**Running head**: Natality declines in Steller sea lions

# Age-structured modeling reveals long-term declines in the natality of western Steller sea lions

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## ABSTRACT

Since the mid-1970s, the western Steller sea lion (*Eumetopias jubatus*), inhabiting Alaskan waters from Prince William Sound west through the Aleutian Islands, has declined by over 80%. Changing oceanographic conditions, competition from fishing operations, direct human-related mortality and predators have been suggested as factors driving the decline, but the indirect and interactive nature of their effects on sea lions have made it difficult to attribute changes in abundance to specific factors. In part, this is because only changes in abundance, not changes in vital rates are known. To determine how vital rates of the western Steller sea lion have changed during its 28-year decline, we first estimated the changes in Steller sea lion age structure using measurements of animals in aerial photographs taken during population surveys since 1985 in the central Gulf of Alaska (CGOA). We then fit an age-structured model with temporally varying vital rates to the age-structure data and to total population and pup counts. The model fits indicate that birth rate in the CGOA steadily declined from 1976 to 2004. Over the same period, survivorship first dropped severely in the early 1980s, when the population collapsed, and then survivorship steadily recovered. The best fitting model predicts that in 2004, the birth rate in the central Gulf of Alaska was 36% lower than in the 1970s, while adult and juvenile survivorship were close to or slightly above 1970s levels. These predictions and other model predictions concerning population structure match independent field data from mark-recapture studies and photometric analyses. The dominant eigenvalue for the estimated 2004 Leslie matrix is 1.0014, indicating a stable population. The stability, however, depends on very high adult survival, and the shift in vital rates results in a population that is more sensitive to changes in adult survivorship. Although our modeling analysis focused exclusively on the central Gulf of Alaska, the eastern Gulf of Alaska and western Aleutians show a similar pattern of declining pup fraction with no increase in the juvenile, or pre-breeding, fraction. This suggests that declining birth rate may be a regional problem across the Gulf of Alaska.

**Keywords**: Leslie matrix, model selection, sensitivity analysis, population modeling, Bering Sea ecosystem, Gulf of Alaska, apex predators, AIC, pinnipeds, sea lions, reproduction

# INTRODUCTION

Apex predators in a variety of taxa, including sea otters, pinnipeds (seals and sea lions) and seabirds, declined across the North Pacific Ocean during the 1970s through 1990s (National Research Council 1996, Merrick 1997, Anderson and Piatt 1999, Trites et al. 1999, Doroff et al. 2003, DeMaster et al. 2006). Declines in three important pinniped species have been especially well-documented: Pacific harbor seals, *Phoca vitulina* (Pitcher 1990, Small et al. 2003, Jemison et al. 2006), Steller sea lions, *Eumetopias jubatus* (Fritz and Stinchcomb 2005), and northern fur seals, *Callorhinus ursinus* (Towell et al. 2006). The affected areas stretch from the western Aleutian Islands to Prince William Sound in the North Pacific Ocean (Fig. 1) and the declines have been severe and sustained. By 2005, these three species had declined to 10-50% of their late-1970s levels in many regions (Angliss and Outlaw 2005). In some marine communities, the cause of the reduction of apex predators is attributed to fishing pressure (Jackson et al. 2001). However, the causes of pinniped declines in the North Pacific remain unclear. Direct human-related mortality, either due to fishing bycatch, intentional mortality, or Alaska native subsistence harvest does not appear to be driving declines observed since 1990 — certainly not for Steller sea lions and northern fur seals (Merrick 1997, Loughlin and York 2000, Doroff et al. 2003, National Research Council 2003, Angliss and Outlaw 2005, DeMaster et al. 2006).

The Steller sea lion (SSL) is the largest eared seal (Otariidae), with adult males weighing up to 2,400 pounds. This fish- and squid-eater is one of the top predators in the Bering Sea ecosystem and is distributed across the entire North Pacific rim from northern Japan to Russia, across the Gulf of Alaska, and south to California (Fig.1). In the early 1970s, SSL abundance began declining in the eastern Aleutian Islands (Braham et al. 1980). By the early 1980s, declines had spread east to the Gulf of Alaska and west to the central Aleutian Islands (Merrick et al. 1987). In 1990, the species was listed as threatened range-wide under the U.S. Endangered Species Act. In 1997, genetic, population trend and other evidence led the National Marine Fisheries Service of the US (NMFS 1997) to recognize two distinct population segments of SSL: western (west of 144° W longitude) and eastern (east of 144° W longitude). At this time, NMFS uplisted the western SSL to endangered (it had declined to 20% of its 1970s levels), while the eastern SSL's status remained threatened (NMFS 1997). The western SSL continued to decline until 2000, after which it began to increase for the first time since the late-1970s (Fritz and Stinchcomb 2005). However, the increase did not occur across the range of the western SSL. Abundance increased in parts of the Aleutian Islands and the Gulf of Alaska, but continued to decline in the central Gulf of Alaska (CGOA; Fig. 2).

Confidently attributing declines in population abundance to specific factors has been difficult for SSL researchers despite a large-scale, well-funded and coordinated research program specifically targeted at this research problem (Ferrero and Fritz 2002, National Research Council 2003). This is largely due to the complexity, indirectness and uncertainty concerning how environmental and biological factors affect SSL populations. The main hypothesized drivers for the decline are killer whale predation (Springer et al. 2003), disease (Burek et al. 2005), nutritional stress caused by natural changes in the prey community (Trites et al. 1999, Benson and Trites 2002, Trites and Donnelly 2003) or the indirect competitive effects of fishing, and direct, anthropogenic mortality (e.g., incidental bycatch in fisheries and legal and illegal shooting) (Loughlin and Merrick 1988, Perez and Loughlin 1991, Ferrero and Fritz 1994, Pascual and Adkison 1994, Hennen 2006). Part of the difficulty in assigning cause is that correlations between rates of population decline or increase and an index for a particular risk factor are not meaningful when multiple factors are simultaneously affecting population dynamics and changing age-specific vital rates in independent and contrary directions. In this case, a risk factor may be having strong effects on one vital rate while the population shows no or countervailing changes in abundance.

In this study, we focus on estimating the changes in age-specific survivorships and birth rates associated with the 28-year decline of the western SSL. Such an analysis helps our understanding of the effects of risk factors and management actions since there is a clearer link from these factors to vital rates than to abundance. To confidently tease apart vital-rate changes from census data, however, age-structure information is required, but the last age survey of the population was in 1984/1985 (York 1994). Before attempting to model the vital-rate changes, we needed to address the critical lack of age-structure information. To do this, we used archived photographs taken during aerial surveys since 1985 and measured the lengths of animals in the photographs. The resultant size distributions provided a metric for the historical changes in age structure. This metric, along with 28 years of census data on newborn pups and total population, allowed us to use age-structured models to estimate the changes in survivorships and birth rates between 1976 and 2004. All modeling analyses involve a myriad of minor or not so minor modeling decisions. We used a multi-pronged approach for evaluating modeling robustness, including calculation of model support using Akaike's Information Criterion (AIC), analysis of sensitivity to model choice across plausible variants, and analysis of sensitivity to data choice. As a final test, we synthesized a wide variety of field studies which gave information on vital rates or population structure for a few specific time periods. These were used to independently cross-validate the model's 28-year retrospective estimates.

# METHODS

We estimated the historical changes in vital rates using a temporally-varying Leslie-matrix model (Caswell 2001). In the model, the pre-decline dynamics (up to 1983) were specified using a Leslie matrix based on a 1970s survey of age distribution and age-specific pregnancy rates (Pitcher and Calkins 1981, Calkins and Pitcher 1982). In the model, natality, juvenile survivorship and adult survivorship were allowed to change independently during four discrete time periods (a step function with four intervals) starting in 1983. In each time period, juvenile survivorships (age 0 to 1 year, age 1 to 2 years, age 2 to 3 years) were scaled together, so that there was only one juvenile-survivorship scaling factor for each period. The same was done for adult survivorship (yearly survival for ages 4 to 32 years) and natality (ages 1 to 32 years). Thus, in each period, only 3 scaling parameters were used for a total of 12 scaling parameters (three scaling factors and four time periods). Using maximum likelihood, we determined the combination of scaling factors that led to the best fit of the 1976-2004 total population, newborn and juvenile-fraction time series. This provided model estimates of the temporal changes in natality, juvenile survivorship, adult survivorship, and age structure.

Our sensitivity analyses addressed sensitivity to matrix choice, time-period choice, and data choices. To study the effects of matrix choice, we repeated this analysis using four different Leslie matrices for the late-1970s SSL population. The matrices ranged in complexity from a simple five-stage matrix using constant adult survivorship and natality to matrices with different vital rates for each age 1 to 32 years. To study the effects of the choice of time periods when vital rates were allowed to change, we repeated the analysis using nine different time-period combinations. The different time periods were based on different hypotheses about the causes of the changes in vital rates. To understand the sensitivity to data choice, we studied the effect of different weightings on the data and repeated the analysis by fitting only to newborn and total population to understand how the results were sensitive to our juvenile-fraction metric. Lastly, we cross-validated the estimates from the best-fit model against available independent field data.

### *Abundance data*

Our analysis focused on the CGOA, which has historically had one of the highest regional abundances and, along with the eastern and central Aleutian Islands, has experienced one of the most severe population declines (Fritz and Stinchcomb 2005). Since 1976, aerial photographic surveys of Alaskan SSLs have been conducted by the NMFS and the Alaska Department of Fish and Game as part of range-wide monitoring (NMFS 1992, Fritz and Stinchcomb 2005). The NMFS survey includes sea lions on rookery and haul-out sites in the Gulf of Alaska and Aleutian Islands during the breeding season (late-June to early-July). Rookeries are sites where adult males defend territories and where mating and birthing occur. Haul-out sites are rocky outcrops where sea lions predictably rest on land but where no or few pups are born. The age and breeding status of individuals differs greatly between rookery and haul-out sites in late-June to early July when the NMFS census occurs. At this time, the majority of breeding-age males and females are on the rookeries, while the majority of pre-reproductive juveniles are on haul-outs. In addition in late-June, the overwhelming majority of adult females on haul-outs will not give birth that year (Withrow 1982). Later in the summer, after the birthing season, these females move to the rookeries (Withrow 1982).

Juveniles and adults are not distinguishable in the NMFS surveys conducted through 2002; only a nonpup count is reported. NMFS designates all major rookeries and certain major haul-outs as trend sites for the purpose of reporting a historically consistent index of the population. These sites have been regularly surveyed using the same methodology since 1976. Sea lion counts on the trend sites account for 70-80% of the total aerial survey each year. For this paper, we used the 1976-2004 total nonpup count on trend rookeries and haul-outs in the CGOA during June/July (raw data and references are provided in Appendix A). There are no observation error estimates available for the NMFS survey data. However, replicate surveys conducted during the same year (though separated by 2-6 days at each site) indicate that the coefficient of variation on regional totals of nonpup counts was approximately 5%.

