Steady declines in Steller sea lion birth rate in the Gulf of Alaska suggest new conservation and research priorities

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Abstract

From the mid-1970s through 2000, the western stock of Steller sea lion (*Eumetopias jubatus*) inhabiting Alaskan (US) waters from Prince William Sound west through the Aleutian Islands declined by over 80%. Other apex predators in the North Pacific Ocean experienced large declines during this same period. In 1990, Steller sea lions were listed as threatened range-wide under the U.S. Endangered Species Act, and in 1997, the western stock was uplisted to endangered. Over $120 million in federal funding was allocated between 2001 and 2004 for research on factors hypothesized to impact the population, but their complexity, indirectness and cumulative impact have made it difficult to associate abundance changes to specific factors. In this study, we used age-structured population models to analyze late 1970s to 2004 abundance and juvenile fraction data for Steller sea lions in the central Gulf of Alaska (CGOA) and estimate the historical changes in survival and birth rate. We compared the results using four different Leslie matrix models based on age-structure and pregnancy data collected from 1975 to 1978. We found strong agreement among models for a steady 30-year decline in birth rate, while at the same time, survivorship increased to pre-decline levels after a severe drop in the early 1980s. We also found a high level of consistency between independent field data and model results. These results suggest that (1) direct sources of mortality are currently low and are not the primary threats to recovery for the western Steller sea lion population, and (2) new research efforts should focus on the reproductive ecology, fitness and energy budgets of adult female Steller sea lions. The study also presents both a caution and a comfort for modelers. Approximate Leslie matrix models based on vital rate data from multiple studies on different populations and different years are commonly used when modeling population dynamics of species of conservation concern, often with limited data. While a population-specific Leslie matrix fit the time series data better than a generic matrix in this analysis, the vital rate estimates were similar. However, the estimates were sensitive to whether the model fitting was constrained with age-structure data in addition to abundance data – and it was not apparent simply from examination of the likelihood surfaces that the vital rates were prone to mis-estimation. This necessitates a careful exploration of the performance of proposed model-fitting analyses to avoid the mistake of assuming that a good fit equates to good performance.

Keywords: Leslie matrix, population modeling, Bering sea ecosystem, Gulf of Alaska, apex predators, AIC

INTRODUCTION

Declines in apex predators in the North Pacific Ocean have been observed across a variety of taxa, including sea otters, pinnipeds (seals and sea lions) and seabirds 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 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 impacted areas stretch from the western Aleutian Islands to Prince William Sound in the central Gulf of Alaska (Figure 1) and the percent declines have been severe. By 2005, these three species had declined to 10-50% of their late-1970s levels in many regions (Angliss and Outlaw 2005). The destabilizing effects of removing apex predators from marine ecosystems has recently become a topic of much concern among marine ecologists, as the extent of depletion of top trophic levels across many different marine ecosystems has become apparent (Merrick 1997, Terborgh et al. 1999, Trites et al. 1999, Jackson et al. 2001, Duffy 2003, Springer et al. 2003, DeMaster et al. 2006). In most marine communities, the cause of the reduction of apex predators is clear -- fishing (Pauly et al. 1998, Jackson et al. 2001, Myers and Worm. 2003). However, the causes of pinniped declines since the early 1980s in the Gulf of Alaska, North Pacific, and Bering Sea, remain unclear. For Steller sea lions and northern fur seals, direct human-related mortality, either due to fishing bycatch, intentional mortality, or tribal subsistence harvest, is well below (less or much less than 10%) of the estimated sustainable levels (Angliss and Outlaw 2005) and does not seem to be driving declines observed since 1990 (Merrick 1997, Loughlin and York 2000, Doroff et al. 2003, National Research Council 2003, DeMaster et al. 2006). For harbor seals, harvest levels are substantially higher albeit still below estimated sustainable levels. In this study, we focus exclusively on understanding the demographic factors driving the decline in western Steller sea lions. The reasons for population declines in other North Pacific pinnipeds may be both similar and idiosyncratic – while they have similar diets throughout much of the year, they also have different life history strategies, seasonal distributions across the North Pacific Ocean, and suffer different predation and mortality rates. Regardless of whether there is a unifying driver across multiple species, Steller sea lion declines are not occurring in isolation and analyses of the causes their declines should be viewed in the context of these long-term and large-scale changes in North Pacific pinnipeds and other apex predators.

The Steller sea lion is the largest eared seal (Otariidae), with adult males weighing up to 2,400 pounds. This fish- and squid-eating predator 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 (Figure 1). In the early 1970s, numbers of Steller sea lions began declining in the eastern Aleutian Islands in the center of its range (Braham et al. 1980), and by the early 1980s, the declines had spread east to the Gulf of Alaska and west to the central Aleutian Islands (Merrick et al. 1987). In 1990, the Steller sea lion was listed as threatened under the U.S. Endangered Species Act across its range. Based on differences in mitochondrial DNA and population trends (Bickham et al. 1996, Loughlin 1997), Steller sea lions were divided into two stocks, the western stock distributed west of 144° W longitude (just east of Prince William Sound, Alaska; Figure 1) and the eastern stock distributed to the east of 144° W. In the mid-1980s, the western Steller sea lion stock began a steep decline, ultimately to approximately 20% of its 1970s population size; in 1997, the western stock was uplisted to endangered. During this same period, numbers in the eastern stock of Steller sea lions increased at approximately 3% per year (Pitcher et al. In press). After 30 years of decline, index counts of the western stock of Steller sea lions in the Gulf of Alaska and Aleutian Islands increased for the first time between the 2000 and 2004 censuses (Fritz and Stinchcomb 2005). The recent increases have not occurred range-wide, however. Numbers rose in parts of both the Aleutian Islands and western and eastern Gulf of Alaska (Figure 2) while numbers continued to decline, albeit slower, in the central Gulf of Alaska. Although the increases are encouraging, western Steller sea lions remain at a small fraction of their 1970s numbers.

Given its distribution across the Gulf of Alaska and eastern Bering Sea where roughly half of the U.S. commercial fishing output is produced, the western stock's status as an endangered species has presented significant challenges to managers of the U.S. groundfish fishery (Fritz et al. 1995, Ferrero and Fritz 2002, McBeath 2004, Hogarth 2005). In 1998, the National Marine Fisheries Service concluded in a biological opinion on the Alaskan walleye pollock fishery that the fishery was likely to jeopardize the continued existence of the western Steller sea lion population, and this led to the implementation of a series of fishery management measures to protect Steller sea lion foraging areas. These measures were successfully challenged in court as insufficient primarily because of the considerable uncertainty about the cause(s) of the population decline, the contribution of commercial fishing to the decline, and the efficacy of the new management measures (McBeath 2004). In response, the U.S. Congress approved an almost 9-fold increase in yearly research funding between 2000 and 2001 on the causes of the Steller sea lion decline. The research budget allocated from 2001 to 2004 was over $120 million (Ferrero and Fritz 2002, McBeath 2004), representing the largest research budget for a U.S. endangered mammal.

The main hypothesized drivers for Steller sea lion population changes in western Alaska are food limitation due to changes in the prey community (Trites et al. 1999, Benson and Trites 2002, Trites and Donnelly 2003), killer whale predation (Springer et al. 2003), disease (Burek et al. 2003), and direct or indirect (e.g., prey or interference competition) effects of fishing (Loughlin and Merrick 1988, Perez and Loughlin 1991, Ferrero and Fritz 1994, Pascual and Adkison 1994, Hennen 2006). But confidently attributing changes in Steller sea lion abundance or population trends to specific factors has been difficult given the complexity, indirectness and uncertainty concerning how these factors, except direct mortality, impact Steller sea lion population dynamics (Ferrero and Fritz 2002, National Research Council 2003). In this study, rather than searching for which external factor drove the population changes, we looked for the internal drivers -- the historical changes in age-specific survivorship and birth rate that best explain the 30-year census data. Previous studies (cited above) have analyzed the impact of hypothesized external drivers by looking at correlations between rates of decline or increase and some index for the external driver. However, most external factors do not affect Steller sea lion abundance directly, but rather indirectly by changing vital rates. Over the course of the population decline, age-specific survivorship and birth rates may not have changed in the same direction, and external factors may not have affected vital rates equally. Thus external factors may be having strong effects on vital rates with conflicting affects on abundance.

In this study, we used demographic models to study the vital rate changes in the Steller sea lion population in the central Gulf of Alaska (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). Population sampling and research conducted from 1975 to 1978 on Marmot Island, one of the largest pre-decline Steller sea lion breeding and birthing sites (rookeries), provided data on population age structure and age-specific pregnancy rates necessary to build a demographic model of the pre-decline population in the CGOA (Calkins and Pitcher 1982). The population model was fit to census data from region- and state-wide surveys by the National Marine Fisheries Service conducted since 1976 and to an estimate of the fraction of the population that was juvenile (1-3 years old), which we obtained from measurements of animals on land in aerial photographs taken between 1985 and 2004.

Other studies (Pascual and Adkison 1994, York 1994, Holmes and York 2003, Winship and Trites 2006) have fit age-structured population models to Steller sea lion abundance data to analyze vital rate changes. All these studies used a single life-history model, a specific Leslie matrix. Winship and Trites (2006) used a generic Steller sea lion Leslie matrix with one juvenile and adult survivorship and fecundity rate and applied it to Steller sea lion rookeries across the Gulf of Alaska and Aleutian Islands. Pascual and Adkison (1994) used a matrix based on age-specific vital rates estimated by Calkins and Pitcher (1982) based on the 1975-1978 Marmot Island population sample. As shown in York (1994), this matrix uses a survivorship schedule that does not reproduce the cumulative age-structure. York (1994) and Holmes and York (2003) used a different matrix that was also derived from the 1970s Marmot Island data, but has a survivorship schedule that produces a cumulative age-structure that more closely fits that observed in 1975-1978. However, all of these studies used matrices with generic data for age-specific birth rates, with each having a constant, non-zero rate after a certain age. By contrast, Calkins and Pitcher (1982) reported a decline in late-term pregnancy rates with age, aka reproductive senescence, after a peak at age 10-12 years.

One of our objectives was to explore the sensitivity of estimated historical vital rate changes to the Leslie matrix used in the analysis. For population modeling, it is common practice to develop a Leslie matrix for a population based on general life-history information and to estimate the individual elements of that matrix from multiple studies based on different populations or different years. For this study, we were in the unique position of having age-structure and age-specific pregnancy data for our study population and thus could rank *apriori* the accuracy of each pre-decline Leslie matrix. Consequently, we could study with field data, rather than simulations, whether accuracy of the Leslie matrix affected the predicted historical changes in vital rates. Uncertainty about the true underlying population model is typical, and an increasingly common practice is to use the data one is trying to fit, in our case, the abundance and juvenile fraction data, to select or weight the model used to fit the data using AIC or BIC (Burnham and Anderson 2003, Ellison 2004, Johnson and Omland 2004). We explore whether the ability of the Steller sea lion Leslie matrix to fit the time series data, as measured by AIC, reflects the known accuracy of the Leslie model. We also investigated to what extent age-structure information constrained model-fitting and selection. Age-structure information is unusual for many species of conservation concern, for which often the only data available are time series of an abundance index for some segment of the population. Thus, it is of practical concern to understand how, beyond making estimates more uncertain (Holmes and York 2003), fitting to abundance data alone affects the results, and whether if only abundance data were available, it would have been obvious to the modeler whether or not the problem was well constrained.

METHODS

Abundance and juvenile fraction

Surveys of Alaskan Steller sea lion populations have been conducted by the National Marine Fisheries Service and the Alaska Department of Fish and Game since 1976 as part of range-wide monitoring (National Marine Fisheries Service 1992, Holmes and York 2003, Fritz and Stinchcomb 2005, and references therein). During aerial surveys, photographs were taken of sea lions on terrestrial rookery and haul-out sites in the Gulf of Alaska and Aleutian Islands during an approximate two week period during the breeding season (June and July). At this time, newborns (pups) and the majority of reproductive adults are on rookeries where adult males defend territories and mating and birthing occur. Based on age and sex-identification using high resolution photographs taken in 2004, approximately 75% of the observed breeding males and females in the CGOA were on the five major rookeries. The remaining ca. 25% of breeding-age adults and the majority (ca. 80% in 2004) of pre-reproductive juvenile sea lions (nonpups up to 3 years old) were observed on 27 CGOA haulout sites, where sea lions predictably rest on land but where no or few pups are born. From the aerial photographs, counts of juveniles and adults were added together to yield a nonpup count. The National Marine Fisheries Service designates all rookeries and some major haulouts as trend sites, which are sites that have been regularly surveyed since 1976. Trend site sea lion counts account for 70-80% of the total counted each year. For this paper, we used the 1976-2004 total nonpup count on trend rookeries and haulouts in the CGOA during June/July (raw data and references are in Appendix A).

Pups have been counted every 1-4 years from 1978 to 2004 at the Marmot, Sugarloaf, Chowiet, Chirokof, and Outer Island rookeries, which together contribute more than 95% of the CGOA pup production (Fritz and Stinchcomb 2005, and references therein). For each of the following years: 1978, 1979, 1984, 1986, 1989, 1990, 1991, 1992, 1993, 1994, 1997, 1998, 2000, 2001, 2002, and 2004; at least three of the five rookeries were surveyed and the other rookeries were surveyed within two years of those years. To create a CGOA pup count for those years, we summed the pups for the five rookeries. For the missing data points, a linear interpolation was used and the interpolated value was used for the missing value. The estimated CGOA pup production for a year represents the sum of the actual rookery pup counts and the interpolated values for those rookeries without a count that year but one within 1-2 years (see Appendix A for the CGOA pup data used in this analysis)

Holmes and York (2003) developed a metric for Steller sea lion population age structure that utilized measurements of animals resting at surveyed CGOA haulouts. We extended this analysis and developed a comprehensive juvenile fraction estimate in the CGOA that used every haulout photograph available (Holmes and York 2003 analyzed a subset). Measurements were taken of sea lions photographed on haulouts during the 1985, 1989, 1990, 1991, 1992, 1994, 1996, 1997, 1998, 2000, and 2002 breeding-season surveys in the CGOA. From the photographs, the longest straight-line length of every animal was measured digitally. The fraction of small animals from all haulout photographs in a given year was used as an index of the juvenile fraction. Only photographs of haulouts were analyzed because few juveniles are on rookeries during the breeding season. No attempt was made to correct for curled animals; instead thousands of measurements were made and it was assumed that the mean curling rate is constant over time and that measurements of thousands of individuals would sufficiently reduce the sampling error from differences in curling tendency in small groups. The average number of measured animals per year was 2827 and the average number of haulout sites per year was 16. The number of animals measured and haulouts is given in Appendix A. Standard errors on the estimated juvenile fraction were estimated via stratified bootstrapping, by haulout and by photographs within haulouts. The data we used include all haulouts in order to maximize sample size. However in the mid-1980s and early-1990s, there were fewer haulouts photographed. The overall pattern in juvenile fraction did not change when we instead used a uniform set of haulouts across all years (comparison is shown in Appendix B, Figure B1).

