

Fecundity declines in Steller sea lions suggest new conservation and research priorities

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From the mid-1970s through 2000, the western stock of Steller sea lion (*Eumetopias jubatus*) declined by over 80%¹. This fish- and squid-eating predator, the largest eared seal (Otariidae), is distributed across the North Pacific Ocean. The western stock breeds on rookeries west of 144°W in Alaska and Russia and the eastern stock breeds to the east and south to the Channel Islands off California. In 1997, the western stock of Steller sea lion was listed as endangered under the U.S. Endangered Species Act, which created new challenges for managers of Alaska's billion dollar groundfish fishery, the most productive in the United States^{2,3,4,5}. Since 2000, over \$120 million^{4,6}, the largest budget for a U.S. endangered species, has been devoted to reducing uncertainty about the factors negatively affecting the population: food limitation, killer whale predation, disease, and direct or indirect impacts from fishing¹. But despite well-funded and large-scale coordinated research⁴, the complexity, indirectness and cumulative effects of these factors have made it difficult to determine which were responsible for the decline and which are primary threats to recovery¹. Here we show how population models using data on the numbers and age distribution of Steller sea lions in the central Gulf of Alaska were used to estimate the historical changes in survivorship and fecundity that drove the decline. We found strong agreement among models for a steady 30-year decline in fecundity, while juvenile survivorship increased to pre-decline levels after a severe drop in the early 1980s, which precipitated the initial population collapse^{7,8} as well as considerable research attention^{2,4,6}. Since 2000, population numbers have stabilized, largely due to increases in survivorship, indicating that direct sources of mortality (e.g., predation) are not primary threats to recovery. Continued declines in fecundity suggest that research should be refocused on indirect factors affecting female condition (e.g., disease, contaminants, natural or anthropogenic food limitations).

The historical record of change in the age distribution within a population is a reflection of underlying changes in the demographic rates, the survivorships and fecundities, which have occurred over time⁹. Life-history models with temporally varying demographic rates can be used to determine what changes in survivorship and fecundity are consistent with the observed time series of population numbers and age distribution^{9,10}. We used this approach to estimate relative changes in Steller sea lion vital rates in the Central Gulf of Alaska (CGOA; Figure 1) from 1976 to 2004. The CGOA has historically been a center of Steller sea lion abundance, and field studies in the 1970s on Marmot Island, where the largest pre-decline sea lion breeding and birthing

site (rookery) was located, provided the data to build an age-specific model for the pre-decline population. We modeled the CGOA population as closed based on previous research supporting this metapopulation structure¹¹.

Three different life-history matrices were used. Each was estimated with different assumptions concerning the sea lion age and fecundity data collected on Marmot Island in the 1970s. To change these into time-varying models, we allowed survivorships and fecundity to change over time according to either shifts in oceanographic conditions¹² or observed changes in Steller sea lion rates of population decline¹¹. The models were fit to sea lion census data from the CGOA, consisting of counts of pups (at approximately 1 month of age) on the five major rookeries, counts of non-pups at haul-out and rookery sites, and a metric of the juvenile to adult ratio in the population (Figure 2). The model was fit using maximum-likelihood estimation assuming normally distributed errors in the data, with confidence intervals specified via likelihood profiling. Models were compared using AIC_c ¹³ with model fits penalized for the number of fitted parameters and model elements. See Methods and supplementary information for details.

The model with the lowest AIC_c was based on the life-history matrix with fecundity senescence and four demographic changes in 1983, 1988, 1993 and 1998 (fits shown with solid lines in Figure 2a-c). The vital rates estimated using this model show fecundity steadily declining from the mid-1980s to 66% of pre-decline levels in 1998-2004, concomitant with juvenile and adult survivorship increasing to near pre-decline levels after being severely reduced in the early-1980s (Table 1). This pattern was seen across all four life-history matrices and four time-period combinations (Figure 3). All models agreed on a very similar pattern of fecundity decline, mirroring the decline in pup-to-non-pup ratios (Figure 2d). For adult and juvenile survivorship, the models differed in the precise pattern of increase although generally agreed on steadily increasing juvenile and adult survivorship with current survivorship being near pre-decline levels (Figure 3).

