part of the decline of Steller sea lions at Marmot Island, and our results were also consistent with a decrease in birth rate having occurred during the 1990s. Nevertheless, as demonstrated by Holmes and York (2003), additional data on the ratio of juveniles to adults improved the precision of estimated changes in vital rates.

Our analysis expanded upon previous Steller sea lion population modeling studies by attempting to estimate the vital rates responsible for the decline in subpopulations other than Marmot Island using counts of pups and non-pups. Finer age-structure data are not available for these subpopulations during the decline. Our model suggested that the changes in vital rates responsible for the decline likely varied among subpopulations and varied with time. For example, juvenile and adult survival rates appear to have been lowest during the 1980s for many, but not all subpopulations. Juvenile survival in some western Aleutian subpopulations appears to have been lower during the late 1990s than during the late 1980s/early 1990s.

It is important to note that there is considerable uncertainty in our modeled estimates of vital rates (wide posteriors), particularly when there were few count data available for a subpopulation. In addition, some of the posteriors had maximal values at the limits of their priors, which is less than ideal. The latter might suggest that either the priors were unrealistic or the model structure was inappropriate. For example, it is possible that birth and survival rates exceeded their assumed maximum values. However, we feel that the bigger problem was an overall lack of precision in parameter estimation arising from using only counts of pups and non-pups on breeding sites and the correlations among birth rates, survival rates, and nuisance parameters. Despite the shortcomings of the data, information about relative changes in birth and survival rates can be obtained from time series of counts of pups and non-pups using a simple age-structured model. Applying this technique to all rookeries in western Alaska had not been done before, and provided a more biologically realistic simulation of these populations into the future than a simpler non age-structured model would have.

Error and Stochasticity

The treatment of observation and process error when fitting models to time-series data affects the resulting parameter estimates (Hilborn and Mangel 1997). It is

difficult to estimate both observation and process error because the two are confounded. Often variability in the data that is not accounted for by the model is attributed to one or the other error types, or the ratio of the variances of the two error types is specified (Ludwig *et al.* 1988). In our analysis of the decline we modeled the variability of the counts about the predicted population trajectories as observation error, and ignored process error. There are techniques for estimating both observation and process error (*e.g.*, Holmes 2001, de Valpine and Hastings 2002), but given the relative complexity of our model and the gaps in the time series that we used, we did not explore these possibilities.

Observation error as estimated by our model represents not only true observation error but also variability in the parameters that scale the counts to total population size (*e.g.*, annual variability in the proportion of juveniles using rookeries). These parameters do not influence the dynamics of the population, and thus the error associated with their estimation can properly be considered part of the total estimated "observation" error. However, in reality, some of the variability in the count data reflects true process error (*i.e.*, variability in birth and survival rates over time due to environmental stochasticity). Not properly accounting for this in our statistical analysis may have biased our parameter estimates and the projected sizes of populations into the future. However, the goal of our decline analysis was to simulate the protracted decline of Steller sea lion populations in western Alaska, not to estimate the natural level of variability in birth and survival rates over time. A modeling study by Pascual and Adkison (1994) suggested that short-term environmental stochasticity was likely not the cause of these declines. Instead their model pointed to some long-term change in the environment or catastrophe as being a more probable explanation. Thus, we simulated historical population dynamics with long-term reductions in vital rates and carrying capacity and ignored short-term variability.

We examined the effect of additional random environmental perturbations affecting birth and survival rates in our future simulations under the density-dependent scenario (III). We found that additional stochasticity resulting in CVs of final population size of 15% was not enough to cause substantial probabilities of extinction for any subpopulation. Thus, if the dynamics of these subpopulations are subject to density-dependent regulation as modeled, the risk of extinction is low at the estimated new carrying capacities given the levels of stochasticity that we examined.

Little is known about long-term stochasticity in the vital rates of Steller sea lion populations. Thus, we modeled stochasticity in a rather crude manner, and were unable to determine what the most realistic level of stochasticity might be. Infrequent, catastrophic decreases in birth and survival rates are more important than annual stochasticity *per se* in determining extinction risk (Pimm and Bass 2002) and have occurred in many populations of otariids (Gerber and Hilborn 2001). Natural catastrophes can be considered extreme events in a continuous distribution of environmental perturbations (Reed *et al.* 2003), but anthropogenic catastrophes can also occur (*e.g.*, over-harvesting).

