

Modeling Spatial Dynamics of Steller Sea Lions (*Eumetopias jubatus*) Using Maximum Likelihood and Bayesian Methods: Evaluating Causes for Population Decline

Gavin Fay and André E. Punt

*University of Washington, School of Aquatic and Fishery Sciences, Seattle,
Washington*

Abstract

The timing and extent of the negative population trend in the abundance of the western stock of Steller sea lions has not been geographically uniform. A stochastic metapopulation dynamics model is developed for Steller sea lions. This model allows for geographical differences in factors affecting population processes, and can be parameterized to represent a wide range of hypotheses for the decline in Steller sea lion abundance. Bayesian and maximum likelihood methods are used to fit this model to pup and non-pup count data, age structure samples, and survival estimates. Inferences from model selection criteria highlight the spatial variability in the types of impact deemed to provide most parsimonious representation of the data. Bayesian posteriors for the estimated model parameters show that many combinations of parameter values are able to provide similar fits to the data, even given a specific hypothesis for the decline. This highlights the uncertainty in the precise nature of the impact of these hypotheses. Indeed, while pup production is generally estimated consistently among models, estimates of the size of other components of the Steller sea lion population (such as total population size) depend greatly on the assumptions regarding the cause of the decline. The results demonstrate that future simulation modeling approaches will require more formal, spatial, and mechanistic descriptions of the manner in which specific hypotheses for the decline affect the population.

Introduction

Data from counts conducted by the National Marine Fisheries Service (NMFS) and the Alaska Department of Fish and Game (ADFG) of pups at rookeries, and of non-pups at rookeries and nonbreeding haul-out sites, suggest that the Alaskan population of Steller sea lions (Otariidae: *Eumetopias jubatus*) declined by approximately 85% between 1956 and 1998 (York et al. 1996, Sease and Loughlin 1999). In 1997, the population of Steller sea lions to the west of 144°W (the western stock) was declared “endangered” under the Endangered Species Act, with the population to the east of this (the eastern stock) remaining “threatened” (Loughlin 1997).

Several reasons for the decline of the western stock of Steller sea lions have been postulated. York (1994) examined changes in the age-composition of samples collected in 1975-1978 and 1985-1986, and concluded that a 20% decline in the annual survival of juvenile females was the simplest explanation for the reduction in abundance. Pascual and Adkison (1994) analyzed several possible reasons for the decline in Steller sea lion abundance, and concluded that transient age-structure dynamics, historical pup harvesting, and short-term environmental stochasticity were unlikely causes, and that long-term environmental changes or a catastrophe of some sort were probably responsible. Other hypotheses regarding the decline of the western stock involve a reduction in birth rate, nutritional stress, predation, direct and indirect competition with fisheries, migration, disease, pollution, and the impact of a regime shift or trophic cascade (Calkins and Pitcher 1982, Merrick et al. 1987, Calkins and Goodwin 1988, Hoover 1988, York 1994, Loughlin and Merrick 1989).

To date, it has not been possible to exclude any of these hypotheses definitively, although past research efforts have eliminated redistribution, pollution, predation, subsistence harvest, disease, and natural fluctuations as the principal causes for the decline (NMFS 1992). Several authors suggest that the cause of the decline may be a combination of various factors (Loughlin and York 2000, Hunter and Trites 2001), and that the primary cause has likely changed over the period of decline (Loughlin and York 2000).

The timing and extent of the negative trend in the size of the western stock has not been uniform over the geographical range of the population. Trites and Larkin (1996) and York et al. (1996) both identified several spatially distinct trends in the abundance of Steller sea lions within the western stock. This suggests that the factors responsible for the decline have not been spatially homogeneous. The behavior of Steller sea lions does create distinct localized populations that may well enable spatial differences in the factors affecting population processes, such as survivorship and fecundity, to be expressed differentially within the overall population. In addition to evidence that Steller sea lions do not

breed other than with their natal stock, Steller sea lions show a degree of tendency toward natal site fidelity in that females return to breed at either the site of birth, or at a site close to the natal site (Pitcher and Calkins 1981). At times other than the pupping and breeding season in the months of May to August, Steller sea lions disperse widely from their breeding areas, and may haul out at sites many hundreds of kilometers from these areas. Immature sea lions show a tendency to disperse even farther than mature animals (Raum-Suryan et al. 2002). Such a population structure, which is typical of otariids, is a good example of a metapopulation, whereby a set of distinct breeding populations are linked through dispersal of individuals, creating a “population of populations” (Hanski and Simberloff 1997).

The high degree of spatial structuring of Steller sea lion populations, and that of management decisions and other human influences likely to affect them, requires a population modeling approach that is spatially realistic. A stochastic, spatially structured, flexible modeling framework for Steller sea lions, which uses the metapopulation concept to account for spatial variability in population trend, is therefore developed. The population dynamics model is appropriate for Steller sea lions, and can be used to mimic the local dynamics of individual regions within the sea lion metapopulation. The implications of a number of different impact scenarios are considered, and model selection criteria used to compare among several different hypotheses regarding the type of impact on this sea lion population.

Methods

The population dynamics model (Appendix A) considers the western stock of Steller sea lions in Alaska as a metapopulation comprising six regions (Fig. 1), each of which includes one or more sea lion rookeries and a number of nonbreeding haul-out sites. Each region is considered within the modeling framework to represent an individual subpopulation in the metapopulation.

The sea lion population in a region is divided into the number of males, immature females, and mature females of each age. The numbers-at-age (by region) are updated each year by:

1. calculating the number of births;
2. allowing immature females to reach maturity; and
3. removing the deaths due to all causes.

Additional trends in birth and death rates can be implemented by imposing forcing functions on survival rate, pregnancy rate, and region-specific carrying capacity (see equations A.7-A.13). These forcing functions can be used to model the effect of unknown stressors on the Steller

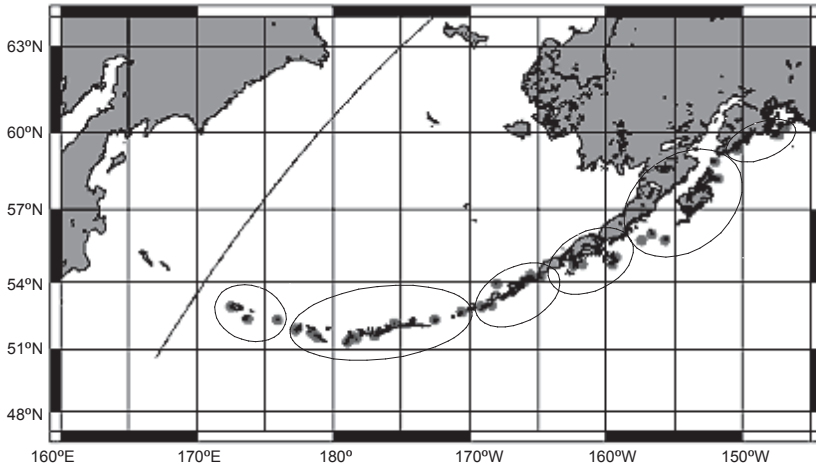


Figure 1. Map of the North Pacific Ocean showing the locations of the six regions of Steller sea lions comprising the Alaskan western stock metapopulation. The six regions are (from west to east): western Aleutian Islands, central Aleutian Islands, eastern Aleutian Islands, western Gulf of Alaska, central Gulf of Alaska, and eastern Gulf of Alaska.

sea lion population, which could result from one or more of the numerous hypotheses for the decline of the western stock. The model is flexible so that these functions can be parameterized to be region-specific, or global, so that one set of parameters determines the trends in survival and/or pregnancy rate in more than one region. The initial conditions (in 1945) correspond to a population at its pre-exploitation level, with the corresponding age-structure, as determined from the survival and maturity rates in Table A.1.

The model is fitted to four sources of data: (a) counts of the total number of pups in a region (which provides an index of the number of pregnant females in the region), (b) counts of non-pups at nonbreeding haul-out sites in a region (which provides a relative index of some component of the 1+ population in the region), (c) survival rates based on a tagging program, and (d) samples of the age-composition of the population in 1985. The survival rate and age-composition data are based on animals from the central Gulf of Alaska, and so these data are used only when estimating the values of the parameters of the population dynamics model for this region.

The parameters of the population dynamics model (Table 1) are either pre-specified based on auxiliary information for Steller sea lions, set to

“guestimates” based on inferences from other species, or determined by fitting the population dynamics model to the available information on pup counts, non-pup counts, survival rate estimates, and the age-structure of the population inferred from collections. The parameters in the model that are related to density dependence are set at fixed values for the analyses of this paper. The resilience parameter, \bar{A} is fixed at 0.22 and the parameter determining the degree of compensation, z , was fixed at 2.39, which corresponds to maximum pup production occurring when the regional non-pup population is at 60% of the equilibrium level.