The photographs provide no direct means of determining absolute size of individuals. Instead, relative size compared to a mature adult male on each photograph was used. Only photographs in which at least one mature adult male (which are distinctive in size and color) was lying completely stretched-out were measured. 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 haulouts was calculated as

$$\frac{J}{T} = \frac{\text{number of animals less than 50\% of the length of the largest male}}{\text{total number of animals in a photograph}}. \quad (1)$$

There is strong consistency in the *J/T* metric between adjacent census years (Figure 3a), which suggests that the metric does not show excessive year-to-year error. For Holmes and York (2003), it was assumed that the *J/T* metric categorized 80% of the actual juveniles correctly based on juveniles being 60-70% of the length of large males (Calkins and Pitcher 1982). In 2004, we were able to test this assumption using high resolution photographs of sea lions on the same CGOA haulouts that were photographed with 35mm slide film in previous years and used to measure animals. We found that 83% of animals categorized as juvenile in the high resolution photographs were being classified as juvenile following Eq 1.

Relating the raw data to the model

We assumed a temporally constant relationship, with error, between the pup numbers and the model total female pup numbers:

$$ln(0.5 \times \text{pups}_{\text{obs}}) = ln(\text{pups}_{\text{model}} \times 0.95) + \varepsilon_p, \quad (2)$$

where ε_p is unknown gaussian distributed observation error with the variance of ε_p treated as an estimated parameter. The observability, 0.95, is based on the fraction of CGOA pups that have been counted off the main rookeries since 2000, and 0.5 is the fraction of female pups at birth (Calkins and Pitcher 1982). The model requires the starting late-1970s expected (in the statistical sense) number of 1-month old female CGOA pups. This value was estimated as a free parameter, p_1, rather than fixing it to a particular value.

The nonpup count is less directly related to the total nonpup count because it represents only animals on trend sites and animals that were also visible at the time of the photographic census. Thus, animals on non-trend sites, those in the water, or those on trend sites but not photographed had to be accounted for in the model:

$$ln(\text{nonpups}_{\text{obs}}) = ln(\text{nonpups}_{\text{model}} \times p_2) + \varepsilon_{np}, \tag{3}$$

where ε_{np} is unknown gaussian distributed observation error whose variance was treated as an estimated parameter. The biological meaning of p_2 is the unknown fraction of the population that is censused on trend sites times the unknown fraction of the population that is female. We estimated p_2 as a free parameter separately for each model. We did not need to specify the starting late-1970s value for the model's female nonpups since this is constrained given by p_1 and the stable age-distribution from the Leslie matrix.

The *J/T* metric is the number of juveniles categorized as juvenile in a photograph divided by the total number of animals photographed on a haulout. We denoted by $m_{j,j}$ the fraction of juveniles in a photograph that are categorized as juveniles, and denoted by h_j and h_a, respectively, the fraction of juveniles and adults that were photographed on haulouts. The *J/T* metric was set so that very few adults would be miscategorized as juveniles. Only a fraction of the juvenile and adult population is photographed since some individuals are in the water, on rookeries, or on the haulout but not photographed. The relationship between the *J/T* metric and the model numbers of female juveniles and adults is then

$$\left(\frac{J}{T}\right)_{obs} = \frac{m_{j,j} h_j J_{\text{mod}\,el} / \phi_j}{h_j J_{\text{mod}\,el} / \phi_j + h_a A_{\text{mod}\,el} / \phi_j} = \frac{m_{j,j} J_{\text{mod}\,el}}{J_{\text{mod}\,el} + \frac{h_a}{h_j} \frac{\phi_j}{\phi_a} A_{\text{mod}\,el}}. \tag{4}$$

Since the model tracks only females and the observed *J/T* metric was based on measurements of all nonpups, males and females, we have to correct for the fraction of juveniles and adults on the haulout that are female: ϕ_j and ϕ_a, respectively These fractions are unknown, as are the constants h_a and h_j. It is known that h_a is considerably smaller than h_j since few adults but most juveniles are on haulouts during the breeding season. The constant ($h_a/h_j \times \phi_j/\phi_a$) was estimated as a free parameter. The constant is denoted, p_3, in Eq. 6. We fixed $m_{j,j}$ to 0.8, thus assuming that 80% of juveniles are classified as juveniles as discussed in the section on measurements of individuals on haulouts..

The relationship between the raw data and the actual nonpup numbers in the population is unknown since we do not know the fraction of the nonpups that is missed by the survey, beyond the rough information from a variety of field studies that puts observability on any one summer day at 30-50% (Merrick and Loughlin 1997, Trites and Porter 2002, Trites et al. 2006). We estimate these fractions during model fitting, but an important assumption is that these fractions do not change systematically over time, and specifically, that observability of nonpups, encapsulated by p_2, has been stable. We feel confident that the fraction of the population that is observed has not changed systematically for two main reasons: the consistency of the survey methods from1976 through 2004 and independent field measurements which concur with the results of the modeling (discussed in the results). A significant violation of this assumption, however, would change our results, although of more concern is that it would mean that the population stabilization observed since 2000 is illusory. We discuss the evidence supporting the assumption of constant observability in Appendix B.

Model and model fitting

The pup, nonpup and juvenile fraction data were fit using time-varying models for the female-only component of the CGOA Steller sea lion population from 1976 to 2004:

$$\vec{N}_{t+1} = \mathbf{Y}_t \cdot \vec{N}_t \qquad (5)$$

$\vec{N}_t$ is the vector of the number of sea lions at each age (0-31 years) at time *t*, with age-0 being pups at age 1-month when they were censused. $\mathbf{Y}_t$ is the 32 x 32 Leslie matrix at time *t* that encapsulates how numbers at year *t* translate to numbers at year *t*+1 (Table 1). This matrix specifies the survivorships from age *i* to *i*+1 and the number of female pups born to females age *i* in year *t+1*. Multiple models were compared, where 'model' refers to Eq. 5 with a specific Leslie matrix and a specific time period combination which specifies when the matrix elements were allowed to change.

We compared how the model fit the data using four different Leslie matrices, each of which was either specified or estimated in a different way from age and pregnancy data from the sample of animals collected, aged and examined for pregnancy near Marmot Island from 1975 to 1978 (Calkins and Pitcher 1982). The four matrices (Figure 4) were: (1) a generic Steller sea lion matrix with constant adult survivorship and birth rates (Winship and Trites 2006), (2) the matrix based on the original survivorship and birth rate schedule estimated by Calkins and Pitcher (1982), (3) the matrix with a re-estimated survivorship schedule from York (1994), and (4) a new matrix estimated in this paper which is based on a re-analysis of the 1975-1978 pregnancy data and incorporates the evidence for reproductive senescence. This last matrix is the most specific to the CGOA population that we are modeling. Details on the estimation of the matrices and the values of the matrix elements are provided in Appendix C.

The modeling implicitly treats the CGOA as a closed population or at least, one that is surrounded by regions with the same dynamics and trends. Previous research (York et al. 1996) revealed that Steller sea lions have independent population dynamics in the Aleutians Islands compared to the Gulf of Alaska, and that the three regions within the Gulf of Alaska, the eastern (EGOA), central and western (WGOA) regions in the Gulf of Alaska (EGOA and WGOA) have experienced similar population trends. In mark-resight studies (Raum-Suryan et al. 2002), 20-30% of females marked as pups on one of the main rookeries on the eastern end of the CGOA, the Sugarloaf and Marmot rookeries (78km apart), were observed to switch between those two rookeries when they gave birth, but only one female was observed to pup on the closest EGOA rookery (288-315km distant). Whether females born near the west end of the CGOA, on Chirikof or Chowiet Islands, move to WGOA rookeries to pup is unknown, however the closest WGOA rookeries are over 200km distant. Juveniles older than 1 year disperse widely (Raum-Suryan et al. 2002), and the nonpup count and juvenile fraction data in the CGOA includes an unknown number of 2-3 year old juveniles born in the WGOA and EGOA. Nonetheless, the juvenile fraction data from the WGOA shows the same pattern as the CGOA data (Figure 3), rather than a mirror images of the CGOA pattern, which suggests there is not directed juvenile movement driving the juvenile fraction patterns. There are currently no data on the juvenile fraction trends in the EGOA. However, pup production in the WGOA and CGOA combined is four to five times larger than in the EGOA; consequently, juvenile numbers in the EGOA should not obscure the juvenile fraction signal for animals born in the CGOA. In total, these data suggest that the closed population assumption should not unduly affect the results.

To change Eq. 5 into a time-varying model, we allowed age-specific survivorships and birth rates in the Leslie matrices to change as a step function during defined time period combinations. For example, in one model, changes were allowed in 1983, 1988, 1992, and 1997. The use of a step function was based on our 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) which indicate that there have been periods with distinct population dynamics. The years when vital rates were allowed to change was in part specified and in part estimated. The timing of the first change can be placed to 1983 based on field work on Marmot Island. Prior to 1983, the fraction of the population on-land composed of juveniles was 15-20% during the breeding season. During 1983, the juvenile fraction on one of Marmot's beaches (#3, the only one sampled that year) started at normal levels but then declined precipitously over the remainder of the breeding season (Chumbley et al. 1997) and juvenile fractions on Marmot beaches remained dramatically below pre-1983 levels for the next 20 years. A second change likely occurred in 1988 or 1989, and was signaled by abrupt changes in the ratio of sea lion 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 set the second change at 1988; the results are the same if we set the second change at 1989. The timing of subsequent declines is difficult to specify based on data separate from the time series used in our analyses. An examination of pup-to-nonpop ratios and population trends suggests that changes in vital rates occurred in both the early and late 1990s. There is evidence of a anomaly in the Bering Sea ocean conditions in 1998 which affected multiple species (Napp and Hunt 2001) and possibly a change to pre-1977 ocean conditions (Hare and Mantua 2000). The evidence for ecosystem change in the early 1990s is unclear, although there is some evidence of change in North Pacific fish communities (McFarlane et al. 2000). For the early 1990s, we fit models with no change, a change in 1992 or a change in 1993. For the last 1990s, we fit models with a change in 1997, 1998, or 1999. In total, nine different time period combinations were used.

Juvenile survivorship (defined in this study as survivorship from age 1 month to 3 years), adult survivorship (age 3 years and older) and birth rate in $\mathbf{Y}_t$ were allowed to change in each time period, such that demographic rates were constant and then changed by separate scaling factors to a new rate during the next time period (Table 2). A separate scaling factor was used for juvenile survivorship, adult survivorship and birth rate in each time period. The only constraints on the scaling factors were that survivorship must be less than 1. In total, we compared 36 different models (4 Leslie matrices x 9 time period possibilities).

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

$$\begin{aligned} S(\theta) = \frac{1}{2}\Big[& k\log\sigma_{\ln N}^2 + \frac{1}{\sigma_{\ln N}^2}\sum_{i=1}^{k}(\ln(N_i) - \ln(p_1 \times (\hat{J}_i + \hat{A}_i)))^2 \\ & + n\log\sigma_{\ln P}^2 + \frac{1}{\sigma_{\ln P}^2}\sum_{i=1}^{n}(\ln(0.5 \times P_i) - \ln(0.95 \times \hat{P}_i))^2 \\ & + m\log\sigma_J^2 + \frac{1}{\sigma_J^2}\sum_{i=1}^{m}((J/T)_i - (m_{j,j}\hat{J}_i/(\hat{J}_i + p_3\hat{A}_i))^2 \;\Big] \\ & + \text{a constant} \end{aligned} \tag{6}$$

where 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, $\hat{P}_1 = 0.5 \times p_1$, was an estimated free parameter. Constants p_1, p_2, p_3 and m_{jj} are defined in Eqs. 2-4. The variances for the errors in the log pup, log nonpup, and juvenile fraction data were unknown and were estimated as free parameters using sequential updating until the variance estimates converged (Green 1984). Confidence intervals on the estimated demographic scaling factors (in Table 3) were estimated using one-dimensional likelihood profiling allowing all other parameters in Eq. 6 to be free (Hilborn and Mangel 1997).

The model fits to the data were compared using Akaike's information criterion corrected for small sample size, AIC$_c$ (Burnham and Anderson 2003). 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. For the $\mathrm{AIC_c}$ calculation, the number of estimated parameters was treated as the number of 'estimable' parameters, K, however the parameters are not orthogonal and thus the effective number of parameters is actually less than the number of estimated parameters. Unfortunately, specification of the number 'estimable' parameters for model-selection purposes where the orthogonality of the parameters is not clear, appears to be an open problem in statistics. It is addressed (in concept) in the section on Takeuchi's (1976) general derivation of AIC (section 7.5, Burnham and Anderson 2003), and the model complexity correction that appears in Takeuchi's general derivation was used recently by Spiegelhalter et al. (2002) to estimate effective parameter size in a Bayesian setting. Using the number of estimated model parameters for K in the $\mathrm{AIC_c}$ calculation results in calculated $\Delta\mathrm{AIC_c}$ values that are smaller than the true values. Thus, if the correct effective parameters size were known, the best fit model would be separated from the next best models by larger $\Delta\mathrm{AIC_c}$ values than are presented here. Nonetheless the ranking of the $\Delta\mathrm{AIC_c}$'s would not change. The total number of data points in the three time series was treated as the sample size for the $\mathrm{AIC_c}$ calculation. This does not adjust for autocorrelation in the residuals, but this was not felt to be a problem in this analysis because 1) there was no clear autocorrelation in the pup and nonpup residuals using the best fit model, 2) half the data points in the time series are separated by 2+ years, and 3) the effect of overestimating sample size is offset by overestimation of the effective parameter size. Nonetheless, to the extent that sample size is overestimated, the presented $\mathrm{AIC_c}$ calculation 'over-favors' models with more parameters.

RESULTS

Vital rate changes in the central Gulf of Alaska

The model with the best fit to the time series data (with the lowest AIC_c) was based on the Leslie matrix that fit the 1975-1978 age-structure and pregnancy data best (matrix HFYS in Figure 4) and had four vital rate changes in 1983, 1988, 1992 and 1997. The predicted pup, nonpup, and juvenile fractions using this model are shown in Figure 5 (black line). The best fit model has a steadily declining birth rate from the mid-1980s to 64% of pre-decline levels in 1997-2004 with juvenile and adult survivorship increasing to near pre-decline levels after being severely reduced in the early-1980s (Table 3).

This pattern was seen in all models with a $\Delta AIC_c < 10$ value relative to the best fitting model (Figure 6). Burnham and Anderson (2003; section 2.6) suggest $\Delta AIC_c < 10$ as a cut-off for 'some' versus 'essentially no empirical support' and $4 < \Delta AIC_c < 7$ as models with some but considerably less empirical support. This agreement in terms of declining birth rate is largely driven by the increase in nonpup to pup ratios, which is seen by the divergence between log pup and log nonpup counts in Figure 3a. While increases in the ratio of nonpups to pups in the mid-1990s could be due in part to a recovery in juvenile survivorship, which would increase counts of nonpups with no rise in pup production, the model accounts for the changing age structure due to increasing juvenile survivorship. Increased juvenile survivorship, leading to more pre-reproductive individuals, cannot by itself explain the long-term increase in nonpup to pup ratios. A concomitant decline in birth rate is required to explain this pattern.