Natural catastrophes are perhaps best modeled with auto-correlation in environmental perturbations over time, while a more general way of modeling unspecified catastrophes is to simply implement extreme events with some frequency in addition to annual stochasticity in vital rates (Breen *et al.* 2003). We modeled the historic decline as a catastrophe, but did not model any future catastrophes. If another catastrophe occurred in the time frame of our future simulations (100 yr), the predicted risks of extinction would have been higher than those we estimated. Unfortunately it is difficult to predict the frequency with which unspecified catastrophes might

occur in Steller sea lion populations given our current understanding. Regardless, another catastrophe with a magnitude similar to that of the observed decline would surely drive many subpopulations to extinction from their currently reduced sizes (and perhaps carrying capacities).

Extinction Risk

The three scenarios we explored produced quite different predictions of the risk of extirpation of the Steller sea lion in western Alaska. Consistent with the findings of previous PVAs (York *et al.* 1996, Gerber and VanBlaricom 2001), we found a large chance that many subpopulations of sea lions will go extinct within 100 yr if the average trends in population size observed during the 1990s continue into the future (*e.g.*, western Aleutian Islands, Fig. 5). However, the outlook is relatively better for some subpopulations than others. In particular, there are two clusters of subpopulations that have a good chance of not going extinct in the next 100 yr if average growth rates observed during the 1990s continue. The risks of extinction for other subpopulations that declined through the early 1990s and potentially began recovering in the late 1990s are also reduced if recent population growth rates continue. Under these scenarios (I and II), there is a relatively low risk of extirpation of the Steller sea lion in western Alaska in the next 100 yr, but individual subpopulations are at a great risk of extinction (majority > 50%).

As expected, the risk of extinction of subpopulations is lower if density-dependent compensation occurs in the future (Scenario III). With density-dependent regulation, the risk of extinction of subpopulations is still low even when additional random environmental stochasticity affecting birth and survival rates was incorporated. However, the number of Steller sea lions in western Alaska is now much lower than it was in 1978, independent of whether or not the carrying capacity has changed. Thus, subpopulations are much more susceptible to potential future catastrophes.

A cautionary finding is that differences in model structure between scenarios affected the precision of parameter estimation and thus affected estimates of extinction risk. The most probable population growth rates in the late 1990s yielded a similar median number of Steller sea lions in western Alaska in 100 yr compared to the predictions made using population growth rates through the 1990s as a whole. However, the model structure (*i.e.*, number of parameters) differed between these two scenarios resulting in more uncertainty in the parameter estimates in the former scenario, and thus higher estimates of the risk of extinction of subpopulations. While it is important to consider multiple models and incorporate uncertainty in parameter estimation into PVAs, the interaction between model structure and parameter estimation, and its effects on the estimation of extinction risk, must be considered.

It is not clear which of the modeled future scenarios we considered is the most likely to occur. This is, in part, because our analysis was unable to determine whether the historic decline was a result of density-independent or density-dependent factors (both models yielded good fits to the data). As Fay (2004) demonstrated, a wide range of models can adequately describe the observed decline in counts of Steller sea lions. A recent review of available empirical data was also unable to conclusively reject any of the hypotheses (National Research Council 2003). Our analysis was never intended to evaluate the likelihood of the different scenarios. Instead, it provides a framework within which current scientific understanding of mechanisms that regulate wildlife populations can be evaluated to develop recovery criteria and guide research and management decisions.

One of the values of our PVA is in the quantification of the uncertainty associated with predicting the risk of extinction, both within and across scenarios. Simply put, there is a lot of uncertainty regarding the risk of extirpation of the Steller sea lion in western Alaska in the near future. This is a common situation with PVAs and has led some to question the value of such endeavors altogether (*e.g.*, Ludwig 1999). Furthermore, it is difficult to evaluate the accuracy of a prediction about the probability of an extinction event (Pielke and Conant 2003). In fact, one experimental study that examined the validity of PVA model predictions concluded that the models' quantitative predictions were generally not accurate (Belovsky *et al.* 1999).