During the 1980s when the western Steller sea lion population dropped 30% over a decade, a variety of field observations and data analyses pointed to low survivorship, particularly for juveniles, as the primary driver^{3,7,8,10}. 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^{1,14,15,16,17,18}. What has been less clear is what vital rate changes were responsible for the declines of the 1990s and what are the current vital rates limiting recovery. The most obvious direct mortality impacts, shooting (legal and illegal) and incidental take in fisheries, were greatly reduced by the 1990s^{1,14,19}. It has been suggested that another source of direct mortality, killer whale predation, increased and replaced the other declining direct factors^{1,16,20}, but the evidence for this hypothesis has been questioned^{21,22}. Our results corroborate the previous studies^{3,7,8,10} indicating a mid-1980s reduction in juvenile survivorship (Table 1), but after the mid-1980s, our analysis indicates that juvenile and adult survivorship steadily improved to pre-decline levels in the late-1990s. Estimates of juvenile survivorship of western Steller sea lion cohorts individually marked in 1987, 1988 and from 2000 to 2004 agree with our finding that juvenile survivorship increased over this period (NMML, unpublished data). Increases in survivorship, however, are not consistent with the hypothesis that killer whale predation

or some other type of direct mortality is currently limiting the population, at least in the CGOA, since high levels of direct mortality would appear as lower survivorship. Rather, our analyses are consistent with the counter hypothesis that direct sources of mortality have not had major impacts on this population since the mid-1990s, at least in the CGOA, and are not currently the primary threats to recovery.

The patterns we found are instead suggestive of impacts from indirect factors, with adult female reproduction rather than juvenile survivorship being predominantly affected. Nutritional stress from fisheries-induced or natural environmental changes in prey abundance, distribution or quality is the indirect factor that has received the most research attention^{14,17,18}, although the effects of diseases²³ and contaminants²⁴ have also been studied. Nutritional stress has been shown to be associated with increased late-term abortion rates, reduced early pup survival and reduced juvenile survival and adult survival, to a lesser degree¹⁷. Recent reviews of the evidence for nutritional limitation in the 1990s and 2000s have found that there is little support from studies on body condition, behavior or pup condition for the conjecture that Steller sea lions are experiencing acute nutritional limitation in the Gulf of Alaska at the present^{17,18}. However, these studies were conducted largely on juvenile sea lions, and there is little information on recent (since 1990) condition of adult females in the wild. 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^{12,17,19,25} and reductions in the abundance and local availability of prey related to commercial fisheries^{3,5,14}.

Bioaccumulation of contaminants, particularly organohalogens, is a documented concern for Arctic predators due to atmospheric cycling that causes the Arctic to be a worldwide sink for airborne pollutants^{26,27}. PCBs and related organohalogens are endocrine disruptors which have been shown to impair reproduction in mammals, including pinnipeds^{24,26,28}. Data on PCB levels in Steller sea lions is limited, however the data available indicate that mean early-1990s PCB levels in juveniles in the Gulf of Alaska were at levels that could compromise reproduction²⁴. The late-1980s and early-1990s juvenile cohort would have been the main reproductive class in the mid- to late-1990s. Nonetheless contaminant screening has not been comprehensive enough to be confident of contaminant levels in reproductive females or to determine if there are regional differences in contaminant levels that might explain regional differences in rates of decline²⁴. Disease is another indirect factor that would be consistent with reduced fecundity despite pre-decline survivorship levels. The limited available surveys have shown that Steller sea lions have high seropositivity for disease organisms, particularly *Chlamydophila psittaci* and caliciviruses, that are associated with reproductive failure in other mammals²³. However in the 1990s samples, seropositivity is high across both declining and non-declining populations, and it is unclear whether this seropositivity is linked to actual negative effects on Steller sea lion fecundity²³. In summary, nutritional limitation, contaminants and disease all have the potential to disrupt fecundity, but research on fecundity has been limited to date and contaminant and disease surveys have not been comprehensive enough to rule out these as factors causing reduced fecundity 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, pup-to-non-pup ratios remain well below the pre-decline levels of the

1970s, and our results point to steadily declining fecundity in a major part of the range, the central Gulf of Alaska. As a consequence, it appears premature to conclude from the small recent increases in non-pup counts alone that the western Steller sea lion is on the road to long-term recovery. Understanding the causes of a population's decline is complex and it is imperative that we undertake comprehensive research to understand how vital rates, and particularly fecundity, are linked to specific indirect factors: nutrition, contaminants and disease. While this research helps us determine the factors affecting the dynamics of the western Steller sea lion population, it may elucidate causes of population declines of other apex predators inhabiting the highly productive North Pacific ecosystem^{1,14, 29}.

