Using Age Structure to Detect Impacts on Threatened Populations: a Case Study with Steller Sea Lions

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Abstract: *A delayed response to change is often a characteristic of long-lived species and presents a major challenge to monitoring their status. However, rapid shifts in age structure can occur even while population size remains relatively static. We used time-varying matrix models to study age-structure information as a tool for improving detection of survivorship and fecundity change and status. We applied the methods to Steller sea lions (*Eumetopias jubatus*), a long-lived endangered marine mammal found throughout the North Pacific Rim. Population and newborn counts were supplemented with information on the fraction of the population that was juvenile, obtained by measuring animals in aerial photographs taken during range-wide censuses. By fitting the model to 1976–1998 data, we obtained maximum-likelihood estimates and 95% confidence intervals for juvenile survivorship, adult survivorship, and adult fecundity in the mid-1980s, late 1980s, and 1990s. We used a series of nested models to test whether the data were best fit by a model with one, two, or three temporal changes in demographic rates, and we fit the models to different lengths of data to test the number of years of data needed to detect a demographic change. The declines in the early 1980s were associated with severely low juvenile survivorship, whereas declines in the 1990s were associated with disproportionately low fecundity. We repeated these analyses, fitting only to the count data without the juvenile-fraction information, to determine whether the age-structure information changed the conclusions and/or changed the certainty and speed with which demographic-rate changes could be detected. The juvenile-fraction data substantially improved the degree to which estimates from the model were consistent with field data and significantly improved the speed and certainty with which changes in demographic rates were detected.*

Utilización de la Estructura de Edades para Detectar Impactos en Poblaciones Amenazadas: Un Estudio de Caso con Lobo Marinos de Steller

Resumen: *Una respuesta diferida al cambio a menudo es una característica de especies longevas y presenta un reto mayor para el seguimiento de su condición. Sin embargo, pueden ocurrir cambios rápidos en la estructura de edades aun cuando la población permanece relativamente estática. Utilizamos modelos matriciales con variación de tiempo para estudiar información sobre la estructura de edades como una herramienta para mejorar la detección de cambio y condición de supervivencia y fecundidad. Aplicamos los métodos a los lobo marinos de Steller (*Eumetopias jubatus*), un mamífero longevo en peligro de extinción que se encuentra en las costas del Pacífico Norte. Los conteos de población y de recién nacidos fueron suplementados con información sobre la fracción de la población que era juvenil, obtenida de medir animales en fotografías aéreas tomadas durante censos en toda el área de distribución. Ajustando el modelo para datos de 1976–1998, obtuvimos estimaciones de la máxima probabilidad de supervivencia de juveniles, supervivencia de adultos y fecundidad de adultos con intervalos de confianza de 95% para mediados de los años 80, fines de los años 80 y 90. Utilizamos una serie de modelos anidados para probar si los datos se ajustaban mejor a un modelo con uno, dos o tres cambios temporales en las tasas demográficas, y ajustamos los modelos a diferentes longitudes de datos para probar el número de años de datos requeridos para detectar un cambio demográfico. Las declinaciones a principios de los años 80 se asociaron con una supervivencia de juveniles marcadamente baja, mientras*

que las declinaciones de los años 90 se asociaron con una fecundidad desproporcionadamente baja. Repetimos estos análisis, ajustando solo para datos de conteo sin información sobre la fracción de juveniles, para determinar si la información de la estructura de edades cambiaba las conclusiones y/o cambiaba la velocidad y la certeza con las que se podían detectar los cambios en las tasas demográficas. Los datos de la fracción de juveniles mejoró sustancialmente el grado en que las estimaciones del modelo fueron consistentes con los datos de campo y mejoraron significativamente la velocidad y certeza con las que se detectaron cambios en las tasas demográficas.

Introduction

Gradual change of population size in response to a perturbation is a characteristic of many long-lived species (Congdon et al. 1994; Crowder et al. 1994; Heppell et al. 1996) and presents a major challenge for their management and conservation (Norse 1993; Dayton et al. 1995). Inertia in a population's response to changes in mortality and fecundity rates delays the detection of negative impacts and hinders evaluation of management actions intended to improve vital rates. Although population numbers for long-lived species typically show a long, gradual response after a perturbation, shifts in age structure often occur in a much shorter time frame (Caswell 1989) and can reveal changes to the underlying rates of survivorship and fecundity that are difficult to see in census data alone (Doak & Morris 1999; Monson et al. 2000). We fit Leslie matrix models to age-structure and population-size data and analyzed historical changes in survivorship and fecundity. We used the resulting information to estimate the changes to these vital rates that have occurred over the last 25 years in the Alaskan population of Steller sea lions (*Eumetopias jubatus*), a long-lived endangered marine mammal whose rapid decline has prompted numerous management decisions affecting resource users in the Bering Sea region.

Steller sea lions are distributed across the North Pacific Ocean Rim (Fig. 1) from the Kuril Islands through the Aleutian Islands and south to central California (Loughlin

et al. 1984). In the early 1970s, Steller sea lion numbers began declining in the eastern Aleutian Islands (Braham et al. 1980), and subsequently declines began spreading westward. By the early 1980s, declines had begun in the central and western Gulf of Alaska (Merrick et al. 1987; Trites & Larkin 1996; York et al. 1996). Between 1956 and 1998, the total population in Alaska declined by approximately 85%, from an estimated 192,000 to 32,200 (Loughlin et al. 1984; Sease & Loughlin 1999). In 1990 the Steller sea lion was listed as threatened under the U.S. Endangered Species Act, and in 1997 the western Alaskan stock was listed as endangered. The ultimate causes of the decline are unknown. Past research efforts have eliminated redistribution, pollution, predation, subsistence use, commercial harvest, disease, and natural fluctuations as principal causes of the most severe declines (review in National Marine Fisheries Service 1992). Current research efforts now focus on ocean climate change, which led to a shift in the prey base of the sea lion (Benson & Trites 2002), and on the potential effects of commercial fishing on sea lion survival and fecundity (Ferrero & Fritz 2002).

Although Steller sea lion population numbers in the Aleutian Islands and Gulf of Alaska have been steadily declining since the early 1980s (Sease & Loughlin 1999), the rate of decline has been changing. The primary collapse in the early 1980s was associated with declines of 10–20% per year, after which the rate moderated to 5–15% per year (York et al. 1996). Field studies (Merrick et al. 1995; Chumbley et al. 1997) and analyses of population data (Pascual & Adkison 1994; York 1994) from the Gulf of Alaska indicate that the initial rapid collapse in the early 1980s was associated with a large decline in juvenile survivorship. It is unknown, however, what survivorship and fecundity rates were associated with the continued, moderated decline since the mid-1980s, and estimating this was the first objective of our analysis. To do this, we used a time-varying Leslie matrix model that we fit to 1976–1998 data on Steller sea lion population size, fecundity, and age structure. We used this model to estimate how and when Steller sea lion rates of survivorship and fecundity have changed throughout the 1980s and into the 1990s.