From a practical standpoint, researchers, managers, policy-makers, and the general public are very interested in the management of wild populations with respect to their risk of extinction. Thus, we feel the quantification of this risk and the associated uncertainty is a worthwhile pursuit. In the case of the Steller sea lion, there is a Recovery Team that is tasked with developing "recovery criteria" that reflect the species' risk of extinction and thus its status under the U.S. Endangered Species Act. Our study provides functional relationships between criteria that might be used to make such decisions, such as population size and population growth rate, and the probability of extinction of actual Steller sea lion subpopulations given different hypotheses about density dependence and environmental variability in the future. These relationships can be used to develop "recovery criteria" (Schultz and Hammond 2003).

Regarding the difficulty in evaluating the accuracy of our predictions, a recent article on ecological forecasting suggested that such probabilistic predictions should be evaluated based on their skill rather than their accuracy (Pielke and Conant 2003). Skill was defined as "the improvement provided by the prediction over a naïve forecast." Our PVA outlines the major alternative hypotheses about the roles of density-independent and density-dependent factors in future and past changes in sea lion numbers, and bounds predictions of the risk of extinction under each of these alternative hypotheses in a common, comparable currency. Thus, our PVA quantifies the currently irreducible uncertainties inherent to estimating the probability that the Steller sea lion will be extirpated in western Alaska and provides useful information for decision-makers beyond that which is simply intuitive.

Ideally, PVA models should incorporate parameters that provide insight into how human actions can influence the risk of extinction (Boyce 1992). Estimated probabilities of extinction can then be used in decision analyses that assess the trade-offs between different management actions (Taylor *et al.* 1996, Harwood 2000). Given the current uncertainty regarding the factors that influence the dynamics of Steller sea lion populations, we did not model specific mechanisms—thus, our models cannot be used to assess the effects of specific management actions on extinction risk. Nevertheless, proposed effects of different management actions can still be considered under each of our scenarios. For example, if a functional relationship is proposed between a specific management action and population growth rate, our results can be used to assess the probability of extinction given different growth rates.

Future Research

One factor we did not consider in our analysis was dispersal among subpopulations. Given the limitations of the data, it was not possible to estimate dispersal in our analysis of the decline. However, scenarios could be examined where new rookeries are formed or extinct rookeries are recolonized by incorporating dispersal in

PVA simulations. Data on dispersal rates between some rookeries in Alaska are now available from the resightings of marked animals (Raum-Suryan *et al.* 2002), and genetics research is also underway to estimate dispersal rates. As more data become available, these scenarios should be explored to refine the predicted spatial patterns of extinction risk.

Continued counts of Steller sea lion pups and non-pups provide a means to reassess extinction risk in the future using the framework we have outlined. Changes in future numbers of pups and non-pups may allow the most likely PVA scenario to be determined (*i.e.*, continued decline, recovery, or adjustment to new carrying capacities). One of the most important research topics that should be explored in the future is the natural level of environmental variability and its effects on the birth and survival rates of Steller sea lions. Improved estimates of this variability are critical for improving estimates of extinction risk. Data that are currently being used to assess this variability and its effect on sea lion populations include biological isotopes, climate records, and genetic variation.

Recent population sizes and trends revealed subpopulations of Steller sea lions in western Alaska that have a relatively lower risk of going extinct than other subpopulations (Fig. 5). Comparative research between these groups of subpopulations may provide insight into the factors responsible for these differences (*e.g.*, diet, predation, human impacts), and thus guide management by determining the specific mechanisms behind extinction risks as predicted in our analysis.

Conclusions

The results of our study provide a mixed view about the future of the Steller sea lion in the Gulf of Alaska and Aleutian Islands. Predictions of the risk of extinction differed depending on the particular scenarios considered. The models predicted that most subpopulations have a >5% chance of extinction within 100 yr if current population trends continue into the future. However the risk of total extirpation is low. The risk of extinction is lower for all subpopulations if compensatory density-dependent mechanisms play a role in population dynamics—even in the presence of environmental variability. Despite such apparent optimism, it is important to recognize that the current sizes of most subpopulations are dramatically smaller relative to their sizes in 1978 under all scenarios and are thus more susceptible to future catastrophes. The available data suggest that some subpopulations may have begun recovering through the 1990s or through the late 1990s. However, only time will ultimately tell the true viability of the Steller sea lion in Alaska. Until then, our study provides information in the face of considerable uncertainty that may help guide research and management decisions, and assist in the recovery of Steller sea lions.

