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The viability of Steller sea lion populations

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Introduction

This paper presents the results of a study that analysed of the historical trends in abundance in the population of Steller sea lions from Alaska and British Columbia. The analysis accounted for (1) the absolute effect of counting errors and heterogeneity in these errors across space and time; and (2) the incomplete nature of surveys for both pups and non-pups so that problems associated with using "trend sites" to assess the population status can be avoided and so that all data about the population is included in assessments, even when surveys were incomplete. These results were then used to generate information at the level of individual sites for the rate of change between years accounting for (1) the effects of local population size; and (2) spatial and temporal autocorrelation in the rate of change. The distributions of potential rates of population change, conditioned on the local population size and autocorrelation effect was then used to investigate scenarios for the future trends in the population used a stochastic population projection. This was designed to test the hypotheses that the population, or sub-sections of the population (e.g. Eastern and Western Distinct Population Segments), comply with a reasonable definition of the population having "endangered" status. For the Steller sea lion the quasi-extinction level has been equated to a total population size of 4,743 Steller sea lions (DeMaster et al., 2004; NMFS, 2008).

The study suggested that (1) current levels of pup productivity within the SSL population are close to the long-term mean; (2) the population across the range appears to be stable and abundance has not changed significantly since 1990; (3) the current population levels may be close to the long-term mean carrying capacity; (4) the dynamics of the Eastern and Western Distinct Population Segments may not be completely disconnected and there is evidence for a net movement of the population distribution from west to east and this could have included the movement of individuals (especially juveniles) during the rapid decline in the West in the 1980s; (5) none of the scenarios investigated showed that the population was endangered and this also applied to the Eastern and Western segments; (6) all other things being equal, the probability of extinction has been extremely small for at least the past 10 years; and (7) management introduced from 1990 appears to have done no harm and may have succeeded in restoring the population to a stable state.

Methods

Count data and definitions

All data were obtained from the Alaska Fisheries Science Center Steller sea lion database (http://www.afsc.noaa.gov/nmml/alaska/Steller_sea_lionhome/databases/) as well as more recent sources (Fritz et al., 2008; Olesiuk, 2008). Although there are rich data sources for Steller sea lion biology, the data that has been collected most consistently and most reliably are counts of pups at "rookeries" across the species range and counts of non-pups (juveniles and adults) at "haulouts" during the breeding season in June and July. In the present study, no distinction was made between "haulouts" (sites where animals rest out of the water) or "rookeries" (where pupping takes place) during the breeding season. This is because the historical distinction appears to be somewhat arbitrary, e.g. Pitcher et al. (2007) decided that any site having <50 pups was classified as a "haulout" rather than a "rookery".

The principal source of data about Steller sea lions came from periodic surveys of these sites. These data have been collected at the resolution of individual sites but had previously been reported at various scales by grouping sites into sub-regions, trend site, regions and stocks (e.g. York et al., 1996). An important underlying feature of the present analysis is that it was based upon the finest scale of data collection and included all count data, not just the 6 range-wide surveys (e.g. as used in the PVA in NMFS 2008). This meant that the analytical approach was designed to cope with partial coverage in some years and missing values for many sites. Consequently the need for aggregation of sites in to "trend" sites (Fritz et al., 2008) or by region (Sease and Gudmundson, 2002; Pitcher et al., 2007; Fritz et al., 2008; Olesiuk, 2008) was avoided. Any aggregation of sites was based upon clustering derived from congruence between the population dynamics shown by sites. However, the analysis aggregated sites across the EDPS and WDPS to allow analysis with respect to the historical approaches to management which have recognised these segments as distinct management unit.

Although past studies have fitted population models to current count data (e.g. York et al., 1996; Winship and Trites, 2006; Holmes et al., 2007), the largely unknown and non-stationary error structure within the count data means that the capacity of the data to support these types of analyses is quite limited. Consequently, the present study did not attempt to directly model the population dynamics of Steller sea lions but it did produce an index of productivity called the "pup ratio", which was the number of pups count as a proportion of the number of non-pups counted.

Observation error

Various methods have been used to count Steller sea lions. These include, aerial photography using 35mm film format normally using an oblique aspect with hand held cameras and no motion compensation; aerial photography using medium-format (5 inch) with motion compensation; aerial photography using digital format with motion compensation; aerial counts using visual estimates; beach/ground counts; viewpoint observations; counts from a skiff near to shore, and counts from a vessel offshore (Supplementary information available on request, Table 1). Each method will have different levels of error and in most cases these have not been quantified.

Five general categories of processes were identified that will lead to error in estimates of Steller sea lion abundance. The main processes leading to error in observation are described in detail in the Supplementary information and these include (1) incomplete coverage of the site; (2) variable capacity to observe animals even if they are present; (3) variance due to the counter; (4) dependency on the timing of the survey in relation to both the time of day when it is carried out and the date in relation to the peak of the season; (5) dependency upon the type of terrain. Many of these processes will interact with one-another and all will vary depending upon survey method. The supplementary information evaluates the range of error associated with each of the factors and these ranges were used to generate an estimate of the overall uncertainty around the counts. This was achieved by assuming that all sources of uncertainty were independent and by modifying each count using a uniform distribution across the range of possible values for each source in the Supplementary information (Available on request, Table 1).

Modelling future trends

The objective was to predict the range of future population trends conditional on past population trends and current population state. A four-step approach was adopted. Step 1 defined the process by which observations, in this case actual counts of Steller sea lions at each site, represented as a set of state vectors $\mathbf{x}_k$, where k denotes a particular site, were translated in to an equivalent set of state vectors $\mathbf{n}_k$ representing the real state of the populations at a particular site. As already described, this involved accounting for the errors within the data and building distributions of possible alternatives of $\mathbf{x}_k$. It follows from this that

$$N_t = \sum_{k=0}^{k=K} \mathbf{n}_k \qquad 1.$$

Where N_t is the total population size in year t.