The model fitting process involves either maximizing the likelihood function detailed in Appendix B (to provide the “best” estimates for the model parameters), or applying Bayesian methods to represent uncertainty in the model parameters and both current and historical population size.

Bayesian estimation

Bayesian estimation requires that prior distributions be placed on all of the “free” parameters of the model being fitted. The priors used when conducting the Bayesian analyses are listed in Table 1. Uniform prior distributions are assigned to all of the parameters except for the regional 1998 pup production (see below). The model is parameterized in such a way so as to be able to define as many estimable parameters as possible as fractions, thus taking values between zero and one. This enabled the placing of more objective uniform $U[0,1]$ priors, and did not necessitate overly subjective choices regarding the bounds for the prior distributions. The parameters determining the reduction in the survival rate of pups and adults were chosen to be defined as fractions of the reduction in juvenile survival rate, because preliminary analyses showed that the survival rate of juveniles was reduced more than that of pups and adults.

The priors for the parameters that determine the year of maximum impact (smooth function), and the start year and impact duration (knife-edge function) are not specified in this manner. The bounds for these priors are constrained by the latest limit of the available data (2001), and either 1970 (for the knife-edge function) or 1980 (smooth function). These latter values reflect an understanding regarding the general timing of the Steller sea lion decline.

While the model is parameterized in such a way that the priors used encompass every possible value for many parameters, the method of parameterization is still somewhat subjective. For example, the impacts on survival rate are modeled with the maximum impact occurring on juveniles. While this is consistent with previous findings by York (1994), no account is made for the possibility that the reduction in the survival rates for adults and/or pups exceeded that for juveniles. Similarly, the years chosen for the bounds of the priors for the parameters determining the timing of the impact functions are arbitrary although they do encompass

Table 1. The parameters of the population dynamics model.

Parameter	Description	How specified	Prior
K^A	Regional pre-exploitation number of non-pups	Calculated	
	Pup production in 1998		Normal $\left[P_y^A, (\sigma_y^{A,P})^2\right]$
X	Dispersal probabilities	Pre-specified	
Y	Mixing probabilities	Pre-specified	
M_a	Proportion mature at age	Pre-specified	
\bar{A}	Density-dependence (resilience) parameter	Pre-specified	
z	Degree of compensation	Pre-specified	
S_a	Age-specific survival rates	Pre-specified	
Parameters that determine the deterministic trend in pregnancy rate			
h_F^A	Maximum impact on pregnancy rate	Estimated	Uniform [0, 1]
y_F^A	Year of maximum impact on pregnancy rate	Estimated	1980 + Uniform [0,20]
$\sigma_{F1/2}^A$	Fraction of impact two years prior/post max.	Estimated	Uniform [0, 1]
v_F^A	Year in which impact on pregnancy rate begins	Estimated	Uniform [1970, 2001]
l_F^A	Length of impact on pregnancy rate	Estimated	Uniform [0, 2002- v_F^A]
Parameters that determine the deterministic trend in survival rate			
h_S^A	Maximum impact on juvenile survival rate	Estimated	Uniform [0, 1]
ϕ_1	Pup selectivity for survival impact	Estimated	Uniform [0, 1]
ϕ_2	Adult selectivity for survival impact	Estimated	Uniform [0, 1]
y_S^A	Year of maximum impact on survival rate	Estimated	1980+ Uniform [0, 20]
$\sigma_{S1/2}^A$	Fraction of impact two years prior/post max	Estimated	Uniform [0, 1]
v_S^A	Year in which impact on survival rate begins	Estimated	Uniform [1970, 2001]
l_S^A	Length of impact on survival rate	Estimated	Uniform [0, 2002- v_S^A]

Table 1. (continued.)

Parameter	Description	How specified	Prior
Parameters that determine the deterministic trend in carrying capacity			
ψ^A	Carrying capacity impact	Estimated	Uniform [0, 1]
y_{ψ}^A	Year in which impact on carrying capacity begins	Estimated	Uniform [1970, 2001]
I_{ψ}^A	Length of impact on carrying capacity	Estimated	Uniform [0, 2002- y_{ψ}^A]

the period for which data are available and the posterior distributions for these parameters show little evidence of probability density “piling up” at the boundaries.

The Bayesian calculations are implemented using the sampling-importance-resampling (SIR) algorithm (Rubin 1987, Gelman et al. 1995, Punt and Hilborn 1997). This algorithm samples parameter vectors from the Bayesian posterior distribution by generating a large number of parameter vectors from the prior probability distribution, and then re-sampling from these vectors with probability proportional to the likelihood. The backwards approach to Bayesian assessments (Butterworth and Punt 1995, Fay 2004) was implemented, with the value for the region-specific initial population size, K^A , (needed to compute the initial age structure), being determined by drawing from a prior distribution for the pup production in 1998, and then using Brent’s method (Press et al. 1996) to solve for the value of K^A that would result in the selected pup production. The most recent pup count is then omitted from the likelihood function because the prior distribution has already been updated using this information. The 1998 pup counts were used when applying the backwards method, rather than the most recent pup count (often for the year 2000 or 2001). This was because maximum likelihood fits suggested that, for some regions, the model did not fit the more recent estimates of pup production very well (the MLE of the 2000-2001 pup count deviated by more than 1 standard error from the observation). The difference in using the count for 1998 rather than the most recent count is almost completely purely computational; the results would be essentially the same irrespective of the choice of year within the last few years.

The SIR algorithm was run until the maximum importance weight assigned to any single parameter vector was less than or equal to 0.5 percent of the total weight of all draws from the prior distributions. This convergence criterion ensured that there was a sufficiently large number of unique parameter vectors in the importance-weighted second sample of 1,000 parameter vectors to enable an investigation of the joint poste-

rior distribution for the model parameters. However, for some regions the count data are highly informative, and very large numbers (several hundred million) of draws from the priors did not attain the convergence criterion.

Scenarios examined

The analyses of this paper consider the six regions of the western stock of Steller sea lions as distinct independent populations, with no movement of animals linking them. Impact functions (time-varying survival rates, changes in pregnancy rate/carrying capacity) in one region do not therefore affect the dynamics of the population in any other region. This assumption greatly simplifies the parameter estimation process because the estimation of the parameters governing the dynamics for each region can be conducted independently. A further simplification for the purposes of the analyses of this paper is that the dynamics are deterministic [$Bin(x,p) = xp$], i.e., no account is taken of demographic stochasticity; results in which demographic stochasticity is taken into account are not qualitatively different from those presented here. It is not presentationally feasible to provide the detailed results for all six regions, and so the results presented focus primarily on the central Aleutian Islands and western Gulf of Alaska regions. Observations resulting from concurrent analyses for the other four regions that are of particular interest are also discussed.

Table 2 lists the nine scenarios considered in this paper. These scenarios are based on different combinations of the impact functions. Table 2 also lists the parameters that are estimated for each scenario. These nine scenarios are compared for each region using maximum likelihood methods, and the Bayesian estimation framework outlined above. The results of the maximum likelihood estimation are compared using Akaike's Information Criteria corrected for small sample size (AIC_c) (Burnham and Anderson 1998). AIC_c allows for model selection among non-nested models, and includes penalties both for lack of fit to the data and model complexity (number of estimated parameters). The results of the Bayesian analyses are compared in a similar way, using the Deviance Information Criterion (DIC) (Spiegelhalter et al. 2002).

Results

Model selection based on AIC_c and DIC

Table 3 lists AIC_c and DIC values for the nine impact scenarios for the six regions and identifies the model with the lowest AIC_c /DIC for each region. Figure 2 shows the fits to pup and non-pup counts, and the estimates of the total number of non-pups for each region for the model selected using AIC_c , while Fig. 3 shows posterior distributions (medians and 95%

Table 2. The nine impact scenarios. The column “free parameters” lists the parameters that are estimated for each scenario in addition to the pre-exploitation number of non-pups, K^A and the parameters that determine the relative availability of non-pups.