Pup production is assessed separately from nonpups and surveys consisted of ground counts conducted every 1-4 years on the major rookeries from 1978 through 2004. In addition, a high-resolution aerial survey (see *'High resolution aerial surveys conducted in 2004 and 2005'* below) was used to count pups on all rookeries and major haul-outs in 2005. To estimate pup production in the CGOA (Fig. 2a), we summed counts at the five major rookeries (Marmot, Sugarloaf, Chowiet, Chirikof, and Outer Islands), which together constitute more than 95% of the CGOA pup production (Fritz and Stinchcomb 2005). Counts were not available every year. We added together the pup counts for those years when 1) at least three of the five major rookeries were surveyed and 2) the other rookeries with missing counts were surveyed within 2 years. For the rookeries missing a count, a linear interpolation was used between the most recent two pup counts, and the interpolated value was used for the missing value. The raw pup numbers for the five rookeries, the interpolated values, and the total pup count used in this analysis are given in Appendix A.

### *Juvenile-fraction data*

Previous researchers have had only the NMFS pup and nonpup time series for modeling analyses. We collected additional data to estimate a time series of the fraction of juveniles in the population. This was based on the metric developed in Holmes and York (2003) that used measurements of the animals photographed in the aerial surveys. We extended the work of Holmes and York (2003) and developed a comprehensive juvenile-fraction estimate for the CGOA (Fig. 2b). This estimate used all haul-outs photographed during the 11 aerial breeding-season surveys between 1985 and 2002. From the photographs, the longest straight-line length of every animal was measured digitally (a total of 28,629 measurements). The fraction of small animals from all haul-out photographs in a given year was used as an index of the juvenile fraction. The average number of measured animals per year was 2827 and the average number of haul-out sites per year was 16. The numbers of animals and haul-outs measured are given in Appendix A. Standard errors on the estimated juvenile fraction were estimated via stratified bootstrapping, by haul-out and by photograph within haul-outs. The data we used include all haul-outs, to maximize sample size. However in the mid-1980s and early-1990s, there were fewer haul-outs photographed. The overall pattern in juvenile fraction did not change when we used a uniform set of haul-outs across all years (comparison is shown in Appendix B, Fig. B1).

The photographs provide no direct means of determining absolute size of individuals. Instead, relative size compared to a mature adult male in each photograph was used. Only photographs with a mature adult male (which are distinctive in size and color) lying fully stretched out were used. The measurements of all other individuals in a photograph were normalized by dividing all animal lengths by the length of the largest mature male. From the set of all normalized measurements, a metric, *J/T*, for the fraction of juveniles on haul-outs was calculated as

$$\frac{J}{T} = \frac{\text{number of animals less than 50\% of the length of the largest male}}{\text{total number of animals measured in all photographs}}. \qquad (1)$$

Juveniles are 60-70% of the length of large males (Calkins and Pitcher 1982), thus the 50% cut-off means that not all juveniles are counted as juvenile in the *J/T* metric. A 50% cut-off was used to ensure that adult females would be rarely categorized as juveniles (Holmes and York 2003). We compared the juvenile numbers on high resolution photographs taken in 2004 (see 'High resolution aerial surveys conducted in 2004 and 2005' below) to the numbers estimated using the 50% cut-off from aerial photographs taken through 2002 and found that 83% of juveniles were categorized as juvenile following the 50% cutoff used in Eq 1.

### *Pre-decline Leslie matrix*

We used a 32 x 32 female-only age-structured life-history matrix (Table 1) for Steller sea lions. Throughout we will refer to this as the HFYS matrix to distinguish it from other matrices used later in the sensitivity analyses (all matrices are named after the authors of the paper in which the matrix was published). The HFYS matrix is a birth-pulse Leslie matrix where row 1 column *i* is the number of 1-month old pups produced by age *i*+1 females multiplied by the survival rate from age *i* to age *i*+1. Thus, when the matrix multiplication, $\vec{N}_{t+1} = \mathbf{A} \times \vec{N}_{t}$, is performed, the first element of $\vec{N}_{{t+1}_t}$ is the female pup numbers (at 1-month of age) in year *t*+1. Rows *i*, *i* > 1, in the matrix contain the survivorships from age *i* to *i*+1, along the diagonal.

The HYFS matrix is based on York (1994) but uses a new natality schedule based on our reanalysis of the 1970s pregnancy data. The Steller sea lion life-history matrix in York (1994) is based on an age and pregnancy survey in the late 1970s off Marmot Island in the CGOA (Pitcher and Calkins 1981, Calkins and Pitcher 1982). The matrix in York (1994) used the natality schedule given in Calkins and Pitcher (1982), but used a reanalyzed survivorship schedule based on a Weibull hazard model. The re-estimated survivorship schedule results in a late-1970s age-distribution that closely matches the observed late-1970s age-distribution. York (1994) did not re-analyze the age-specific pregnancy rates used in Calkins and Pitcher (1982), and there were a number of inconsistencies between the actual pregnancy data and Calkins and Pitcher's natality schedule. In particular, both Calkins and Pitcher (1982) and York (1994) set natality at a constant level after age 6; however, no late-term pregnancies were observed in females over the age of 21 in the 1970s data. Reproductive senescence has been documented in a variety of other pinnipeds including Antarctic fur seals (*Arctocephalus gazelle*) (Lunn et al. 1994), northern fur seals (*Callorhinus ursinus*) (Lander 1981), harp seals (*Pagophilus groenlandicus*) (Bowen et al. 1981), harbor seals (*Phoca vitulina*) (Härkönen and Heide-Jørgensen 1990) and grey seals (*Halichoerus grypus*) (Bowen et al. 2006).

We revisited the raw pregnancy data from Marmot Island for the late-1970s and re-estimated the late-term pregnancy rates using a logistic regression model (McCullagh and Nelder 1989) of the form:

$$\log\left(\frac{p_{a,m}}{1-p_{a,m}}\right) \sim \beta_a + \gamma\, m, \tag{2}$$

where $p_{a,m}$ is the probability that a female Steller sea lion in age group $a$ is pregnant $m$ months after mating in July; the age group is one of the following categories, 3, 4, 5, 6, 7-9, 10-16, 16-20, or 21-30 year, and represents the age at which a female becomes pregnant, but she gives birth when she is one year older. $p_{a,m}$ is assumed to be the expectation of a Bernoulli random variable, and we modeled its logit as a linear function of *m*. The form of this model is conceptually different from that of Calkins and Pitcher (1982). They modeled late-term pregnancy rates as a product of an age-specific maturity rate, a constant conditional pregnancy rate given a female is mature, and a constant monthly decay rate in pregnancy rate. Our model is an age-group specific pregnancy rate at the time of implantation with a constant monthly decay in pregnancy rate. This new model leads to a natality schedule that includes reproductive senescence and that closely fits the observed age-specific pregnancy data from the late-1970s.

### *Model*

The HFYS matrix for the late-1970s population was used as the starting Leslie matrix in a time-varying Leslie matrix model. In this model, there were five time periods with dynamics in each time period governed by a different Leslie matrix (denoted by the **A**s):

$$\begin{aligned}
\vec{N}_{t+1} &= \mathbf{A}_{\text{predecline}} \cdot \vec{N}_t, \text{ for } 1976 \le t \le t_1 \\
\vec{N}_{t+1} &= \mathbf{A}_{T1} \cdot \vec{N}_t, \text{ for } t_1 < t \le t_2 \\
\vec{N}_{t+1} &= \mathbf{A}_{T2} \cdot \vec{N}_t, \text{ for } t_2 < t \le t_3 \\
\vec{N}_{t+1} &= \mathbf{A}_{T3} \cdot \vec{N}_t, \text{ for } t_3 < t \le t_4 \\
\vec{N}_{t+1} &= \mathbf{Y}_{T4} \cdot \vec{N}_t, \text{ for } t_4 < t \le 2004
\end{aligned} \quad . \tag{3}$$

$\vec{N}_t$ is the vector of the number of sea lions at each age at time *t*, with age-0 being pups at age 1-month which is the census age. $\mathbf{A}_{\text{predecline}}$ is the 32 x 32 Leslie matrix for the pre-decline period. The time periods used were mid-1980s to late-1980s, late-1980s to early 1990s, early 1990s to late-1990s and late-1990s to 2004. The time periods blocks were based on previous analyses of pinniped population trends and oceanographic changes in the Gulf of Alaska. The exact years of change were varied by 1-2 years as part of the sensitivity analyses to reflect biological and oceanographic influences.

The matrices, $\mathbf{A}_{T1}$, $\mathbf{A}_{T2}$, $\mathbf{A}_{T3}$, $\mathbf{A}_{T4}$, were relative to $\mathbf{A}_{\text{predecline}}$ by scaling juvenile survivorship, adult survivorship and birth rate relative to their pre-decline values (Table 2). Thus, in time period 1, all adult survivorships, $s_3$ to $s_{30}$ in Table 1, were scaled up or down together by a factor $p_{a,1}$, all juvenile survivorships, $s_0$ to $s_2$ in Table 1, were scaled by a factor $p_{j,1}$, and all fecundities were scaled by $p_{f,1}$. The only constraint on the scaling factors was that survivorship must be less than 1. Analogous to $\mathbf{A}_{T1}$, the $\mathbf{A}_{T2}$, $\mathbf{A}_{T3}$, and $\mathbf{A}_{T4}$ matrices were defined relative to $\mathbf{A}_{\text{predecline}}$, each with their own three independent scaling factors. The scaling factors for adjacent time periods were independent, and the matrices were not forced to change in each time period; it was possible for the scaling factors to remain constant between time periods. The objective of the model fitting was estimation of the scaling factors for each time period and thus estimation of the change (or lack of change) in vital rates over time.

### *Model fitting*

For model fitting, we needed to specify the relationship between model numbers of animals and observed data. The observed pup numbers were related to the model's total female pup numbers as:

$$\log(\text{pups}_{\text{model}}) = \log(0.5\ \text{pups}_{\text{obs}}/0.95) + \varepsilon_p. \tag{4}$$

This was based on the fraction of CGOA pups that have been counted on the main rookeries since 2000 (95%) and on the sex ratio at birth (50%) (Calkins and Pitcher 1982, Fritz and Stinchcomb 2005). $\varepsilon_p$ is Gaussian distributed observation error with mean zero. The variance of $\varepsilon_p$ was unknown and treated as an estimated parameter. The model needs as an initial value the true number of female pups in the late-1970s. This was estimated as a free parameter, $p_1$. Two pup counts were available for the late-1970s, so $p_1$ was not entirely unknown and the estimated $p_1$ was between these two counts.

The NMFS nonpup count represents only animals visible on the NMFS trend sites during the aerial survey. Thus, animals on non-trend sites, in the water, or on trend sites but not photographed had to be accounted for in the model fitting:

$$\log(\text{nonpups}_{\text{model}}) = \log(\text{nonpups}_{\text{obs}}/p_2) + \varepsilon_{np}. \tag{5}$$

Here $\varepsilon_{np}$ is unknown Gaussian-distributed observation error whose variance was treated as an estimated parameter. The biological meaning of $p_2$ is the fraction of total nonpups that was counted in the NMFS census divided by the fraction of the nonpup population that is female. We estimated $p_2$ as a free parameter. A critical assumption is that $p_2$ did not change systematically over time, meaning that observability and sex-ratio have not changed systematically between 1976 and 2004. A significant violation of this assumption would change our results; it would also mean that the population stabilization observed since 2000 is illusory. However, we are confident with this assumption for two reasons. First the survey methods have been consistent from 1985 through 2004. Although year-to-year variability in the survey counts is certain, a serious systematic change in observability would be needed to negate the increasing trend in nonpup to pup ratios. Specifically, the current nonpup count would need to be inflated by ca. 67%. Second, the estimated sex ratio in nonpups in the late-1970s was 70% female, which is similar to the percent female estimated from the 2004 high-resolution photographs. Although it is possible that the sex-ratio has shifted somewhat, the change in sex ratio would have to be extreme to negate the decline in pup to nonpup ratios, specifically from 70% of nonpups being female to 40% of nonpups being female in 2000-2004.