Step 2 defined the potential distribution θ of λ which is the proportional change in the state of each successive element in the state vector $\mathbf{n}_k$. This defines the historical trends in the population. Assuming exponential growth or decay, the rate of population change (λ) was derived as follows:

$$n_{k,t} = n_{k,t-\tau} e^{r\tau} \qquad 2.$$

Where $n_{k,t}$ was the number of non-pups or pups in the population at time t, $n_{t-\tau}$ was the number at the previous time of survey, defined by a time interval of τ years and r was the growth rate where $\lambda = e^r$. Both $n_{k,t}$ and $n_{k,t-\tau}$ were measured variables. The exponential rate of increase was derived as:

$$r = \frac{\ln(n_{k,t}) - \ln(n_{k,t-\tau})}{\tau} + \xi \qquad 3.$$

In this case ξ was a random deviate defined by the standard deviation around the principal eigenvalue of a Lefkovitch matrix representing pup, juvenile and adult stages in the population and where the principal eigenvalue was equal to λ. The Weiner process described by Dennis et al. (1991) was used to estimate the value of ξ. This log-linear relationship, together with uncertainty, was used to interpolate the number of pups and non-pups at each site for years when surveys did not take place.

Step 3 was the process by which the elements within the population state vector at a site, $n_{k,t}$, was updated to define scenarios for future population trajectories. This used the distribution θ_n, where θ was subscripted by n, because λ varied depending upon the size of the population at each site. Thus the population at each site was

$$n_{k,t} = f(n_{k,t-\tau}, \theta_{n_{k,t}}) \qquad 4.$$

In this case, τ was equal to unity in the projections. The value of λ, drawn from the distribution θ (Equation 4) was selected to satisfy the condition of a first order Markov process in which $\lambda_{k,t} = \lambda_{k,t-\tau}\alpha_\tau$, where α was a random variate drawn from a distribution defined by the direct observation of the autocorrelation between values of λ at different values of τ.

Step 4 involved aggregating the results for sites across different scales of relevance to management and assessing the probability of recovery criteria being met.

Modelling spatial and temporal correlation between sites

The objective of the analysis to determine spatial correlation was to define the extent to which the future trends at each site could be modelled independently or as part of a cluster of sites. The complexities of the data variance-covariance matrix, due to missing values, did not permit the use of standard statistical procedures. As a result a multiple regression approach was used to cluster sites based upon congruence between the value of the historical population trajectories at each site. This approach made use of the relationship:

$$\mathbf{b} = \mathbf{S}^{-1}\mathbf{y} \qquad 5.$$

Where **S** was the *i* x *i* symmetrical matrix containing the sum of squares-sum of products matrix for a set of sites defined as the independent variables in a multiple regression. The vector **y** of length *i* was the sum of products for the site designated as the dependent variable. In each case, the years included in the data set were those in which the sites in **S** contained no missing values during the years in **y** when there were also no missing values. The number of sites included as independent variables to derive **S** was defined to be less than the number of years represented by the data. The minimum number of years of data required for a site to be included was 6. In order to maximise the power of this analysis log-linear interpolation was also used to estimate the number of animals present in years between counts and to reduce the effects of missing data. This allowed the estimation of **b** which was a vector containing the partial regression coefficients for each site designated as an independent variable.

A systematic analysis was conducted using each site as the independent variable and all permutations of different sets of all other 431 sites. The goodness of fit of each model was assessed using the AIC and the best-fitting model was chosen for each site. Note that the AIC was only used to compare among models using the same dependent variable this avoiding the effects of over-parameterisation due to serial correlation. This had the effect of selecting a small set of sites that were statistically most closely related to each site, in terms of their population dynamics, with either a positive or a negative relationship.

The sets of sites used as independent variables were then inspected to determine which sites occurred with greatest frequency as independent variables in the most favoured models. The correlation between these sites and other sites was preserved in the population projections of the dependent sites. Those sites for which there was no significant relationship with a trend site were treated as behaving independently of all other sites in projections.

Density limitation

There was no direct information available about the carrying capacity. However, it can be assumed that there are upper limits to the number of Steller sea lions at particular sites, because of limits on space or because of limits on the local environmental productivity. To allow for this type of limit within the model, it was assumed that each site had an upper limit drawn from the distribution of maximum observed values across all sites.

Model definitions

Several models were used to investigate possible future trends in the population and these are summarised in Table 1. Spatial correlation of sites was included in Model 2 but not in Model 1. Both models were run on data for the whole population and also separately for the Western and Eastern segments (WDPS and EDPS respectively) of the population (York et al., 1996; NMFS, 2008). Results from all these combinations of models were investigated using data from the complete time series (a); from 1990 to the present (b) and from 2000 to the present (c). These data sets in (b) and (c) represent two different phases of conservation management. Before 1990 there were no conservation management measures; after 1990

measures to reduce human impacts were introduced and after 2000 measures to reduce possible indirect effects of fishing were expanded. Consequently, population projection using data from 1990 and 2000 respectively assumed similar types of management will be extended in to the future.

	Model 1			**Model 2**		
	a	b	c	a	b	c
Spatial clustering included					✓	
Temporal correlation included		✓			✓	
Basic data at the scale of rookeries and haulouts (June/July)		✓			✓	
Sampled λ from empirical distribution across the all years	✓			✓		
Sampled λ from empirical distribution across phase A and B only (post 1990)		✓			✓	
Sampled λ from empirical distribution across B only (post 2000)			✓			✓
Results modified to reflect the observation process, including error and bias		✓			✓	

Table 1. Definitions of the different population risk analyses undertaken. All of these scenarios were investigated with and without density limits.

Results

Data available

The complete data set contained a sample of 7,175 counts of non-pups and 906 counts of pups at individual sites. After exclusion of data outside the June/July pupping season and taking averages for repeated counting at individual sites within years, the total sample of site counts for non-pups was 4,530 and 828 for pups. The total sample of sites from the region included within the present analysis for non-pups was 431 and the total number of rookeries was 312.