Scenario	Impact			Free parameters
	Survival rate	Pregnancy rate	Carrying capacity	
1	Smooth impact	None	None	$h_S^A, \phi_1, \phi_2, \gamma_S^A, \sigma_{S1/2}^A$
2	None	Smooth impact	None	$h_F^A, \gamma_F^A, \sigma_{F1/2}^A$
3	Smooth impact	Smooth impact	None	$h_S^A, \phi_1, \phi_2, \gamma_S^A, \sigma_{S1/2}^A, h_F^A, \gamma_F^A, \sigma_{F1/2}^A$
4	Knife-edged impact	None	None	$h_S^A, \phi_1, \phi_2, v_S^A, I_S^A$
5	None	Knife-edged impact	None	h_F^A, v_F^A, I_F^A
6	Knife-edged impact	Knife-edged impact	None	$h_S^A, \phi_1, \phi_2, v_S^A, I_S^A, h_F^A, v_F^A, I_F^A$
7	None	None	Knife-edged impact	$\psi^A, \gamma_\psi^A, I_\psi^A$
8	Smooth impact	Knife-edged impact	None	$h_S^A, \phi_1, \phi_2, \gamma_S^A, \sigma_{S1/2}^A, h_F^A, v_F^A, I_F^A$
9	Knife-edged impact	Smooth impact	None	$h_S^A, \phi_1, \phi_2, v_S^A, I_S^A, h_F^A, \gamma_F^A, \sigma_{F1/2}^A$

probability intervals) for the time-trajectories of total regional non-pups, pup production, and the fits to the non-pup counts for each region for the model selected using DIC.

The model selected by AIC_c varied among regions. Models with impacts on both survival and pregnancy rates were favored for four of the six regions (eastern and central Gulf of Alaska, and the eastern and central Aleutians). For the eastern Gulf of Alaska, the model with a knife-edged impact on both survival and pregnancy rate (model 6) was selected, whereas for the other three regions, the model that had a knife-edged impact on survival and a smooth impact on pregnancy rate (model 9) was selected. The “best” model for the western Gulf of Alaska was deemed to be that which only had a smooth impact function affecting pregnancy rate

Table 3. AICc and DIC values for the nine impact scenarios for each of the six regions. Values in bold for each region indicate the model with the lowest AICc/DIC value.

Scenario	Eastern GoA	Central GoA	Western GoA	Eastern Aleutians	Central Aleutians	Western Aleutians
AICc						
1	95.40	83.47	53.55	73.68	63.15	42.46
2	82.92	75.94	33.40	83.35	61.26	56.00
3	62.21	58.96	51.11	54.94	60.81	89.02
4	94.31	145.23	68.94	99.03	80.22	35.49
5	69.95	1343.48	124.45	162.20	164.19	46.56
6	40.71	131.03	51.10	74.98	86.08	48.63
7	70.53	1496.99	169.34	174.04	187.41	86.54
8	45.97	91.87	67.20	80.13	79.40	65.27
9	54.01	57.22	47.12	52.91	55.44	64.75
DIC						
1	80.57	69.48	40.88	61.28	49.35	23.93
2	75.79	70.03	26.96	77.87	44.33	38.16
3	23.59	38.53	17.8	32.54	32.06	15.17
4	77.11	121.73	51.79	83.86	68.55	20.82
5	65.27	1338.67	116.58	156.52	149.16	37.62
6	16.77	54.70	24.53	57.05	28.98	10.73
7	64.33	1494.38	151.75	159.59	173.71	30.58
8	18.13	70.19	43.38	59.21	43.80	14.31
9	45.89	35.41	13.14	30.81	30.42	16.74

(model 2), while for the western Aleutian Islands region, the model with a knife-edged reduction in survival rate (model 4) was selected.

For the regions toward the center of the range of the western stock, the models selected using DIC are similar to those selected using AIC_c. Model 9 was chosen as the “best” model for the central and western Gulf of Alaska, and the eastern Aleutian Islands regions. For the eastern Gulf, central Aleutians and western Aleutian Islands regions, model 6 (knife-edged reductions in both survival and pregnancy rate) was chosen as the “best” model. The impact scenarios selected by AIC_c therefore differ from those selected by DIC for the central and western Aleutians, and also for the western Gulf of Alaska.

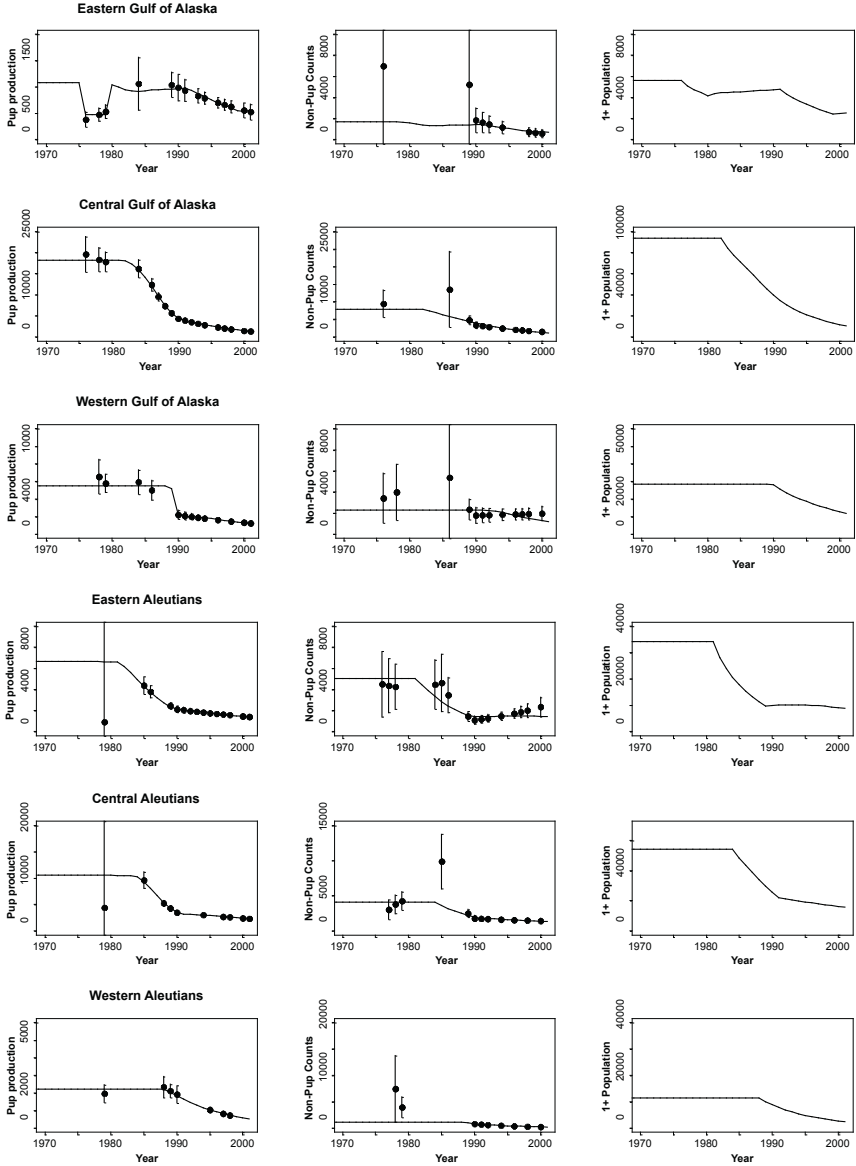


Figure 2. Fits to the pup and non-pup count data, and estimates of total non-pups, corresponding to the maximum likelihood estimates obtained from the models selected by AIC_c for all six regions.