Although the pattern of declining birth rate and increasing survivorship was seen across all model with a $\Delta AIC_c < 10$, the precise estimates fell into two types. Models that allowed an early 1990s change in vital rates, estimated a more severe decline in birth rate and estimated that current adult survivorship is higher than in the 1970s while juvenile survivorship is slightly lower (Figure 6). But four models which were not allowed a vital rate change in the early 1990s also had $\Delta AIC_c < 10$.

These models could not fit the *J/T* data (Figure 5, grey line), but compensated with a high estimated variance for the *J/T* data; recall that the error variances are treated as estimated parameters. The result is that the poor fit to the *J/T* data is not penalized as much. If all models, including these with no early 1990s change, were forced to fit the *J/T* data by treating the variances as fixed parameters, models without an early 1990s vital rate change would have $\Delta AIC_c >> 10$ since they are unable to fit the *J/T* data. Regardless of whether an early 1990s vital rate change was included, all models estimated steadily declining birth rate combined with steadily increasing survivorship from the early 1980s through 2004.

Comparison of the modeling results and independent field studies on survivorship, reproduction and population structure

In 1987-1988, 751 Steller sea lion pups born on Marmot Island were individually and permanently marked (hot-branded) to study cohort survivorship (Merrick et al. 1996, Raum-Suryan et al. 2002, Pendleton et al. 2006, NMML Unpublished data). The marking program was resumed in 2000 in the Gulf of Alaska, and through 2003 and 2004, a total of 659 and 844 pups, respectively, were branded on two CGOA (Marmot and Sugarloaf) and two EGOA (Seal Rocks and Fish Island) rookeries (NMFS-AFSC-NMML unpublished data). Using a mark-resight model that estimates survivorship by sex,and age (Pendleton et al. 2006), the 1987-1988 and 2000-2004 cohort resight histories were analyzed to estimate female juvenile survival from 1988 to 1992, and from 2000 to 2005. Two different sets of capture histories were analyzed for the 2000-2003 and the 2000-2004 cohorts.

Resightings of the 1987 and 1988 cohorts were an order of magnitude lower than that expected given juvenile survival rates in the 1970s (Raum-Suryan et al. 2002). Based on the resight histories for this cohort, juvenile survivorship in the late 1980s was approximately 20% lower than in the 1970s values (Figure 6a, circles). The estimated proportional declines vary depending on the assumed 1970s Leslie matrix; the multiple points represent the effect of assumptions about the 1970s juvenile survivorship. These estimate overlap the proportional declines estimated by the best-fitting models (Figure 6a). As of 2006, estimates of the juvenile survivorship from the 2000-2004 marked cohorts are preliminary due to the limited number of resight years available. However, based on the resight data collected up to 2005, the cumulative survivorship to age 4 of the 2000-2004 branded cohorts is 35-40% greater than that of the 1987-1988 cohorts. This translates to juvenile survivorship still below 1970s levels, but much higher than in the 1980s. Again, these field estimates closely mirror the model estimates of juvenile survivorship from the best fitting models from this study (Figure 6a, circles).

Field data on pregnancy rates is more limited than for survivorships. Other than the 1975-1978 collections on Marmot Island, direct measurements of pregnancy rates are only available from the mid-1980s. In 1985 and 1986, females were sampled from Marmot Island and pregnancy status was determined (Pitcher et al. 1998). There were 64 females collected in April and May, when late-term pregnancies would be observed, for which pregnancy status is known. Of these, 35 or 54.7% were pregnant. We compared this to the expected number using the 1970s age-specific pregnancy probabilities (given in Appendix C for the HFYS matrix). The expected pregnancy rate for this sample of 64 females is 63.3% (95% CIs = 41.7-- 67.2%). Thus the actual number of pregnancies was 14% lower than expected. This could have occurred by chance (the 95% CIs do overlap the 1970s expected value), nonetheless it closely matches the 13% model-estimated decline in pregnancy rate for this period (Table 3; Figure 6b).

The third piece of independent field data is an estimate of the juvenile fraction in the CGOA Steller sea lion population from high resolution photographs of all CGOA haulouts and rookeries in 2004 (Fritz and Stinchcomb 2005; NMML, unpublished data). From these photographs of sea lions on all rookeries and haulouts, adult males, subadult males, adult females, juveniles and pups were separately identified based on size, color, behavior, and spatial configuration relative to males defending harems. These measurements are independent of those used in the analysis in this paper, and use different planes, photographs and analysts. A total of 2259 adult females and 1198 juveniles were counted on all CGOA terrestrial sea lion sites surveyed via the high photographs in 2004. Assuming a 50:50 sex-ratio in juveniles, the juvenile fraction of the female population is 21% (1198 x 0.5/2259). Animals on haulouts are more likely to not be photographed, since small sites are visually counted. This will tend to underestimate juvenile fraction since there are more juvenile on haulouts. If we assume that 20% of haulout animals are missed, a high-end assumption, the juvenile fraction estimate increases to 23%. These estimates compare well with the 24% juvenile fraction predicted by the best fit model for 2004, and is considerably smaller than the 34% in the late 1970s based on the stable age-distribution calculated from the best-fitting Leslie matrix (HFYS).

Effect of the Leslie matrix on the results

The Akaike information criteria (AIC) estimates the Kullback–Leibler information about some given sample data that are lost by approximating the unknown complex process that produced the data by a less-complex approximate model (Burnham and Anderson 2003). AIC is estimated by fitting a model to the sample data and penalizing for model complexity. In this study, it is a way to judge the ability of different Leslie matrix models and different historical vital rate changes to fit the time series data. We can formally ask whether there are alternate equally supported models that fit the data at hand. The ability of the Leslie matrices to fit the age-structure and age-specific pregnancy data from the approximately stable pre-decline population provide an independent estimate of how well the Leslie matrix models describe the pre-decline population's survivorship and birth rate schedules. From worst to best the ranking is: WT2006, CP1982, Y1994, HFYS. There is no *apriori* reason to assume that the model using a matrix that fits the snap-shot of the 1970s age-structure data best is also the model that fits the 1976-2004 time series data best. With 15-18 estimated parameters, one might assume that all could manage to fit the data well; however this was not the case. Figure 8 shows the ΔAIC_c values across all 36 models. The black lines show the values when the models are fit to the pup, nonpup and juvenile fraction data. The grey lines show the values when the models are fit only to the pup and nonpup data. When the juvenile fraction data were fit, the model using the most population-specific Leslie matrix (HFYS) consistently had the lowest ΔAIC_c (best fit) For many time period combinations, the relative ΔAIC_c values mirrored how well the Leslie matrix fit the 1975-1978 age-structure data, with ΔAIC_c increasing as less to more generic matrices were used; the most population-specific Leslie matrix (HFYS) had a ΔAIC_c much lower than the generic matrix in all cases except one. This pattern was caused mainly by the ability of the HFYS matrix to fit the juvenile fraction data much better than the WT2006 matrix. When models were fit to only the pup and nonpup data, the HFYS matrix no longer consistently best fit the time series data (Figure 8, grey lines), and the matrices typically had similar ΔAIC_c values for each time period combination.

Although matrix accuracy improved the model's ability to fit the juvenile fraction data, the vital rate estimates were not appreciably affected by the matrix used as long as the estimated variance for the *J/T* data was low (Figure 9, top). High variance estimates occurred when the model was unable to closely fit the *J/T* data. With a high variance estimate for the *J/T* data, the model's maximum likelihood could reach a higher maximum despite its inability to fit the *J/T* data. This resulted in certain cases where the $\Delta\mathrm{AIC}_c$ values were similar but the 1997-2004 juvenile survivorship estimates were very different (Figures 6a and 9). When models were unable to fit the *J/T* data, all pups born in the most recent period (1997-2004) were estimated to have survived (100% survival, and 120% of pre-decline juvenile survivorship) and birth rates were 75-80% of pre-decline values across all models (Figure 7 and 9, bottom). Besides being an unrealistic result, these results also contradict both juvenile survivorship estimates from the recently branded 2000-2004 CGOA cohorts and the lower (not higher) estimated juvenile fraction of the female population compared to 1975-1978 from the 2004 high resolution photographs.

That the overall conclusions were similar using a generic versus specific matrix when fitting to the abundance and age-structure data may provide comfort to population modelers who often must use a generic Leslie matrix. However, caution is advised when the estimation problem may be poorly constrained, in this case when fit only to the pup and nonpup data, or when it is unknown what the error variance should be for specific data, in this case, the *J/T* data. In our analyses, a best fit to the abundance data alone, without juvenile fraction information, translated to estimates of juvenile survivorship and population juvenile fraction that were inconsistent with independent field data. If the models had been fit only to the abundance data and no field data were available to cross-validate some of the predictions, we may have mistakenly concluded that juvenile survivorship was currently much higher than 1970s levels, particularly since there was a high $\Delta\mathrm{AIC}_c$ (ca. 50) for the alternative fit with lower juvenile survivorship. This conclusion would have been consistent across all model variants fit to the abundance data alone, and emphasizes the need for critical thinking about model selection sensitivity and problem-specification sensitivity beyond just a calculation of model selection metrics (such as AIC). In our study of Steller sea lion vital rates, we have a metric for juvenile fraction plus independent field studies that provide approximate current juvenile survivorship and juvenile fraction. All of this evidence agrees with the model fits indicating juvenile survivorship still slightly below pre-decline levels along with a steady decline in birth rates.

Relationship of the results to other modeling analyses of the western stock of Steller sea lions

Recently, Winship and Trites (2006) used data from all rookeries in the western stock (from the western Aleutians to the eastern Gulf of Alaska) and estimated survivorship and birth rate changes between the late 1970s and 2002 by fitting separate models to each of the individual rookery's nonpup and pup counts. Their model analysis concluded, as did ours, that survivorship has been steadily increasing after the 1980s in the central Gulf of Alaska. Our results differ from Winship and Trites', however, in the estimate of current birth rates in the central Gulf of Alaska. Their analysis indicates birth rates in the region increasing to near pre-decline levels, after declining in the mid-1990s. In contrast, our analyses indicated that current birth rates are severely below pre-decline levels (ca. 65% of pre-decline levels), suggesting that the declining pregnancy rate seen in the mid-1980s field data (Pitcher et al. 1998) has continued into the late 1990s and early 2000s. This is a significant divergence in conclusions about the current conditions in the central Gulf of Alaska and could have resulted from one or more of the following differences between our analyses: 1) we analyzed lumped rookery plus haulout data across the entire CGOA versus Winship and Trites' rookery by rookery analyses, 2) we fit to age-structure information in addition to pup and nonpup data, 3) we used life-history models that more closely fit the age and pregnancy data collected on Marmot Island in the 1970s, and 4) we allowed adult survivorship to increase above that estimated in the 1970s versus constraining adult survivorship to a maximum equal to the pre-decline survivorship.

After repeating our analysis using the life matrix used in Winship and Trites (2006) and fitting only to the pup and nonpup data, we conclude that the differences in our results are due to our analysis allowing adult survivorship to increase above pre-decline levels. Fitting to the juvenile fraction data affects our estimate of how low the current birth rate is, but not whether it has steadily declined. When adult survivorship is constrained, the solution with high adult survivorship, lower juvenile survivorship, and low birth rate is not allowed. Current adult survivorship above the 1970s levels may be due to management efforts that have largely eliminated shooting and incidental take Steller sea lions in the Alaska fisheries (Perez 2003). Direct mortality of adult Steller sea lions associated with fisheries operations were likely highest in the early 1980s but also occurred in the late 1970s (Perez and Loughlin 1991).

DISCUSSION

The western Steller sea lion population experienced its severest decline during the 1980s, and a variety of field observations and data 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). Evidence indicated that both direct impacts (e.g., predation, illegal shooting, incidental take in fisheries) and indirect impacts (e.g., disease, pollutants, nutritional stress related to climate change or the competitive effects of fisheries) 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). What has been less clear is what vital rate changes were responsible for the continuing, though less severe declines of the 1990s and what vital rate changes are associated with the increase in nonpup numbers 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 declining direct factors (Springer et al. 2003, Williams et al. 2004). However, evidence for this hypothesis has been questioned and recent field observations and analyses of killer whale trophic level based on fatty acids and stable isotopes suggest that Steller sea lions are a relatively modest component of the diet of Alaskan killer whales (DeMaster et al. 2006, Krahn 2006, Mizroch and Rice 2006).

Our results corroborate previous studies indicating a severe mid-1980s reduction in juvenile survivorship, but after the mid-1980s, our analysis concludes that juvenile and adult survivorship steadily improved to near pre-decline levels by the late-1990s. Recent estimates of juvenile survivorship of western Steller sea lion cohorts individually marked in 1987-1988 and in 2000-2004 corroborate our conclusion that juvenile survivorship has increased since the mid-1980s to near pre-decline levels for pups born since 2000. Increases in survivorship, however, 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. This pattern of steadily increasing juvenile and adult survivorship was also found by Winship and Trites (2006) in their rookery-by-rookery analysis of vital rate changes.

At the same time that survivorship was increasing, our analysis concluded that birth rate was doing the opposite and has been steadily declining in the central Gulf of Alaska since at least the early 1980s. Decreased pregnancy rates relative to 1975-1978 were found in females sampled in 1985-1986 (Pitcher et al. 1998), with lactating females having significantly lower pregnancy rates than lactating females in 1975-1978. Our analysis suggests that birth rates have continued to erode in the almost 20 years since Pitcher et al.'s samples were taken. Our result is driven by the increasing nonpup to pup ratio seen in the census data combined with a decreasing fraction of the nonpup population in the class of pre-reproductive juveniles. Given this pattern, the maximum likelihood fits from all the models indicated a pattern of steadily declining birth rate. The best fitting models indicate that the current average per-female birth rates are 36% lower than pre-decline levels.

We analyzed the census data using models only for the central Gulf of Alaska given that there is an estimate of the pre-decline population structure for that region only and we were concerned that errors in the assumed life-history model could affect estimates for other regions. However, we have data on nonpup to pup ratios and juvenile female fractions in the western Gulf of Alaska and the eastern Aleutian Islands (Figure 3d,f). Nonpup to pup ratios in both of these regions have increased since the early 1990s as evidenced by the widening gap between pup and nonpup numbers on the log scale (Figure 3c,e). At the same time, the *J/T* data show no evidence of increasing juvenile fraction on the haulouts (Figure 3d,f). The estimated fraction of female nonpup juveniles from the 2004 high resolution photographs was 20% and 23% for the western Gulf of Alaska and eastern Aleutian Islands, respectively, which are similar to the 21% estimated for the central Gulf of Alaska. Thus, the same pattern of nonpup to pup ratios above pre-decline levels along with no evidence of increased juvenile fraction appears to be present to the west of the CGOA and suggests that low birth-rate is a region-wide problem for Steller sea lions in the Gulf of Alaska.