Our second objective was to evaluate the value of age-structure information for detecting changes in underlying demographic rates of survivorship and fecundity. Estimating the age structure of a Steller sea lion population is not

Figure 1. Range of Steller sea lions in Alaska, with Marmot Island indicated.

trivial. Indeed, determining the complete age structure involves either long-term mark-recapture studies or examination of teeth removed from a representative sample of individuals. Neither of these types of data were available historically, and they may be difficult to obtain in the future given the Steller sea lion's endangered status. Instead we examined the value of simple age-structure metrics. In particular, we looked at whether an index of the juvenile fraction within the population would improve the precision and speed with which changes in demographic rates could be detected. Although the collection of age-structure data (even simple age-structure metrics) can require a significant increase in monitoring costs, gathering such data may be justified if it significantly improves detection of demographic changes and population status, thereby aiding the management of species of conservation concern.

Methods

Steller Sea Lion Censuses

Aerial and ground censuses 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 (for descriptions see National Marine Fisheries Service 1992; Sease & Loughlin 1999). During the aerial surveys, the entire Gulf of Alaska and Aleutian Island portion of the range (Fig. 1) is flown during the course of one day, and aerial photographs are taken of the rookery and haul-out sites, where sea lions are found on land. During the breeding season surveys (June–July), newborns (pups) and reproductive adults are observed on rookeries, where adult males defend territories and mating and birthing occur. Adults that are not breeding that year and pre-reproductive juveniles (age 1 to <3 years old) are observed on haul-out sites, where sea lions predictably rest on land but where few or no pups are born. Non-pups, which denotes juveniles plus adults but not newborn pups, are surveyed via aerial photography of rookeries and haul-out sites, whereas pups are surveyed via ground counts on rookery beaches. The National Marine Fisheries Service designates rookeries and haul-out sites as trend or nontrend sites (National Marine Fisheries Service 1992). Trend sites have been regularly censused since 1976, whereas nontrend sites have not been counted in all censuses. Animals on trend sites account for 60–70% of the census (Sease & Loughlin 1999).

For the purpose of fitting the matrix model, we focused on data from the central Gulf of Alaska (CGA), for which a pre-decline (1970s) life-history model has been developed (Calkins & Pitcher 1982; York 1994). We fit the model to (1) 1976–1998 data on the total non-pup count on trend rookeries and haul-out sites in the CGA during June–July (Merrick et al. 1992; Sease & Loughlin 1999), (2) 1978–1998 data on the total pup count on Marmot Island rookeries (Fig. 1) in the CGA (Chumbley et al. 1997; Sease & Loughlin 1999), and (3) 1985–1998 data on the fraction of the population that is juvenile (described below). Only the Marmot Island pup counts were used because 13 counts were available versus only 8 for the total CGA, and the proportion of Marmot Island pups within the total CGA pup count was steady (30–40%) between 1979 and 1998.

A Metric for Age Structure

Initially we explored a variety of age-structure fractions, such as the fraction of the population that is juvenile, newborn, or breeding. We conducted a preliminary sensitivity analysis by using age-structured models to determine which metric would be most informative. This preliminary analysis indicated that an index for the fraction of juveniles in the population would be most sensitive to the type and magnitude of survivorship and fecundity changes that we anticipated had occurred in Steller sea lion populations. The other metrics, although easier to estimate from existing census data, turned out to be relatively insensitive.

To estimate the historical juvenile fractions, we measured sea lions in the aerial photographs of haul-out sites taken during the 1985, 1989, 1992, 1994, 1996, 1997, and 1998 breeding-season surveys in the CGA. From the photographs, the longest straight-line length of every animal was measured digitally. The fraction of small animals from all haul-out photographs in a given year was used as an index of the juvenile fraction. Given the low numbers of juveniles located on rookeries during breeding season, we analyzed only haul-out, not rookery, photographs. Photographs from both trend and non-trend haul-out sites were analyzed (20 sites total). In sum, 5841, 1385, 1636, 826, 1161, and 1385 animals were measured for the 1985, 1989, 1992, 1994, 1996, 1997, and 1998 censuses, respectively. Photographs were selected in which there was at least one mature adult male (distinctively large and light in color) laying completely stretched out. We normalized the measurements by dividing all animal lengths in a photograph by the length of this largest mature male in that photograph. Variation in the lengths of adult males is relatively low (Calkins & Pitcher 1982), and thus they provided a natural scale. Calkins et al. (1998) found no evidence of a change in the size of large females between 1985 and 1997, although a decline was found prior to that. If large males follow the same trend, then our ruler was relatively stable over the time period (1985–1998) we took size measurements. In addition, a sensitivity analysis, which looked at the effect of variation in the measurement of the largest male, indicated that our juvenile-fraction metric was robust to the anticipated level of variation in the measurement of large males.

From the data set of all normalized measurements, we calculated the metric for the fraction of juveniles on haul-out sites:

$$\frac{J}{T} = \frac{\text{number of animals} < 50\% \text{ of the length of the largest male}}{\text{total number of animals in a photograph}}.$$

Although when they are laying straight juveniles are 60–70% of the length of large males (Calkins & Pitcher 1982), few animals in the photographs were laying stretched out. Cross-checking our normalized measurements with visual categorization of animals indicated that a 50% cut-off would categorize the majority of juveniles as juveniles and minimize miscategorization of adults. The relationship between our (J/T) metric and the true numbers of juveniles and adults is

$$\frac{J}{T} = \frac{\text{number of juveniles counted as juvenile in photograph}}{\text{total number of animals photographed on haul outs}}$$

$$= \frac{m_{jj} h_j J_{\text{true}}}{h_j J_{\text{true}} + h_a A_{\text{true}}} = \frac{m_{jj} J_{\text{true}}}{J_{\text{true}} + \frac{h_a}{h_j} A_{\text{true}}}, \tag{1}$$

where we assumed that m_{jj} is the fraction of juveniles that are categorized as juveniles, and h_j and h_a are, respectively, the fraction of juveniles and adults photographed on haul-out sites. (Obviously, only a fraction of the juvenile and adult population is photographed because some individuals are in the water, on rookeries, or on the haul-out sites but not photographed.) The value of m_{jj} was 0.8, although our results were not particularly sensitive to the exact value. The constants h_a and h_j were unknown, except that h_a is considerably smaller than h_j because most adults but few juveniles are on the rookeries during the breeding season. We estimated the ratio h_a/h_j by fitting model D (described below) to the non-pup, pup, and J/T data, allowing h_a/h_j to be a free variable along with the other free variables in model D. The resulting fit was $h_a/h_j = 0.21$ (using $m_{jj} = 0.8$), which is in line with the expected relative values of h_a and h_j. For the rest of the analyses, h_a/h_j and m_{jj} were fixed at 0.21 and 0.8, respectively.