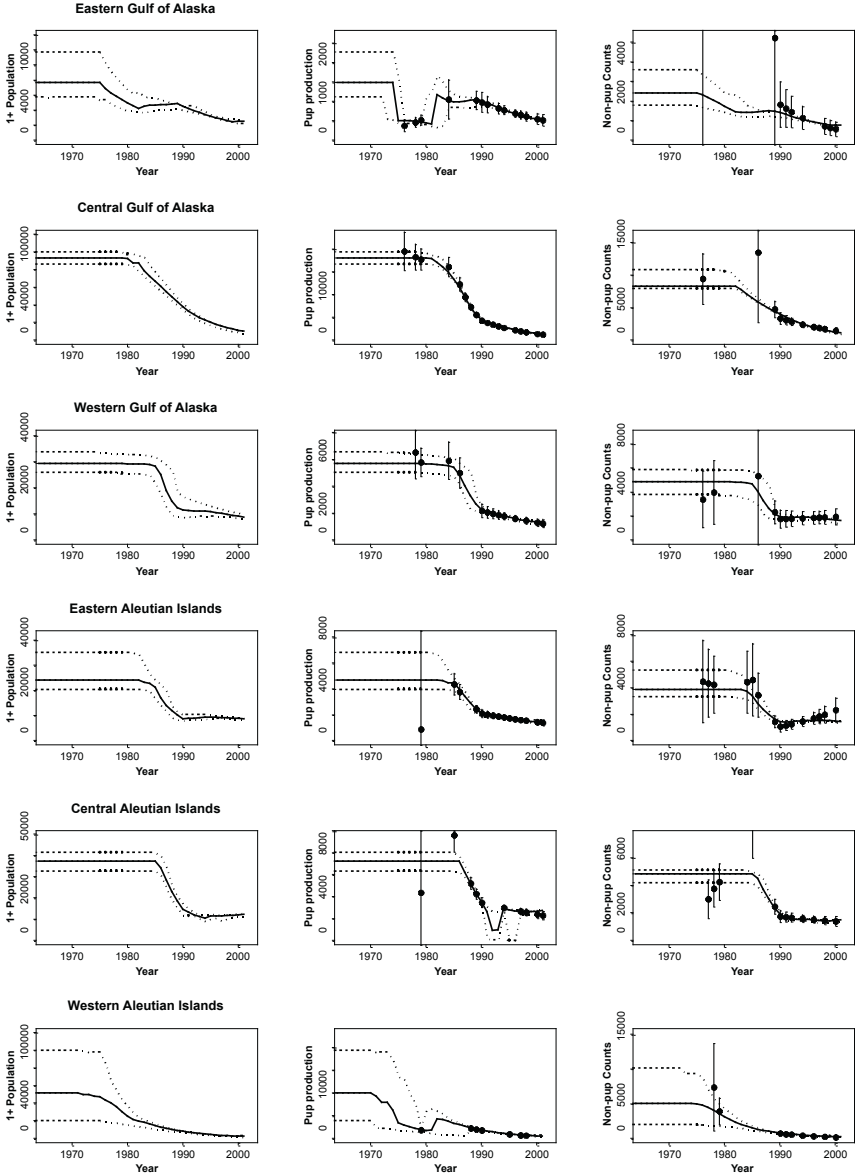


Figure 3. Median and central 95% probability intervals for the time trajectories of total regional non-pups, pup production, and estimated non-pup counts on haul-outs, for all six regions, for the models selected by DIC.

The models in which there is only a knife-edged reduction in pregnancy rate (model 5), or a knife-edged reduction in carrying capacity (model 7)—which implies a density-dependent increase in pregnancy rate—provided markedly poorer fits to the pup and non-pup count data than the other models for all six regions (Table 3).

The differences in AIC_c/DIC values between the “best” model and the next best model are not very large for some of the regions. This is particularly apparent for the central Gulf of Alaska, where model 3, the model with a smooth impact function on both survival and pregnancy rate, has an AIC_c value of 58.96 compared to a value of 57.22 for the “best” model (model 9). The importance of this is that, under a model-averaging procedure using AIC weights (Burnham and Anderson 1998), this “second best” model would receive almost as much weight as the “best” model. The other regions in which model 9 was selected by AIC_c as the “best” model (the eastern and central Aleutian Islands) also had an AIC_c value for model 3 that was close to the minimum value corresponding to model 9 (Table 3).

Region-specific results

Western Gulf of Alaska

The model selected by AIC_c for the western Gulf of Alaska as the “best” model was model 2, the impact scenario in which pregnancy rate (only) declined smoothly (Table 3; Fig. 2, third row of panels). There is no obvious trend in non-pup counts for this region after 1990, and there is little information in the non-pup counts for this region prior to 1990 (all estimates for the years pre-1990 for this region have very high CVs) (Fig. 2, third row). Consequently, there is little information that would suggest a reduction in survival as the cause of the decline in pup production inferred by the pup count data for this region, as opposed to a reduction in pregnancy rate.

The two impact scenarios selected by AIC_c and DIC for the western Gulf of Alaska lead to very similar estimates of historical (1945) numbers of non-pups; the central 95% of the posterior probability for this size lies between 25,924 and 33,764 sea lions for model 9, and between 26,280 and 32,910 for model 2 (Figs. 3 and 4). Inspection of the posterior distributions for the impact parameters for model 9 (Fig. 5a) reveals that the primary cause of the decline was a large impact on the survival rate of juveniles in the mid-late 1980s. The posteriors for the survival impacts on juveniles, pups, and even adults, span a wide range of values, suggesting that different combinations of relative impacts on these three classes of animals can provide almost equally good fits to the data. The posterior for y_F^A (“y F” in Fig. 5a) suggests that the pregnancy rate had to be reduced toward the end of the time series to fit the data for this model.

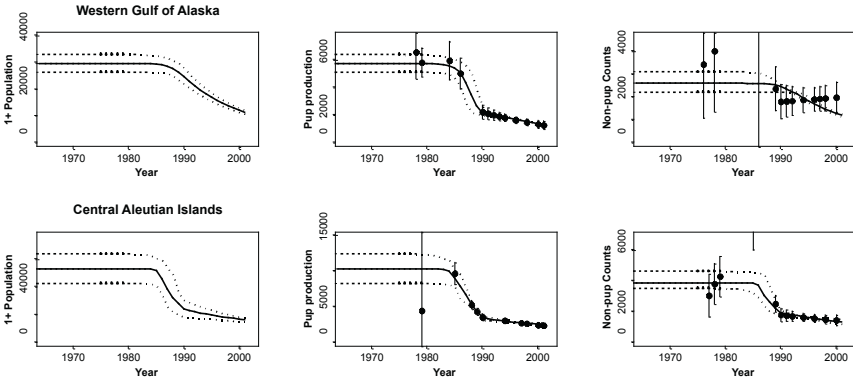


Figure 4. Median and central 95% probability intervals for the time trajectories of total regional non-pups, pup production, and estimated non-pup counts on haul-outs, for the models selected by AIC_c when the results of AIC_c differed to those of DIC: model 2 (western Gulf of Alaska), and model 9 (central Aleutian Islands).

For the model that assumed only a smooth reduction in pregnancy rate (model 2), the posteriors indicate that a 50-60% reduction in pregnancy rate occurred during the late 1980s, and that the pregnancy rate is still depressed (see the posteriors for h_F^A - "h F" and σ_{F2}^A - "sigma F2" in Fig. 5b). The wide posterior for the parameter determining the shape of the left-hand side of the smooth pregnancy rate function (σ_{F1}^A - "sigma F1" in Fig. 5b) indicates that, although the mode of the posterior for the year of maximum impact is around 1990, pregnancy rate was reduced for much of the late 1980s for all parameter vectors in the posterior. The magnitude of the impact on pregnancy rate is correlated with regional non-pup carrying capacity (Fig. 6), and interestingly, the magnitude of the impact in pregnancy rate did not change with the timing of the impact (Fig. 6, lower panels).

Central Aleutian Islands

The model selected by DIC for the central Aleutian Islands region was model 6, which differed from that selected by AIC_c (model 9). Unlike the situation for the western Gulf region, the fits to the data and the 95% posterior intervals for the time trajectory of non-pups for the central Aleutians region for the models selected using AIC_c and DIC differ appreciably (Figs. 3 and 4). The nine models imply quite different trends in the size of the regional population prior to the decline. Estimates of both the number of non-pups in 1945 for this region and the width of the central 95% posterior intervals of this quantity vary greatly among models. For

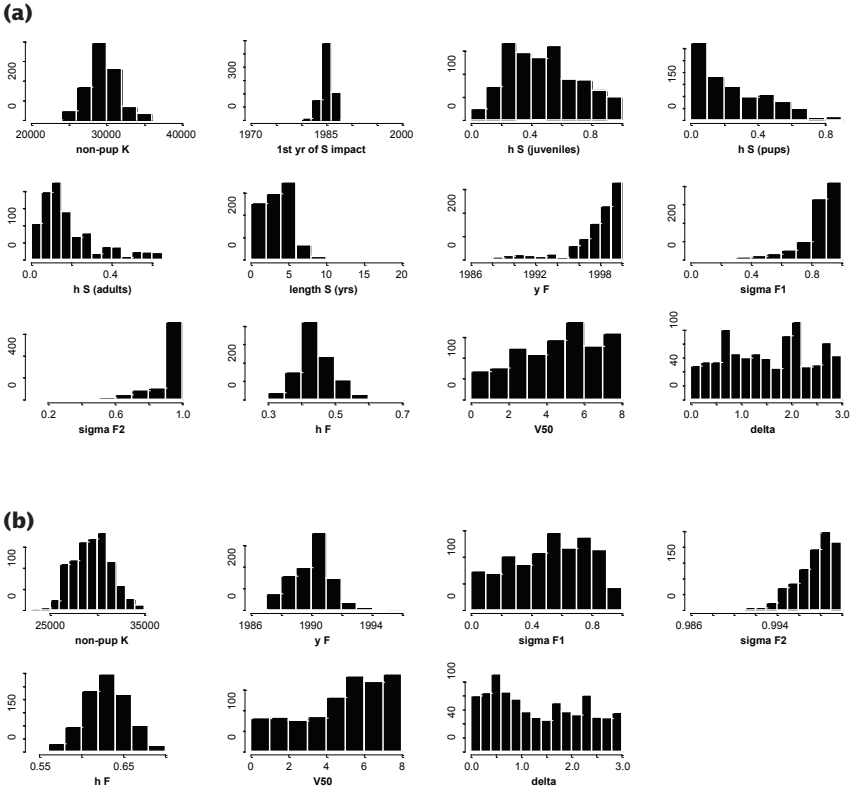


Figure 5. Posterior distributions for some of the model parameters based on fitting (a) model 9, and (b) model 2 to the data for western Gulf of Alaska. Parameter labels on panels are the same as those used in Table 1, except for “1st yr of S impact” (v_S^A), and “length S (yrs)” (I_S^A).