Observation errors

Taking information from the whole data set where there were repeated counts of a site within a single year, the coefficient of variation (CV) followed a log-normal distribution with a mean of 0.28 (sd = 2.492). The distribution of CVs (Fig. 1) is unlikely to have completely captured

the biases associated with the characteristics of the different sites because it tested for internal consistency in within-site counts and says little about consistency among sites. Unfortunately, there was very little that could be done to assess the differences in count bias among sites even though it is possible that this could be important. For example, Cumbley et al. (1997) showed clear differences in the seasonal pattern of abundance among neighbouring beaches on Marmot Island. There was also evidence of large inter-site variation in the apparent proportion of non-pups hauled out at sites during the breeding season. The local conditions that drive these differences are not understood but all may add significantly to the overall uncertainty around counts.

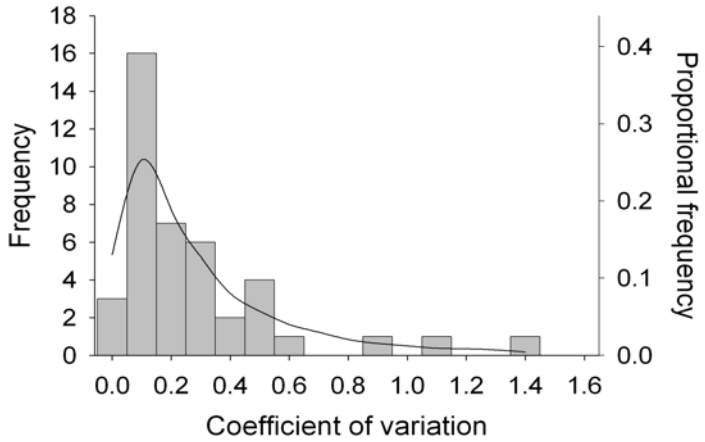

Figure 1. The frequency distribution (histogram) of the coefficient of variation found for repeated counts of non-pups at the same site in the same breeding season. The skewed form of the distribution meant that counting error was modelled using a log-normal distribution (solid line plotted as a proportional frequency scaled to the observed frequency). The geometric mean was 0.280 (sd = 2.492).

The overall effect of the procedure used to account for error and bias is shown in Figure 2 for non-pup counts. This shows how the true population is likely to be distributed as a multiple of observed population.

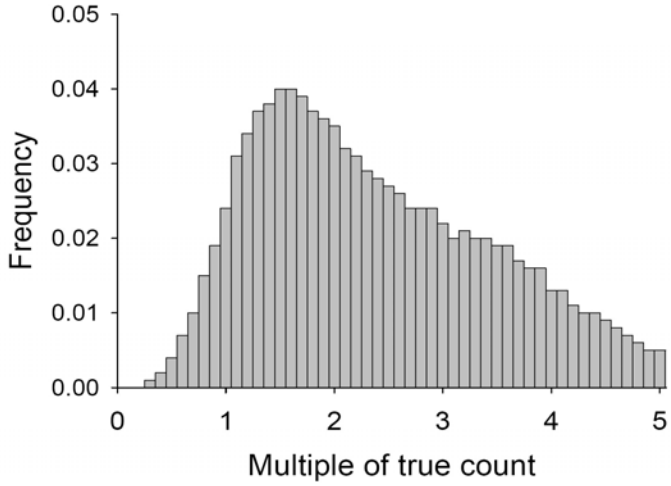

Figure 2. The frequency distribution of N_{true} for non-pup counts expressed as a proportion of N_{obs} for non-pup counts.

Historical abundance

The original interpolated counts across the whole population, together with counts corrected for error and bias are shown in Figures 3a & 3d. Although the number of pup and non-pup Steller sea lions counted apparently increased between 1960 and 1980, relatively few sites were surveyed through this period so much of this increase could be caused by increased observation effort. The total number of pups and non-pups declined after 1980 even though the observation effort, in terms of number of sites included within the surveys, continued to increase.

The number of non-pups counted declined almost linearly through the 1980s so that, by 1990 <50% of the numbers observed at the peak in 1980 were being counted (Figure 3a). However, from 1990, the total number of non-pups has remained stable and the apparent observation effort based on the number of sites included in the counts has also changed little through this time.

The number of pups observed did not begin a sustained decline until after 1985, and suggested a roughly 5-year delay between declines in non-pup abundance and declines in pup abundance (Figure 3d). This decline continued until about 2000 and thereafter numbers counted have increased at about the same rate as the previous decline. The rapid increase in the number of sites surveyed for pups since 2000 partly reflects greater observation effort but it also reflects a reclassification of some sites into a larger number of smaller units.

The application of the procedure to account for error in the counting methods caused an increase in the estimated number of pups and non-pups. As expected from the distribution illustrated in Figure 2, accounting for counting errors led to an approximate doubling of the number of non-pups (Figure 3a). The confidence limits around the mean estimate narrowed through time reflecting the increasing accuracy of the counting methods used and the relative level of uncertainty was greater for pups than non-pups. Thus, based on this account, the total number of non-pup Steller sea lions within Alaska and British Columbia is between 130,000 and 150,000. The trends in these estimates follow those for the observed numbers.

The "pup ratio" before 1980 was excluded as unreliable (Fig. 3g). These data suggest that relative productivity increased through the 1980s, when the population was in decline. The pup ratio then declined through the 1990s when the population had stabilised and began to increase again after 2000.