METHODS

Data We used the range-wide census data collected by the National Marine Fishery Service on the western stock of Steller sea lions since the mid-1970s. These data consist of ground counts of pups (newborns) on the major rookeries and aerial photographic counts of non-pups on haul-outs and rookeries (Figure 2a,b). From the aerial photographs, we measured animals to derive a historical metric of the juvenile to adult ratio (Figure 2c). This data, references, and a discussion of the relationship between the unobserved true population counts and the observed population indices are provided in the supplementary methods.

Model We fit this data using a time-varying model, equation (1), for the CGOA Steller sea lion population dynamics 1976 to 2004:

$$\bar{N}_{t+1} = \mathbf{Y}_t \cdot \bar{N}_t \quad (1)$$

\bar{N}_t is the vector of the number of sea lions at each age (0-31 years) at time t . \mathbf{Y}_t is the 32 x 32 age-structured life-history model at time t that encapsulates how numbers at year t translate to numbers at year $t+1$. This matrix specifies the survivorships from age i to $i+1$ and the number of pups born to females age i in year t . We compared how models fit the data using three different life-history matrices, \mathbf{Y} 's, estimated from age and fecundity data collected on Marmot Island in the 1970s: the matrix estimated by Calkins and Pitcher (1982)³⁰, the re-estimated matrix by York (1994)⁸, and a new matrix estimated in this paper which was based on a re-analysis of pregnancy data from the 1970s and which incorporated the evidence for fecundity senescence. The life-history matrices are given in the supplementary tables. Their background and development is discussed in the supplementary methods.

In equation (1), we allowed juvenile survivorship (survivorship from age 0 to 1, 1 to 2, and 2 to 3), adult survivorship (age 3 to 4, 4 to 5 ...) and fecundity in \mathbf{Y}_t to change as a step-function, such that demographic rates were constant for a period of years and then changed by a scaling factor to a new rate. A separate scaling factor was used for juvenile survivorship, adult survivorship and adult fecundity. A step function was used based on analyses of the population growth rates¹¹ which indicated that there have been distinct periods with distinct population dynamics and based on research which shows that climatic and oceanographic physical parameters in the Bering Sea changed abruptly during different distinct time periods¹². We used models with two sets of time-period changes, along with two minor variations on those. Our first set was based on the

oceanographic periods¹²: 1970-1976, 1977-1988, 1989-1997, 1998-2004. The second time period combination was based on the time periods with different Steller sea lion population trends^{11,10}: 1970-1982, 1983-1987, 1988-1992, 1993-1997, 1998-2004. We added two additional sets of time periods by adding variations to the oceanographic time periods: changing the late-1980s shift to 1988 and adding an additional early 1990s shift. In total, thus, we compared 12 different models (3 life-history matrices x 4 time period possibilities). The matrix with scaled parameters is shown in the supplementary tables and discussed in the supplementary methods. The number of parameters varied in the models depending on the number of time-period changes. In addition, the analyses^{11,10} showing changes in population trends is based on data which also appear in our analysis, namely the CGOA non-pup data. For this reason, the model using the population-trend time periods was penalized with an extra four parameters to account for the fact that the number of time-periods was in effect partially estimated from the data at hand. The two variations on the time periods based on the oceanographic rates were each penalized by one parameter for the added time period change.