example, with the exception of model 9 (the model selected by AIC_c), the models that included a reduction in survival rate predict that the Steller sea lion population in this region is currently either stable or increasing (Fig. 7) while the models that just considered a reduction in pregnancy rate (models 2, 5, and 8), as well as model 9, suggest otherwise, with the 95% probability intervals for the trend in non-pups in the recent years showing a further decline (Fig. 7).

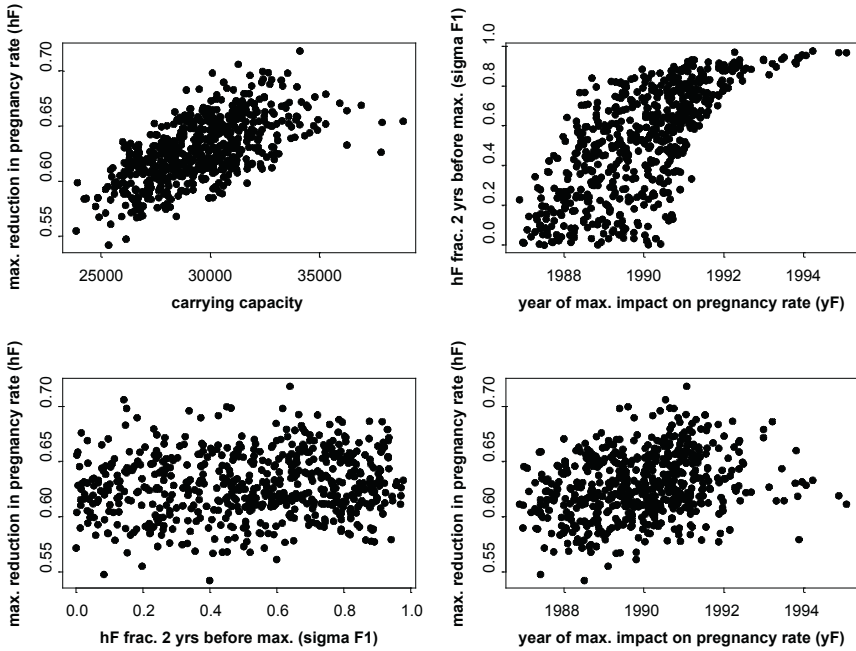


Figure 6. Correlation plots of some of the model parameters from the posteriors obtained for the western Gulf of Alaska region for model 2, the model with a smooth reduction in pregnancy rate only.

Discussion

Estimation of trends and population size

The current and pre-decline pup production was generally estimated consistently regardless of the impact scenario considered as the cause of the decline (perhaps with the exception of models 5 and 7, knife-edged reductions in pregnancy rate and carrying capacity respectively, although these models tended to provide poorer fits to the data than the alternative models). The pup count data were generally mimicked very well (e.g., Figs. 2-4). In contrast, the models were often very inconsistent when estimating the sizes of other population components, such as the total number of non-pups (e.g., Fig. 7). In some regions, the estimated number of non-pups at equilibrium differed by up to two orders of magnitude depending on the impact scenario. This clearly reflects the nature of the assumed impact on the population, as this will determine how the relationship between the pups and the non-pups changes over time. As the non-pup counts are assumed to be relative indices of female abundance,

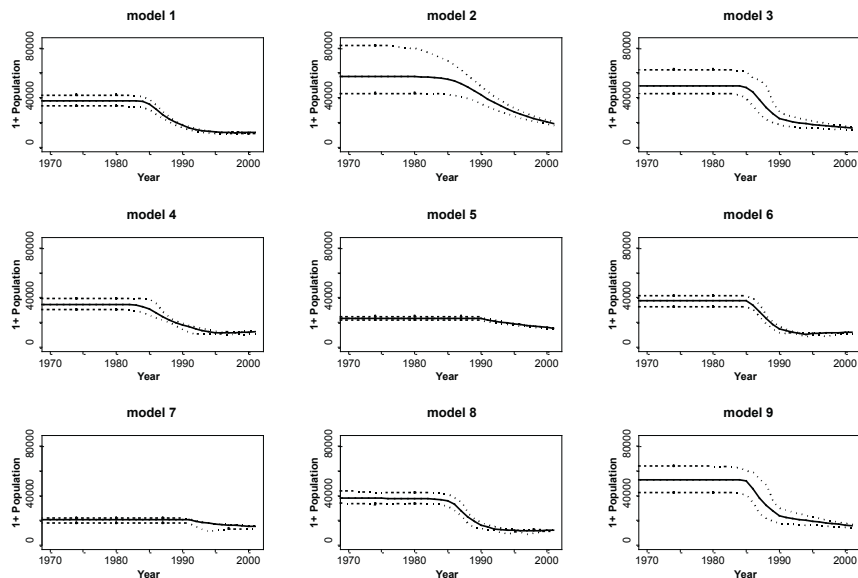


Figure 7. Median and central 95% probability intervals for the time-trajectory of the total number of non-pups for the central Aleutian Islands region for each of the nine models.

estimates of the numbers of non-pups will change depending on how the impact affects changes in pup production. The results of the Bayesian analyses demonstrate further the level of uncertainty associated with estimating regional total non-pup population sizes.

Model selection results, along with model predictions, were also observed by Fay (2004) to be sensitive to the choice of data set. Analyses for the central Gulf of Alaska that omitted the estimates of survival rates resulted in model 2 (smooth reduction in pregnancy rate), being selected by AIC_c as the “best” model, as opposed to models that included a survival impact (Table 3). This is unsurprising, because the estimates of survival rate are lower than those assumed under equilibrium (Table A.1).

The selection by AIC_c and DIC of different models depending on the region being analyzed demonstrates the benefits of adopting a spatial approach over one in which no account is made for differing impacts among regions. For those regions where the same type of impact scenario was selected as the most parsimonious representation of the data, the estimates of the values for the parameters providing that representation were markedly different. If the same impact scenario is assumed to apply to all regions and those regions are parameterized using the same

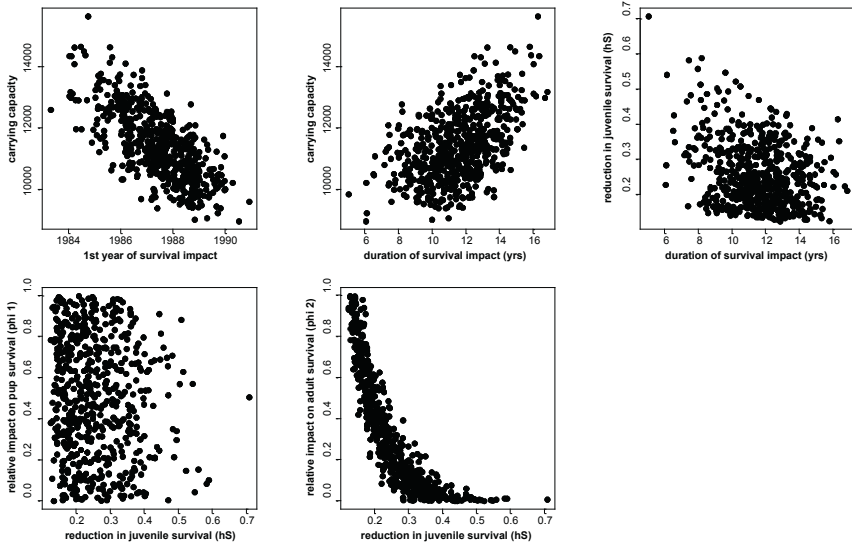


Figure 8. Correlation plots of some of the model parameters from the posteriors obtained for the western Gulf of Alaska region for model 9, the model with a knife-edged reduction in survival and a smooth reduction in pregnancy rate.

values for the parameters of the impact functions, then the fit to the data is extremely poor compared to that obtained when it is assumed that the values for the parameters are region-specific. For example, fitting model 9 to the data for all regions leads to a negative log-likelihood of 43.94 when the impact parameters are allowed to vary by region, and a value of 654.35 when the values for the model parameters related to impacts are assumed to be the same across all regions. The AIC_c resulting from this example is 299.93 for the independently parameterized version of the model compared to 1343.5 for the “global” scenario. This demonstrates that adopting a spatially heterogeneous view enables more of the trend in the data to be explained, supporting the spatially explicit parameter estimation procedure adopted here.