Using Models to Analyze Changes in Steller Sea Lion Demography

We fit an age-structured Steller sea lion model with temporally varying rates of survivorship and fecundity to the pup, non-pup, and juvenile-fraction data. The base matrix model (Table 1) was parameterized by York (1994) based on data from the late 1970s on Marmot Island. The York matrix is a modified Leslie matrix that follows the female portion of the population at the start of the breeding season just after parturition. The matrix represents a stable Steller sea lion population in the late 1970s, and the estimated λ (population growth rate) is 1.0 by design. The model assumes that there is no density dependence. We

Table 1. York (1994) matrix for a stable Steller sea lion population in the central Gulf of Alaska.

age 0	1	2	3	4	5	6	...	31
0	0	0.0788	0.1669	0.2376	0.2819	0.2785[b]	...	0
0.782	0	0	0	0	0	0	...	0
0	0.782	0	0	0	0	0	...	0
0	0	0.782	0	0	0	0	...	0
0	0	0	0.930	0	0	0	...	0
0	0	0	0	0.909	0	0	...	0
0	0	0	0	0	...[b]	0	...	0
0	0	0	0	0	0	...	...	0

[a]*The matrix was parameterized with data from Marmot Island (Calkins & Pitcher 1982). The York matrix is a 32 × 32 matrix following females from age 0 (newborn pups) up to the maximum age of 31 years. Age denotes age (in years) during the breeding season (June–July). Fecundity for age 3–5 years does not match with that found by York (1994) because of a typographical error in that paper. The first row is survival from age i to i+1 times fecundity at age i+1. When the matrix is multiplied by the current population vector, row 1 of next year's population vector is the pup count in the next year. The first nine rows of the matrix are shown.*
[b]*Fecundity of females age 0 to 31 is 0, 0, 0, 0.1008, 0.1795, 0.2614, 0.315, 0.315, ... (fecundity age 6 to 31 is 0.315). The elements for the columns are fecundity age i+1 times survivorship from age i to i+1. The rest of the matrix continues with survivorship from age i to i+1 along this diagonal. The survivorships from age i to i+1, starting with age 0 to 1, are, respectively, 0.782, 0.782, 0.782, 0.930, 0.909, 0.895, 0.884, 0.875, 0.867, 0.859, 0.853, 0.847, 0.841, 0.836, 0.831, 0.827, 0.822, 0.818, 0.814, 0.810, 0.807, 0.803, 0.800, 0.797, 0.794, 0.791, 0.788, 0.785, 0.782, 0.780, 0.777.*

thought this a reasonable simplification because we used the model to study a declining population.

The age structure and population size of females just after the start of the breeding season (June–July) were specified by the population vector N_t. In this vector, the first rows is the pup count, rows 2 and 3 are the juveniles, and rows 4+ are the adults. The starting population vector, N_0, was the late 1970s age structure in the CGA calculated by York (1994), with population sizes normalized to reflect our estimate of the total female population size (58,450) in the late 1970s. The York matrix (denoted **Y**) is a modified Leslie matrix model because in the first row of the matrix the element in column i is $s_i f_{i+1}$ (survivorship of from age i to $i + 1$ times fecundity at age $i + 1$). In this way when the matrix **Y** is multiplied by the vector N_t, the first element of N_{t+1} is the pups in the next year ($t + 1$). The model (model D) with temporally varying rates of survivorship and fecundity was specified as follows:

$$\text{For } t = 1976 \text{ to } 1982,$$
$$N_{t+1} = \mathbf{Y}_{76} \cdot N_t$$
$$\text{For } t = 1983 \text{ to } 1987,$$
$$N_{t+1} = \mathbf{Y}_{83} \cdot N_t \tag{2}$$
$$\text{For } t = 1988 \text{ to } 1992,$$
$$N_{t+1} = \mathbf{Y}_{88} \cdot N_t$$
$$\text{For } t = 1993 \text{ to } 1998,$$
$$N_{t+1} = \mathbf{Y}_{93} \cdot N_t.$$

The $\mathbf{Y}_{76}$ is the base York matrix denoting conditions in 1976. The $\mathbf{Y}_{83}$, $\mathbf{Y}_{88}$, and $\mathbf{Y}_{93}$ represent modified York matrices after fecundity, juvenile survivorship, and adult survivorship have been changed to new levels by multiplying the base 1976 rates of fecundity, juvenile survivorship, and adult survivorship by p_f, p_j, and p_a, respectively. The $\mathbf{Y}_{83}$, $\mathbf{Y}_{88}$, and $\mathbf{Y}_{93}$ matrices are different (or can be) because the p_f, p_j, and p_a multipliers for each of the three different matrices are independent free variables.

Although it is certain that vital rates did not change as step functions, the rapidity with which the age structure and pup numbers changed does suggest rapid shifts. Furthermore, examination of the trends in population size indicates that there were periods in which the exponential rate of decline was constant and then changed to a new rate of decline. York et al. (1996) found that Steller sea lions in the CGA declined at different rates in each of the periods 1975–1985, 1985–1989, and 1989–1994. Extending York et al.'s analysis, the subsequent 1994–1998 period also had its own rate of decline. Model D (Eq. 2) was set up such that demographic rates were allowed to change 1–2 years before a new rate of decline was observed.

We fit model D to the pup, non-pup, and juvenile-fraction data by independently varying each of the p_f, p_j, p_a multipliers for the $\mathbf{Y}_{83}$, $\mathbf{Y}_{88}$, and $\mathbf{Y}_{93}$ matrices. The best fit was determined by maximum-likelihood estimation following the methods of Pascual et al. (1997). In the fitting procedure we assumed that all residual errors were due to sampling error (Pascual & Kareiva 1996; Hilborn & Mangel 1997). We calculated the distance between the observed data and model predictions with the negative log-likelihood function summed over the censuses:

$$S(\theta) = \frac{1}{2\sigma_{\ln N}^2} \sum_{i=1}^{k} (\ln(N_i) - \ln(0.524(\hat{J}_i + \hat{A}_i)))^2$$

$$+ \frac{1}{2\sigma_{\ln P}^2} \sum_{i=1}^{n} (\ln(P_i) - \ln(0.323\hat{P}_i))^2 \qquad (3)$$

$$+ \frac{1}{2\sigma_J^2} \sum_{i=1}^{m} ((J/T)_i - (0.8\hat{J}_i/(\hat{J}_i + 0.21\hat{A}_i)))^2$$

$$+ \text{a constant,}$$

where N_i, P_i, and $(J/T)_i$ are the ith CGA non-pup counts, Marmot Island pup counts, and the juvenile fraction, respectively. The parameters $\hat{P}_i$, $\hat{J}_i$, and $\hat{A}_i$ are the model predictions of total counts of pups, juveniles, and adults. The relationship between the model's total number of female non-pups and total number of male and female non-pups observed on trend sites, $\hat{N}_i = 0.524(\hat{J}_i + \hat{A}_i)$ in Eq. 3, was determined by preliminary fitting of the model to the trend count data, allowing the relationship to be a free variable. The relationship between the Marmot Island pup count and total CGA pup count, $0.323\hat{P}_i$, was calculated from the

average ratio of the 1978 and 1979 Marmot pup counts to the total 1979 CGA pup count.