The *J/T* metric is the number of small animals on haul-outs divided by the total number of animals photographed on haul-outs that year. The relationship between the *J/T* metric and the total numbers of female juveniles and adults in the population is specified as:

$$\left(\frac{J}{T}\right)_{\text{haulout}} = \frac{m_{j,j} h_j J_{\text{total}} / \phi_j}{h_j J_{\text{total}} / \phi_j + h_a A_{\text{total}} / \phi_j} = \frac{m_{j,j} J_{\text{total}}}{J_{\text{total}} + \dfrac{h_a}{h_j} \dfrac{\phi_j}{\phi_a} A_{\text{total}}} . \tag{6}$$

The constant $m_{j,j}$ is the fraction of juveniles in a photograph that are categorized as less than 50% the length of the largest male (estimated to be 83%). The fraction of juveniles and adults that were photographed on haul-outs, as opposed to being in the water, on rookeries, or otherwise not photographed, is denoted by $h_j$ and $h_a$, respectively. Since the model tracks only females and the *J/T* metric was based on measurements of males and females, we had to correct for the fraction of juveniles and adults on the haul-out that are female: $\phi_j$ and $\phi_a$, respectively. These fractions, along with the constants $h_a$ and $h_j$, are unknown. However, it is known from high resolution photographs (see 'High resolution aerial surveys conducted in 2004 and 2005' below*)* that $h_a$ is considerably smaller than $h_j$. The constant ($h_a\phi_j / h_j\phi_a$) was estimated as a free parameter ($p_3$, in Eq. 6). We assumed that the observed *J/T* was related to the true $(J/T)_{\text{haulout}}$ with Gaussian observation errors with an unknown variance which was estimated as a free parameter.

The models were fit using maximum likelihood with a negative log-likelihood function, $S(\theta)$, based on normally distributed errors in the data:

$$\begin{aligned} S(\theta) = \frac{1}{2}\Big[ & k \log \sigma^2_{\log N} + \frac{1}{\sigma^2_{\log N}} \sum_{i=1}^{k} (\log(N_i / p_2) - \log(\hat{J}_i + \hat{A}_i))^2 \\ & + n \log \sigma^2_{\log P} + \frac{1}{\sigma^2_{\log P}} \sum_{i=1}^{n} (\log(0.5 \times P_i / 0.95) - \log(\hat{P}_i))^2 \quad . \\ & + m \log \sigma^2_J + \frac{1}{\sigma^2_J} \sum_{i=1}^{m} ((J/T)_i - (m_{j,j} \hat{J}_i / (\hat{J}_i + p_3 \hat{A}_i))^2 \Big] \end{aligned} \tag{7}$$

Here $N_i$, $P_i$, and $(J/T)_i$ are the data: the *i*-th CGOA nonpup count, pup count, and the juvenile fraction metric, respectively. The variables, $\hat{P}_i$, $\hat{J}_i$, and $\hat{A}_i$ are the model predictions of total female pups, juveniles and adults, except that the initial number of female pups, $\hat{P}_1 = 0.5\, p_1$, was an estimate. Constants $p_1$, $p_2$, $p_3$ and $m_{jj}$ are defined in Eqs. 4-6. The variances for the errors in the log pup, log nonpup, and *J/T* data were unknown. They were estimated as free parameters using sequential updating until the variance estimates converged (Green 1984). Confidence intervals on the estimated scaling factors (*p*'s in Table 2) were estimated using one-dimensional likelihood profiling allowing all other parameters in Eq. 7 to be free (Hilborn and Mangel 1997). There were a total of 18 free parameters per model; three scaling parameters for each of four time periods, three variances, and three constants. In the sensitivity analyses, we also compared a model with three time periods; this model had 15 free parameters.

### *Sensitivity to matrix choice and time-period choice*

The effect of model choice on the results was tested by comparing the results for 36 different model variants (four pre-decline Leslie matrices x 9 time-period possibilities). The four pre-decline matrices were: 1) an SSL matrix with one constant adult survivorship and birth rate; this matrix is denoted WT (Winship and Trites 2006); 2) a matrix based on the original survivorship and birth rate schedule estimated by Calkins and Pitcher (1982) for the CGOA; this matrix is denoted CP; 3) the CP matrix with a re-estimated survivorship schedule from York (1994); this matrix is denoted Y; and 4) the CGOA matrix discussed previously which is based on a re-analysis of the 1975-1978 pregnancy data, and denoted HFYS. All matrices have the same form (Table 1), but have different natality and survivorship schedules. The differences are shown in Fig. 3. A discussion on the background of the WT, CP and Y matrices and parameter values for all four matrices are given in Appendix C.

The use of disjoint time periods, rather than smoothly varying functions, was based on previous analyses of population growth rates (York et al. 1996, Holmes and York 2003), field work (Chumbley et al. 1997), and declines in other pinnipeds in the CGOA (DeMaster et al. 2006). These studies indicate that there have been distinct periods with different population dynamics. The timing of the first change ($t_1$) can be placed at 1983 based on field work on Marmot Island. Prior to 1983, juveniles comprised 15-20% of the animals on the Marmot beaches during the breeding season. During 1983, the juvenile fraction on Marmot Island started at normal levels but then declined precipitously over the remainder of the breeding season (Chumbley et al. 1997) and remained well below pre-1983 levels for the next 20 years. A second change ($t_2$) in population dynamics occurred in 1988 or 1989 and was signaled by abrupt changes in the ratio of pups to nonpups and a change in the rate of population decline in both CGOA sea lions and harbor seals (DeMaster et al. 2006). A change in oceanographic conditions also occurred at this time (Hare and Mantua 2000, Benson and Trites 2002). We fixed $t_2$ at 1988; the results were the same when it was set at 1989. The timing of subsequent changes in vital rates is less clear. Examination of the ratio of pups to nonpups and population trends suggests that changes in vital rates occurred in both the early and late 1990s. There is evidence of an anomaly in the Bering Sea ocean conditions in 1998 which affected multiple species (Napp and Hunt 2001) and possibly a reversion to pre-1977 ocean conditions (Hare and Mantua 2000). The evidence for ecosystem change in the early 1990s is unclear, although there is evidence of a change in North Pacific fish communities at this time (McFarlane et al. 2000). For the early 1990s, we fit models with no $t_3$, a $t_3$ in 1992, or a $t_3$ in 1993. For the late 1990s, we fit models with a $t_4$ in 1997, 1998, or 1999. In total, nine different time period combinations were compared: three possible early 1990s years and three possible late-1990s years.

The model fits were compared using the AIC corrected for small sample size, $AIC_c$ (Burnham and Anderson 2003): $AIC_c = -2 \log L + 2K + 2K(K+1)/(n - K - 1)$, where L is the likelihood, $K$ is the number of estimable parameters and $n$ is the sample size. The $AIC_c$ values, maximum-likelihood estimates of the scaling factors, and the number of free parameters for each of the 36 model variants are given in Appendix D. The number of estimated parameters was used for $K$, however the parameters are not orthogonal and thus the estimable number of parameters is actually less than the number of estimated parameters. If the estimable parameters were used, the best fit model would be separated from the next best models by larger $\Delta AIC_c$ values than are presented here. Nonetheless the ranking of the $\Delta AIC_c$s would not change. Unfortunately when the orthogonality of parameters in a model is ambiguous, as it is in our model, specification of the number of estimable parameters for model-selection purposes appears to be an open problem in statistics. For $n$, the total number of data points in the three time series was treated as the sample size for the $AIC_c$ calculation. This does not adjust for possible autocorrelation in the residuals; however, 1) half the data points in the time series are separated by two or more years, and 2) any effect of overestimating sample size is somewhat offset by overestimation of the effective parameter size. Nonetheless, to the extent that sample size is overestimated, the presented $AIC_c$ calculation unduly favors models with more parameters.

### *High resolution aerial surveys conducted in 2004 and 2005*

High-resolution photographs were taken of all known CGOA rookeries and haul-outs in 2004 to count nonpups; a similar comprehensive survey of all rookeries and major haul-outs was conducted in 2005 to count pups (Fritz and Stinchcomb 2005; NMFS-NMML, unpublished data). In these photographs, animals were identified as pup, juvenile, sub-adult male, adult male and adult female based on color, size, morphology and location within the rookery. The number of animals assigned to each age-sex category using the 2004 high-resolution photographs is independent of the aerial survey numbers and the *J/T* metric to which our models were fit.

## RESULTS

The model fits to the pup, nonpup and juvenile-fraction data indicate a steady decline in the per-capita natality in the Central Gulf of Alaska (CGOA) from the late-1970s through to 2004 (Fig. 4). Survivorships of adults and juveniles initially declined (for juveniles much more than for adults), but since the late 1980s-early 1990s, both have increased (Fig. 4). This pattern of increasing survivorship and decreasing natality was seen across all models, using either the WT, CP, Y or HFYS Leslie matrices and using any of the nine possible variations on the years when vital rates were allowed to change (Fig. 4). This agreement in terms of a long-term declining birth rate is largely driven by the increase in nonpup to pup ratios in the data, which is shown by the divergence between log pup and log nonpup counts in Fig. 2a. A widening pup-to-nonpup ratio, however, does not by itself indicate that natality is declining, since it could be due to increased juvenile survivorship leading to more pre-reproductive individuals or to a shift in adult survivorship leading to more older and non-reproductive females. The model analysis indicated that neither increased juvenile survivorship nor a shift towards older females can by itself explain the long-term increase in nonpup to pup ratios. A concomitant decline in birth rate is required.

The model with the best fit (as measured by the lowest AICc; Burnham and Anderson 2003) to the time-series data was based on the HFYS Leslie matrix with vital rate changes in 1983, 1988, 1992 and 1997. This model was separated from the second-best model by a $\Delta AIC_c$ of 3.46 (Appendix D). The fits of this model to the pup counts, nonpup counts, and juvenile fractions are shown in Fig. 5 (thick grey line). The best fit model shows a steady decline in per-capita natality to 64% of pre-decline levels and steady increase in juvenile and adult survivorship to near pre-decline levels after a severe reduction in survivorships in the early 1980s (Table 3). This indicates a shift in the vital rates driving Steller sea lion declines. In the 1980s, declines were driven by low juvenile and adult survivorship, but by the late 1990s, survivorship recovered and continued declines and lack of recovery were caused by low birth rate.

Our best estimate for the 2004 Leslie matrix for the CGOA is given by the scaling parameters in Table 3 combined with the HFYS pre-decline matrix (Table 2, Appendix C). The dominant eigenvalue of this 2004 matrix is 1.0014. This indicates that the population is currently stable; however, the increase in adult survivorship combined with a decrease in natality leads to a shift in the survivorship elasticities (Fig. 6). The change in elasticities indicates that the population is more sensitive to changes in adult survivorship and less sensitive to changes in juvenile survivorship relative to the pre-decline population.