Can the existing data identify the population processes that caused the decline?

Even given the assumption of a certain impact scenario as the cause of the decline in Steller sea lion abundance for a region, the Bayesian posteriors demonstrate that there are many parameter combinations that are consistent with the data (Figs. 6 and 8). That is, the way in which a given impact scenario may be expressed within the population is not

necessarily easily determined. This is particularly true for the survival impacts, where the relative impact on the survival rate of adults is correlated with that for juveniles for some regions (e.g., Fig. 8), implying a number of different ways in which an impact perturbs the population while providing similar predictions of model quantities such as total number of non-pups.

The lack of correlation among some of the other parameters (Fig. 8) also presents challenges, as this suggests that a very large number of combinations of parameter values can provide adequate fits to the data. The results show that there is a distinct inability to elucidate from the count data the precise nature in which a type of impact could affect the population, even given a particular impact scenario. In the instance of an adult survival impact versus a juvenile survival impact, additional data on the age structure of the population would probably assist in determining the real cause of the observed trend.

Several authors suggest it is likely that a number of factors were/are responsible for the decline in abundance of the western stock (Loughlin and York 2000, Hunter and Trites 2001). The scenarios considered in the analyses above assume only one type of each impact (i.e., one reduction in survival, along with one reduction in pregnancy rate), and assume that the vital rates affected by these impacts will return to their pre-impact levels following the cessation of the impact. Allowing for more than one forcing function affecting, for example, survival could allow the population dynamics model to accommodate a larger number of possible causes for the decline. However, prior knowledge regarding the likely effects of the modeled hypotheses would be required to prevent confounding among the parameters of these impact functions.

While the analyses of this paper have considered a number of different impact scenarios, little effort has been made to relate these to the various mechanistic hypotheses for the cause of the Steller sea lion decline. That the results of these investigations suggest a number of ways in which it is possible to fit the data means that, to properly assess the likelihood/importance of a given hypothesis for the decline, a mechanistic understanding of the manner in how that hypothesis could affect vital rates (such as survival and pregnancy rates) of Steller sea lions is necessary. This is important, as many of the postulated causes of the decline may ultimately express themselves in the Steller sea lion population in the same way (e.g., by a reduction in survival). However, the spatial and temporal trends in such an expression may be sufficiently different among hypotheses to enable isolation of a particular cause from another. As such, it will be necessary to obtain a detailed idea of the likely spatial/temporal effect of a given hypothesis, in addition to the section of the population likely impacted, before any final conclusions can be drawn. The flexible nature of the modeling framework presented in this paper does, however, enable the incorporation of such detailed information, should it be available.

Acknowledgments

Funding for this work was provided by NOAA Fisheries and the North Pacific Universities Marine Mammal Research Consortium. The comments by Milo Adkison (University of Alaska) are gratefully acknowledged.

References

- Burnham, K.P., and D.R. Anderson. 1998. Model selection and inference: A practical information-theoretic approach. Springer-Verlag, New York.
- Butterworth, D.S., and A.E. Punt. 1995. On the Bayesian approach suggested for the assessment of the Bering-Chukchi-Beaufort seas stock of bowhead whales. Rep. Int. Whal. Comm. 45:303-311.
- Calkins, D.G., and E. Goodwin. 1988. Investigation of the declining sea lion population in the Gulf of Alaska. Alaska Department of Fish and Game. 76 pp.
- Calkins, D.G., and K.W. Pitcher. 1982. Population assessment, ecology and tropic relationships of Steller sea lions in the Gulf of Alaska. Alaska Department of Fish and Game, Final Report RU243. 128 p.
- Calkins, D.G., D.C. McAllister, K.W. Pitcher, and G.W. Pendleton. 1999. Steller sea lion status and trend in southeast Alaska: 1979-1997. Mar. Mamm. Sci. 15:462-477.
- Fay, G. 2004. A Bayesian stochastic metapopulation model for Steller sea lions in Alaska. M.S. thesis, University of Washington, Seattle. 253 pp.
- Gelman, A., B.P. Carlin, H.S. Stern, and D.B. Rubin. 1995. Bayesian data analysis. Chapman and Hall, London.
- Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. In: I. Hanski and M.E. Gilpin (eds.), Metapopulation biology: Ecology, genetics and evolution. Academic Press Inc., San Diego, pp. 5-26.
- Hoover, A.A. 1988. Steller sea lion, *Eumetopias jubatus*. In: J.W. Lentfer (ed.), Selected marine mammals of Alaska: Species accounts with research and management recommendations. Marine Mammal Commission, Washington, D.C., pp. 159-193.
- Hunter, A.M.J., and A.W. Trites. 2001. An annotated bibliography of scientific literature (1751-2000) pertaining to Steller sea lions (*Eumetopias jubatus*) in Alaska. Fish. Res. Centre Res. Rep. 9(1):1-45.
- Loughlin, T.R. 1997. Using the phylogeographic method to identify Steller sea lion stocks. In: A. Dizon, S.J. Chivers, and W.F. Perrin (eds.), Molecular genetics of marine mammals. Soc. Mar. Mammal. (Spec. Publ. 3), pp. 159-171.
- Loughlin, T.R., and R.L. Merrick. 1989. Comparison of commercial harvest of walleye pollock and northern sea lion abundance in the Bering Sea and Gulf of Alaska. In: Proceedings of the International Symposium on the Biology and Management of Walleye Pollock. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 679-700.

- Loughlin, T.R., and A.E. York. 2000. An accounting of the sources of Steller sea lion, *Eumetopias jubatus*, mortality. *Mar. Fish. Rev.* 62:40-45.
- Merrick, R.L., T.R. Loughlin, and D.G. Calkins. 1987. Decline in abundance of the northern sea lion, *Eumetopias jubatus*, in Alaska, 1956-86. *Fish. Bull. US.* 85:351-365.
- NMFS. 1992. Final Recovery Plan for the Steller sea lion (*Eumetopias jubatus*). Prepared by the Steller Sea Lion Recovery Team for the National Marine Fisheries Service (NMFS), Silver Spring, Maryland. 92 pp.
- Pascual, M.A., and M.D. Adkison. 1994. The decline of the Steller sea lion in the Northeast Pacific: Demography, harvest or environment. *Ecol. Appl.* 4:393-403.
- Pitcher, K.W., and D.G. Calkins. 1981. Reproductive biology of Steller sea lions in the Gulf of Alaska. *J. Mammal.* 62:599-605.
- Press, W.H., B.P. Flannery, S.A. Teukolsky, and W.T. Vetterling. 1996. Numerical recipes in FORTRAN. 2nd edn. Cambridge University Press, Cambridge.
- Punt, A.E., and R. Hilborn. 1997. Fisheries stock assessment and decision analysis: The Bayesian approach. *Rev. Fish Biol. Fish.* 7:35-63.
- Raum-Suryan, K.L., K.W. Pitcher, D.G. Calkins, J.L. Sease, and T.R. Loughlin. 2002. Dispersal, rookery fidelity, and metapopulation structure of Steller sea lions (*Eumetopias jubatus*) in an increasing and a decreasing population in Alaska. *Mar. Mamm. Sci.* 18:746-764.
- Rubin, D.B. 1987. Comment: The calculation of posterior distributions by data augmentation. *J. Am. Statist. Assoc.* 82:543-546.
- Sease, J.L., and T.R. Loughlin. 1999. Aerial and land-based surveys of Steller sea lions (*Eumetopias jubatus*) in Alaska, June and July 1997 and 1998. NOAA Tech. Memo. NMFS-AFSC-100. 61 pp.
- Spiegelhalter, D.J., N.G. Best, B.R. Carlin, and A. van der Linde. 2002. Bayesian measures of model complexity and fit. *J.R. Statist. Soc. B.* 64:583-616.
- Trites, A.W., and P.A. Larkin. 1996. Changes in the abundance of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1956 to 1992: How many were there? *Aquat. Mamm.* 22:153-166.
- Trites, A.W., and B.T. Porter. 2002. Attendance patterns of Steller sea lions (*Eumetopias jubatus*) and their young during winter. *J. Zool. Soc. (Lond.)* 256:547-556.
- Winship, A.J., A.W. Trites, and D.G. Calkins. 2001. Growth in body size of the Steller sea lion (*Eumetopias jubatus*). *J. Mammal.* 82:500-519.
- York, A.E. 1994. The population dynamics of northern sea lions, 1975-1985. *Mar. Mamm. Sci.* 10:38-51.
- York, A.E., R.L. Merrick, and T.R. Loughlin. 1996. An analysis of the Steller sea lion metapopulation in Alaska. In: D.R. McCullough (ed.), *Metapopulations and wildlife conservation*. Island Press, Covela, pp. 259-292