There are a number of biological mechanisms that would 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 of the mature female population combined with a non-uniform age-specific reproduction, to name several. The model is only able to rule out the last of these - lower reproduction because of a change in the age-distribution of mature females - since it explicitly models the age structure of females and includes age-dependent rates of birth. Distinguishing which other factors are causing or interacting to cause decreased birth rates is not possible using simply the pup, nonpup and juvenile fraction data described here. Such a determination requires research and field studies directed specifically at sea lion fertility, maturation, pregnancy and abortion rates, which have not been conducted in almost two decades because of conservation concerns related to handling, sedating, and collecting a large number of adult females. However, field data are available on post-partum pup survival from the percentage of dead pups observed during on-land pup counts at rookeries in the eastern Aleutian Islands, and western and central Gulf of Alaska (NMML, 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). These findings do not support the conjecture that an increase in early pup mortality (birth to 1-month of age) is causing the decline in birth rate. There also does not seem to be evidence of mate-limitation since the adult sex-ratio observed in the 2004 high resolution photographs is similar to that calculated for the late 1990s. The remaining conjectures for the biological factors driving a declining birth rate are those directly linked to female reproduction, such as older age at first reproduction, reduced impregnation rates, or increased abortion rates.

Three main stressors are either known or hypothesized to impair Steller sea lion reproductive performance: nutritional stress, contaminants and disease. Nutritional stress from fisheries-induced or natural environmental changes in prey abundance, distribution or quality has received significant research attention as a hypothesis for the Steller sea lion declines (National Research Council 2003, Trites and Donnelly 2003, Fritz and Hinckley 2005). Nutritional stress is known to be associated with increased late-term abortion rates, reduced early pup survival and reduced juvenile survival and, to a lesser degree, adult survival (Trites and Donnelly 2003). Recent reviews of the evidence for nutritional limitation in the 1990s and 2000s have found little support from studies of body condition, behavior or pup condition that Steller sea lions are currently experiencing acute nutritional limitation in the Gulf of Alaska (Trites and Donnelly 2003, Fritz and Hinckley 2005). However, these studies were conducted largely on juvenile sea lions and focused on acute nutritional limitation (starvation). There is little information on chronic nutritional limitation and stress in adult females. The study of pregnancy rates in adult females conducted in 1985-1986 (Pitcher et al. 1998) found a reduction compared with the 1970s only in lactating, but not in non-lactating females, which could have resulted from chronic nutritional stress. Factors that could cause chronic nutritional stress and affect reproduction include natural changes in the composition of the prey-community in the Gulf of Alaska (Anderson and Piatt 1999, Benson and Trites 2002) and reductions in the abundance and local availability of prey related to commercial fisheries (National Research Council 1996, 2003, Fritz and Brown 2005). However, even if lactating females were nutritionally limited in the mid-1980s, the population declined significantly for at least another 15 years; factors affecting birth rate then may not be the same as those limiting birth rate now. Other factors known to affect reproduction may also be at play.

The effects of contaminants and disease/parasitism on Steller sea lions have been investigated to differing degrees, but both could be associated with reduced birth rates and 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 can impair reproduction in mammals, including pinnipeds (Reijnders 1984, Aguilar et al. 2002, Barron et al. 2003). Data on PCB levels in Steller sea lions is limited, however the data available indicate that average early-1990s PCB levels in juveniles in the Gulf of Alaska were at levels that could compromise reproduction (Barron et al. 2003). 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 if regional differences in rates of population decline are related to differences in contaminant loads. The limited disease and parasite survey data available have shown that 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. 2003). In samples collected in the 1990s, high seropositivity was unrelated to regional population trend, and, similar to the results on contaminants, it is unclear whether exposure to these disease organisms reduced Steller sea lion reproduction relative to pre-decline periods (Burek et al. 2003).

In summary, nutritional limitation, contaminants and disease all have the potential to disrupt reproduction, but research on reproduction has been limited to date and contaminant and disease surveys have not been comprehensive enough to rule out these as factors affecting birth rate in Steller sea lions in the Gulf of Alaska. The past five years have seen an encouraging abatement of the decline of the endangered western Steller sea lion population across the Gulf of Alaska and Aleutian Islands. However, nonpup to pup ratios 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, the Gulf of Alaska. High adult survivorship and low birth rate is a life-history trait combination that tends to make a species sensitive to negative impacts and limit its ability to recover quickly from a perturbation (Pimm et al. 1988, Fagan et al. 2001). Based on our reconstruction of 30 years of its population dynamics, Steller sea lions in the Gulf of Alaska appear to be more extreme in these attributes than before the severe 1980s declines. As a consequence, it may be premature to conclude from the small recent increases in nonpup counts alone that the western Steller sea lion is on the road to long-term recovery.

Population biologists studying Steller sea lions in the central Gulf of Alaska are fortunate that an estimate of pre-decline age-dependent survivorship and birth rate, as well as long-term census and other field data are available for analysis. However, this is not the normal situation for many species of conservation concern. Instead Leslie matrices used to describe the survivorship and reproduction of these species are usually generic in some sense: they are based on general life-history information from multiple studies or they borrow parameter estimates from other populations or species. In this study, we found that using a generic Leslie matrix did not significantly change the results relative to the more accurate Leslie matrix model. Instead the results depended on whether the models fit the age-structure data, not on the matrix per se. If the models were forced to fit the juvenile fraction data, they yielded estimates of current juvenile survivorship that were just below pre-decline levels (as the branding data also suggested). If the models were fit only to the pup and nonpup data or were allowed a large error variance for fitting to the juvenile fraction data, all models estimated that current age 0 to 1 survival is essentially 100%, an unrealistic result. All models using every Leslie matrix and every time period combination produced this estimate when fit only to the pup and nonpup data. This is troubling because it would suggest high robustness in the estimate of very high juvenile survivorship. In this case, plotting the likelihood surface would reveal that the 2-dimensional juvenile versus adult survivorship surface has two peaks, one with juvenile survivorship near 100% and one with juvenile survival slightly below pre-decline levels, but the ΔAIC_c between these two peaks is high (ca. 50), which would suggest considerable support for very high current juvenile survivorship. Thus in this example, fitting to only abundance data would lead to a model that fit the abundance data well, in fact perfectly to the eye, but it would not be in agreement with independent field measurements on vital rates and population age-structure.

Life-history modeling is a commonly used and powerful tool for understanding a population's past, present and future dynamics. Consideration of the sensitivity of one's results to model uncertainty is a crucial step, and it is increasingly a common feature of modeling analyses. However, careful thought must also be given to how or whether a metric for model fit actually reflects the uncertainty in the analysis as a whole. Beyond just narrow confidence or credibility intervals, one wants the whole model-fitting process to be sufficiently constrained so that it is both robust -- the same conclusion would be reached regardless of the modeling decisions made along the way -- and commutative -- if one produces some data using a particular model and then chooses among multiple model using that data, the original model is the model selected rather than one that differs in some fundamentally important way. Experience suggests that the commutative property should rarely be presumed, and that detecting problems in model fitting performance, such as alternate solution sets and a poorly constrained problem, is not likely to be detected by examining metrics of model fit, such as AIC, alone.

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Table 1. The 32 x 32 age-structured life-history matrix. 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 x 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 x f_{i+1} so that when the matrix multiplication is done, $N_{0,t+1} = \Sigma N_{i,t} \times s_i \times f_{i+1}$ 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 at the nonpup count. The parameters values for the four versions of the matrix are given in Appendix C.

	age 0 (pup)	age 1 yr	age 2 yr	age 3 yr	…	age 31 yr
birth rate	$s_0 \times f_1 \times s_n$	$s_1 \times f_2 \times s_n$	$s_2 \times f_3 \times s_n$	$s_3 \times f_4 \times s_n$	…	$s_{31} \times f_{32} \times s_n$
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.

Table 2**.** The 32 x 32 age-structured life-history matrix with perturbation terms 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*.

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

Table 3. Estimated demographic rates relative to pre-decline levels for the best fit model. Pre-decline level is 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 χ^2 with one-degree of freedom which is based on the asymptotic likelihood-ratio distribution.

	Juvenile survivorship ML (95% CIs)	Adult survivorship ML (95% CIs)	Birth rate (pups/♀) ML (95% CIs)
1976-1982	1.0	1.0	1.0
1983-1987	0.42 (0.38, 0.50)	0.90 (0.88, 0.92)	0.87 (0.82, 0.91)
1988-1991	0.73 (0.68, 0.80)	0.93 (0.91, 0.95)	0.76 (0.72, 0.80)
1992-1996	0.57 (0.53, 0.61)	1.00 (0.98, 1.02)	0.70 (0.67, 0.73)
1997-2004	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 (W of 144°W) and eastern stocks of 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. Changes in the abundance of the western stock of Steller sea lions by region, 1976 to 2004. Numbers shown are the nonpup counts on a consistently surveyed group of rookeries and haulouts used to monitor population trend by the National Marine Fisheries Service since 1984. The regions are the eastern, central and western Gulf of Alaska (EGOA, CGOA, WGOA), and the eastern, central, and western Aleutian Islands (EAI, CAI, WAI).

Figure 3. 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 pup and nonpup counts for each region represent different fractions of the total pup and nonpups in those regions. They are population indices meant to be consistent over time, but do not represent equal fractions (see data references in Appendix A). The juvenile fraction plots (B, D, and E) show the fraction of haulout 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 4. Age-specific female survivorship and birth rate (of female pups) schedules for the four different Leslie matrix models. The matrices are described in Appendix B.

Figure 5. Historical trends in juvenile fraction, nonpup, and pup counts in the central Gulf of Alaska. The circles show the observed 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 haulouts with a large male, b) adult and juvenile (nonpup) counts on rookery and haulout 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. Maximum likelihood estimates of the vital rates across all model variants with ΔAIC_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. The estimates of juvenile survivorship, adult survivorship, and pregnancy rate that are available from independent studies (discussed in text) are shown with open circles.

Figure 7. Maximum likelihood estimates when models were fit to pup and nonpup data only. The estimates were similar across the time periods, but only two time periods are shown: the time period with lowest ΔAIC_c's for models fit to the abundance alone (1983, 1988, 1997) and the time period with lowest ΔAIC_c's for models fit to the abundance and juvenile fraction metric, (1983, 1988, 1992, 1997) .

Figure 8. ΔAIC_c values across all 36 model variants fit to pup, nonpup and juvenile fraction data (black lines) or fit to pup and nonpup data only (grey lines). On the x-axis, Leslie matrices used in the models are referenced by number from most population specific Leslie matrix to least specific: #1) HFYS, #2) Y1994, #3) CP1982 and #4) WT2006. The time periods are shown above each block of ΔAIC_c values with the years shown when vital rates are allowed to change to new values. Appendix D gives the raw AIC_c values for each model fit.

Figure 9. Estimated 1997-2004 survivorship and birth rate estimates using the HFYS (+) matrix versus the most generic Leslie matrix, WT2006 (o). Top panel) estimates for the 9 time periods

plotted against the estimated error variance for the *J/T* data. Bottom panel) estimates plotted against their $\Delta\mathrm{AIC}_c$ values.


Russia
Alaska
(USA)
Canada
Commander Is.
(Russia)
Bering Sea
Attu I.
(USA)
Sugarloaf I.
Outer I.
Chowiet I.
Marmot I.
Chirikof I.
Central
Gulf of Alaska
Western
Stock
Eastern
Stock

Figure 1.

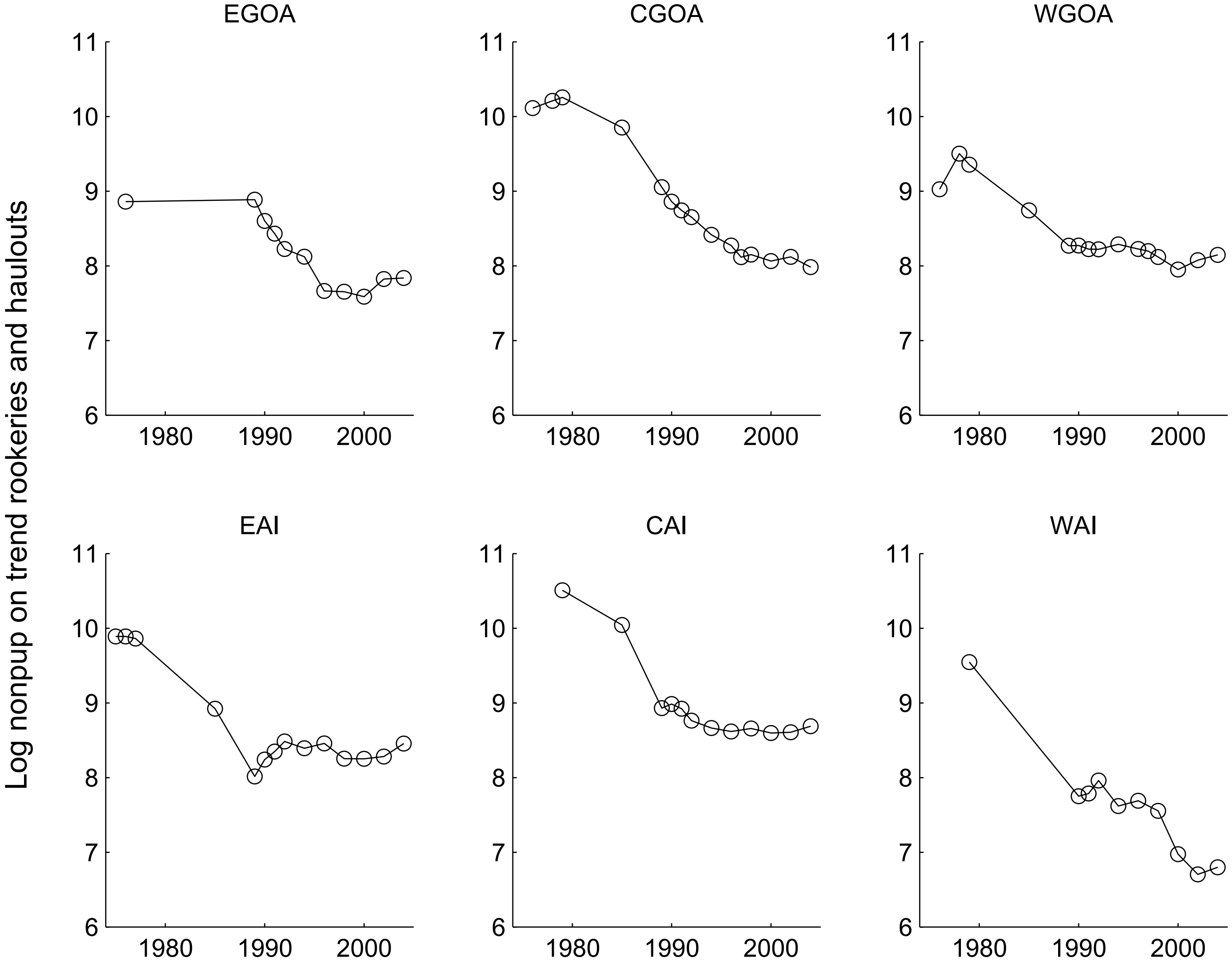

EGOA
CGOA
WGOA
EAI
CAI
WAI
Log nonpup on trend rookeries and haulouts
11
10
9
8
7
6
1980
1990
2000