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Table A2. Counts of Steller sea lion non-pups at rookeries in western Alaska during June and July 1978–2000. Counts are mainly from aerial photographs, but include counts from terrestrial and offshore observation points. Sources were Early *et al.* (1980), Fiscus *et al.* (1981), Calkins and Pitcher (1982), Merrick *et al.* (1987), Byrd and Nyswander (1988), Calkins and Goodwin (1988), Douglas and Byrd (1990), Merrick *et al.* (1991), Loughlin *et al.* (1992), Merrick *et al.* (1992), NMFS (1992), Sease *et al.* (1993), Chumbley *et al.* (1997), Strick *et al.* (1997), Sease and Loughlin (1999), Sease *et al.* (2001), Sease and Gudmundson (2002) and the NMML Steller sea lion non-pup count database (<http://nmml.afsc.noaa.gov/AlaskaEcosystems/ss/home/Databases/Adult%20count%20database.htm>).

| | Year | | | | | | | | | | | | | | | | | | | | | | | | |
|------------------------------|-------|--------|----|----|----|----|-------|-------|-------|----|-------|-------|-------|-------|-------|-----|-------|-----|-------|-----|-------|-----|-----|----|-------|
| Rookery | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 00 | 01 | 02 |
| Seal Rocks | 2,463 | 2,961 | | | | | | | | | | 2,159 | 1,471 | 1,220 | 784 | | 636 | | 544 | | 730 | 624 | 749 | | 768 |
| Wooded | | | | | | | | | | | | 1,333 | 1,232 | 1,350 | 1,005 | | 649 | | 502 | | 330 | 311 | 396 | | 396 |
| Outer (Pye) | 3,142 | 3,155 | | | | | | | | | | 1,127 | 589 | 334 | 243 | | 406 | | 319 | | 225 | 344 | 262 | | 226 |
| Marmot | 8,506 | 8,450 | | | | | | | | | 3,460 | 2,331 | 1,766 | 1,459 | 1,581 | | 1,091 | | 1,102 | | 781 | 694 | 671 | | 848 |
| Sugarloaf | 4,810 | 4,374 | | | | | 8,122 | 4,983 | 7,049 | | | 1,861 | 1,319 | 1,216 | 1,184 | | 976 | | 741 | | 625 | 646 | 706 | | 736 |
| Chirikof | 3,699 | 5,199 | | | | | 2,346 | 2,059 | | | | 1,278 | 1,061 | 946 | 770 | | 433 | | 360 | | 295 | 266 | 276 | | 320 |
| Chowiet | 4,419 | 4,441 | | | | | | | | | | 737 | 897 | 716 | 771 | | 599 | | 592 | | 538 | 515 | 504 | | 582 |
| Atkins | 3,943 | 5,000 | | | | | | 1,562 | 1,129 | | | 755 | 728 | 616 | 792 | | 571 | | 624 | | 544 | 602 | 537 | | 560 |
| Chernabura | 2,758 | 1,504 | | | | | | 487 | 456 | | | 544 | 442 | 650 | 459 | | 676 | | 422 | | 729 | 624 | 496 | | 496 |
| Pinnacle Rock | 3,692 | 2,731 | | | | | | 1,588 | 1,932 | | | 1,366 | 1,305 | 1,049 | 1,092 | | 977 | | 1,027 | | 1,007 | 865 | 868 | | 1,034 |
| Clubbing Rocks | 2,663 | 1,1623 | | | | | | 1,251 | 1,023 | | | 856 | 1,021 | 920 | 970 | | 931 | | 957 | | 934 | 858 | 712 | | 830 |