Model fitting and comparison The models were fit using maximum likelihood with a negative log-likelihood function, $S(\theta)$, based on normally distributed errors in the data¹⁰:

$$\begin{aligned}
S(\theta) = & \frac{1}{2} \left[\log \sigma_{\ln N}^2 \sum_{i=1}^k \ln(N_i) + \frac{1}{\sigma_{\ln N}^2} \sum_{i=1}^k (\ln(N_i) - \ln(p_1(\hat{J}_i + \hat{A}_i)))^2 \right. \\
& + \log \sigma_{\ln P}^2 \sum_{i=1}^n \ln(P_i) + \frac{1}{\sigma_{\ln P}^2} \sum_{i=1}^n (\ln(P_i) - \ln(p_2 \hat{P}_i))^2 \\
& \left. + \log \sigma_J^2 \sum_{i=1}^m (J/T)_i + \frac{1}{\sigma_J^2} \sum_{i=1}^m ((J/T)_i - (0.8 \hat{J}_i / (\hat{J}_i + p_3 \hat{A}_i)))^2 \right] \\
& + \text{a constant}
\end{aligned} \tag{2}$$

where N_i , P_i , and $(J/T)_i$ are the data: the i -th CGOA non-pup count, pup count, and the juvenile fraction, respectively. The variables, \hat{P}_i , \hat{J}_i , and \hat{A}_i are the model predictions of total pups, juveniles and adults. The relationship between the model's total number of female non-pups and the total number of male and female non-pups observed on trend sites is p_1 , and the relationship between the J/T fraction and the juvenile and adult numbers is p_3 . These were treated as free parameters. The relationship between the total pup count and the observed CGOA pup count was treated as a fixed parameter, $p_2 = 0.95$ based on both the nature of this data and the uniformity of p_2 estimates across models (see supplementary methods). The relationship between the data and the model values is discussed more fully in the supplementary methods. Confidence intervals on the estimated demographic scaling factors were estimated using one-dimensional likelihood profiling allowing all other parameters in equation (1) to be free¹⁰. The model fits to the data were compared using Akaike's information criterion (corrected for small sample size: AIC_c)¹³. The AIC_c values, maximum-likelihood estimates of the scaling factors, and the number of free parameters for each model are given in Table 5 in the Supplementary Information.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author contributions E.H and L.F. were the primary writers of this paper. E.H. did the model-fitting and development of the analysis. K.S. and L.F. worked on the measurements of sea lions from the census photographs. E.H., L.F. and K.S. worked together on assembling the data and data-error checking. A.Y. estimated the life-history matrices. E.H., L.F., and A.Y. reviewed the analyses, discussed the results and commented on the manuscript.

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Table 1. Estimated demographic rates relative to pre-decline levels for the best fit model

	Juvenile survivorship ML (95% CIs)	Adult survivorship ML (95% CIs)	Fecundity (pups/♀) ML (95% CIs)
1976-1982	1.0	1.0	1.0
1983-1988	0.44 (0.38, 0.50)	0.90 (0.88, 0.92)	0.87 (0.82, 0.91)
1989-1992	0.74 (0.68, 0.80)	0.94 (0.92, 0.96)	0.72 (0.69, 0.77)
1993-1998	0.61 (0.56, 0.67)	1.01 (0.99, 1.03)	0.67 (0.63, 0.70)
1999-2004	0.96 (0.89, 1.04)	1.08 (1.05, 1.08)	0.61 (0.58, 0.65)

Maximum likelihood estimates of juvenile survivorship, fecundity and adult survivorship relative to 1976 levels (pre-decline). The 95% confidence intervals, in parentheses, were determined by one-dimensional likelihood profiling allowing all other parameters in equation (1) 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.

Figure 1. Principal breeding locations (rookeries) in Alaska, USA, of the western (W of 144°W) and eastern stocks of Steller sea lion. Names of islands with rookeries in the central Gulf of Alaska are shown.

Figure 2. Historical trends in juvenile fraction, non-pup, and pup counts in the central Gulf of Alaska. The circles show the observed data. The lines show the estimates from the best-fitting temporally varying Leslie matrix model. In this model, juvenile survivorship, fecundity and adult survivorship were allowed to change in 1983, 1988, 1993, and 1998. a) Index of juvenile fraction from all photographed trend and non-trend haul-outs with a large male. b) Adult and juvenile (non-pup) counts on rookery and haul-out trend sites. c) Total pup counts from the five major central Gulf of Alaska rookeries. d) Ratio of pup-to-non-pup counts at trend haul-out and rookery sites in the central Gulf of Alaska.