Figure 2

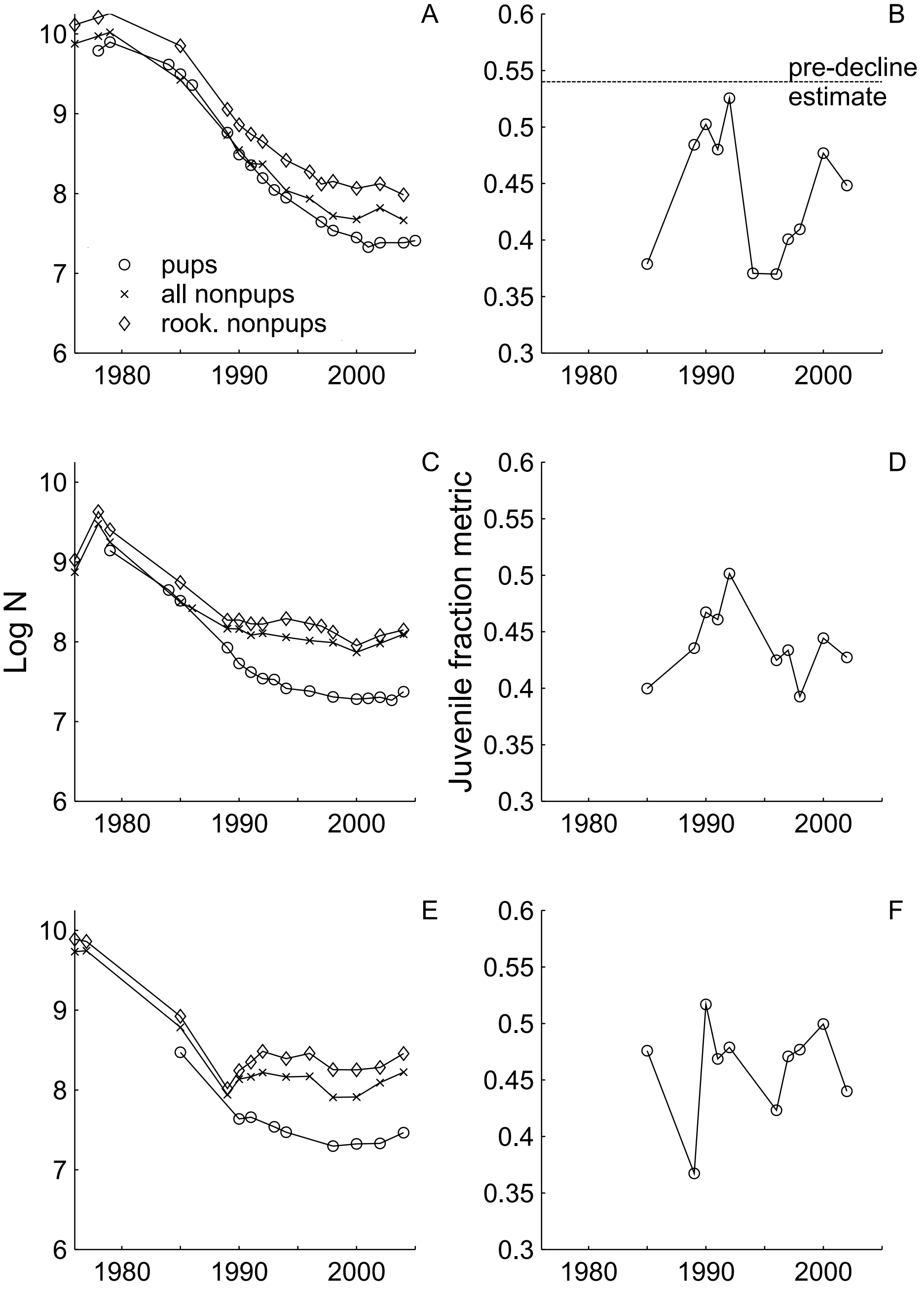

A
B
C
D
E
F
Log N
Juvenile fraction metric
pups
all nonpups
rook. nonpups
pre-decline
estimate
10
9
8
7
6
0.6
0.55
0.5
0.45
0.4
0.35
0.3
1980
1990
2000

Figure 3

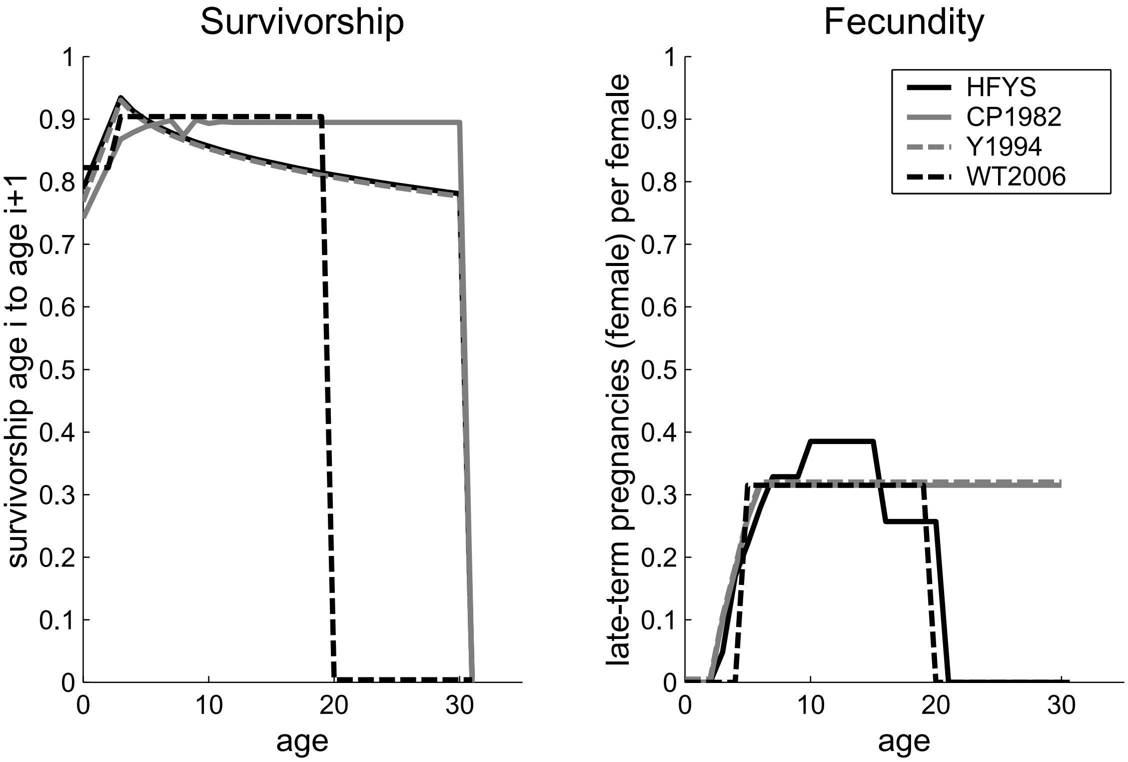
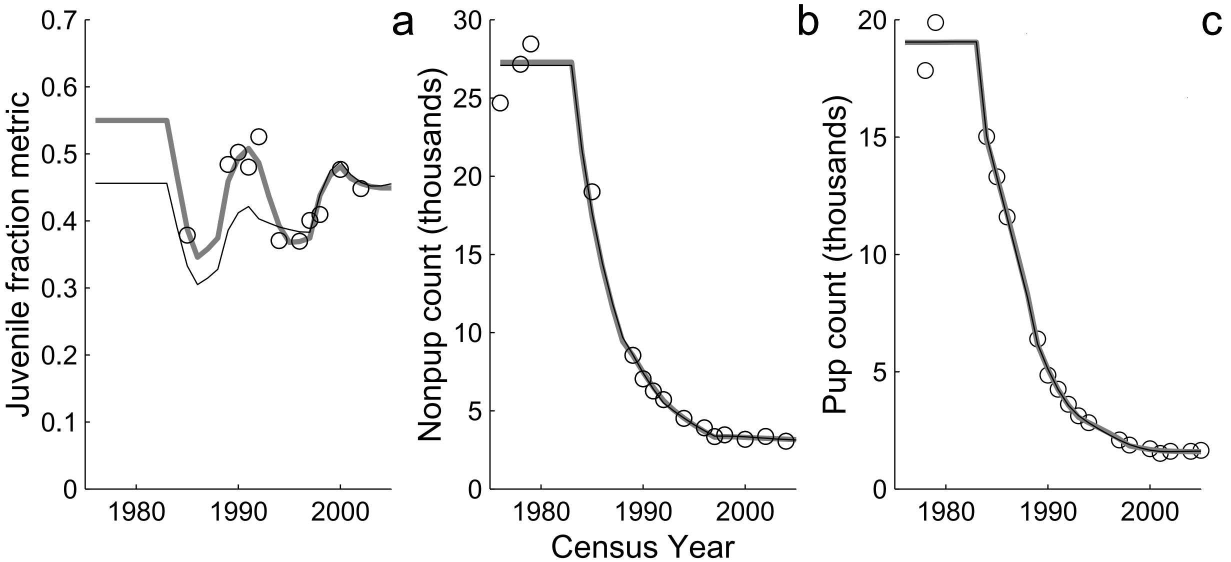

Survivorship
Fecundity
survivorship age i to age i+1
late-term pregnancies (female) per female
age
age
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
10
20
30
HFYS
CP1982
Y1994
WT2006

Figure 4



a
b
c
Juvenile fraction metric
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Nonpup count (thousands)
30
25
20
15
10
5
0
Pup count (thousands)
20
15
10
5
0
1980
1990
2000
Census Year

Figure 5

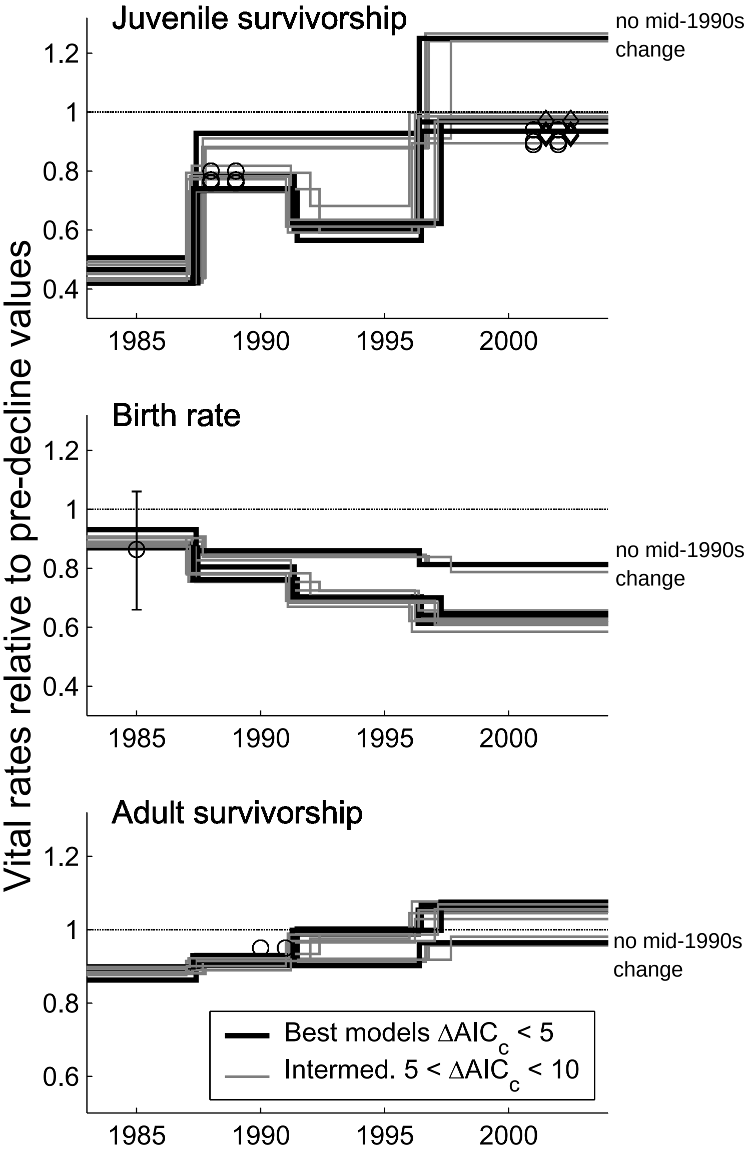

Juvenile survivorship
no mid-1990s change
1.2
1
0.8
0.6
0.4
1985
1990
1995
2000
Birth rate
no mid-1990s change
1.2
1
0.8
0.6
0.4
1985
1990
1995
2000
Adult survivorship
no mid-1990s change
1.2
1
0.8
0.6
1985
1990
1995
2000
Best models ΔAIC$_c$ < 5
Intermed. 5 < ΔAIC$_c$ < 10
Vital rates relative to pre-decline values