The Eastern and Western Distinct Population Segments (Figs. 3b, 3c, 3e & 3f) followed roughly opposite trends (Fig. 4). The rapid decline in abundance through the 1980s in the WDPS meant that the population reached about 20% of its peak size and it has shown a much slower overall decline since then (Fig. 3c). The decline in pup numbers in the western segment of the population lagged behind the change in the population as a whole (Fig. 3f) and this is reflected in the increasing pup ratio through the 1980s. The pup ratio in the western population segment then declined rapidly between about 1990 and 1997 and has remained unchanged at an intermediate level, or has shown a slight overall increase (Fig. 3i).

In contrast to the western segment, the number of non-pups and pups in the eastern segment has shown a near-monotonic increase since before 1980 (Figs. 3b & 3e). The pup ratio in the

eastern segment declined through the 1980s (Fig. 3h), at a time when the pup ratio in the west was high or increasing and when the non-pup portion of the population was in rapid decline. The pup ratio in the east has remained relatively low or increased slightly since 1990, but at a level equivalent to the pup ratio in the western population segment in recent years. The apparent low pup ratios in the eastern population segment during the early 2000s could have been caused by unaccounted bias within a single survey.

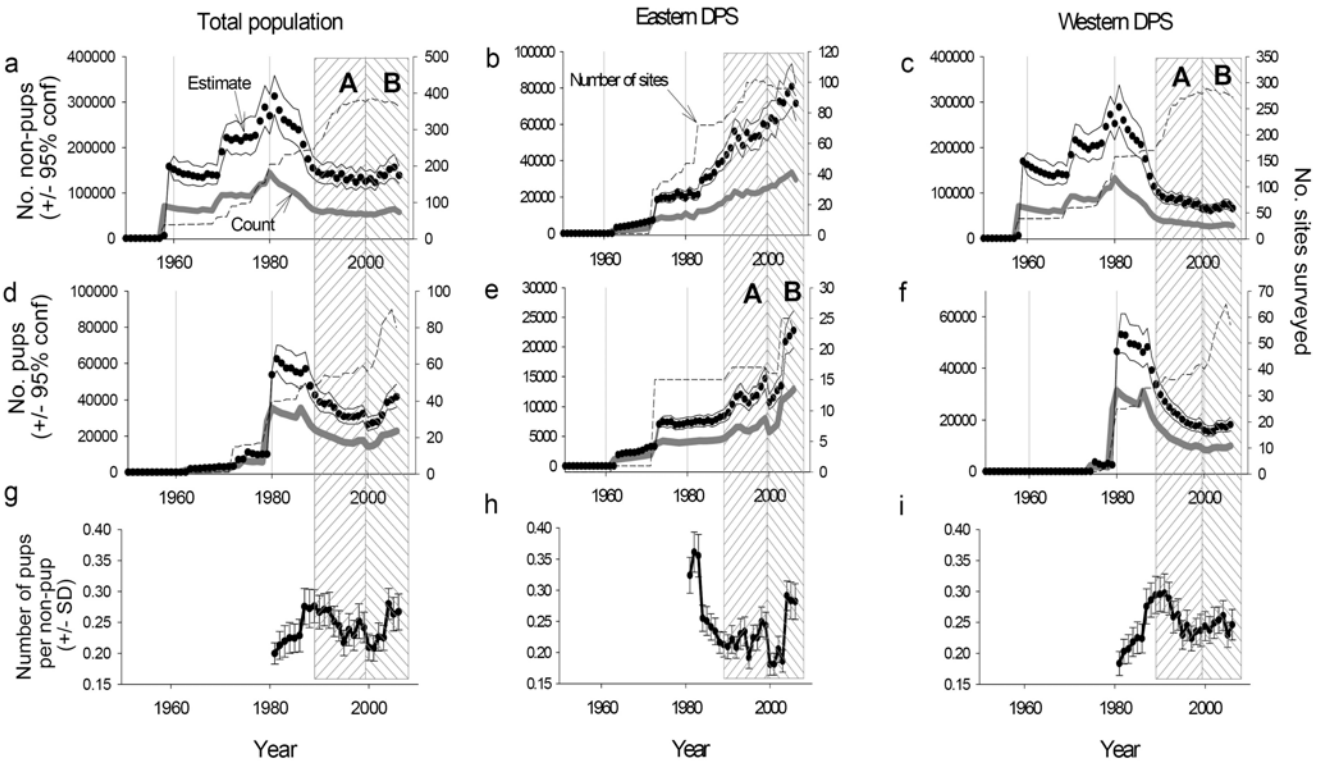

Figure 3. Changes in the observed number of non-pup (a, b, c) and pup (d, e, f) Steller sea lions at rookeries and haulouts during the June-July pupping season (shown as a broad grey line to reflect that there is uncertainty about these numbers). The decline in numbers at the end of the time series was caused by reduced data availability. Log-linear interpolation with Weiner diffusion was used to account for missing values. The dots show equivalent numbers adjusted for bias and errors in the observation process. The solid lines above and below these dots show ± 95% confidence intervals on these mean values. The dashed line shows the number of sites included in the estimation during each year. In panels g, h, and i the ratio of pups in the population to non-pups is shown ± 1 SD. The shaded block show the two phases of conservation management of Steller sea lions.

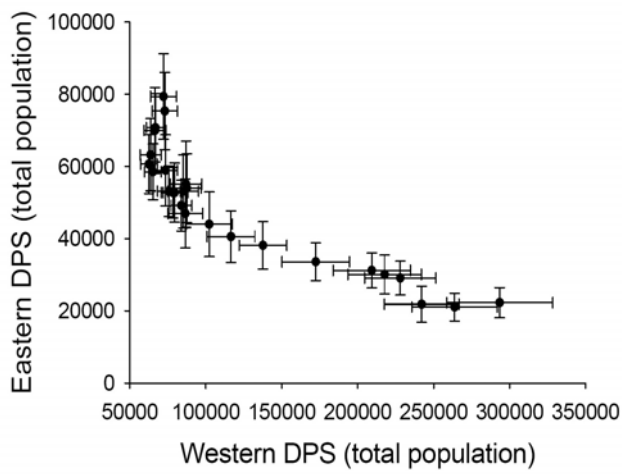

Figure 4. The relationship between the total number of Steller sea lions estimated within in the western and eastern parts of their range. Data from 1980-2006.