The maximum-likelihood (ML) estimates of p_f, p_j, p_a multipliers for the $\mathbf{Y}_{83}$, $\mathbf{Y}_{88}$, and $\mathbf{Y}_{93}$ matrices were obtained by minimizing $S(\theta)$. The σ values in Eq. 3 weight the contribution of the data based on its variability. However, the variances of the observations relative to the true values were unknown. Therefore, iteratively reweighted least squares (Green 1984) were used following Pascual et al. (1997). This is a process by which parameters are fit holding unknown σs constant, and then the unknown σs are re-estimated from the residuals. This is repeated until the estimates of the unknown σs and the parameter estimates do not change significantly between iterations. For the model with three temporal changes fit to the pups, non-pups, and juvenile fraction,

$$\sigma_{\ln N}^2 = 0.0031, \quad \sigma_{\ln P}^2 = 0.0096, \quad \sigma_J^2 = 0.0004.$$

We established confidence intervals for the estimated parameters using one-dimensional likelihood profiles (Hilborn & Mangel 1997), as follows. Separately, each of the nine parameters (p_f, p_j, p_a for $\mathbf{Y}_{83}$, $\mathbf{Y}_{88}$, and $\mathbf{Y}_{93}$) was incrementally set above or below its mL value and held constant at that perturbed level while the other parameters were re-estimated according to maximum likelihood. The $S(\theta)'$ estimates as each parameter was perturbed away from its ML value described the negative log-likelihood profile for that parameter. Confidence intervals for each parameter at the 95% level were given by the parameter range for which $|2(S(\theta)' - S(\theta))| < \chi^2(0.95, 1) = 3.95$, where $S(\theta)$ is the minimum negative log likelihood when all parameters are at their mL values.

Testing One versus Multiple Historical Survivorship and Fecundity Changes

We used likelihood ratio tests (Hilborn & Mangel 1997) to test different nested hypotheses about whether one or multiple temporal changes in rates of survivorship and fecundity produced the historical data:

MODEL A

Only one survivorship and fecundity change occurred (in 1983).

$$\text{For } t = 1976 \text{ to } 1982,$$
$$\mathbf{N}_{t+1} = \mathbf{Y}_{76} \cdot \mathbf{N}_t, \text{ and}$$
$$\text{For } t = 1983 \text{ to } 1998, \qquad (4)$$
$$\mathbf{N}_{t+1} = \mathbf{Y}_{83} \cdot \mathbf{N}_t.$$

There were three free parameters in model A: p_f, p_j, p_a in $\mathbf{Y}_{1983}$.

MODEL B

Two changes occurred (1983 and 1988).

For $t = 1976$ to 1982,

$$N_{t+1} = \mathbf{Y}_{76} \cdot N_t$$

for $t = 1983$ to 1987,

$$N_{t+1} = \mathbf{Y}_{83} \cdot N_t \qquad (5)$$

for $t = 1988$ to 1998,

$$N_{t+1} = \mathbf{Y}_{88} \cdot N_t.$$

There were six free parameters: p_f, p_j, p_a for $\mathbf{Y}_{83}$ and $\mathbf{Y}_{88}$.

MODEL C

Two changes occurred (1983 and 1993).

For $t = 1976$ to 1982,

$$N_{t+1} = \mathbf{Y}_{76} \cdot N_t$$

for $t = 1983$ to 1993,

$$N_{t+1} = \mathbf{Y}_{83} \cdot N_t \qquad (6)$$

for $t = 1993$ to 1998,

$$N_{t+1} = \mathbf{Y}_{93} \cdot N_t.$$

There were six free parameters: p_f, p_j, p_a in $\mathbf{Y}_{83}$ and $\mathbf{Y}_{93}$.

MODEL D (SAME AS EQ. 2)

Three changes occurred (1983, 1988, and 1993). There were nine free parameters: p_f, p_j, p_a for $\mathbf{Y}_{83}$, $\mathbf{Y}_{88}$, and $\mathbf{Y}_{93}$.
Using

$$\sigma^2_{\ln N} = 0.0031, \sigma^2_{\ln P} = 0.0096, \sigma^2_J = 0.0004$$

(the estimate from reweighting using model D), we fit models A, B, C, and D by maximum likelihood to the P, N, and J/T data and obtained the minimizing $S(\theta)$. The test criteria for a significantly better fit of model D versus A, D versus B, and D versus C at the $p = 0.05$ level were, respectively,

$$2(S(\theta)_A - S(\theta)_D) > \chi^2(0.95, 6) = 12.59,$$
$$2(S(\theta)_B - S(\theta)_D) > \chi^2(0.95, 3) = 7.81, \qquad (7)$$
$$2(S(\theta)_C - S(\theta)_D) > \chi^2(0.95, 3) = 7.81,$$

where the degrees of freedom of the χ^2 distribution is given by the difference between the number of free parameters in the competing models.

Effect of Age-Structure Data on mL Estimates

To study the extent to which juvenile-fraction data decreased the uncertainty in parameter estimates, we fit model D to the pup and non-pup data alone, without the additional juvenile-fraction data. The model was fit as described previously for the full data set, including estimation of the variances via iterative re-weighting. Fit to the pup and non-pup counts only, the estimated variances were

$$\sigma^2_{\ln N} = 0.0023 \text{ and } \sigma^2_{\ln P} = 0.0088.$$

To test whether the juvenile-fraction information improved the speed with which changes in survivorship and fecundity would be detected, we compared the number of years of data required to conclude that a change in rates of survivorship and/or fecundity occurred in 1988. We did this analysis twice: first using juvenile-fraction plus pup and non-pup counts (i.e., the full data set) and second using only count data (with no juvenile-fraction data). We used the likelihood ratio test

$$2(S(\theta)_A - S(\theta)_B) > \chi^2(\alpha, 3)$$

to determine whether model B (changes in 1983 and 1988) was significantly better than model A (change in 1983 only) at the $\alpha = 0.95$ and $\alpha = 0.99$ significance levels. The tests were made using progressively longer data sets, first using 1976–1989 data only, second using 1976–1990 data, third using 1976–1991 data; and on up to 1976–1998 data. For each time period of data, the analysis was done as if that were the only data available (e.g., as if we were in 1992, say, trying to determine whether vital rates had changed). Thus, b_a/b_j and the relationship between trend and total population counts were re-estimated from the data. We did not use the iterative reweighting algorithm because it performed poorly when fit to two to four data points (e.g., when fit to the 1976–1989 or 1976–1991 period). Instead, we used a fixed relative weighting of