Appendix A. The population dynamics model

Basic dynamics

The dynamics of animals aged 1 and older are governed by the equations¹:

$$\begin{aligned}
 N_{y+1,a+1}^{m,A} &= \tilde{N}_{y,a}^{m,A} + \sum_{A' \neq A} \text{Bin}(\tilde{N}_{y,a}^{m,A'}, X_{y,a}^{m,A',A}) - \sum_{A' \neq A} \text{Bin}(\tilde{N}_{y,a}^{m,A}, X_{y,a}^{m,A,A'}) \\
 N_{y+1,a+1}^{l,A} &= \tilde{N}_{y,a}^{l,A} + \sum_{A' \neq A} \text{Bin}(\tilde{N}_{y,a}^{l,A'}, X_{y,a}^{l,A',A}) - \sum_{A' \neq A} \text{Bin}(\tilde{N}_{y,a}^{l,A}, X_{y,a}^{l,A,A'}) \\
 N_{y+1,a+1}^{M,A} &= \tilde{N}_{y,a}^{M,A} + \sum_{A' \neq A} \text{Bin}(\tilde{N}_{y,a}^{M,A'}, X_{y,a}^{M,A',A}) - \sum_{A' \neq A} \text{Bin}(\tilde{N}_{y,a}^{M,A}, X_{y,a}^{M,A,A'})
 \end{aligned} \tag{A.1}$$

where

$N_{y,a}^{m/l/M,A}$ is the number of males, immature females, and mature females of age a in region A at the start of year y^2 ,

$\tilde{N}_{y,a}^{m/l/M,A}$ is the number of males, immature females, and mature females of age a in region A at the end of year y (after mortality and maturation but before dispersal):

$$\begin{aligned}
 \tilde{N}_{y,a}^{m,A} &= \bar{N}_{y,a}^{m,A} && \text{Males} \\
 \tilde{N}_{y,a}^{M,A} &= \bar{N}_{y,a}^{M,A} + (\bar{N}_{y,a}^{l,A} - \tilde{N}_{y,a}^{l,A}) && \text{Mature females} \\
 \tilde{N}_{y,a}^{l,A} &= \bar{N}_{y,a}^{l,A} - \text{Bin}(\bar{N}_{y,a}^{l,A}, \beta_{a+1}) && \text{Immature females}
 \end{aligned} \tag{A.2}$$

$$\bar{N}_{y,a}^{m/l/M,A} = \sum_{A'=1}^R \text{Bin}(N_{y,a}^{m/l/M,A} Y_{y,a}^{m/l/M,A,A'}, S_{y,a}^{m/l/M,A'}) \tag{A.3}$$

$X_{y,a}^{m/l/M,A,A'}$ is the probability during year y that a male, immature female, or mature female of age a in region A at the end of the year disperses to region A' ,

$Y_{y,a}^{m/l/M,A,A'}$ is the probability during year y that a male, immature female, or mature female of age a belonging to the population in region A is found in region A' and thus experiences the survival impacts specific to region A' ,

$S_{y,a}^{m/l/M,A}$ is the survival rate for males, immature females, and mature females of age a in region A during year y ,

β_a is the probability that an immature animal of age $a-1$ matures at age a , and equals $(M_a - M_{a-1}) / (1 - M_{a-1})$ where

¹Equation A.1 is modified appropriately for age x , which is treated as a plus-group. This plus group is defined as being at age 6 because all females are mature at this age.

²The “start” of the year refers to the start of the model “year,” which begins with the pupping season, which occurs in June, in the middle of the calendar year.

M_a is the probability that an animal of age a is mature,

$Bin(x, p)$ is a (x, p) binomial random variable with expectation xp , and variance $xp(1-p)$, and

R is the number of regions in the model.

Equation (A.3) allows for demographic variability in the probability of suffering mortality, and equation (A.1) allows for demographic variability in the dispersal rate.

Pups

The number of pups (immature animals of age $a = 0$) in region A at the start of year y , B_y^A , depends on both the number of mature females in that region and the pregnancy rate:

$$\begin{aligned}
 B_y^A &= \sum_{a=1}^x B_{y,a}^A; & B_{y,a}^A &= Bin(N_{y,a}^{m,A}, b_y^A) \\
 N_{y,0}^{m,A} &= \sum_{a=1}^x Bin(B_{y,a}^A, 0.5); & N_{y,0}^{l,A} &= B_y^A - N_{y,0}^{m,A}
 \end{aligned}
 \tag{A.4}$$

where

$B_{y,a}^A$ is the number of pups produced by mature females of age a , and

b_y^A is the probability, during year y , that a mature female in region A pups.

The pregnancy rate in region A during year y is given by:

$$b_y^A = f_0^A (1 + \bar{A} (1 - P_y^A / \bar{P}_y^A)^z) h_y^A
 \tag{A.5}$$

where

f_0^A is the pregnancy rate/infant survival rate at pre-exploitation equilibrium for region A , determined by the expected age structure at pre-exploitation equilibrium, which, given the values for survival and maturity in Table A.1, results in a value of 0.63,

\bar{A} is the (resilience) parameter that determines the extent of density-dependence in birth rate,

z is the parameter that determines the degree of compensation,

h_y^A is a factor to impose a trend over time in the pregnancy rate in region A ,

P_y^A is the number of mature females at the start of year y :

$$P_y^A = \sum_{a=1}^x N_{y,a}^{M,A} \quad (\text{A.6})$$

\tilde{P}_y^A is the carrying capacity for mature females in region A during year y .

Equation (A.5) allows for density dependence in the pregnancy rate, and is the only manner in which a density-dependent response is incorporated into the general modeling framework. This density dependence can be viewed as being expressed in either the pregnancy rate, or early infant mortality.

Trend in survival rate

The probability that an animal of stage m/I/M and age a in region A survives the impact of natural mortality, $S_{y,a}^{m/I/M,A}$, is given by:

$$S_{y,a}^{m/I/M,A} = S_a k_{y,a}^A \quad (\text{A.7})$$

where

S_a is the survival rate for animals of age a at pre-exploitation equilibrium (Table A.1).

Equation (A.7) includes the factor $k_{y,a}^A$ to impose an impact on survival rate over time, which could represent impacts from a number of different sources, depending on the hypotheses being modeled for the decline. The functional forms of the impact on survival rate allow for different impacts on pups (age 0), juveniles (ages 1-4) and adults (ages 5+):

$$k_{y,a}^A = \begin{cases} 1 - \phi_1 \tilde{k}_y^A & \text{if } a = 0 \\ 1 - \tilde{k}_y^A & \text{if } 1 \leq a \leq 4 \\ 1 - \phi_2 \tilde{k}_y^A & \text{otherwise} \end{cases} \quad (\text{A.8})$$

where

ϕ_1 is the parameter that determines the relative impact of changes in survival rate for pups compared to that for juveniles,

ϕ_2 is the parameter that determines the relative impact of changes in survival rate for adults compared to that for juveniles, and

\tilde{k}_y^A is the impact during year y on the expected survival rate of juveniles.

The impact in a given year \tilde{k}_y^A can be determined from two different functional forms:

- a) An asymmetrical smooth forcing function which allows the maximum impact on survival to be approached at a different rate to that at which survival rate is returned to the level prior to the impact.

$$\tilde{k}_y^A = \begin{cases} h_s^A \exp(\ln(\sigma_{s1}^A) [y - y_s^A]^2 / 4) & \text{if } y \leq y_s^A \\ h_s^A \exp(\ln(\sigma_{s2}^A) [y - y_s^A]^2 / 4) & \text{otherwise} \end{cases} \quad (\text{A.9})$$

h_s^A is the parameter that determines the magnitude of the impact on the survival rate,

y_s^A is the year in which the impact on survival rate is greatest,

σ_{s1}^A is the fraction of the maximum impact on the survival rate two years prior to year y_s^A , and

σ_{s2}^A is the fraction of the maximum impact on the survival rate two years after year y_s^A .