Figure 6

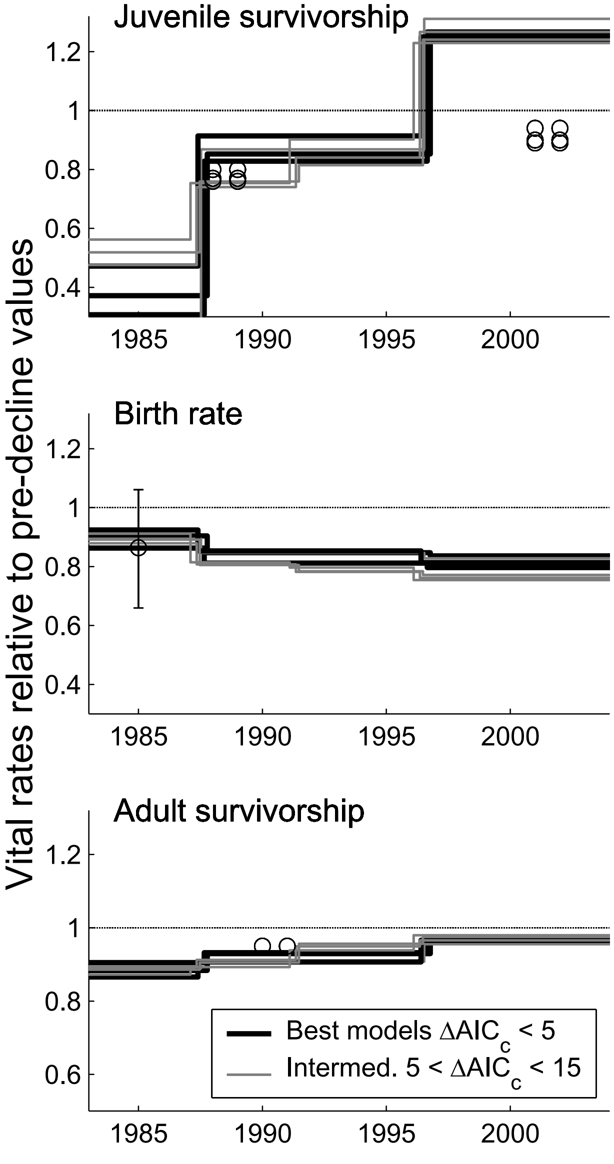
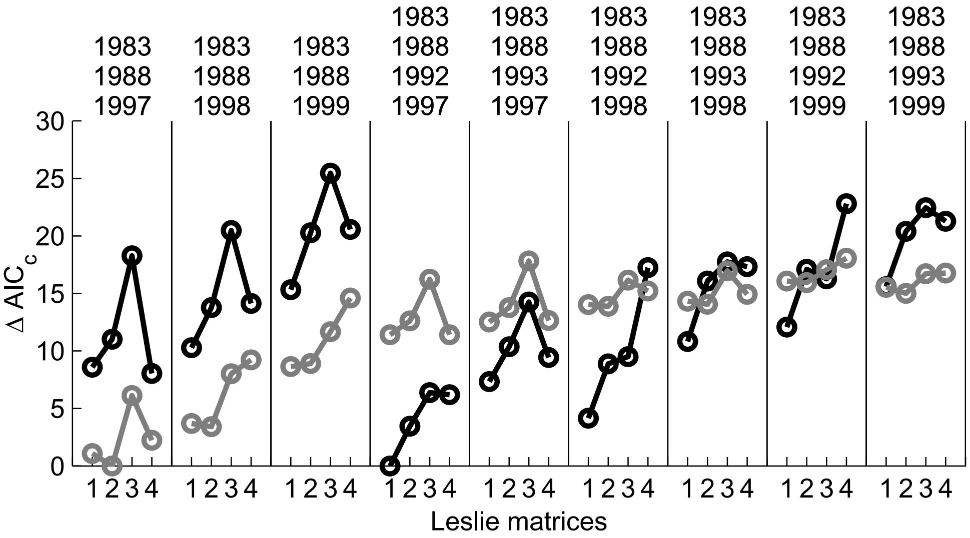
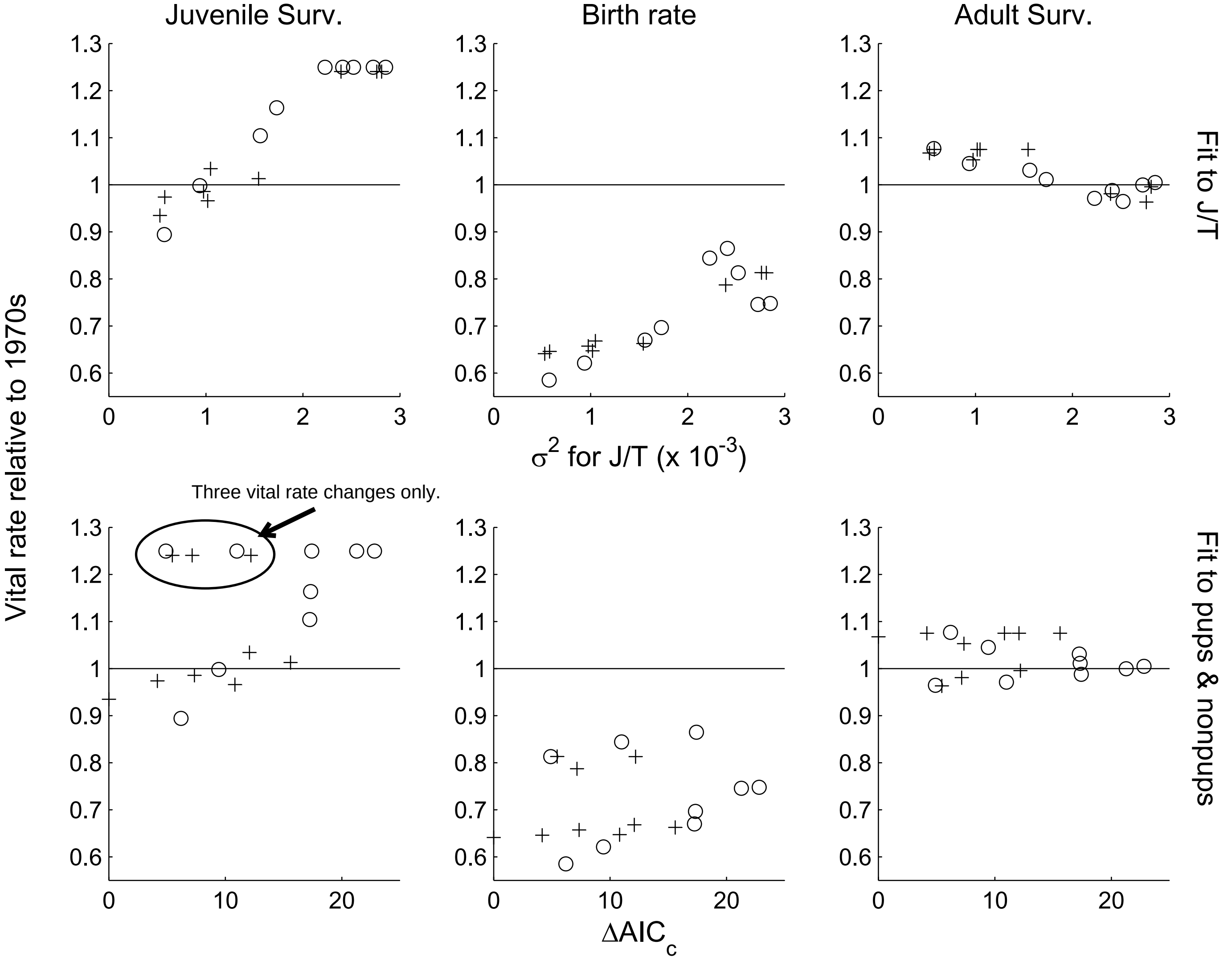

Juvenile survivorship
Birth rate
Adult survivorship
Vital rates relative to pre-decline values
1.2
1
0.8
0.6
0.4
1985
1990
1995
2000
Best models ΔAIC_c < 5
Intermed. 5 < ΔAIC_c < 15

Figure 7



1983 1988 1997
1983 1988 1998
1983 1988 1999
1983 1988 1992 1997
1983 1988 1993 1997
1983 1988 1992 1998
1983 1988 1993 1998
1983 1988 1992 1999
1983 1988 1993 1999
30
25
20
15
10
5
0
Δ AIC$_c$
1 2 3 4
Leslie matrices

Figure 8



Juvenile Surv.
Birth rate
Adult Surv.
Fit to J/T
Fit to pups & nonpups
Vital rate relative to 1970s
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0
1
2
3
σ² for J/T (x 10⁻³)
Three vital rate changes only.
0
10
20
ΔAIC_c

Figure 9

Appendix A Raw data tables with references

Table A1. The raw data for the central Gulf of Alaska

Year	Non-pup count	Pup count[1]	*J/T* metric[6]	Sample size for *J/T* metric # of measurements (# of haulouts)
1976	24678[2]	no data	no data	n.a.
1977	no data	no data	no data	n.a.
1978	27155[7]	17835	no data	n.a.
1979	28460[7]	19886	no data	n.a.
1980	no data	no data	no data	n.a.
1981	no data	no data	no data	n.a.
1982	no data	no data	no data	n.a.
1983	no data	no data	no data	n.a.
1984	no data	15019	no data	n.a.
1985	19002[2]	no data	0.3788	7182 (13)
1986	no data	11598	no data	n.a.
1987	no data	no data	no data	n.a.
1988	no data	no data	no data	n.a.
1989	8552[2]	6394	0.4843	3039 (11)
1990	7050[2]	4648	0.5025	2752 (16)
1991	6273[2]	4057	0.4801	2468 (16)
1992	5721[2]	3646	0.5255	2409 (19)
1993	no data	3176	no data	n.a.
1994	4520[3]	2831	0.3706	2536 (19)
1995	no data	no data	no data	n.a.
1996	3915[3]	no data	0.3698	1971 (17)
1997	3352[3]	2056	0.4007	1924 (15)
1998	3467[4]	1876	0.4095	2090 (16)
1999	no data	no data	no data	n.a.
2000	3180[4]	1675	0.4769	2489 (17)
2001	no data	1540	no data	n.a.
2002	3366[4]	1608	0.4483	2237 (18)
2003	no data	no data	no data	n.a.
2004	3055[5]	1578	no data	n.a.

1. Based on the sum of the Marmot, Sugarloaf, Chowiet, Chirokof, and Outer Island rookery's pup counts. Table 8 in Fritz, L. W. and C. Stinchcomb. 2005. Aerial and ship-based surveys of Steller sea lions (*Eumetopias jubatus*) in the western stock in Alaska, June and July 2003 and 2004. U.S. Department of Commerce., NOAA Tech. Memo. NMFS-AFSC-153, 56 p. and Sease, J. L., J. P. Lewis, D. C. McAllister, R. L. Merrick and S. M. Mello. 1993. Aerial and ship-based surveys of Steller sea lions (*Eumetopias jubatus*) in Southeast Alaska, the Gulf of Alaska, and Aleutian Islands during June and July 1992. U.S. Department of Commerce., NOAA Tech. Memo.

NMFS-AFSC-17, per interpolation discussed in supplementary methods. The 1978 Outer Island, pup count was interpolated (interpolated value = 843) since the actual count was a rough estimate from a boat rather than a ground count.

2. The nonpup here is the nonpup count for trend rookeries and haulouts. Table 4 in Sease, J. L., J. P. Lewis, D. C. McAllister, R. L. Merrick and S. M. Mello. 1993. Aerial and ship-based surveys of Steller sea lions (*Eumetopias jubatus*) in Southeast Alaska, the Gulf of Alaska, and Aleutian Islands during June and July 1992. U.S. Department of Commerce., NOAA Tech. Memo. NMFS-AFSC-17.
3. Table 4 in Sease, J. L., and T. R. Loughlin. 1999. Aerial and ship-based surveys of Steller sea lions (*Eumetopias jubatus*) in Alaska, June and July 1997 and 1998. U.S. Department of Commerce., NOAA Tech. Memo. NMFS-AFSC-100.
4. Table 3 in Sease, J. L., and C. J. Gudmundson. 2002. Aerial and ship-based surveys of Steller sea lions (*Eumetopias jubatus*) from the western stock in Alaska, June and July 2001 and 2002. U.S. Department of Commerce., NOAA Tech. Memo. NMFS-AFSC-100.
5. Table 4 in Fritz, L. W. and C. Stinchcomb. 2005. Aerial and ship-based surveys of Steller sea lions (*Eumetopias jubatus*) in the western stock in Alaska, June and July 2003 and 2004. U.S. Department of Commerce., NOAA Tech. Memo. NMFS-AFSC-153. This is the count adjusted for the increased accuracy of the new medium-format photography which replaced the 35mm photographs used previously. This adjustment is based on a cross-validation discussed in Fritz and Stinchcomb (2005). The unadjusted count was 2944.
6. The *J/T* measurement method was initially presented in Holmes and York (2003). The measurements listed here do not exactly match those in Holmes and York (2003) since more haul-out measurements were taken to supplement those used in that paper.
7. Interpolated based on rookery only counts these years.

Table A2. The raw data from the western Gulf of Alaska used in Figure 3. Footnote references are the same as for Table A1 except where supplemental information is added below table.

Year	Non-pup count	Pup count[1]	*J/T* metric[6]	Sample size for *J/T* metric # of measurements (# of haulouts)
1976	8311[2]	no data	no data	n.a.
1977	no data	no data	no data	n.a.
1978	15229[7]	no data	no data	n.a.
1979	12128[7]	9351	no data	n.a.
1980	no data	no data	no data	n.a.
1981	no data	no data	no data	n.a.
1982	no data	no data	no data	n.a.
1983	no data	no data	no data	n.a.
1984	no data	5700	no data	n.a.
1985	6275[2]	4985	0.3997	3225 (7)
1986	no data	no data	no data	n.a.
1987	no data	no data	no data	n.a.
1988	no data	no data	no data	n.a.
1989	3908[2]	2771	0.4356	808 (6)
1990	3915[2]	2271	0.4673	1130 (6)
1991	3734[2]	2036	0.4608	1569 (10)
1992	3720[2]	1879	0.5015	1960 (13)
1993	no data	1857	no data	n.a.
1994	3982[3]	1662	no data	n.a.
1995	no data	no data	no data	n.a.
1996	3741[3]	1605	0.4247	3567 (17)
1997	3633[3]	no data	0.4337	3525 (15)
1998	3361[4]	1493	0.3927	2865 (16)
1999	no data	no data	no data	n.a.
2000	2840[4]	1451	0.4443	1908 (17)
2001	no data	1466	no data	n.a.
2002	3221[4]	1487	0.4273	1898 (18)
2003	no data	1432	no data	n.a.
2004	3456[5]	1593	no data	n.a.

1. References are the same as for Table A1. Pup count is a sum of counts on the Atkins, Chernabura, Clubbing Rocks and Pinnacle Rocks rookeries.

Table A3. The raw data from the eastern Aleutian Islands used in Figure 3. Footnote references are the same as for Table A1 except where supplemental information is added below table.

Year	Non-pup count	Pup count[1]	*J/T* metric[6]	Sample size for *J/T* metric # of measurements (# of haulouts)
1975	19769[2]	no data	no data	n.a.
1976	19743	no data	no data	n.a.
1977	19195	no data	no data	n.a.
1978	no data	no data	no data	n.a.
1979	no data	no data	no data	n.a.
1980	no data	no data	no data	n.a.
1981	no data	no data	no data	n.a.
1982	no data	no data	no data	n.a.
1983	no data	no data	no data	n.a.
1984	no data	no data	no data	n.a.
1985	7505[2]	4778	0.4758	2717 (12)
1986	no data	no data	no data	n.a.
1987	no data	no data	no data	n.a.
1988	no data	no data	no data	n.a.
1989	3032[2]	no data	0.3674	215 (4)
1990	3801[2]	2075	0.5169	563 (3)
1991	4231[2]	2119	0.4687	879 (11)
1992	4839[2]	no data	0.4789	1564 (14)
1993	no data	1879	no data	n.a.
1994	4421[3]	1756	no data	n.a.
1995	no data	no data	no data	n.a.
1996	4716[3]	no data	0.4232	1635 (16)
1997	no data	no data	0.4709	2064 (15)
1998	3847[4]	1474	0.4769	2661 (14)
1999	no data	no data	no data	n.a.
2000	3840[4]	1516	0.4995	1996 (14)
2001	no data	no data	no data	n.a.
2002	3956[4]	1525	0.4400	2234 (19)
2003	no data	no data	no data	n.a.
2004	4707[5]	1744	no data	n.a.