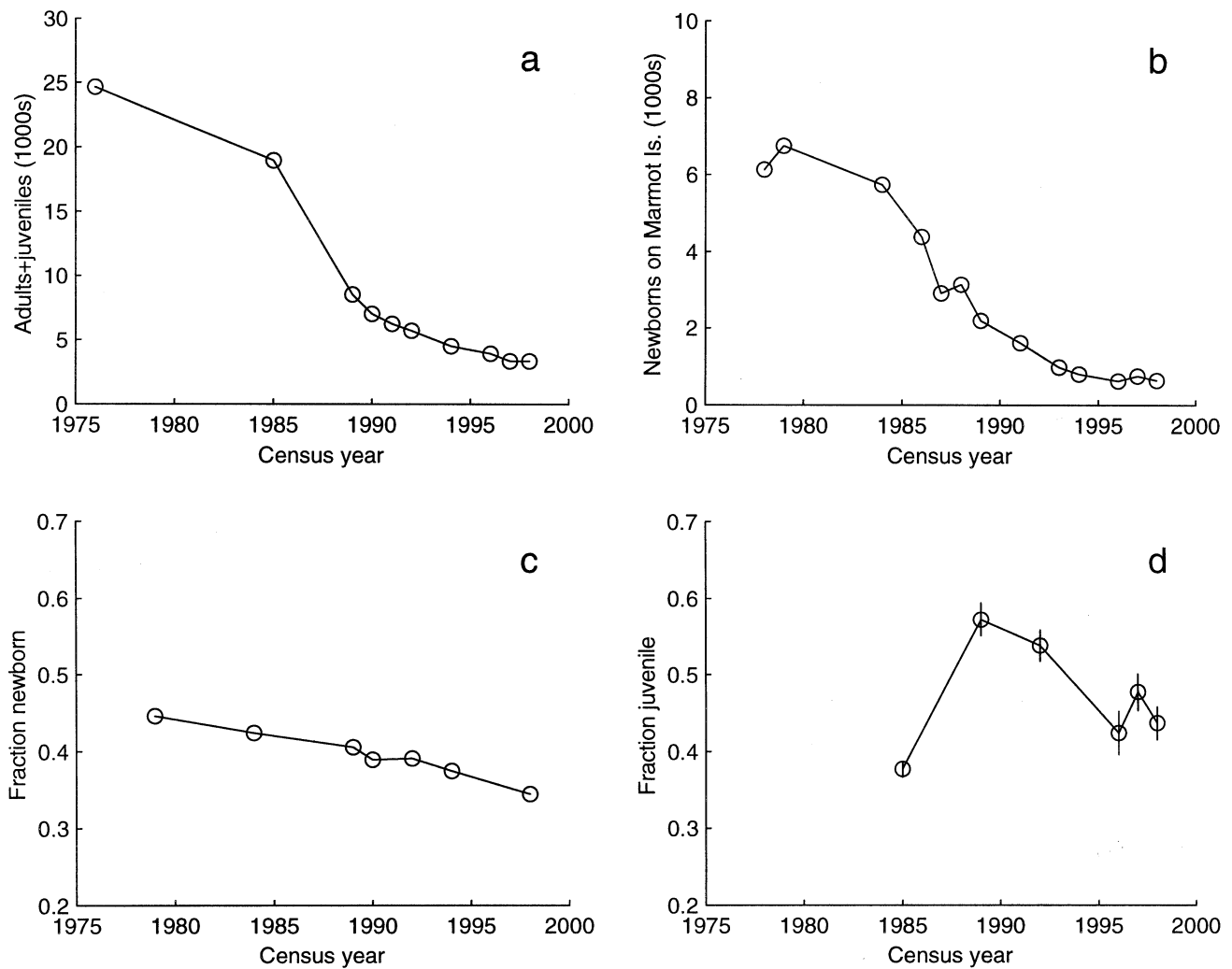$$\sigma^2_{\ln P}/\sigma^2_{\ln N} = 1 \text{ and } \sigma^2_{\ln J}/\sigma^2_{\ln N} = 0.1.$$

We did a similar analysis to examine how quickly and simply an increase in juvenile survivorship would be detected. This test was done analogously to that described above, except that model B was compared with model B−, in which juvenile survivorship was held constant after 1983 and adult survivorship and fecundity were allowed to change in 1988. The test was

$$2(S(\theta)_{B-} - S(\theta)_B) > \chi^2(\alpha, 1),$$

given that there was one parameter difference between these two nested models.

Results

Historical Changes in Steller Sea Lion Survivorships and Fecundity

Pup and non-pup counts in the CGA declined steadily between 1976 and 1998 (Fig. 2a & 2b). If demographic rates had been constant during the decline, the age structure
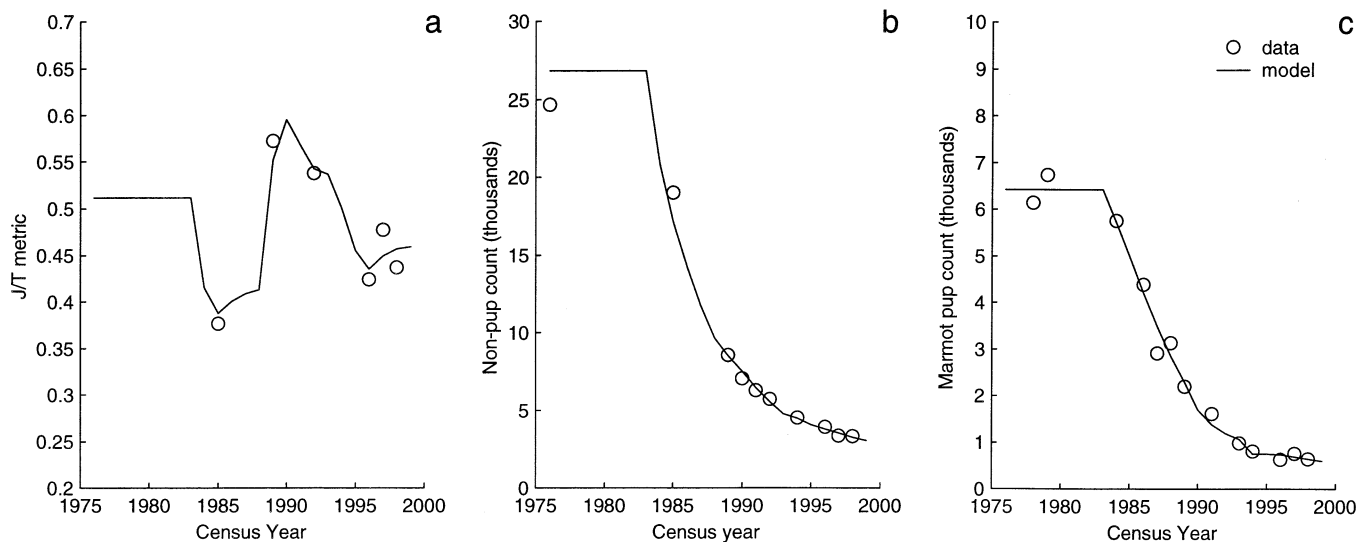
Figure 2. Historical trends of Steller sea lions in the central Gulf of Alaska (CGA): (a) Adult plus juvenile (non-pup) counts on rookery and haul-out trend sites. (b) Pup counts on the Marmot Island rookery. (c) Index of pup to non-pup ratio (total CGA pup count divided by the total CGA trend non-pup count). The index illustrates how the relative ratio of pups to non-pups changed but was not used in the analysis because it is a combination of the count data. (d) Index of juvenile fraction from photographs of trend and non-trend haul-out sites. Vertical lines show the 95% confidence intervals on the measured juvenile fractions.

would have been constant. Throughout this period, however, the age structure, as indicated by the newborn and juvenile fractions, also changed. The newborn fraction of the population declined steadily (Fig. 2c), and the juvenile fraction fluctuated (Fig. 2d). The newborn fraction illustrated age-structure changes but was not used for model fitting because it was derived from the pup and non-pup counts already used for model fitting. Likelihood-ratio tests indicated that the model with change in vital rates occurring in 1983, 1988, and 1993 (model D; Fig. 3) fit the data significantly better than model C, with changes in 1983 and 1993 only ($p < 0.001$), model B, with changes in 1983 and 1988 only ($p < 0.001$), or model A, with change in 1983 only ($p < 0.001$). The maximum-likelihood fit specified a Leslie matrix model governing each period: 1983–1987, 1988–1992, and 1993–1998. From these ma-

trices, we calculated the underlying population rate of decline, λ, during each period. The rates of decline were 0.80, 0.87, and 0.92 for the respective periods, indicating a gradual moderation in the intrinsic rate of population decline over time.