Rate of increase (λ) and the distribution of λ

The overall rate of increase at sites was heavily centred on unity (Fig. 5) which reflects the fact that most of the data came from a population that has been showing little directional change in recent years. The distribution was highly leptokurtic. Although this type of distribution could potentially be modelled using the Parieto or Generalised Extreme Value distributions, to avoid additional uncertainty due to model fitting, bootstrap re-sampling from the empirical distribution was used to model future population growth at each site.

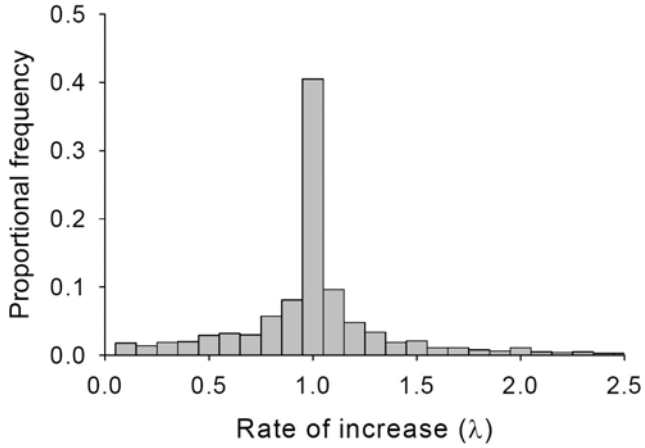

Figure 5. The frequency distribution of λ for non-pups at rookery sites during June and July across all sites irrespective of population size (n=2874).

However, the rate of increase appeared to be affected by population size in that increasing population size resulted in lower rates of increase (Krukal-Wallis, Chi-square= 46.07, df=10, p<0.001). Population size had a particularly strong effect upon the variance in λ. This was mainly because of high variability in λ at low population sizes presumably because of an increasing effect of immigration and emigration. Consequently, population size was used as a covariate in the choice of rates of increase to model future population growth (see Equation 4).

There was strong evidence that the rate of increase at individual sites was dependent upon the rate of increase at the previous time of measurement (Fig. 6). This autocorrelation was also included in population projections.

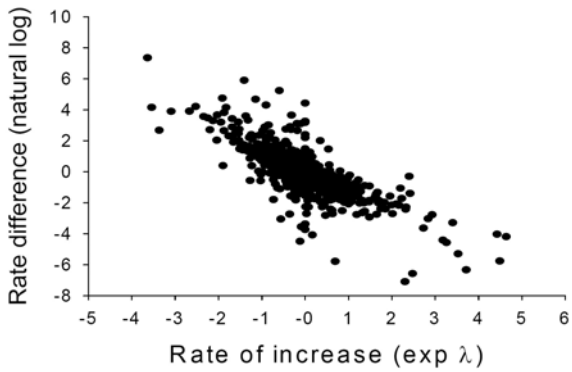

Figure 6. The relationship between the rate of increase at each site and the change in the rate of increase the next time it was measured. Extreme values at each end of these distributions are attributable to fluctuations at small population size, which was a significant co-variate in this relationship. Ln Rate difference = -0.0729-1.2138xln(λ); r^2=0.642.

Future trends in abundance

Model 1

The results of population projections using Model 1, which included temporal correlation but no spatial correlation (Fig. 7), showed the risk of extinction depended upon which parts of the time-series of historical counts was used to model the rate of change in the population. The population as a whole (Fig. 7a) when modelled using all historical data had a probability of extinction that exceeded the management objective until 1993 and after that the probability of extinction was <0.1 in 100 years (referred to here as the "conservation objective"). The terminal population size after 100 years was considerably greater in the case where no density limits were used and this pattern was the same across the population segments and irrespective of which prior distribution of rates was used (contrasting Models a, b and c). The western population segment (WDPS, Fig 7e) showed less of a tendency to meet the conservation objectives early in the time series but using the full range of historical data, it was compliant with the conservation objective after 2005. Using Model 1 and only the later parts of the time series of λ to project the population forward showed that in no circumstances did the stochasticty included here result in the extinction of the populations (Models 1 and 1c; Figs. 7b, 7d and 7f). The terminal size of the population as a whole (Fig. 7a) and of the western stock (Fig. 7c) continued to increase as additional data were added, reflecting the addition of information about the population as it has stabilised through time (Figs. 3a and 3c) and suggesting that this period of stability is increasing confidence that the population is robust to extinction. There was little apparent effect on the probability of extinction of the addition of new years to the time series. This analysis suggested that the predicted risk to the population was relatively insensitive to the addition of new data.

Model 2

The results of population projections using Model 2, which included temporal correlation and spatial correlation, are shown in Figure 8. Overall, the addition of correlation increased the probability that the population would not meet the conservation objective but this effect was

only present in Model 2a (Fig. 8a, 8c & 8d) and not in Models 2b and 2c, and the present probability of not meeting the conservation objective was very low. Adding density limits produced an increased probability that the populations would not meet the conservation objective and this is illustrated by the pattern in Figure 8c where even the eastern population segment failed to meet the conservation objective up to 1995. As with Model 1, the total terminal populations after 100 years were predicted to increase to a roughly constant level, showing that the prediction appears to be robust to the duration of the time series used to derive the sample distributions of λ.

Use of the time series from 1990 (Phase A in the management history, Figs 8b, 8d and 8f) showed slightly elevated terminal populations compared with the scenarios using the complete time series. The terminal population levels derived using only the data from Phase B of the management history (post 2000) were similar to those derived from the distribution of λ from Phase A of the management history. When the population changes during Phases A and B were used, all scenarios suggested that the population met the conservation objective.