- b) A knife-edge function, whereby survival is reduced by a fixed amount for the duration of the impact.

$$\tilde{k}_y^A = \begin{cases} 0 & \text{if } y < v_s^A \\ h_s^A & \text{if } v_s^A \leq y < (v_s^A + I_s^A) \\ 0 & \text{if } (v_s^A + I_s^A) \leq y \end{cases} \quad (\text{A.10})$$

v_s^A is the year in which the impact on survival rate begins, and

I_s^A is the duration of the impact on survival.

Trend in pregnancy rate

As with the survival rate, an impact on pregnancy rate can be modeled using either a smooth function, or a knife-edge reduction.

- a) Smooth forcing function:

$$h_y^A = \begin{cases} 1 - h_f^A \exp(\ln(\sigma_{f1}^A) [y - y_f^A]^2 / 4) & \text{if } y \leq y_f^A \\ 1 - h_f^A \exp(\ln(\sigma_{f2}^A) [y - y_f^A]^2 / 4) & \text{otherwise} \end{cases} \quad (\text{A.11})$$

where

h_f^A is the parameter that determines the magnitude of the impact on pregnancy rate,

y_f^A is the year in which the impact on pregnancy rate is greatest,

σ_{f1}^A is the fraction of the maximum impact on pregnancy rate two years prior to year y_f^A , and

σ_{F2}^A is the fraction of the maximum impact on pregnancy rate two years after year y_F^A .

b) Knife-edge forcing function:

$$h_y^A = \begin{cases} 1 & \text{if } y < v_F^A \\ 1 - h_F^A & \text{if } v_F^A \leq y < (v_F^A + I_F^A) \\ 1 & \text{if } (v_F^A + I_F^A) \leq y \end{cases} \quad (\text{A.12})$$

where

v_F^A is the year in which the impact on pregnancy rate begins, and

I_F^A is the duration of the impact on pregnancy rate.

Changes in carrying capacity

The population dynamics can also be impacted by a region-specific change in carrying capacity:

$$\tilde{P}_y^A = \begin{cases} \tilde{P}^A & \text{if } y < y_\psi^A \\ \psi^A \tilde{P}^A & \text{if } y_\psi^A \leq y < (y_\psi^A + I_\psi^A) \\ \tilde{P}^A & \text{if } (y_\psi^A + I_\psi^A) \leq y \end{cases} \quad (\text{A.13})$$

where

ψ^A is the parameter that determines the extent of the change in carrying capacity for region A,

y_ψ^A is the year in which there is a change in carrying capacity for region A, and

I_ψ^A is the duration of the change in carrying capacity for region A.

Table A.1. Expected survival probabilities for females, and the probability of being mature as a function of age (source: York 1994, Table 1).

	Age (yrs)						
	0	1	2	3	4	5	6+
Survival S_a	0.782	0.782	0.782	0.93	0.909	0.895	0.851
Maturity M_a	0	0	0	0.32	0.57	0.83	1.00

Appendix B. Likelihood function

Pup counts

The pup counts are assumed to be unbiased, normally distributed indices of the total numbers of pups (both sexes) by region at the start of the year concerned. The contribution of the pup count data to the likelihood function for region *A* is therefore given by:

$$\prod_y \frac{1}{\sqrt{2\pi}\sigma_y^{A,P}} \exp\left(-\frac{[P_y^A - (N_{y,0}^{m,A} + N_{y,0}^{l,A})]^2}{2(\sigma_y^{A,P})^2}\right) \quad (\text{B.1})$$

where

P_y^A is the pup count for region *A* and year *y*, and

$\sigma_y^{A,P}$ is the standard deviation of the pup count for region *A* and year *y*.

The product in equation (B.1) is restricted to those years for which pup counts are actually available.

Non-pup counts

In contrast to the pup counts, it is not reasonable to assume that the non-pup counts are unbiased indices of the number of animals aged 1 and older. This is because some (unknown) fraction of the non-pups will be on the sites that are surveyed, and this fraction is likely to be age-specific (Calkins et al. 1999, Trites and Porter 2002). Therefore, the non-pup counts are assumed to be relative indices of the total number of females aged 1 and older, adjusted for the probability of being sighted by age. The use of the non-pup count data in this manner is somewhat questionable. For example, the non-pup count data include data for both males and females. Unfortunately, the age-specific survival rate estimates (Table A.1) pertain only to females—assuming the same values for males (particularly the older males) is questionable as large males are expected to have a lower survival rate than equivalently aged females (Calkins and Pitcher 1982, Winship et al. 2001). The validity of assuming that the non-pup counts index the number of females therefore depends on how the number of females changes relative to how the number of males changes. Other problems with the use of the non-pup counts as indices of “available females” include that the haul-out probabilities may differ between the sexes and older females may be less likely to be counted on nonbreeding haul-outs during the breeding season as they will be involved in breeding activities on rookeries.

The contribution of the non-pup counts to the likelihood function is given by:

$$\prod_y \frac{1}{\sqrt{2\pi}\sigma_y^{A,Q}} \exp\left(-\frac{(Q_y^A - \hat{Q}_y^A)^2}{2(\sigma_y^{A,Q})^2}\right) \quad (\text{B.2})$$

where

Q_y^A is the non-pup index for region A and year y ,

\hat{Q}_y^A is the model-estimate corresponding to Q_y^A :

$$Q_y^A = \sum_{a>1} V_a (N_{y,a}^{I,A} + N_{y,a}^{M,A}) \quad (\text{B.3})$$

V_a is the relative probability of an animal of age a being available to be sighted:

$$V_a = \frac{V_\infty}{1 + \exp(-[a - V_{50}]/\delta)} \quad (\text{B.4})$$

V_∞ is an overall scaling factor,

V_{50} is the age at which 50% of the animals are available (relative to the age that is most available),

δ is a parameter which determines the width of the age-specific availability ogive, and

$\sigma_y^{A,Q}$ is the standard deviation of the non-pup index for region A and year y .

The logistic equation (B.4) was chosen as opposed to a dome-shaped function, which would indicate that availability on haul-outs declines with age. While this is a reasonable assumption (older animals are more likely to be mothers nursing pups on rookeries), a parameter that determines the extent to which availability declines with age would be confounded with the reduction in survival rate with age. Given the paucity of the data, the simpler functional form was deemed more preferable.

Survival rates

Estimates of survival rates based on tagging are available for the animals pupped in 1987 and 1988 (i.e., the 1987 and 1988 cohorts) (Anne York, NMML, pers. comm.). Separate survival rates are available for ages 0-5 (both cohorts) and ages 5+ (separately by cohort). The contribution of the estimates of survival rate to the likelihood function is based on the assumption that these estimates are normally distributed about their expected values.³ The survival rates were determined from animals tagged at Marmot Island and so are used only for the analyses for the central Gulf of Alaska.

³The assumption of normality is unlikely to impact the qualitative outcomes of any analysis as the standard errors for the survival estimates are fairly low.

Age composition data

The age-composition data for 1976-1981 (ADFG, unpubl. data) were used to calculate the survival rates in Table A.1, and are consequently not included in the likelihood function. The contribution of the (female) age-composition data for 1985⁴ to the likelihood function is based on the assumption that the age-composition data are a random sample from the 3+ component of the population that is available to being sighted/sampled (see equation B.4). The contribution of the 1985 age-composition data to the likelihood function (ignoring constants independent of the model parameters) is therefore:

$$\prod_{a \geq 3} (\hat{p}_a^A)^{N_{\text{age}} p_a^{\text{obs}}} \quad (\text{B.5})$$

where

p_a^{obs} is the proportion which females of age a made up of the 1985 age-composition sample of 3+ animals,

N_{age} is the weight assigned to the age-composition data (the effective sample size, taken to be 100—largely unimportant as age data are available for only one year), and

\hat{p}_a^A is the model-estimate of the proportion which females of age a made up of the available population in 1985:

$$\hat{p}_a^A = \frac{V_a (N_{y,a}^{M,A} + N_{y,a}^{L,A})}{\sum_{a' \geq 3} V_{a'} (N_{y,a'}^{M,A} + N_{y,a'}^{L,A})} \quad (\text{B.6})$$

⁴Age-composition data are also available for 1986 but these data are ignored because the sample size is very small.