Figure 4 (a–c) shows model D's estimates for juvenile survivorship, adult fecundity, and adult survivorship in 1983, 1988, and 1993 relative to 1976 levels. The model fits indicated a severe decline in juvenile survivorship in the early 1980s, with moderate declines in adult fecundity and survivorship. The 95% confidence intervals did not overlap the 1976 levels (the dotted line), indicating that all rates were below the corresponding vital rates estimated for 1976. However, given that the 1976 rates were estimated and the proximity of the estimated fecundity confidence intervals to the 1976 estimates, this

Figure 3. Fits of the temporally varying Leslie matrix model (Eq. 2) to the (a) juvenile fraction, (b) non-pup counts on haul out and rookery sites in the central Gulf of Alaska and (c) Marmot Island pup counts. The model was fit by allowing juvenile survivorship, adult fecundity, and adult survivorship to change in 1983, 1988, and 1993.

data analysis only weakly supported a decline in fecundity during this period. In contrast, the support for a decline in juvenile and adult survivorship was strong. In the late 1980s, the model fit predicted that juvenile survivorship recovered to within 1976 levels, whereas adult survivorship dropped significantly and adult fecundity stayed slightly below 1976 levels. Finally, in the early 1990s, the model fit predicted that adult survivorship improved to within 1976 levels, whereas adult fecundity declined significantly and well below 1976 levels (Fig. 4b).

The overall picture was one of low juvenile survivorship during the early declines, low adult survivorship during the declines of the late 1980s to early 1990s, and low fecundity during declines through the 1990s. There appeared to be periods of stasis in some vital rates. For example, from the late 1980s to the late 1990s, no significant change in juvenile survivorship was detected, whereas throughout the 1980s no significant change in fecundity was detected. Given that the 1976 fecundity was estimated, and given the proximity of the 1980s confidence intervals for fecundity to the point estimates of 1976 fecundity, this analysis did not unequivocally detect a decline in fecundity, relative to 1976 levels, until the early 1990s. In contrast, adult survivorship appeared to be shifting during each period throughout the 1980s and 1990s. These results were robust to shifting the years when the changes were allowed (i.e., using a 1982 or 1984 start of the decline, a 1987 mid-change, and a 1992 or 1994 change).
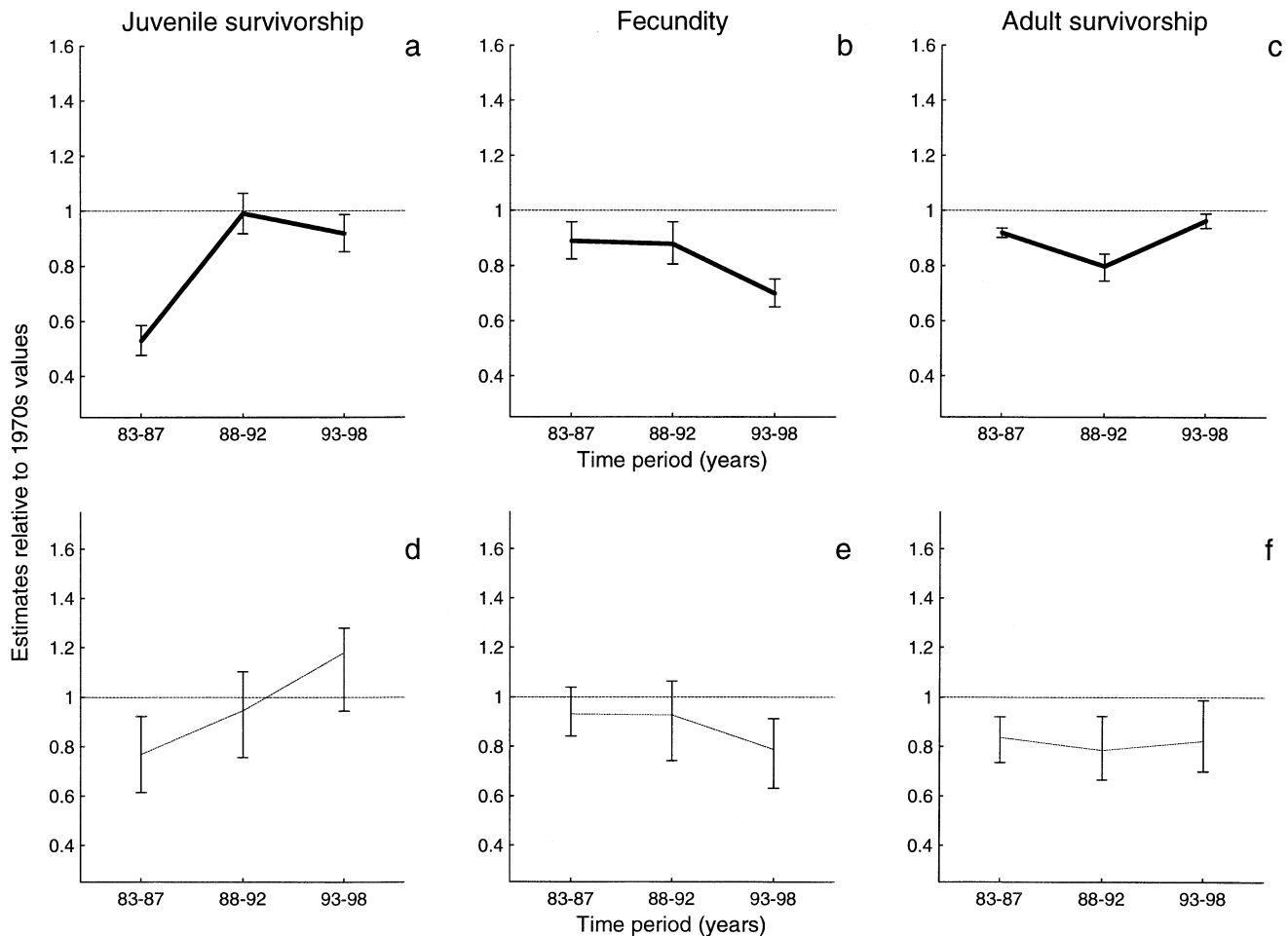
Effect of Age-Structure Data on Estimates

When the model was fit to the count data alone, the picture was qualitatively similar (compare Fig. 4a–c, with

d–f), and except for the estimates of juvenile survivorship in the early 1980s, the 95% confidence intervals for the estimates from the count data alone (d–f) overlapped with the 95% confidence intervals for the estimates from the full data set (a–c). The most striking difference was for the mid- to late 1990s, when the fit to the count data alone predicted that adult survivorship and fecundity were both low, whereas juvenile survivorship was well above the 1976 level. In contrast, the fit to the full data set gave estimates indicating that adult fecundity was disproportionately low in the 1990s, with juvenile and adult survivorship both slightly below 1976 levels.