Although the estimates of the 1976-2004 vital-rate changes were not appreciably affected by the Leslie matrix used in the model, models with different matrices did differ in how well they fit the data. Models using the HFYS Leslie matrix (the most CGOA-specific matrix) also fit the 1976-2004 abundance and juvenile-fraction time series the best. There is no a priori reason to assume that this would be the case. With 18 estimated parameters, one might assume that all the Leslie matrices we used could manage to fit the data equally well; however, this was not the case. Models using the HFYS matrix consistently had the lowest $\Delta AIC_c$ and models using the least population-specific matrix (WT) had the highest or next to highest $\Delta AIC_c$ (Appendix D). This resulted from the fact that the models using the HFYS matrix were better able to fit the juvenile-fraction data compared to models using the Y, WT or CP matrices.

Although the pattern of declining birth rate and increasing survivorship was seen across all models, the estimates fell into two types (Fig. 4). One type had a more severe (36%) decline in natality combined with an increase in juvenile survival to slightly below pre-decline levels and an increase in adult survival to above pre-decline levels. The second type had a less severe (20%) decline in natality with juvenile survivorship increasing well above pre-decline levels and adult survivorship increasing to slightly below pre-decline levels. The first type of estimate had the best fit overall—lowest $AIC_c$—but further analysis revealed that selection of this estimate type was being determined by whether the model was able to fit the juvenile-fraction data (Fig. 7). The models were not forced to fit the *J/T* data; the variance in the *J/T* metric was unknown and was an estimated parameter. Models that were capable of fitting the *J/T* data had a low estimated variance for *J/T*, and with these models, the estimate with the more severe decline in natality (Fig. 7) had the lowest $AIC_c$. If a model were unable to fit the *J/T* data, then the *J/T* variance estimate would be high, and the *J/T* data would be ignored. In that case, the lowest $AIC_c$ was provided by the second type of estimate with high juvenile survivorship. We did not have independent information on how well the models should fit the *J/T* data relative to the other data. To distinguish more confidently between these two estimate types and to test the modeling analysis as a whole, we used independent field data to cross-validate model predictions.

### *Comparison of the modeling results to independent field studies*

Although field data were not available to determine long-term trends in per-capita natality or survival, vital rate estimates were available for a handful of specific years. In addition, the 2004 high-resolution aerial survey provided independent estimates of juvenile fraction and per-capita natality to compare against the 2004 model predictions. None of the field data we discuss below appear in the data to which our model was fit or from which the pre-decline matrices were estimated.

*Mark-resight studies*—In 1987 and 1988, 751 SSL pups born on Marmot Island were individually and permanently marked to study cohort survivorship (Merrick et al. 1996, Raum-Suryan et al. 2002, Pendleton et al. 2006). The marking program was resumed in 2000. Between 2000 and 2004, a total of 659 pups were branded on two CGOA rookeries, Marmot and Sugarloaf Islands (NMFS-NMML, unpublished data). Using mark-resight data from the 1987 and 1988 cohorts, Pendleton et al. (2006) estimated juvenile survivorship for the 1988 to 1992 period using two models: a Cormack-Jolly-Seber (CJS) model and a Barker model. Each model uses a somewhat different resight dataset. Their estimate of mean juvenile survival, age 1-month to 3 years, was 0.627 (s.e. = 0.094) using the CJS model and 0.672 (s.e. = 0.0365) using the Barker model. This is 23-28% below the average age 1-month to 3-year survival of 0.874 for the pre-decline period in the HFYS matrix and corresponds closely to the best-fit model predictions for this time period (Fig. 8a, Table 3). Pendleton et al. (2006) also calculated an average adult survivorship for 1990 to 2003: 0.856 via the CJS model and 0.826 via the Barker model. This spans three time periods in our model across which adult survivorship was changing. To compare the Pendleton et al. estimates to the predicted average adult survival from the best-fit model, we simulated a 1987 and 1988 marked cohort surviving and being resighted through the

1988.5-1992.5, 1992.5-1997.5, and 1997.5-2003 time periods in Table 3. The average adult survival 1990-2003 was then estimated from the simulated resight histories using a standard CJS model. The resight probabilities in the simulation were varied between 0.4 and 0.7, corresponding roughly to the resight probabilities estimated in Pendleton et al. (2006). The 1990 to 2004 average adult survival estimated from a CJS model from the simulated cohorts varied between 0.848 and 0.869. This closely corresponds to the CJS estimate of 0.856 for average annual adult survival 1990 to 2003 of Pendleton et al. (2006) (Fig. 8c).

Using the CJS model described in Pendleton et al. (2006), the resight histories for the 2000-2004 marked cohorts were analyzed to estimate female juvenile survival from 2000 to 2005 (NMFS-NMML, unpublished data). These estimates are preliminary due to the limited number of resight years available. However, based on the data collected up to 2005, the cumulative survivorship to 36 months of the 2000-2004 cohorts is 35-40% greater than that of the 1987-1988 cohorts. This translates to yearly juvenile survivorship still below 1970s levels, but much higher than in the 1980s. Again, the model estimate of juvenile survivorship from the best fitting model closely mirrors these independent field estimates (Fig. 8a).

*Pregnancy rates and ratios of pups to adult females*—Field data on pregnancy rates are more limited than data on survivorships. Other than the 1975-1978 collections on Marmot Island, direct measurements of pregnancy rates are available only from 1985 and 1986 when samples of females were taken near Marmot Island and their pregnancy status was determined (Pitcher et al. 1998). Of the 64 females collected in April and May, when late-term pregnancies would be observed, 35 (54.7%) were pregnant. Using the known ages of the females in the sample and the age-specific pregnancy rates for the HFYS matrix (Appendix C), we calculated the expected number of pregnancies given the pre-decline pregnancy rates. The expected pregnancy rate for this sample of 64 females was 63.3% (95% CI = 41.7 - 67.2%). Thus, the actual number of pregnancies was 14% lower than expected using pre-decline rates. This closely matches the 13% model-estimated reduction in pregnancy rate for this period (Fig. 8b); however, the 95% CI is wide.

From the 2004 high resolution photographs taken of CGOA rookeries and haul-outs, 2537 animals were counted on rookeries, of which 1751 were adult females; 1949 animals were counted on haul-outs, of which 594 were adult females. Although pups were counted in the 2004 high-resolution photographs, this survey was completed in the early part of the birthing season to maximize nonpup counts and missed the pups born later that year. Consequently, we used photographs from the 2005 high resolution pup survey, which was timed to maximize pup counts. In the 2005 pup survey, a total of 1753 pups were counted on all CGOA rookeries and major haul-outs. To use these counts to estimate pups per adult females, we required estimates of sightability or the percentage of time females rest on land at rookeries or haul-outs during daylight hours (Appendix E provides a summary of sightability studies). The sightability of females nursing a pup in late June has been found to be between 48.5% and 66% (Merrick and Loughlin 1997, Brandon 2000, Milette and Trites 2003, Maniscalco et al. 2006). Less is known about the sightability of females without pups. In winter, sightability of adult females with 6-8 month old pups or yearlings has been measured at 10% to 22% (Merrick and Loughlin 1997, Trites and Porter 2002). For summer, we found no data on adult females without pups; however, studies on females in late-summer, when females are nursing 1-3 month old pups, indicate that sightability declines as pups get older. Sightability of females with 1 to 3 month old pups has been found to be between 30% and 40% (Higgins et al. 1988, Milette and Trites 2003, Maniscalco et al. 2006). The sightability of non-lactating females in June is likely to be lower than the sightability of females with 1-3 month old pups and higher than the sightability of non-lactating females in winter. However, we used estimates for these types of females as a surrogate for sightability of non-lactating females given the lack of other information.

We combined the sightability estimates and the MF counts of adult females (AF) to calculate an estimate of 1-month old pups per adult female in the CGOA as follows: (June pup count) ÷ (AF haul-out count/AF haul-out sightability + AF rookery count/ AF rookery sightability). We computed pups per adult females using all possible combinations of haul-out and rookery sightability estimates. In total, we had 5 sightability estimates for females on the haul-outs in June: we used the winter studies on non-lactating females and the summer studies for females with older pups. In late-June, Withrow (1982) found that over 90% of females on haul-outs do not give birth that year, so are either non-lactating or nursing a 12-month old pup. We also had 5 sightability estimates for females on rookeries in June: we used data on the sightability of females with young pups since the overwhelming majority of adult females on the rookeries in late-June have pups. We computed pups per adult females for all possible combinations of the five haul-out and five rookery sightability estimates to get 25 total estimates of pup to females in the CGOA. Fig. 8b shows a box plot of the estimates. Although variable, due to the variable sightability numbers, the mean estimates correspond closely with the model predictions.

*Fraction of females that are juvenile*—The third piece of independent field data was an estimate of the fraction of females that are juvenile. Using the best-fit model (Table 3), the estimated juvenile fraction in 2004 was 24%, which is 70% of the pre-decline estimate obtained using the HFYS matrix (the pre-decline estimate of the fraction of juveniles is 34%). We estimated the actual juvenile fraction in 2004 using the high resolution survey data. A total of

1386 juveniles were counted on CGOA haul-outs and rookeries. Again, to translate the high resolution numbers, we used sightability estimates. We found three studies that measured juvenile sightability in the GOA. These found 43% and 50% sightability in summer (Loughlin et al. 2003, Call et al. 2007) and 40% in winter (Trites and Porter 2002), respectively. Assuming a 50:50 sex-ratio in juveniles and trying all combinations of juvenile and adult sightabilities, the mean estimated fraction of females that are juvenile is 21% (ranging from 13% to 29% with an s.e. of 0.006), which is 62% of the pre-decline fraction (Fig. 8c). To the east of the CGOA, the eastern Gulf of Alaska (EGOA) has a high proportion of juveniles which researchers believe is due to preferential dispersal into the EGOA by juveniles from the CGOA and the western Gulf of Alaska (WGOA), as well as from Southeast Alaska. Using the high resolution survey data for the Gulf of Alaska as a whole (EGOA + CGOA + WGOA), the mean calculated juvenile fraction is 23%, which is 68% of the pre-decline fraction (Fig. 8c).

All of these field estimates for the population-level vital rates and juvenile fraction have high uncertainty. Some depend on estimates of the sightability of adult non-lactating females on haul-outs, for which there is limited information. Nonetheless, these independent field estimates are consistent with the predictions of the best fitting model—birth rate is much lower than in the late-1970s and mid-1980s, the fraction of juveniles in the population is less than it was in the late-1970s, juvenile survivorship has increased but remains slightly below pre-decline levels, and adult survival increased in the 1990s.