| Sea Lion Rocks (Amak) | 1,386 | | | | | | 1,298 | 558 | 527 | | | 344 | 286 | 300 | 329 | | 480 | | 590 | | 452 | 445 | 258 | | 507 |
| Ugamak/Round | | | | | | | 1,358 | 1,503 | 1,751 | | | 450 | 945 | 1,063 | 954 | | 971 | | 854 | | 840 | 744 | 746 | | 1,044 |
| Akun (Billings Head) | | | | | | | 760 | 435 | | | | 150 | 118 | 156 | 271 | | 220 | | 346 | | 247 | 213 | 254 | | 275 |
| Akutan (Cape Morgan) | 2,796 | | | | | | 2,084 | 1,269 | 1,338 | | | 578 | 765 | 818 | 1,061 | | 908 | | 934 | | 760 | 681 | 739 | | 783 |
| Bogoslof | | 1,463 | | | | | 1,379 | 1,287 | | | | 682 | 713 | 558 | 540 | | 413 | | 382 | | 274 | | 347 | | 356 |
| Ogchul | | | | | | | 712 | 547 | 486 | | | 217 | 240 | 229 | 235 | | 209 | | 155 | | 167 | 137 | 117 | | 105 |
| Adugak | | | | | | | | 955 | 915 | | | 392 | 350 | 395 | 322 | | 314 | | 277 | | 231 | 270 | 201 | | 201 |
| Yunaska | | 1,497 | | | | | | 1,071 | | | | 466 | 391 | 398 | 393 | | 462 | | 340 | | 210 | 241 | 276 | | 276 |
| Seguam (Saddleridge) | | 4,018 | | | | | | 2,942 | | | | 602 | 833 | 684 | 696 | | 658 | | 553 | | 586 | 570 | 666 | | 666 |
| Kasatochi | | 1,953 | | | | | | 1,170 | | | | 659 | 641 | 466 | 376 | | 288 | | 331 | | 351 | 390 | 529 | | 529 |
| Adak (Cape Yakak/Lake Point) | | 1,242 | | | | | | 1,289 | | | | 424 | 592 | 847 | 615 | | 765 | | 618 | | 683 | 874 | 821 | | 821 |
| Gramp Rock | | 1,705 | | | | | | 1,290 | | | 872 | 747 | 712 | 773 | 691 | | 537 | | 582 | | 571 | 580 | 600 | | 600 |
| Tag | | 1,740 | | | | | | 944 | | | | 590 | 478 | 440 | 370 | | 310 | | 321 | | 371 | 301 | 279 | | 279 |
| Ulaik | | 2,170 | | | | | | 2,729 | | | | 1,123 | 1,324 | 1,046 | 1,059 | | 866 | | 844 | | 698 | 663 | 481 | | 481 |
| Amchitka (Column Rocks) | | 1,943 | | | | | | 728 | | | | 197 | 233 | 194 | | | 188 | | 137 | | 113 | 92 | 71 | | 71 |
| Ayudak | | 1,463 | | | | | | 702 | | | | 389 | 401 | 324 | 313 | | 285 | | 281 | | 179 | 146 | 182 | | 182 |
| Kiska (Lief Cove) | | 4,953 | | | | | | 1,715 | | | | 510 | 528 | 506 | 357 | | 359 | | 341 | | 285 | 272 | 174 | | 174 |
| Kiska (Cape St. Stephen) | | 2,202 | | | | | | 1,351 | | | | 464 | 564 | 380 | 248 | | 233 | | 258 | | 224 | 152 | 126 | | 126 |
| Buldir | | 5,118 | | | | | | | | | 1,396 | 1,058 | 729 | 589 | 454 | | 345 | | 313 | | 336 | 129 | 94 | | 94 |
| Agattu (Cape Sabak) | | 6,394 | | | | | | 3,130 | | | 1,783 | 1,680 | 1,199 | 1,428 | 1,304 | | 961 | | 1,001 | | 827 | 480 | 307 | | 307 |
| Agattu (Grillon Point) | | 756 | | | | | | | | | | 806 | | | 670 | 773 | | 509 | | 595 | 481 | 306 | | | 258 |
| Attu (Cape Wrangell) | | 2,141 | | | | | | | | | 1,196 | | | 736 | 755 | | 839 | | 721 | | 584 | 310 | | | 264 |