Although the point estimates for the vital rates in the three time periods were not radically different (except in for the 1990s), when the juvenile-fraction information was added to the data set, the certainty in the estimated vital rates changed substantially. Indeed without the juvenile-fraction information, the confidence intervals for all vital rates and all time periods overlapped, with one exception: juvenile survivorship in the early 1980s versus the early 1990s. Thus, without the juvenile-fraction information, it could not be determined that vital rates have been changing over the 1980s and 1990s—except that juvenile survivorship increased. Without the juvenile-fraction information, the predictions were not only less certain but were also less robust to the details of the model. Specifically, without the juvenile-fraction data, the estimated vital rates changed substantially with slight changes in the years at which changes in the vital rates were allowed to occur. For example, with slightly different years—1982, 1987, and 1993 instead of 1983, 1988, and 1993—parameter estimates from the fit to the count data alone changed dramatically, to values inconsistent with field and data analyses and inconsistent

Figure 4. Maximum-likelihood estimates of juvenile survivorship, adult fecundity, and adult survivorship for 1983–1987, 1988–1992, and 1993–1998 relative to 1976 levels (shown by the dotted line at 1.0). The 95% confidence intervals were determined by one-dimensional likelihood profiling. The top panels (a-c) show the estimates when the model was fit to both the pup and non-pup counts and the juvenile-fraction data. The bottom panels (d-f) show the estimates when the model was fit to the pup and non-pup counts only (without the juvenile-fraction information). Comparison of the top and panels show how, without the juvenile-fraction information, the uncertainty in the parameter estimates increases substantially. In d-f all the 95% confidence intervals overlap except the 1983–1987 and 1993–1998 juvenile-survivorship confidence levels.

with estimates based on the full data set (with the juvenile-fraction data). In contrast, when the model was fit to the full data set, the results were qualitatively and quantitatively insensitive to the precise year that change was assumed to have occurred (within a 1–2 year range).
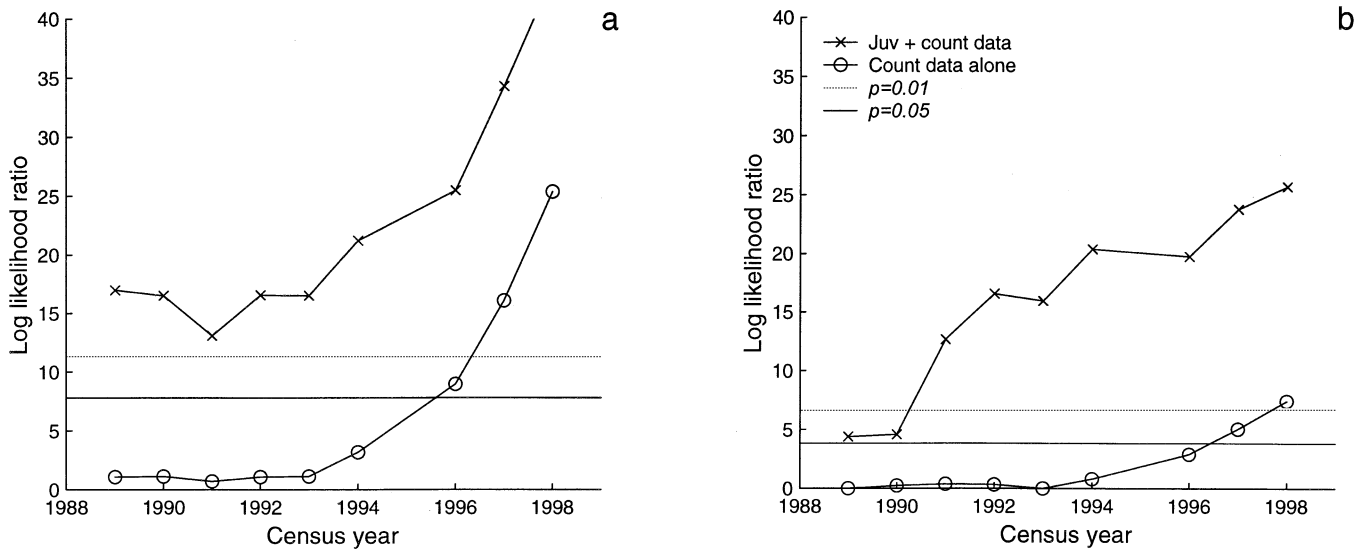
Effect of Age-Structure Data on the Rapidity of Change Detection

The juvenile-fraction data also allowed demographic change to be detected more rapidly. With the juvenile-fraction data, a significant ($p = 0.0007$) 1988 demographic change could be detected by 1989 (Fig. 5a), although with only count data, a significant 1988 change was not detected at the $p < 0.05$ level until 1996. Thus, the additional juvenile-fraction information allowed a

1988 demographic change to be detected 7 years earlier. When the test was posed to determine whether juvenile survivorship increased in 1988 (rather than simply any demographic-rate change), the juvenile-fraction data allowed an increase in juvenile survivorship to be detected by 1989 ($p < 0.05$). With only the count data, an increase was not detected until 1997, 8 years later, at the $p < 0.05$ level (Fig. 5b).

Discussion

Using model-fitting and likelihood ratio tests, we examined whether there is significant evidence of multiple changes in the vital rates of Alaskan Steller sea lions during their steady 20-year decline and estimated how the vital

Figure 5. Effect of juvenile-fraction data on the number of years of censuses required to determine whether a demographic change occurred in 1988. (a) Test for a change in any of the vital rates in 1988. The y-axis shows the ratio of the minimum-log likelihood for a model with demographic change in 1983 only to the minimum-log likelihood for a model with demographic change in 1983 and 1988. These two nested models were compared with progressively more data: 1976–1989, 1976–1990, up to 1976–1998. A significant demographic change in 1988 is detected when the log-likelihood ratio crosses the p = 0.05 (solid) or p = 0.01 (dashed) lines. (b) Analogous to the analysis for (a) except here a change in only juvenile survivorship is tested. The model in which all vital rates are allowed to change in 1983 and 1988 is compared to a model in which juvenile survivorship is allowed to change only in 1983, whereas adult survivorship and fecundity are allowed to change in both 1983 and 1988.

rates compared with 1976 levels during the decline. The pattern of population decline could not be explained by a single change occurring in the early 1980s and persisting into the present (due for example to the shift in the fish community structure). Neither could the data be fit well by only two periods of change (such as 1980s and 1990s), each with different vital rates. Instead, a model with early 1980s, late 1980s, and early 1990s changes in rates of survivorship and fecundity closely fit the data, and even accounting for the increase in free parameters associated with such a model, this model fit the data significantly better than the models with fewer temporal changes.