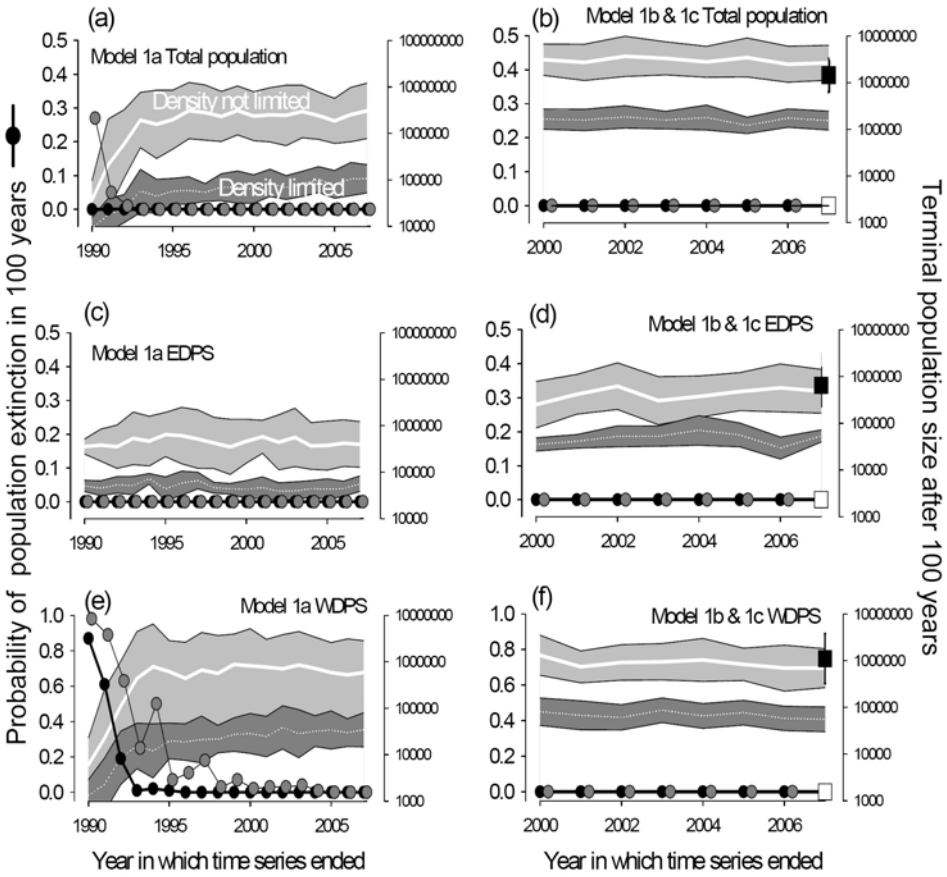

Figure 7. The evolution of population projections for 100 years in to the future using Model 1a (a), (c) and (e), and Models 1b and 1c (b), (d) and (f) . The projections used historical time-series that included all the available historical data up to the year in which the time series was terminated to illustrate how the predictions evolved as new data were collected. The probability of extinction during the future 100 years is shown as dots and the terminal population size is shown as a mean (white lines) ± 1 standard deviation (shaded regions). The result of running the models without density limits at individual sites (light grey shading, grey dots) is contrasted with running the models using density limits (dark grey shading, black dots). The projections using Model 1b used historical time-series that included data

collected after 1990 when management measures were introduced to promote conservation of the Steller sea lion (phases A & B in Fig. 4). The projection using Model 1c used historical time-series from 2000 to 2006 (phase B in Fig. 4) and the output is shown as a single shaded square (± 1 standard deviation) for the predicted terminal population size and an unshaded square to show the probability of extinction. The output for Model 1c with density limits in place is not shown. EDPS signifies the Eastern stock of Steller sea lions and WDPS signifies the western stock.