## DISCUSSION

Western Steller sea lions experienced a precipitous decline during the 1980s, and a variety of field observations and modeling analyses have pointed to low survivorship, particularly of juveniles, as the primary driver (Pascual and Adkison 1994, York 1994, Chumbley et al. 1997, Holmes and York 2003, Winship and Trites 2006). A variety of evidence indicates that both direct impacts (predation, illegal shooting, and incidental take in fisheries) and indirect impacts (disease, pollutants, and nutritional stress due tochanges in their prey community) combined to cause this severe depression in juvenile survivorship (National Research Council 1996, Pitcher et al. 1998, National Research Council 2003, Trites and Donnelly 2003, Fritz and Hinckley 2005). Less clear is what vital rate changes were responsible for both the continuing, though less severe, declines of the 1990s and the apparent population stabilization observed since 2000. The most obvious direct mortality impacts, shooting (legal and illegal) and incidental take in fisheries, were greatly reduced by management regulations implemented in the 1990s (Perez and Loughlin 1991, Alverson 1992, National Research Council 1996, 2003, Perez 2003). It has been suggested that another source of direct mortality, killer whale predation, increased in the late 1970s and replaced the other direct mortality factors (Springer et al. 2003, Williams et al. 2004). SSLs are an important component of the diet of mammal-eating killer whales in the Gulf of Alaska (Heise et al. 2003, Herman et al. 2005, Wade et al. 2007); however, recent analyses have found little evidence to support the hypothesis that killer whale prey-switching (from whales to pinnipeds and sea otters) drove successive declines in Steller sea lions, harbor seals and sea otters (DeMaster et al. 2006, Mizroch and Rice 2006, Wade et al. 2007).

The results from our modeling analysis concur with previous studies indicating that a severe reduction in juvenile survivorship occurred in the mid-1980s. After the mid-1980s, our analysis indicates however, that juvenile and adult survivorship steadily improved to near pre-decline levels by the late-1990s. Recent estimates of juvenile and adult survivorship from mark-resight studies corroborate our conclusion that survivorship has increased since the mid-1980s, and the estimates from these independent studies closely match our model predictions. Increases in survivorship are not consistent with the hypothesis that killer whale predation or some other type of direct mortality is currently limiting recovery of the population, at least in the CGOA.

At the same time that survivorship was recovering, our analysis indicates that birth rates were steadily declining. Decreased late-term pregnancy rates relative to 1975-1978 were first observed in the field in a sample of females taken in 1985-1986 (Pitcher et al. 1998). In this sample, lactating females had significantly lower late-term pregnancy rates than lactating females in 1975-1978; no change in late-term pregnancy rates of non-lactating females was observed. In our analysis, we estimated that birth rates first declined in the early 1980s, to the levels observed by Pitcher et al., and then continued to steadily erode over the next 20 years. Our estimate is that the current average per-female birth rate is 36% lower than the 1975-1978 level. On the surface, this conclusion appears to contradict observations of good pup health and a high birth rate by females on the rookeries. However, rookeries are sites where females give birth and rookery studies focus on females that are giving birth in a particular year. In contrast, our analysis estimates the birth rate across all females, those that return to the rookeries and those that do not. This combination of good pup health but declining birth rate implies that currently, a substantially larger fraction of females are forgoing reproduction in some years than in the past, and thus not returning to the rookeries to pup.

We fit models only to data from the CGOA because pre-decline age-structure and fecundity data are available only for this area. These data were needed to estimate the pre-decline Leslie matrix used by our models. However, patterns in the ratios of nonpups to pups and the juvenile fraction can help in determining whether the trends in vital rates we observed in the CGOA may have occurred in other areas as well. We analyzed the aerial survey photographs for the western Gulf of Alaska and the eastern Aleutian Islands in the same way as for the CGOA to determine the changes in juvenile fractions for these regions (Fig. 2d,f). These data provided no evidence that the juvenile fraction of the populations in these areas had increased. At the same time, the ratios of nonpups to pups in both of these regions have increased since the early 1990s as evidenced by the widening gap between nonpup and pup numbers in the NMFS aerial survey data (Fig. 2c,e). Thus, to the west of the CGOA, we see the same pattern as in the CGOA: increasing ratios of nonpups to pups with no evidence of increased juvenile fraction. This suggests that low birth rate is a regional problem for SSLs in the Gulf of Alaska and eastern Aleutian Islands.

There are a number of biological mechanisms that could lead to lower birth rate: lower impregnation rates, higher abortion rates, lower post-partum pup survival, increased average number of years between successful breeding, older average age of first reproduction, and a shift in the age structure toward post-reproductive females, to name several. The model does not support the last of these since it explicitly models the age structure of females; however, it should be noted that we did not allow the possibility that prime-age breeding females have lower survival than older senescent females. Distinguishing which other factors might be causing decreased natality requires field data on reproduction and neonate mortality. Some information is available on neonate mortality from the percentage of dead pups observed during the NMFS pup counts (NMFS, unpublished data). These data indicate that the proportion of dead pups has not increased since the late-1970s, but instead has declined. In addition, pup birth weights and growth rates, measured in the 1990s, are not lower in the CGOA compared to southeast Alaska where no population declines have occurred nor is there evidence that pups in the CGOA are nutritionally stressed (reviewed in Trites and Donnelly 2003). There is also no evidence of mate-limitation because the adult sex-ratio observed in the 2004 high resolution survey is similar to that calculated for the late 1970s. The remaining biological factors are those directly linked to female reproductive parameters.

Three main stressors are known to impair female reproduction in pinnipeds: nutritional stress, contaminants and disease. Nutritional stress from fisheries-induced or natural environmental changes in abundance, composition, distribution, or quality of fish prey has received significant research attention as a hypothesis for the Steller sea lion declines (National Research Council 2003, Trites and Donnelly 2003, Fritz and Brown 2005, Fritz and Hinckley 2005). Nutritional stress negatively affects pregnancy in pinnipeds in a variety of ways: decreased implantation rates during early pregnancy, increased late-term abortion rates, and increased age of sexual maturity (Bengtson and Siniff 1981, Bowen et al. 1981, Huber et al. 1991, Lunn and Boyd 1993, Lunn et al. 1994, Boyd 2000, Pistorius et al. 2001, Trites and Donnelly 2003). Recent studies of body condition, behavior and pup condition indicate that Steller sea lions in the Gulf of Alaska are not currently under acute nutritional limitation (Trites and Donnelly 2003, Fritz and Hinckley 2005). However, these studies were conducted largely on juvenile sea lions and focused on acute limitation (starvation). It is not known if adult females, or more specifically lactating females, are experiencing food limitation causing a trade-off between maintenance and reproduction.

While it is known that food limitation reduces reproduction, it is generally assumed that reproductive parameters do not change in isolation. The classic paradigm for long-lived mammals is that in response to food limitation, demographic rates have a specific order of sensitivity: juvenile survival is most severely impacted, followed by age of maturity, adult female reproduction and lastly adult survival (Fowler 1981, Eberhardt 2002). Numerous studies of pinnipeds undergoing severe nutritional stress during El Niño events have shown this pattern (Trillmich and Ono 1991). Our estimates of the demographic changes in SSLs in the early 1980s during the initial population collapse show this pattern also, but our finding that survival increased while reproduction output declined after the early 1980s does not. One explanation is that SSLs are experiencing moderate or seasonal food limitation that is not so severe as to limit juvenile survival but severe enough to reduce the ability of females to meet the energetic needs of lactation concomitant with gestation. Because females nursing pups are limited in the distances they can travel and foraging time at sea, they may be more affected by seasonal prey changes than juveniles or adults females that are not nursing a pup. Another explanation is that some factor other than food limitation is causing low natality.

The effects of contaminants and disease or parasitism on Steller sea lions have been investigated to differing degrees, but both could cause reduced birth rates with near normal survivorship levels. The bioaccumulation of contaminants, particularly poly-chlorinated biphenyls (PCBs) and other organo-halogens, is a serious conservation concern for apex predators in Arctic and sub-Arctic regions due to atmospheric cycling that causes this region to be a worldwide sink for airborne pollutants (Norstrom and Muir 1994, Borrell and Reijnders 1999, Aguilar et al. 2002). Organo-halogens act as endocrine disrupters and are known to impair reproduction in pinnipeds (Reijnders 1984, 1986, Aguilar et al. 2002, Barron et al. 2003). Data on PCB levels in Steller sea lions are limited. The data available indicate that PCBs levels are currently low, but that in the early-1990s, PCB levels in juveniles in the Gulf of Alaska were very high and at levels that could compromise later reproduction (Barron et al. 2003). During this same late-1980s and early 1990s period, PCB levels in sea otters (family Mustelidae) in the

Eastern Aleutians were found to be 38 times higher than in southeast Alaska (Bacon et al. 1999). Sea lions born in the late-1980s and early 1990s would have been the main reproductive cohorts in the mid- to late-1990s. Contaminant screening has not been comprehensive enough, however, to be confident of contaminant levels in reproductive females or to determine whether regional differences in rates of population decline are related to differences in contaminant loads. The limited disease and parasite surveys available have shown that western Steller sea lions have high seropositivity for a number of organisms, particularly *Chlamydophila psittaci* and caliciviruses, that are associated with reproductive failure in other mammals (Burek et al. 2005). In samples collected in the 1990s, high seropositivity was unrelated to regional population trend, and it is unclear whether exposure to these disease organisms has changed relative to pre-decline periods and whether exposure affects Steller sea lion reproduction (Burek et al. 2005).

The past 5 years have seen an encouraging abatement of the population declines seen in the 1980s and 1990s across the Gulf of Alaska and Aleutian Islands. However, ratios of nonpups to pups remain well above the pre-decline levels of the 1970s, and our results point to steadily declining birth rate in a major part of the range as the cause. Our best-fit Leslie matrix for the 1997-2004 period has a dominant eigenvalue of $\lambda = 1.0014$, indicating a stable population. However, the current population vital rates have shifted towards higher adult survivorship and lower birth rate, further decreasing the population's ability to recover quickly from perturbations.

Overall our results have important conclusions for the conservation and recovery of the endangered western Steller sea lion. More research is needed on their reproductive ecology, including sampling of females without pups, which are less likely to be on rookeries in the summer. Basic survey information is lacking on risk factors that are known to affect reproduction, particularly winter nutritional limitation which the mid-1980s pregnancy data suggest was affecting birth rates at that time (Pitcher et al. 1998) and contaminant exposure which was high in one survey (Barron et al. 2003). While per-capita birth rates have declined, survivorship has improved substantially, indicating that direct or indirect mortality is not limiting recovery. Instead, with per-capita natality currently much lower than prior to the decline, it is high survivorship that is preventing further declines. Consequently, protections to limit the mortality of breeding adults are now more critical than ever. At the same time, with survivorship already high and perhaps approaching the maximum that is possible, our results indicate that the long-term recovery of the western Steller sea lion hinges on increasing per-capita birth rates.

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## APPENDIX A

The raw data used in the analyses and figures: the central Gulf of Alaska, the western Gulf of Alaska and the eastern Aleutian Islands are available in ESA's Electronic Data Archinve: *Ecological Archives* Exxx-xxx-A1.

## APPENDIX B

A figure of the sensitivity of the *J/T* metric to the haul-out sample is available in ESA's Electronic Data Archinve: *Ecological Archives* Exxx-xxx-A2.

## APPENDIX C

Background and parameters for the Leslie matrices are available in ESA's Electronic Data Archinve: *Ecological Archives* Exxx-xxx-A3.

## APPENDIX D

The parameter estimates from the model fits with their $\mathrm{AIC}_{cc}$'s matrices are available in ESA's Electronic Data Archinve: *Ecological Archives* Exxx-xxx-A4.

## APPENDIX E

A summary of Steller sea lion sightability studies is available in ESA's Electronic Data Archinve: *Ecological Archives* Exxx-xxx-A5.