1. References are the same as for Table A1. Pup count is a sum of pup counts on the Adugak, Akun, Akutan, Bogoslof, and Ugamak rookeries.

Appendix B A critical evaluation of the assumptions affecting the modeling results

We subjected our analysis to many different tests of its sensitivity to the various assumptions that we made and we found that the pattern of decreasing birth rate combined with increasing survivorship is very robust to all except two central assumptions about constant observability and sex-ratio over the time period analyzed. If these assumptions are systematically violated, this would alter our basic conclusion concerning a long-term decline in birth rate. We address these assumptions here.

The assumption that observability of animals has been steady

We assume that while there are year-to-year fluctuations in the observability of animals, there has not been a systematic increase (or decrease) in observability. If there has been a systematic increase in observability over the 30-year period analyzed in this study, this would mean that the nonpup counts in the latter years of the survey are overestimating the nonpup numbers relative to the early years of the survey. Such a systematic overestimation of nonpup numbers would mean that the population in the CGOA has actually continued its 1980s decline and the observed stabilization in population numbers is an artifact of increased observability. If observability were sufficiently increased, the true nonpup to pup ratio would not have increased as seen in Figure 3a, and the model fits would not have indicated a decline in birth rate. In this case, to explain the population decline (which is obscured by increased observability), survivorship would have to have been declining throughout the 1990s and onward. The reasons why this is implausible are:

1) To negate the increasing trend in nonpup to pup ratios, the current nonpup count would need to be inflated by ca. 67%. Thus a significant change in observability is needed to negate our conclusions.
2) The nonpup trend survey is based on a consistent set of trend haul-outs and rookeries that have been surveyed every year since the early 1980s. The fraction of the population on the trend sites fluctuates year-to-year but has not been systematically increasing. The survey covers a large geographic area – the entire CGOA – so it averages over local variability. The same survey methods, including date, aircraft types, and photographic methods, have been used. There have been no significant changes in methodology, until 2004.
3) Branding studies in the late 1980s and in 2000-2003 found that juvenile survivorship severely declined in the 1980s (as the model also concluded), but that in the early 2000s, juvenile survivorship increased closer to pre-decline levels (as the model here also concluded). None of the biological factors that are hypothesized to impact Steller sea lions would be expected to cause adult survivorship to decline while juvenile survivorship increased. To the contrary, it biologists expect that juvenile survivorship is more sensitive than adult survivorship.
4) Given that survey methods have not changed, observability should only increase by Steller sea lions spending less time in the water during the day. However, the survey is done during the height of the breeding season. Reproductive males defending a territory rarely leave their territories at this time, and females leave for foraging primarily in the evening and return by morning.

5) Steller sea lions do show predator avoidance when killer whales are present and will leave the water. However, the entire CGOA is photographed in one to two days, and there are not enough killer whales to patrol the entire CGOA at once, particularly since only a small number of killer whales in the Gulf of Alaska appear to specialize on Steller sea lions. Even if killer whales happen to scare every sea lion onto the rocks at one of the major rookeries, it would not cause a substantial increase in the CGOA-wide survey count since the survey includes such a large number of rookeries and haul-outs.

The assumption that the sex ratio has been constant

We implicitly assume that the sex-ratio has been steady, albeit showing year-to-year fluctuations, when we are fitting the model to the non-pup count, which includes males and females. If the fraction of males increased substantially through the 1980s and 1990s, then again the non-pup survey is not giving a consistent measure of the number of non-pup females, and it would have a similar effect on our conclusions as would a systematic change in observability. A change in the sex ratio that would be sufficient to change our results appears implausible for the following reasons:

1) The change in sex ratio would have to be extreme to negate the decline in pup to non-pup ratios, specifically from 70% of non-pups being female (the approximate proportion in the late 1970s and in 2004) to 40% of non-pups being female in 2000-2004. Mammals with harem social structures like Steller sea lions are characterized by female dominated sex ratios in adults. A change to a male-dominated sex ratio would be extremely unusual.

2) The approximate fraction of the nonpups that are females can be calculated for the late 1970s based on the male and female survivorship schedules estimated for that period, and the estimate is that ca. 70% of the population was female. This is the same approximate fraction observed in high-resolution photographs of CGOA rookeries and haul-outs in 2004. In addition, there has been no observed change in the sex-ratio of pups (which is approximately 50/50) throughout the survey period.

Thus the available data are not consistent with a large change in sex ratio. This is not to argue that there have not been sex ratio changes over the years. In fact during the declines in the 1980s, the ratio of males to females on Marmot Island did increase, however the magnitude of observed change is much less than the change needed to reverse the conclusions concerning declining birth rate.

The assumption that the J/T ratio was not affected by changes in the number of haulouts sampled in the 1980s versus 1990s

The *J/T* was analyzed by including only those haulout surveyed for all years, those surveyed regularly in the 1990s, and all surveyed haulouts. The results are shown in Figure B1.

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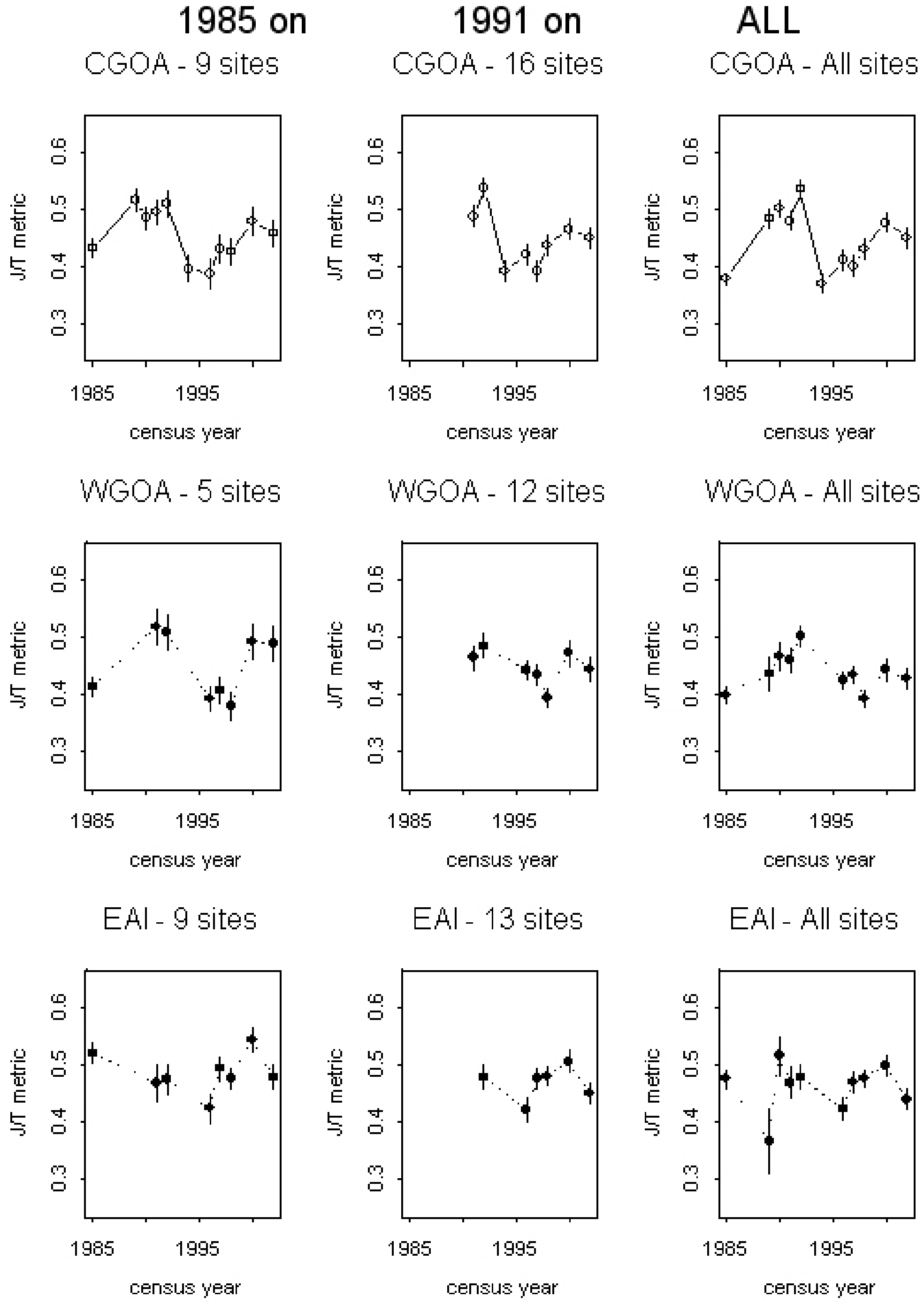
Figure B1. *J/T* ratio using different sets of haulouts.



Appendix C Life-history matrices

The 32 x 32 female-only age-structured life-history matrix for Steller sea lions (**Y** in Eq. 5 in the main text) is shown in Table 1 (main text). The 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, $\vec{N}_{t+1} = \mathbf{Y} \times \vec{N}_t$, is performed, the first element of $\vec{N}_{t+1t}$ 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 s_i and f_i terms in **Y** have been estimated different ways in different published studies based on data from 1975-1978 on Marmot Island, and these different estimates give rise to the four different life-history matrices are used in this study. Although each matrix is based on a published matrix, there are some slight modifications, namely a non-flat juvenile survivorship pattern across all matrices and inclusion of neonate survivorship. The number of female 1-month old pups produced by females of age *i* equals f_i, the late-term pregnancy rate times 0.5 to get female fetuses only, multiplied by s_n, neonate survivorship from age 0 (late-term fetus) to age 1-month when the pup survey occurs. This early pup survivorship was estimated as 0.949 from the average of the fraction of dead pups observed during the 1978 and 1979 pup counts in the CGOA: 492 (dead) to 6720 (live) in 1978 and 526 (dead) to 14763 (live) in 1978. The rest of the s_i and f_i terms which specify the survivorship and fecundity schedule for each matrix are discussed below and given in Table C1.

A matrix based on Calkins and Pitcher (1982) – CP1982

For this matrix, the survivorships, s_i, were those estimated originally by Calkins and Pitcher (1982) as presented in their Table 24. These estimates are from the age-distribution observed in the longitudinal sample of Steller sea lions around Marmot Island in the 1970s, which was done by shooting a random sample of animals from the population. Given their smaller size and lack representation near rookeries, individuals younger than 3 years were not equally sampled and were excluded from the analyses. Age was determined by counting the enamel layers in cross-sections of the canine teeth, and pregnancy rates were determined from pregnancies observed in the sampled females. The survivorships in Table C1 are taken from York (1994) Table 1 with the exception of s_0, s_1 and s_2. Juvenile survivorship could not be estimated directly from the data. Instead, York (1994) and Calkins and Pitcher (1982), set juvenile survivorship such that the resulting matrix would be stable (maximum eigenvalue equals 1.0). York (1994) made juvenile survivorship equal for the 1st three years while Calkins and Pitcher (1982) had juvenile survivorship increasing with age. In this analysis, we used Calkins and Pitcher's method, which eliminates a sudden jump from older juvenile survival to young adult survival. Thus s_1 and s_2 increase linearly from s_0 towards s_3, and s_0 is set so that the matrix is stable. Late-term pregnancy rate, f_i, is based on 'percent mature' x 'birth rate' in Table 26 in Calkins and Pitcher (1982) x 0.5 pup sex ratio. 'birth rate' is not precisely birth rate, however, rather it is late-term pregnancy rate. The f_i given in Table C1 are from York (1994), Table 1. Note that the age or i column in both York (1994) and Calkins and Pitcher (1982) is confusing. Early maturing females first become mature at age 3 but give birth at age 4, so f_i is 0 for age 0-3.

Winship and Trites (2006) used a very generic model of Steller sea lions based on the Calkins and Pitcher survivorship and fecundity schedules. The matrix (Table C1) has high adult survivorship, lower age 1-3 survivorship, and a uniform late-term pregnancy rate after age 5. For this study, we changed juvenile survivorship so that juvenile survivorship increased linearly from s_0 to s_4 as for the other matrices. If this is not done, the time-varying model can have the biologically odd behavior of high juvenile survivorship (age 1-3) followed by a sudden step-drop to a much lower survivorship at age 4. No animals are allowed to live beyond age 20 in this model, thus the model has fecundity senescence of a sort since no animals give birth after age 20.

Matrix based on York (1994)'s re-analysis of survivorship rates – Y1994

The Calkins and Pitcher (1982) survivorships result in an equilibrium age-distribution that does not precisely fit the observed age-distribution. York (1994) re-estimated the Calkins and Pitcher (1982) survivorships using a Weibull hazard model which is a standard model for survivorship. The re-estimated survivorships result in an age-distribution that closely matches the sampled cumulative age-distribution. Table C1 gives the re-estimated survivorship schedule.

There are two differences between the matrix used in this paper and the matrix published in York (1994) in Table 1 in that paper. York (1994) made juvenile survivorship equal for the 1st three years. Here, we used Calkins and Pitcher's method as above and allowed juvenile survivorship to increase with age. Thus s_1 and s_2 were set to increase linearly from s_0 towards s_3, and s_0 adjusted so that the matrix is stable. The second difference is in the f_i terms. In the matrix described in York (1994), females erroneously give birth the year that they become pregnant, whereas females give birth in the year after becoming pregnant. Thus the fecundities should be shifted forward by one year. This error is corrected in the f_i values given in Appendix A. This same error appears in the matrix given in Holmes and York (2003). This error does not change the conclusions of either paper, although it does change slightly the estimated natality rate in Holmes and York (2003).

Matrix based on a re-analysis of the pregnancy data -- HFYS

York (1994) did not re-analyze the age-dependent pregnancy rates used in Calkins and Pitcher (1982), and there were a number of inconsistencies between the actual pregnancy data collected in the 1970s and the age-specific rates presented in Calkins and Pitcher (1982) and later in York (1994). In particular, Calkins and Pitcher (1982) and York (1994) set f_i at a constant level after age 6; however no late-term pregnancies were observed in females over the age of 21. Data on fecundity senescence in pinnipeds is limited due to the lack of 20-year plus studies of branded individuals. The best data are from monk seals in Hawaii (Thea Johanos-Kam, NMFS, personal communication), northern fur seals (*Callorhinus ursinus*) on the Pribilof Islands (Lander 1981), harp seals (*Pagophilus groenlandicus*) (Bowen et al. 1981), and grey seals (*Halichoerus grypus*) (Boyd 1985). Fecundity senescence has been measured in the monk seals, harp seals and fur seals, but not in grey seals.