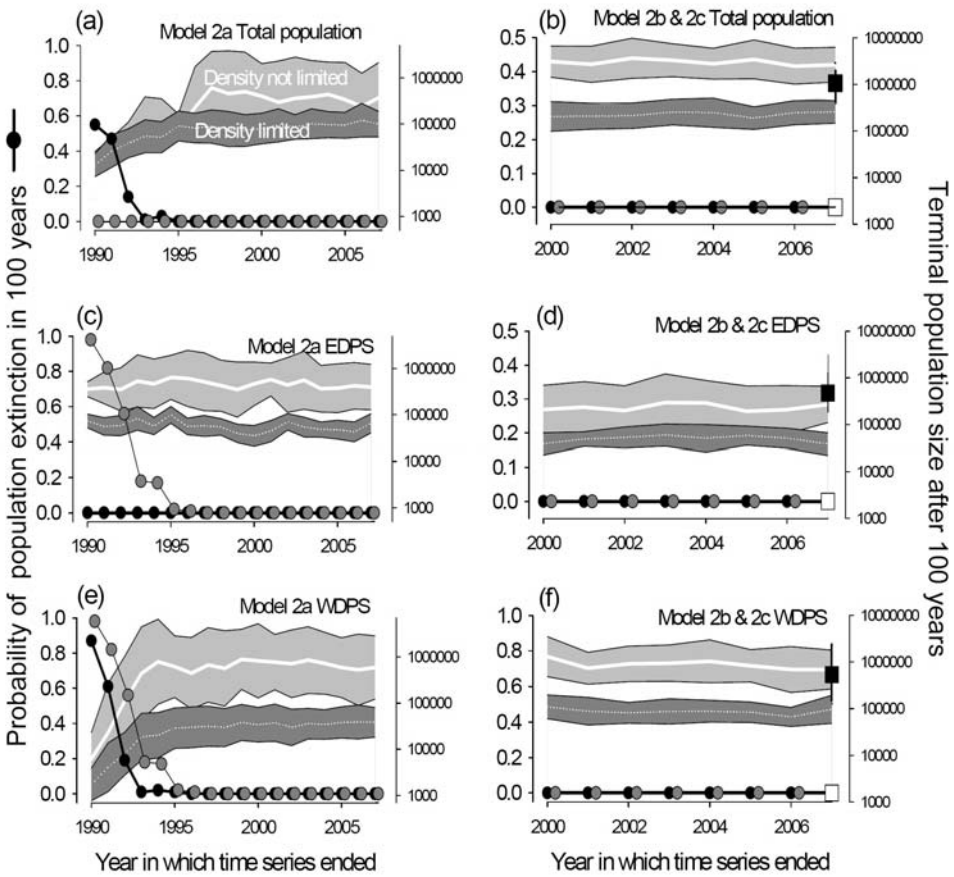

Figure 8. The evolution of population projections for 100 years in to the future using Model 2a (a), (c) and (e), and Models 2b and 2c (b), (d) and (f). Refer to the caption for Figure 7 for further details about the meaning of each symbol.

Discussion

Observation process

Count data contained errors only some of which have been taken in to account in past analyses of population trends (e.g. NMFS, 2008; Fritz et al., 2008). Past analyses have either accepted count data without error or with generalised error terms used when fitting models (e.g. Winship and Trites, 2006; Wolf and Mangel, 2008). The error defined here was approximately log-normal (Fig. 2) but the mean and variance of this distribution will vary with the counting methods used and has changed through time. Overall, the present analysis suggests that past approaches to understanding the population dynamics of the Steller sea lion have generally underestimated the uncertainties within the raw population data.

There has been an accumulation in the number of sites surveyed through time. We cannot be sure what proportion of this accumulation reflects the dispersal process as sea lions move to occupy new rookeries and haulouts and what proportion represents increasing diligence on the part of those conducting surveys. However, it is unlikely that the relative number of sites surveyed between the start and end of the time series (Fig. 3) is directly proportional to the observation effort.

Data considerations

Time-series count data from marine mammals are frequently complex and difficult to interpret mainly because it is often difficult to carry out truly synoptic surveys of widely spread marine mammal populations, not all animals are available to be surveyed, the relationship between the observed number and the true number is often obscure and difficult to assess, and there are often missing values caused by stochastic factors such as weather, funding, equipment failure, platform availability and, in the case of the Steller sea lion, withdrawal of permits to conduct surveys. More often than not, those involved in surveys have to make a leap of faith that the numbers they count are at least internally consistent because quantitative assessment of all the errors that could occur is extremely difficult. However, the type of post-hoc assessment of the scale of error applied here can provide additional information that is relevant to management.

The approach adopted in the present study using sites as the unit of sampling overcomes having to manage incomplete surveys or surveys that have a regional focus that shifted between years, often by excluding the data completely (e.g. NMFS, 2008). However, the data set did not include sites from Washington, Oregon or those from Russia that are not included within the NMFS data base. It would be simple to include these in future if data were made available at the level of individual sites. Lack of these data is unlikely to have seriously affected the outcome of this analysis because these regions make a comparatively small contribution to the overall population (Pitcher et al., 2007; NMFS, 2008). Future synoptic analyses of the Steller sea lion population would be simplified if all data holders could contribute to a common data base.

The analysis also allowed the data to dictate the cluster structure rather than geography, genetics or past perceptions of population sub-divisions. A number of analyses have sought to sub-divide the population demographically, geographical, politically and using genetics. O'Corry-Crowe et al., (2006) showed high levels of mitochondrial DNA diversity within Steller sea lions but, because of the recent trajectory of the population, it is not possible to know whether the distribution of haplotypes in the population is a cause or a consequence of

these demographic changes. Consequently, the present study has not made any underlying assumptions about the structure of the population. However, because of the historical management approach taken to Steller sea lions, the effects of considering the eastern and western segments separately has been investigated, but there seems to be no *a priori* reason, other than historical precedence, to view these population segments as distinct.

Historical trends in abundance

The data presented in Figure 3 need to be interpreted with care in terms of fine-scale changes shown. Even the estimates adjusted for error cannot account for the relatively low observer effort in the early part of the time series. The results of the present assessment of the Steller sea lion population trends before 1980 are in broad agreement with earlier estimates (Loughlin et al., 1984; Loughlin et al., 1992; Trites and Larkin 1992). The present analysis indicates that Steller sea lion numbers may have increased through the 1960s and 1970s. It appears that some status reviews of Steller sea lions (e.g. NMFS, 2008) and some PVAs (e.g. York et al., 1996; Gerber and VanBlaricom, 2001; NMFS, 2008) reflect an assumption that the counts of the population before 1980 greatly underestimated the overall population and these PVAs appear to have used the counts after 1980 as a benchmark for the pre-1980 estimates of Steller sea lion numbers, even though there is little evidence for this within the available data. After 1980, the non-pup population declined consistently for 10 years from a high of ~312,000 in 1980 to a low of ~135,000 in 1990, an annual rate of decline of 8%. There is no evidence of a significant decline or increase in the overall non-pup population since this time. However, local or regional dynamics may differ (e.g. York, 1994; Trites and Larkin, 1996) meaning that it is difficult to draw conclusions about population status based upon regionally-based surveys.

There are potentially important implications of these historical data for setting management objectives. It appears that the population size in 1980 could have been a peak and could have been greater than the long-term carrying capacity. Consequently, the return of the population since 1990 to a level similar to that measured in the 1960s may represent a level that is closer to the long-term mean carrying capacity. This suggests that management objectives could be most usefully focused upon maintaining the current population level rather than attempting to "recover" the population towards an historic high (NMFS, 2008), unless it can be shown that the environment has returned to the conditions of the 1970s (see Trites et al., 2006).