Table 1. The 32 x 32 age-structured life-history matrix for Steller sea lions. This is a pulse-birth Leslie matrix model for the female only segment of the population. $f_i$ is fraction of age $i$ females with late-term pregnancies times 0.5 to get female fetuses only. $s_n$ is neonate survivorship from late-term fetus to 1-month of age when the pup survey occurs. For all matrices, $s_n$ was set to 0.949 based on the average of the fraction of dead neonate pups observed during the 1978 and 1979 pup counts. $s_i$ is survivorship from age $i$ to age $i$+1. Line 1 is $s_i f_{i+1}$ so that when the matrix multiplication is done, $N_{0,t+1} = \Sigma N_{i,t} s_i f_{i+1}$ which is sum of the number of age $i$ individuals that survive to age $i$+1 and give birth to a pup at age $i$+1. When the Leslie matrix is written this way, $N_0$ is always the pup count in the same year as the nonpup count. The parameters values for the matrix are given in Appendix C.

| | Age 0 (pup) | Age 1 yr | Age 2 yr | Age 3 yr | … | Age 31 yr |
|---|---|---|---|---|---|---|
| birth rate | $s_0 f_1 s_n$ | $s_1 f_2 s_n$ | $s_2 f_3 s_n$ | $s_3 f_4 s_n$ | … | $s_{31} f_{32} s_n$ |
| surv. age 0* to 1 | $s_0$ | 0 | 0 | 0 | … | 0 |
| surv. age 1 to 2 | 0 | $s_1$ | 0 | 0 | … | 0 |
| surv. age 2 to 3 | 0 | 0 | $s_2$ | 0 | … | 0 |
| surv. age 3 to 4 | 0 | 0 | 0 | $s_3$ | … | 0 |
| … | … | … | … | … | … | … |
| surv. age 30 to 31 | 0 | 0 | 0 | 0 | … | 0 |

* Age 0 starts at 1-month of age. Ages are always age in late June when breeding surveys are done.

Table 2**.** The 32 x 32 age-structured life-history matrix with scaling factors added. The parameters, $f_i$ ,$s_n$, and $s_i$ are defined as in Table 1. The parameters $p_{j,k}$, $p_{a,k}$, and $p_{f,k}$ are the scaling terms for juvenile survivorship, adult survivorship and birth rate, respectively, at time period $k$. Time in the model is June to June since births are predominately in June.

| | Age 0 (pup) | Age 1 | Age 2 | Age 3 | … | Age 30 | Age 31 |
|---|---|---|---|---|---|---|---|
| birth rate | $s_0\,p_{j,k}\,f_1\,s_n\,p_{f,k}$ | $s_1\,p_{j,k}\,f_2\,s_n\,p_{f,k}$ | $s_2\,p_{j,k}\,f_3\,s_n\,p_{f,k}$ | $s_3\,p_{a,k}\,f_4\,s_n\,p_{f,k}$ | … | $s_{30}\,p_{a,k}\,f_{31}\,s_n\,p_{f,k}$ | $s_{31}\,p_{a,k}\,f_{32}\,s_n\,p_{f,k}$ |
| surv. age 0 to 1 | $s_0\,p_{j,k}$ | 0 | 0 | 0 | … | 0 | 0 |
| surv. age 1 to 2 | 0 | $s_1\,p_{j,k}$ | 0 | 0 | … | 0 | 0 |
| surv. age 2 to 3 | 0 | 0 | $s_2\,p_{j,k}$ | 0 | … | 0 | 0 |
| surv. age 3 to 4 | 0 | 0 | 0 | $s_3\,p_{a,k}$ | … | 0 | 0 |
| … | … | … | … | … | … | … | … |
| surv. age 29 to 30 | 0 | 0 | 0 | 0 | … | 0 | 0 |
| surv. age 30 to 31 | 0 | 0 | 0 | 0 | … | $s_{30}\,p_{a,k}$ | 0 |

Table 3. Vital rates relative to pre-decline levels estimated using the best-fit model. The best fit model uses the HFYS matrix with the time periods in the table. Pre-decline levels are indicated with 1.0, and estimates are shown relative to that value (e.g., juvenile survivorship in 1983-1987 was 42% of its pre-decline value). The 95% confidence intervals, in parentheses, were determined by one-dimensional likelihood profiling allowing all other parameters in the model to be free. The α-levels for the CIs are based on two-tailed $\chi^2$ with one-degree of freedom, which is based on the asymptotic likelihood-ratio distribution. The time scale in the model is June-June since animals are born in June; thus, the 0.5 on the years.

| | Juvenile survivorship ML (95% CIs) | Adult survivorship ML (95% CIs) | Birth rate (pups/♀) ML (95% CIs) |
|---|---|---|---|
| 1976-1983.5 | 1.0 | 1.0 | 1.0 |
| 1983.5-1988.5 | 0.42 (0.38, 0.50) | 0.90 (0.88, 0.92) | 0.87 (0.82, 0.91) |
| 1988.5-1992.5 | 0.73 (0.68, 0.80) | 0.93 (0.91, 0.95) | 0.76 (0.72, 0.80) |
| 1992.5-1997.5 | 0.57 (0.53, 0.61) | 1.00 (0.98, 1.02) | 0.70 (0.67, 0.73) |
| 1997.5-2004 | 0.94 (0.89, 1.04) | 1.07 (1.05, 1.08) | 0.64 (0.61, 0.67) |

**Figure 1**. Principal breeding locations (rookeries) in Alaska, USA, of the western (west of 144°W) and eastern Steller sea lion. Rookeries in the eastern, central and western Gulf of Alaska (GOA), and the eastern Aleutian Islands (AI) are labeled separately.

**Figure 2**. Trends in pup counts, nonpup counts, and the juvenile fraction metric for the central Gulf of Alaska (CGOA; panels a and b), western Gulf of Alaska (WGOA; panels c and d) and eastern Aleutian Islands (EAI; panels e and f). The pup and nonpup plots (a, c, and e) are on a log-scale; thus an increasing difference between the pup and nonpup lines indicates an increasing nonpup to pup ratio. The nonpup counts are animals older than 1 year on rookeries and haul-outs used to monitor population trend by the NMFS since 1984. The pup and nonpup counts for each region are indices and represent different fractions of the total pup and nonpups in each region. The juvenile fraction plots (b, d, and e) show the fraction of haul-out animals that are less than 50% the length of a mature male. Raw data and sample sizes for the juvenile fraction measurements are given in Appendix A.

**Figure 3**. Age-specific female survivorship and female-pup birth rate schedules for the four different Leslie matrix models. The matrices are described in Appendix B.

**Figure 4**. Maximum-likelihood estimates of the vital rates across all model variants with $\Delta AIC_c$ values less than 10. Models were fit to the pup, nonpup, and juvenile-fraction metric. The y-axes show the survivorship and birth rates relative to the 1975-1978 pre-decline estimated rates in the pre-decline matrix.

**Figure 5**. Model fits to the central Gulf of Alaska data. The grey lines show the estimates from the best-fitting temporally varying Leslie matrix model. In this model, juvenile survivorship, adult survivorship, and birth rates were allowed to change in 1983, 1988, 1992, and 1997. The model was fit to a) the index of juvenile fraction from all photographed haul-outs with a

large male (with 95% CIs shown), b) adult and juvenile (nonpup) counts on rookery and haul-out trend sites, and c) total pup counts from the five major central Gulf of Alaska rookeries. The thin black lines show the fits using a model without a 1992 change in vital rates.

**Figure 6**. Elasticities of the age-specific survivorships and fecundities. The thin lines show the survivorship elasticities and the thick lines show the natality elasticities. The total elasticity to juvenile survivorship (the sum of elasticities age 1-3) is 0.27 for the late-1970s and 0.25 for 2004. The total elasticity to adult survivorship (the sum of elasticities age 4-32) is 0.63 for the late-1970s and 0.67 for 2004. The total elasticity to natality (sum across all ages) is 0.09 for the late-1970s and 0.08 for 2004.

**Figure 7**. Estimated 1997-2004 survivorship and birth rate estimates using the HFYS (+) matrix versus the simplest Leslie matrix, WT2006 (o). Model using each of the 9 possible time periods are plotted against each model's estimated error variance for the *J/T* data.

**Figure 8**. Comparison of best-fit model predictions to independent field data. The solid lines in all panels show the model predictions from the best-fitting temporally varying Leslie matrix model: this uses the HFYS matrix with vital rate changes in 1983, 1988, 1992, and 1997. The vital rate scaling parameters for the best-fit model are given in Table 3. The model predictions are compared to observations from the four independent field studies discussed in the text: a mark-resight study of the 1987 and 1988 cohorts using either the Cormack-Jolly-Seber or Barker models to analyze the data (denoted 'MR 87/88 cohorts(CJS)' and 'MR 87/88 cohorts(B)', respectively, in the legends), a mark-resight study of the 2000 to 2004 cohorts using the Cormack-Jolly-Seber model to analyze the data (referred to as 'MR 00/04 cohorts(CJS)' in the legends), pregnancy data from females sampled in the late 1980s

(denoted ‘direct pregnancy survey’ in the legends), and a high-resolution photographic survey in 2004 (referred to as ‘HR photo survey’ in the legends). The box plots in panels b and c show the inner first quartiles (enclosed in the boxes) and the 95% range of the estimates (whiskers) using all combinations of sightability estimates with the counts from the high-resolution photographic survey (see text). The error bars on the point estimates in panels a, b, and d are the 95% confidence intervals from the analyses of the mark-resight data.

Figure 1 (sized so that fonts should be min 6pt when reduced to 3 inch wide)