Figure 3. Maximum likelihood estimates of the vital rates across all 12 model variants. The y-axes show the survivorship and fecundity rates relative to the 1970s pre-decline estimated rates. Table 5 in the Supplementary Information shows the AIC_c values for each model.

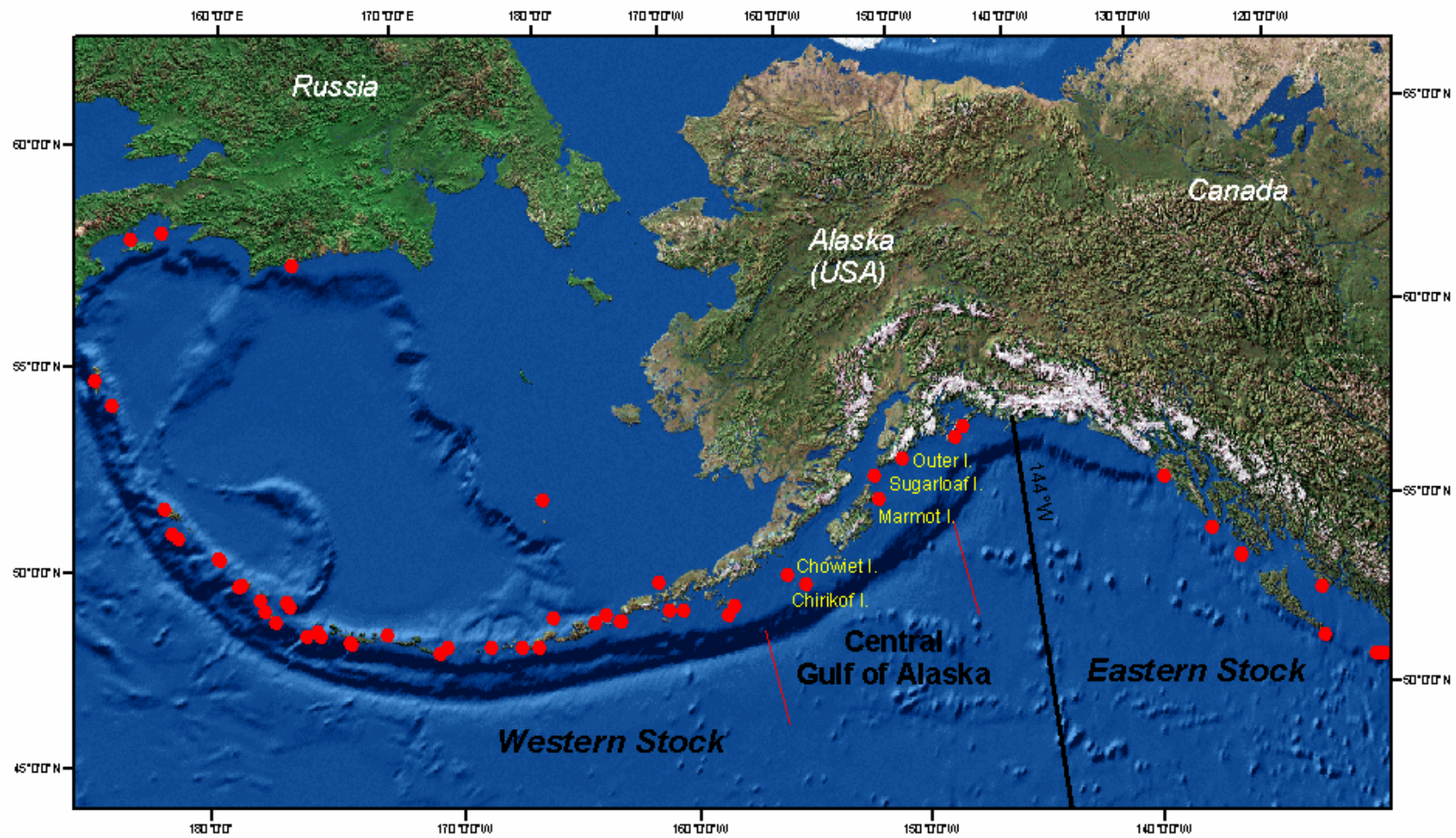


Figure 1