We revisited the raw pregnancy data from Marmot Island and re-estimated the f_i's as follows. We estimated late-season pregnancy rates for female Steller sea lions as the predicted values from a logistic regression model (McCullagh and Nelder 1989) of the following form:

$$\log\left(\frac{p_{a,m}}{1-p_{a,m}}\right) \sim \beta_a + \gamma\, m, \qquad \text{(C1)}$$

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. We used the statistical program R (R Development Core Team 2004) for model estimation and prediction.

The form of this model is conceptually different from that of Calkins and Pitcher (1982). They modeled late-season 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 to account for reproductive failures. 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 fecundity schedule that includes fecundity senescence.

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Table C1. Fecundity and survivorships terms used in the four life-history matrices. Matrix codes refer to matrices based on different papers: WT2006 (Winship and Trites 2006), CP1982 (Calkins and Pitcher 1982), Y1994 (York 1994), and HFYS (this paper). In all matrices, $s_n = 0.949$.

i	f_i	f_i	f_i	f_i	s_i	s_i	s_i	s_i
age	WT2006	CP1982	Y1994	HFYS	WT2006	CP1982	Y1994	HFYS
0[*]	0	0	0	0	0.8001[3]	0.7420[3]	0.7680[3]	0.7845[3]
1	0	0	0	0	0.8334[3]	0.7840[3]	0.8221[3]	0.8331[3]
2	0	0	0	0	0.8667[3]	0.8260[3]	0.8761[3]	0.8316[3]
3	0	0	0	0	0.9	0.8680[1]	0.9302[1]	0.9302[1]
4	0	0.1008[1]	0.1008[1]	0.0480[2]	0.9	0.8790	0.9092	0.9092
5	0.315	0.17955	0.17955	0.1695	0.9	0.8880	0.8951	0.8951
6	0.315	0.26145	0.26145	0.2215	0.9	0.8930	0.8839	0.8839
7	0.315	0.315	0.315	0.27950	0.9	0.8980	0.8746	0.8746
8	0.315	0.315	0.315	0.3285	0.9	0.8740	0.8665	0.8665
9	0.315	0.315	0.315	0.3285	0.9	0.8990	0.8593	0.8593
10	0.315	0.315	0.315	0.3285	0.9	0.8930	0.8527	0.8527
11	0.315	0.315	0.315	0.3885	0.9	0.8960	0.8468	0.8468
12	0.315	0.315	0.315	0.3885	0.9	0.8950	0.8412	0.8412
13	0.315	0.315	0.315	0.3885	0.9	0.8950	0.8360	0.8360
14	0.315	0.315	0.315	0.3885	0.9	0.8950	0.8312	0.8312
15	0.315	0.315	0.315	0.3885	0.9	0.8950	0.8266	0.8266
16	0.315	0.315	0.315	0.3885	0.9	0.8950	0.8223	0.8223

17	0.315	0.315	0.315	0.2570	0.9	0.8950	0.8182	0.8182
18	0.315	0.315	0.315	0.2570	0.9	0.8950	0.8142	0.8142
19	0.315	0.315	0.315	0.2570	0.9	0.8950	0.8105	0.8105
20	0.315	0.315	0.315	0.2570	0.9	0.8950	0.8069	0.8069
21	0.315	0.315	0.315	0.2570	0	0.8950	0.8034	0.8034
22	0	0.315	0.315	0	0	0.8950	0.8001	0.8001
23	0	0.315	0.315	0	0	0.8950	0.7968	0.7968
24	0	0.315	0.315	0	0	0.8950	0.7937	0.7937
25	0	0.315	0.315	0	0	0.8950	0.7907	0.7907
26	0	0.315	0.315	0	0	0.8950	0.7878	0.7878
27	0	0.315	0.315	0	0	0.8950	0.7850	0.7850
28	0	0.315	0.315	0	0	0.8950	0.7822	0.7822
29	0	0.315	0.315	0	0	0.8950	0.7795	0.7795
30	0	0.315	0.315	0	0	0.8950	0.7769	0.7769
31	0	0.315	0.315	0	0	0	0	0

f_i is the fraction of age i females with late-term pregnancies x 0.5 to get female fetuses only (note age i females mate and become impregnated at age i-1). s_i is the survivorship from age i to i+1.

* age 0 denotes 1-month of age which is the age of pups when the survey occurs.

1. Table 1 from York (1994). Note that in Table 1 (York 1994) the age ‘To’ column represents the numbering for f_i, whereas the age ‘From’ column represents the numbering for s_i.
2. Re-estimated in this paper from the original 1970s data. See notes above.
3. s_1 and s_2 increase linearly from s_0 towards s_3, and s_0 is set so that the matrix is stable.

Appendix D Parameter estimates and AIC_c values for model fits

Table D1. Maximum likelihood estimated historical survivorship and birth rate relative to pre-decline levels. The number of free parameters, K, is the number of scaling factors, 3, times the number of time periods, 3 to 4, plus 3 constants, p_1, p_2, p_3, and the 3 variances in the likelihood function. $p_{j,k}$ is the scaling factor for juvenile survivorship in time period k. Juvenile survivorship in time period k is (pre-decline juvenile survivorship) x $p_{j,k}$. $p_{a,k}$ is the scaling factor for adult survivorship in time period k. $p_{f,k}$ is the scaling factor for birth rate in time period k. For all models, the first time period starts in 1983, and the second starts in 1988. The third and fourth (if present) start in the first and second years in column 1, respectively. The Leslie matrices are described in Appendix C.

Time periods	Leslie matrix	$\Delta\mathrm{AIC}_c$	K	$p_{j,1}$	$p_{j,2}$	$p_{j,3}$	$p_{j,4}$	$p_{f,1}$	$p_{f,2}$	$p_{f,3}$	$p_{f,4}$	$p_{a,1}$	$p_{a,2}$	$p_{a,3}$	$p_{a,4}$
1997	HFYK	5.454	15	0.436	0.877	1.241	-	0.908	0.841	0.813	-	0.879	0.921	0.963	-
1997	Y1994	7.884	15	0.421	0.882	1.267	-	0.891	0.846	0.809	-	0.89	0.913	0.957	-
1997	CP1982	15.133	15	0.443	0.93	1.311	-	0.924	0.873	0.83	-	0.872	0.892	0.952	-
1997	WT2006	4.9	15	0.506	0.928	1.25	-	0.931	0.86	0.813	-	0.863	0.902	0.965	-
1998	HFYK	7.148	15	0.43	0.911	1.241	-	0.903	0.839	0.787	-	0.881	0.918	0.981	-
1998	Y1994	10.631	15	0.41	0.911	1.267	-	0.885	0.844	0.81	-	0.893	0.91	0.971	-

1998	CP1982	17.332	15	0.442	0.998	1.311	-	0.929	0.902	0.84	-	0.869	0.882	0.963	-
1998	WT2006	10.993	15	0.504	0.952	1.25	-	0.934	0.869	0.844	-	0.863	0.899	0.971	-
1999	HFYK	12.193	15	0.39	0.901	1.241	-	0.897	0.829	0.813	-	0.885	0.925	0.996	-
1999	Y1994	17.131	15	0.454	0.955	1.267	-	0.899	0.871	0.872	-	0.886	0.897	0.976	-
1999	CP1982	22.312	15	0.393	0.991	1.311	-	0.913	0.872	0.879	-	0.878	0.888	0.974	-
1999	WT2006	17.42	15	0.487	0.945	1.25	-	0.925	0.844	0.865	-	0.866	0.905	0.988	-
1992;1997	HFYK	0	18	0.42	0.734	0.565	0.935	0.869	0.762	0.703	0.641	0.899	0.928	1.002	1.068
1992;1997	Y1994	3.46	18	0.465	0.787	0.603	0.967	0.882	0.805	0.701	0.613	0.894	0.916	0.988	1.053
1992;1997	CP1982	6.385	18	0.481	0.818	0.621	0.998	0.903	0.827	0.725	0.628	0.882	0.889	0.965	1.029
1992;1997	WT2006	6.197	18	0.453	0.731	0.592	0.894	0.887	0.755	0.67	0.585	0.884	0.921	0.989	1.077
1993;1997	HFYK	7.341	18	0.42	0.739	0.591	0.986	0.871	0.754	0.724	0.657	0.898	0.934	1	1.053
1993;1997	Y1994	10.365	18	0.493	0.827	0.666	1.054	0.89	0.82	0.732	0.645	0.889	0.908	0.978	1.029
1993;1997	CP1982	14.262	18	0.506	0.85	0.675	1.08	0.91	0.834	0.754	0.657	0.877	0.887	0.961	1.013
1993;1997	WT2006	9.436	18	0.491	0.794	0.682	0.998	0.905	0.783	0.707	0.621	0.876	0.915	0.976	1.045
1992;1998	HFYK	4.161	18	0.42	0.74	0.622	0.974	0.871	0.761	0.7	0.646	0.899	0.929	0.998	1.075

1992;1998	Y1994	8.877	18	0.451	0.783	0.635	0.982	0.874	0.784	0.684	0.615	0.899	0.922	0.986	1.069
1992;1998	CP1982	9.504	18	0.428	0.772	0.611	0.968	0.882	0.78	0.69	0.608	0.893	0.901	0.969	1.056
1992;1998	WT2006	17.248	18	0.552	0.778	0.798	1.104	0.909	0.792	0.719	0.67	0.874	0.902	0.958	1.031
1993;1998	HFYK	10.82	18	0.395	0.712	0.627	0.966	0.864	0.738	0.708	0.647	0.902	0.941	1.006	1.075
1993;1998	Y1994	16.075	18	0.523	0.868	0.823	1.191	0.897	0.835	0.757	0.706	0.885	0.898	0.951	1.005
1993;1998	CP1982	17.738	18	0.479	0.828	0.716	1.085	0.896	0.801	0.727	0.649	0.885	0.893	0.959	1.03
1993;1998	WT2006	17.327	18	0.543	0.829	0.869	1.164	0.92	0.815	0.747	0.697	0.869	0.902	0.952	1.011
1992;1999	HFYK	12.072	18	0.433	0.731	0.678	1.034	0.868	0.757	0.694	0.668	0.898	0.927	0.998	1.075
1992;1999	Y1994	17.105	18	0.47	0.779	0.684	1.013	0.88	0.794	0.679	0.628	0.895	0.918	0.99	1.075
1992;1999	CP1982	16.272	18	0.378	0.695	0.578	0.897	0.871	0.753	0.653	0.593	0.9	0.911	0.987	1.081
1992;1999	WT2006	22.803	18	0.594	0.796	0.935	1.25	0.923	0.825	0.776	0.748	0.868	0.888	0.938	1.005
1993;1999	HFYK	15.595	18	0.409	0.705	0.691	1.013	0.865	0.738	0.703	0.663	0.901	0.939	1.007	1.075
1993;1999	Y1994	20.396	18	0.55	0.867	0.937	1.266	0.909	0.86	0.792	0.752	0.879	0.89	0.939	0.992
1993;1999	CP1982	22.458	18	0.597	0.916	0.964	1.311	0.943	0.904	0.827	0.778	0.862	0.866	0.927	0.983
1993;1999	WT2006	21.272	18	0.574	0.828	0.964	1.25	0.93	0.838	0.786	0.746	0.865	0.894	0.942	1

Table D2. Maximum likelihood estimated of the constants and variances for each model. See text for explanation of the constants. Column 3 translates to the expected average thousands of pre-decline female pups in the CGOA. The value, p_2, from column 4 translates is the scaling factor that translates the nonpup trend count into the total (unobserved) number of nonpup females in the population: $(1/p_2)$ x nonpup trend count = total number (unobserved) of nonpup females. p_3 is the scaling factor for the juvenile fraction metric (see text).

Time periods	Leslie matrix	p_1 (÷1000)	p_2	p_3	σ^2 nonpup (x1000)	σ^2 pup (x1000)	σ^2 J/T (x1000)
1997	HFYK	9.52	0.458	0.359	3.097	0.914	2.761
1997	Y1994	9.50	0.478	0.368	3.121	0.892	3.555
1997	CP1982	9.52	0.498	0.379	3.662	1.183	3.68
1997	WT2006	9.53	0.446	0.37	3.659	0.794	2.521
1998	HFYK	9.53	0.456	0.359	4.362	0.811	2.392
1998	Y1994	9.51	0.478	0.369	4.744	0.749	3.254
1998	CP1982	9.52	0.5	0.405	5.575	0.955	3.431

1998	WT2006	9.50	0.452	0.377	5.66	0.873	2.227
1999	HFYK	9.51	0.462	0.347	5.497	0.8	2.81
1999	Y1994	9.50	0.482	0.396	6.719	0.847	3.15
1999	CP1982	9.51	0.502	0.387	7.452	0.891	4.023
1999	WT2006	9.51	0.452	0.364	7.683	0.908	2.409
1992;1997	HFYK	9.52	0.458	0.229	2.403	0.934	0.527
1992;1997	Y1994	9.52	0.472	0.253	2.426	1.195	0.501
1992;1997	CP1982	9.53	0.496	0.254	2.742	1.312	0.483
1992;1997	WT2006	9.52	0.45	0.22	2.762	1.148	0.571
1993;1997	HFYK	9.53	0.456	0.241	2.538	0.917	0.975
1993;1997	Y1994	9.53	0.47	0.287	2.534	1.178	0.901
1993;1997	CP1982	9.54	0.494	0.284	2.956	1.257	0.946
1993;1997	WT2006	9.53	0.446	0.259	2.77	0.992	0.937
1992;1998	HFYK	9.51	0.458	0.233	3.158	0.883	0.576
1992;1998	Y1994	9.52	0.474	0.246	3.845	1.106	0.49

1992;1998	CP1982	9.52	0.498	0.224	4.279	1.062	0.475
1992;1998	WT2006	9.53	0.444	0.282	3.175	1.002	1.56
1993;1998	HFYK	9.52	0.458	0.227	3.132	0.912	1.019
1993;1998	Y1994	9.53	0.468	0.331	3.359	0.938	1.425
1993;1998	CP1982	9.53	0.494	0.269	4.164	1.088	1.001
1993;1998	WT2006	9.54	0.444	0.31	3.051	0.971	1.729
1992;1999	HFYK	9.54	0.456	0.242	3.219	0.935	1.048
1992;1999	Y1994	9.52	0.472	0.255	3.489	1.527	0.737
1992;1999	CP1982	9.52	0.5	0.194	3.712	1.418	0.702
1992;1999	WT2006	9.53	0.444	0.328	3.125	0.949	2.852
1993;1999	HFYK	9.53	0.456	0.237	2.813	1.026	1.543
1993;1999	Y1994	9.52	0.47	0.364	2.976	0.999	2.287
1993;1999	CP1982	9.50	0.494	0.377	3.006	1.215	2.074
1993;1999	WT2006	9.53	0.444	0.338	2.849	0.972	2.724