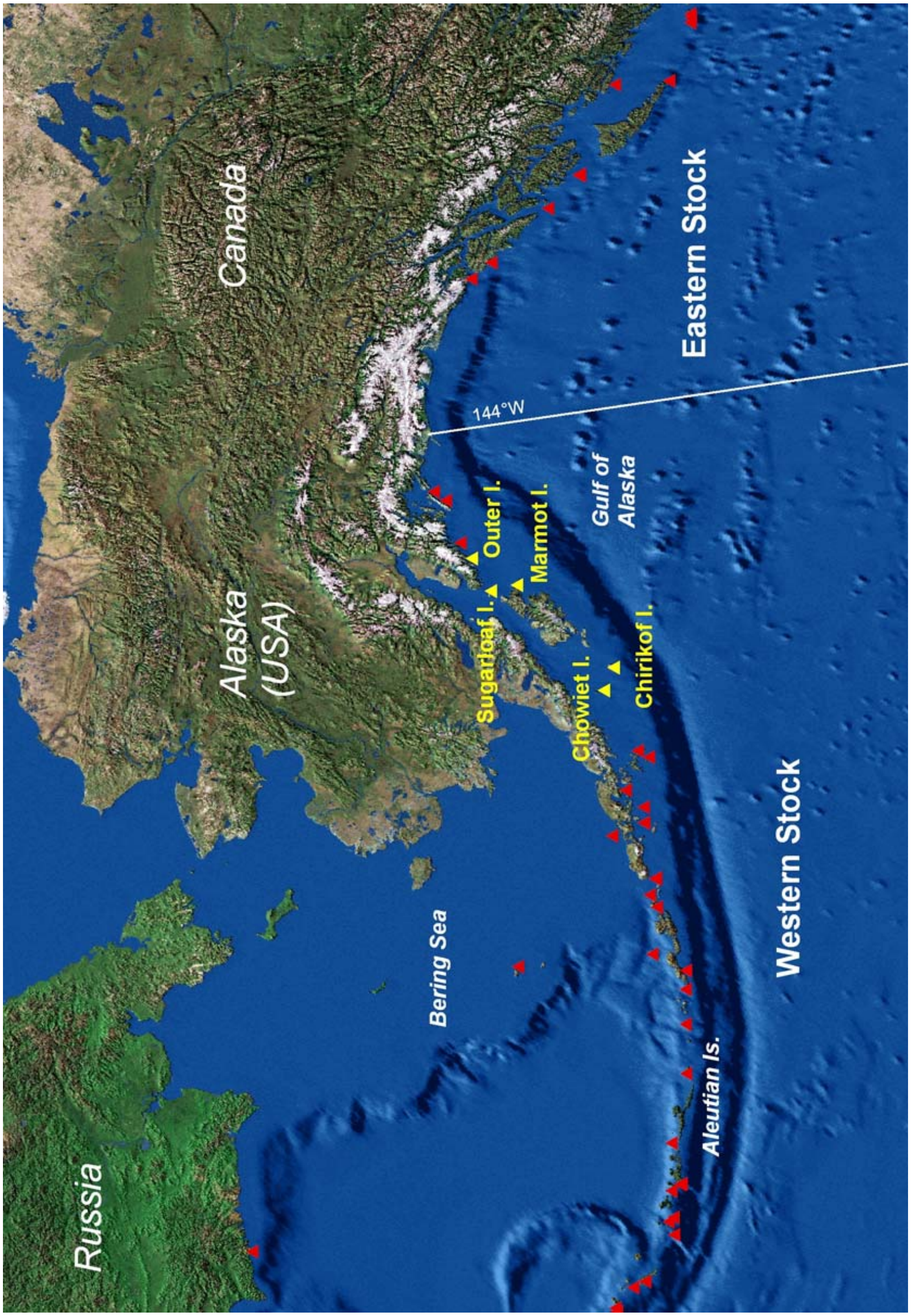
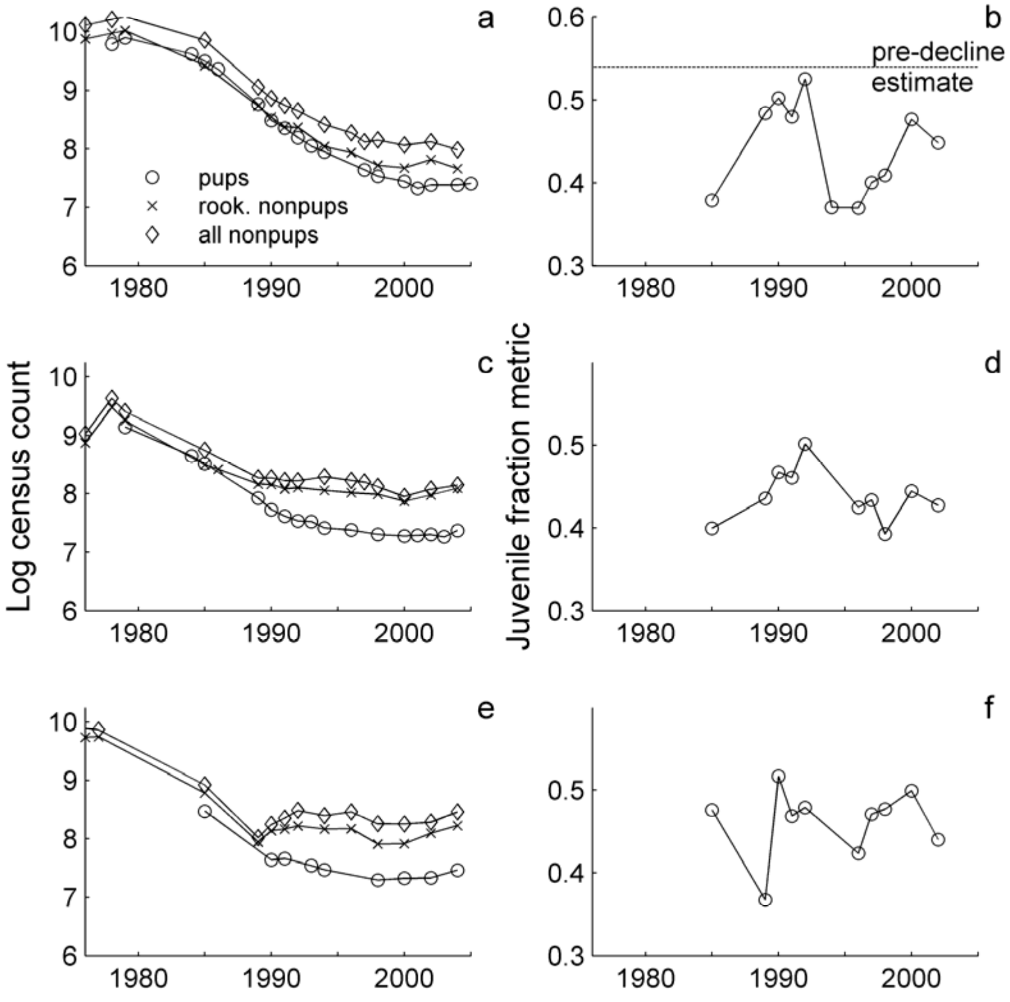


Figure 2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0.6

Figure 3

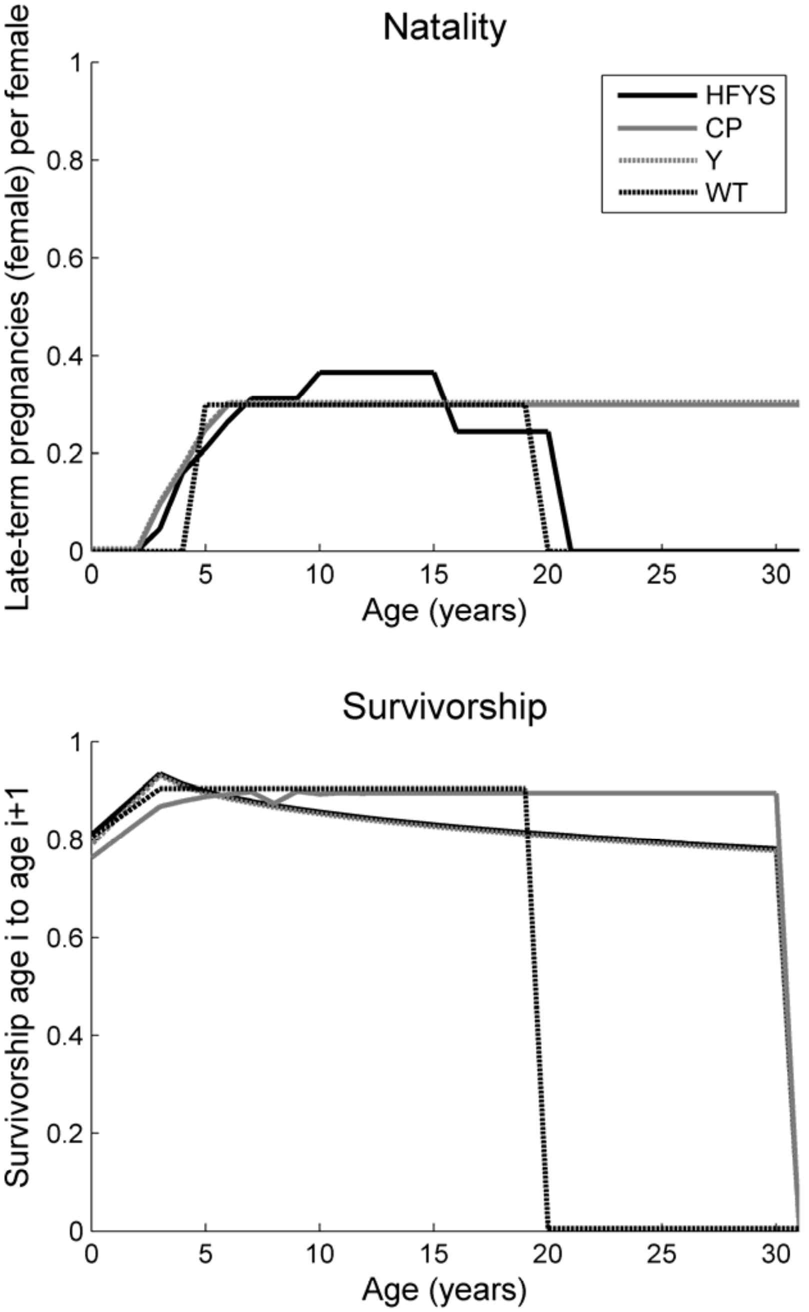

Natality
Late-term pregnancies (female) per female
Age (years)
0
0.2
0.4
0.6
0.8
1
0
5
10
15
20
25
30
HFYS
CP
Y
WT
Survivorship
Survivorship age i to age i+1
Age (years)
0
0.2
0.4
0.6
0.8
1
0
5
10
15
20
25
30

Figure 4

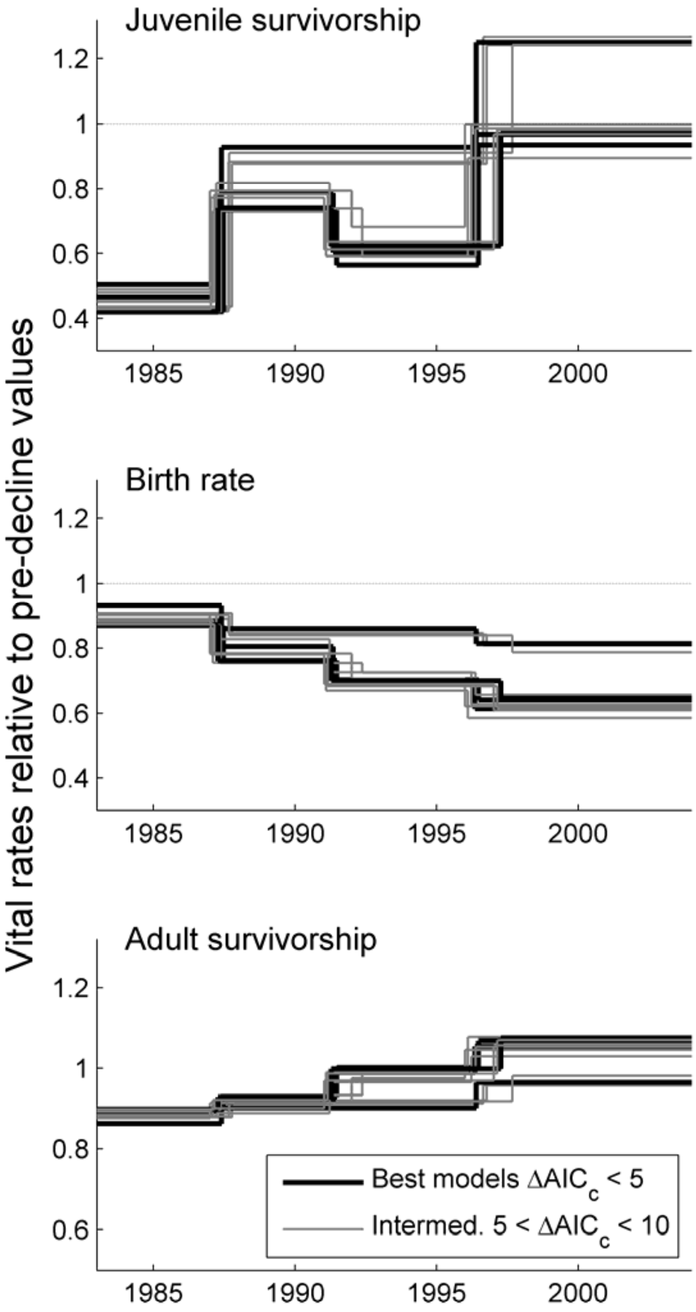

Vital rates relative to pre-decline values
Juvenile survivorship
1.2
1
0.8
0.6
0.4
1985
1990
1995
2000
Birth rate
1.2
1
0.8
0.6
0.4
1985
1990
1995
2000
Adult survivorship
1.2
1
0.8
0.6
1985
1990
1995
2000
Best models ΔAIC$_c$ < 5
Intermed. 5 < ΔAIC$_c$ < 10