Overall, the population has declined in the west and increased in the eastern part of its range (Fig. 3). While data from genetics, mark-recapture, and satellite tagging (Raum-Suryan et al., 2002; O'Corry-Crowe et al., 2006; NMFS, 2008; Lander et al., 2009) do not suggest that there are regular movements of individuals from west to east, it remains likely that these opposing trends reflect a re-distribution of favoured habitat and a shift in the distribution of food. The pup ratios (Fig. 3) may indicate changing population productivity but they could also indicate movement of non-pups, most likely juveniles. It may be significant that the pup ratios in the eastern segment of the population declined at the same time as they increased in the western segment and at a time when the absolute size of the non-pup population in the eastern segment of the population began to increase (Fig. 3h compared with Fig. 3i and Fig. 3f). Rather than interpreting these as changes as being caused by internal dynamics within the eastern and western segments of the population, these could indicate recent emigration of juveniles from the western segment with subsequent recruitment in to the eastern segment. This hypothesis could be tested by reassessing the genetics data against the hypothesis generated by the present study, although since few samples are likely to be available that pre-date the changes in the 1980s even this may be inconclusive. The outcome has implications for

the approaches to management of the Steller sea lion as two separate stocks because of the effects that dispersal could have on meeting management objectives (Taylor, 1997).

Some features of the population data may reflect the potential causes the decline in the Steller sea lion population during the 1980s. The lag of 5 years between the start of the decline in pups compared to adults and the increase in the pup ratio through the same period supports the hypothesis (York, 1994; Holmes and York, 2003) that the decline through the 1980s was largely the consequence of low juvenile survival, but it could also have been caused by the emigration of juveniles (see above). This trend appears to have been driven by changes in the west of the range. In other words, the time lag in the decline in pup production was probably a consequence of the loss of females recruiting to the adult population and the increasing pup ratio in the early 1980s was probably because adults remained relatively unaffected. However, the ratio of pups in the population then declined and this suggests that adult fecundity declined through the 1990s, possibly as a delayed effect of the processes going on in the 1980s. Nevertheless, the subsequent increase in the pup ratio, with the apparent increase in the non-pup population, suggests that fecundity is once again recovering. This conclusion contrasts with that of Holmes et al., (2007) who suggest that fecundity is lower than expected and probably warrants further investigation. Differences may be caused by the smaller spatial scales used by Holmes et al., (2007) and we know that the population dynamics can be volatile at these scales (York, 1994; Trites and Larkin, 1996).

Scenarios for future trends

Simulations of future trends in abundance showed that if one assumes that there is a stationary distribution of λ across the full range of the data available, the probability of the population as a whole meeting the conservation objectives (probability of extinction <0.01 in 100 years) was met under all circumstances (Figs 7 & 8). The density-limited cases of both Model 1 and Model 2 constrained the growth of the population within reasonable boundaries and, even in these circumstances, the population met the conservation objectives. Only when distributions of λ that excluded observations for the past 10 years were used were the conservation objective not met. Model 2 included a more complex but potentially more realistic representation of the population processes. Inclusion of information about metapopulation structure, as opposed to considering all sites as independent populations, tended to increase the vulnerability of the population to extinction. This result is similar to that found by Melbourne and Hastings (2008). Apparent vulnerability to extinction will increase further if the Eastern and Western segments of the population are considered to be internally freely-mixing. This has often been assumed within past studies that have modelled the extinction probability of the Steller sea lion in terms of eastern and western distinct population segments (e.g. Gerber and VanBlaricom, 2001; NMFS, 2008), even though genetic studies have tended to indicate that these sub-sections of the population are not freely mixing (Bickham et al., 1998; O'Corry-Crowe et al., 2006; Hoffman et al., 2006). Consequently, making the assumption that the eastern and western segments are freely mixing sub-populations is likely to result in an unrealistically inflated estimate of the extinction probability calling in to question the results of some past risk assessments of the Steller sea lion population.

Although there was some level of density dependence included in the model, because the mean value of λ declined as population size increased, the only explicit form of density regulation in these models was the upper limit set on the number of sea lions that could be present on each site. This was introduced as an additional stochastic variable so the predictions will have accounted for uncertainty in the effects of density. There is no information from Steller sea lions about how density-dependent regulation actually operates

but the overall effect of limiting the total number of sea lions within a site is likely to be a reasonable surrogate.

There are reasons to believe that the distribution of λ was not stationary. Inspection of the population trends in Figure 3 suggest that a different set of conditions applied to the population before and after 1980 and before and after 1990. The threshold at 1990 is further supported by the introduction of extensive conservation measures at that time, and further measures were introduced after 2000 (NMFS, 2008). Consequently, if it is assumed that management approaches similar to the current conservation measures are maintained, then repeating the population projections using the distribution of λ from after 1990 and after 2000 are likely to provide a more realistic prediction of future risks. This demonstrated that the Steller sea lion population as a whole, or if considered in the two segments, met the conservation objectives (Fig. 7b, 7d, 7f, 8b, 8d and 8f).

Implications for conservation actions

The conclusions of previous assessments of the risks to the Steller sea lion population were based upon the data that were available at the time they were developed (e.g. York et al., 1996). Although none of the previous studies has examined the population as a whole (preferring instead to consider it as two distinct populations or even sub-sections of these populations), the results of the present study suggest that both the eastern and western segments of the population have probabilities of persistence that mean they do not meet the criteria for classification as endangered. They also suggest that conservation actions undertaken to date have either been successful or neutral in their effect. Even if one takes the most precautionary approach by assuming that management actions have had no positive effect the best risk models to apply would be Models 1a and 2a that have density limits in place. Both of these demonstrate compliance with conservation objectives. Considering that there will be cost-benefit trade-off associated with conservation measures, the conservation benefits accruing to Steller sea lions from additional management actions may be negligible. However, the present study has also demonstrated that the success of management can be assessed by updating analyses of risk with new data within a stochastic framework, using scenarios built upon the empirical distributions of directly measured population indicators, rather than through the use of complex process models of the population or by the making assessments based on the latest information alone.

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