Figure 5

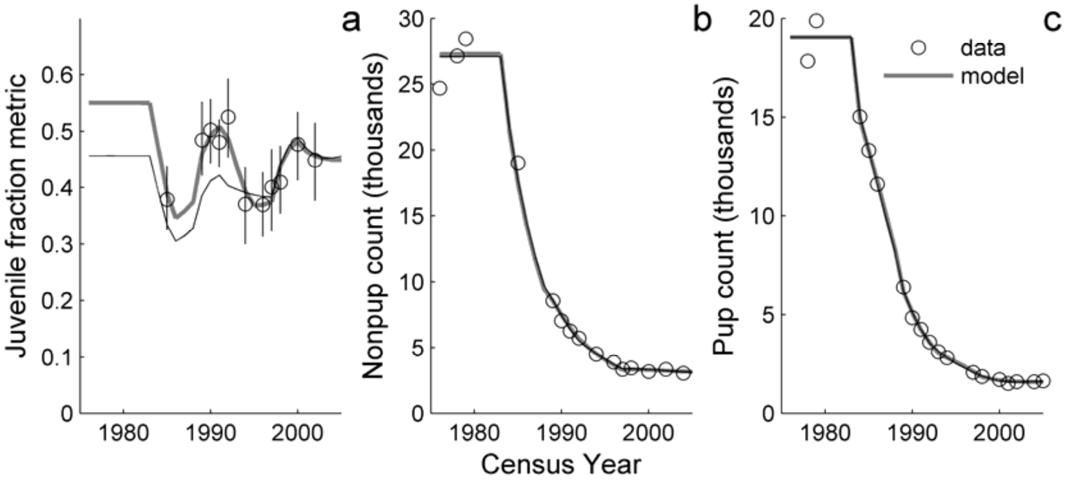

a
b
c
Juvenile fraction metric
0
0.1
0.2
0.3
0.4
0.5
0.6
Nonpup count (thousands)
0
5
10
15
20
25
30
Pup count (thousands)
0
5
10
15
20
1980
1990
2000
Census Year
data
model

Figure 6

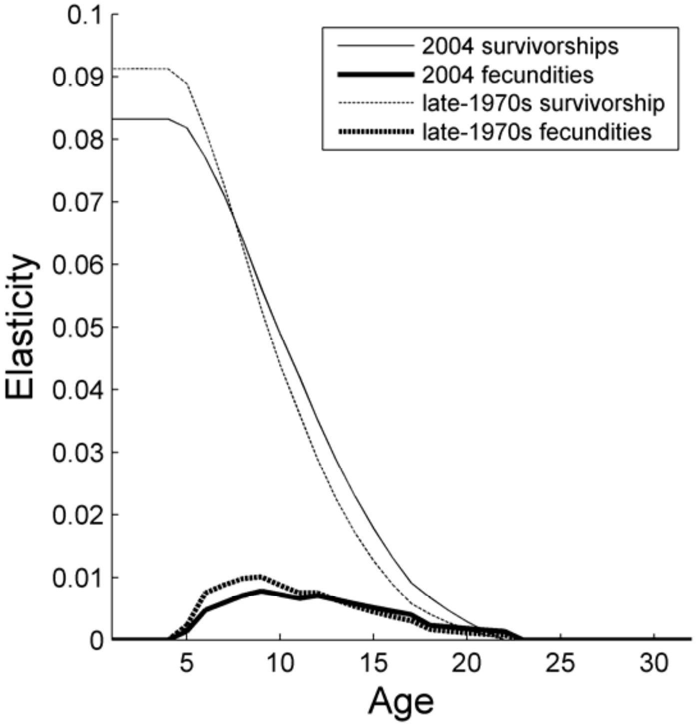

0.1
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
Elasticity
5
10
15
20
25
30
Age
2004 survivorships
2004 fecundities
late-1970s survivorship
late-1970s fecundities

Figure 7

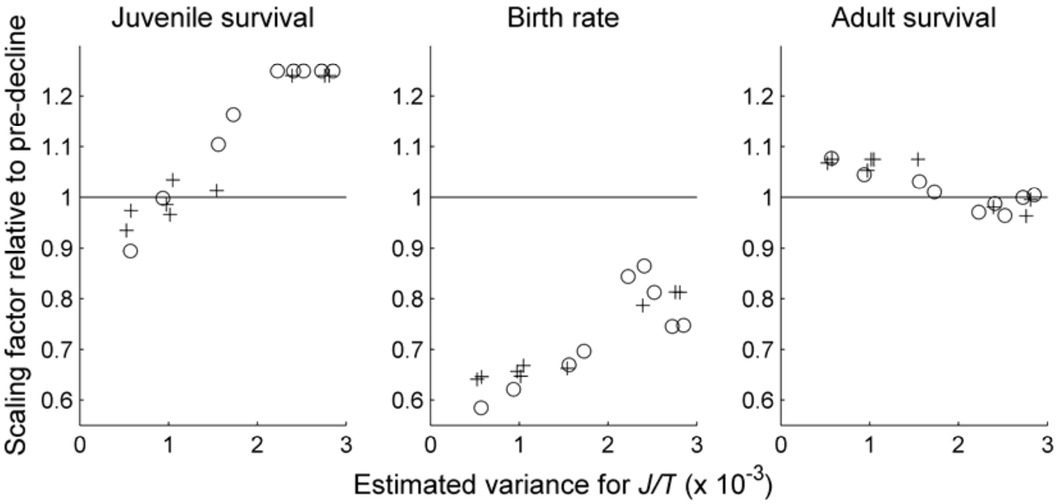
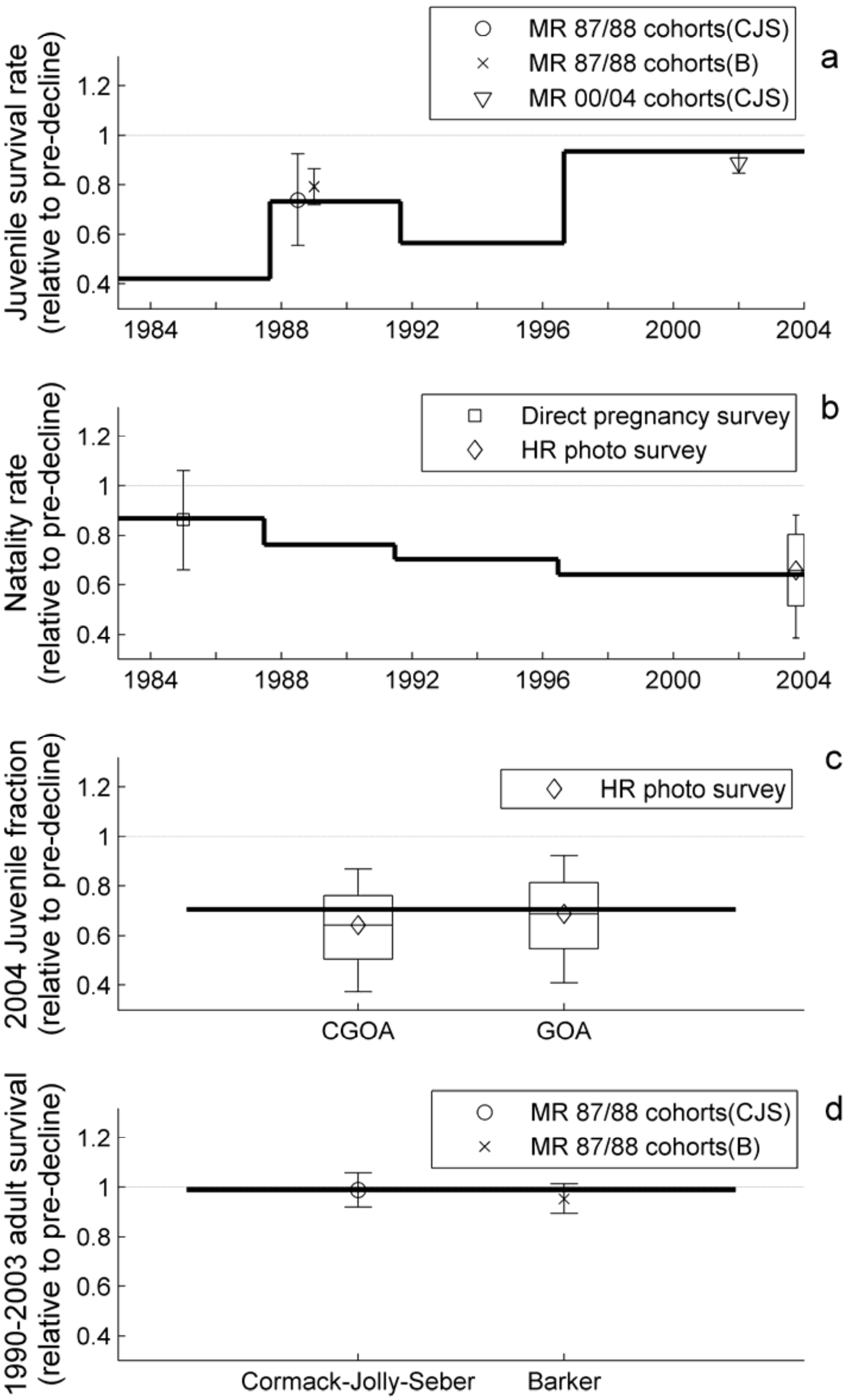

Juvenile survival
Birth rate
Adult survival
Scaling factor relative to pre-decline
1.2
1.1
1
0.9
0.8
0.7
0.6
0
1
2
3
Estimated variance for J/T (x 10-3)

Figure 8


a
Juvenile survival rate (relative to pre-decline)
MR 87/88 cohorts(CJS)
MR 87/88 cohorts(B)
MR 00/04 cohorts(CJS)
1.2
1
0.8
0.6
0.4
1984
1988
1992
1996
2000
2004
b
Natality rate (relative to pre-decline)
Direct pregnancy survey
HR photo survey
1.2
1
0.8
0.6
0.4
1984
1988
1992
1996
2000
2004
c
2004 Juvenile fraction (relative to pre-decline)
HR photo survey
1.2
1
0.8
0.6
0.4
CGOA
GOA
d
1990-2003 adult survival (relative to pre-decline)
MR 87/88 cohorts(CJS)
MR 87/88 cohorts(B)
1.2
1
0.8
0.6
0.4
Cormack-Jolly-Seber
Barker

1