During the three periods, we found a shifting pattern of demographic impacts on Steller sea lions. In the 1983–1987 period, juvenile survivorship was severely affected and almost 50% below 1976 levels, whereas adult survivorship and fecundity showed much smaller declines. In the early 1990s, adult survivorship was the lowest (20% below 1976 levels), whereas juvenile survivorship and adult fecundity were relatively high. Finally, during the declines in the mid- to late 1990s, adult and juvenile survivorship were within 5–10% of 1976 levels, whereas adult fecundity was disproportionately low and well below 1976 levels. These data analyses support the suspicions of biologists working on Steller sea lions that the rates of survivorship and fecundity have been changing and that the factors that led to the early 1980s collapse

were not the same as those causing the continuing declines in the 1990s (DeMaster & Atkinson 2002).

Our estimates for the early to mid-1980s (corresponding to the period of the initial population collapse) concur with those of other studies on the survivorship and fecundity of Alaskan Steller sea lion populations during this period. Data analyses (Pascual & Adkison 1994; York 1994) and field and cohort studies (Merrick et al. 1995; Chumbley et al. 1997) all indicate that juvenile survivorship was disproportionately depressed during the early 1980s. However, despite an abundance of research throughout the late 1980s and 1990s (Hunter & Trites 2001; Ferrero & Fritz 2002), information on the demographic rates of Steller sea lions during the more recent declines is limited and largely inferential. Much research has been conducted on the physical condition of sea lions to investigate the hypothesis that food limitation plays an important role in the current declines. The assumption is that food limitation could affect both survivorship and fecundity. As of yet, there is little evidence of reduced body size and condition in the regions where population declines are occurring (Merrick et al. 1995; Calkins et al. 1998; Rea et al. 1998; Davis et al. 2002). Other researchers have looked at a range of impacts, including disease, entanglement, harvest, predation, pollution, and fishery interactions (reviews in Hunter & Trites 2001; DeMaster & Adkinson 2002). These studies generally indicate that

mortality or lower fecundity are associated with these impacts, but it is difficult to determine their role in the declines because increasing populations in southeast Alaska experience many of the same impacts. Our quantitative analysis of pup, non-pup, and juvenile-fraction information is the first we know of that has determined which vital rate changes are consistent with the observed declines in the late 1980s to late 1990s and compared estimates of the current vital rates to those before the declines began.

Our analysis indicates not only that the vital rates have been shifting but also that as they have shifted the rate of decline of the Steller sea lion in the Gulf of Alaska has been moderating. From the maximum-likelihood fits to the 1976–1998 data, we estimated that the population rates of decline, λ, were 0.80, 0.87, and 0.92 for the periods 1983–1987, 1988–1992, and 1993–1998, respectively. These λs translate to declines of 20%, 13%, and 8% per year, respectively. What vital rates were primarily driving the rate of decline during these different periods? Although the mid-1980s were associated with disproportionately low juvenile survivorship and the mid- to late 1990s with low adult fecundity, this does not mean they were the primary drivers of the observed rate of decline in these periods. It is often the case for long-lived species that population growth rate is disproportionately sensitive to adult survivorship (Caswell 1989), and this has been shown for pinnipeds, including fur seals (Wickens & York 1996) and Steller sea lions (Pascual & Adkison 1994; York 1994). To investigate the extent to which the rate of decline in the mid-1980s (with $\lambda = 0.80$) could be attributed to juvenile survivorship, adult survivorship, or adult fecundity alone, we sequentially recalculated λ after lowering only one of the rates to our mid-1980s estimates while holding the rest at 1976 levels. Seventy-two percent of the low λ in the early 1980s was explained solely by the estimated decline in juvenile survivorship, 6% was attributed to the estimated low adult fecundity, and 22% to the estimated low adult survivorship. In this case, it appears that low juvenile survivorship was the primary demographic driver of the early 1980s declines.

For the mid-1990s, when $\lambda = 0.92$, 32% of the low λ was explained solely by the estimated decline in juvenile survivorship, 45% was attributed to the estimated decline in adult fecundity, and 26% to the estimated decline in adult survivorship. Thus, although it appears that adult fecundity was severely low in the 1990s (30% lower than 1976 levels), with adult and juvenile survivorship only slightly depressed (5–10%), the smaller declines in juvenile and adult survivorship were also driving the late-1990s declines, to a much greater extent than their relatively small depression might suggest. This should lend a cautionary note to the interpretation of the current work emerging on nutritional limitation, predation, and other "minor" impacts on adult and juvenile Steller sea lions. Although a variety of research indicates that adults and juveniles are not nutritionally limited (Pitcher 2002), and although

many researchers believe predation has a minor effect (DeMaster & Atkinson 2002), Steller sea lion declines are sensitive to impacts on adult and juvenile survivorship, and even a small depression of these may be significantly contributing to current declines (even though our analyses and the declining ratio of pups to non-pups indicate that fecundity is well below 1976 levels).

Although our analyses shed light on the changing vital rates in Alaskan Steller sea lion populations, they do not allow us to determine the natural or anthropogenic causes of these changes. Steller sea lions are affected by a variety of factors, including competition with fisheries, ocean climate change, predation from killer whales and sharks, and environmental pollutants (National Marine Fisheries Service 1992; DeMaster & Atkinson 2002; Loughlin & York 2002); they have also been affected, we assume, by management actions over the last 20 years, including reduction of shooting of sea lions, fisheries closures, and buffer zones around rookeries. These impacts are likely to be interacting in a variety of unknown ways, which ultimately produce the given suite of demographic rates at a given point in time. Although our analyses cannot determine the ultimate causes of the decline, understanding the proximate survivorship and fecundity changes can help one evaluate the importance of these different ultimate drivers. In addition, analysis of the survivorship and fecundity of an endangered or threatened species is critical to setting management and research priorities and determining population status. Indeed, monitoring to detect a change in status and viability, whether in response to management actions or environmental perturbation, is a standard aspect of most management plans (cf. Morris et al. 2002).

In most of these plans, however, only population size or some index thereof is monitored, and, unfortunately, detecting demographic change and status with simple census data can be difficult, especially for long-lived species. A well-studied example of these difficulties is the delayed effect of management actions on adult sea turtle numbers (Crowder et al. 1994; Heppell et al. 1996; Bjorndal et al. 1999). Researchers typically found that 10 or more years were required to see substantial changes in the numbers of nesting female sea turtles after institution of management actions. In general, whether the species of concern is long-lived or not, census data alone is often insufficient for detecting status and change within populations unless many census years are available and/or the count variability is low (Schroeter et al. 1993; Taylor & Gerrodette 1993; Thompson et al. 2000).

Our study and other recent studies indicate that supplementing census data with age-structure information can help overcome some of these problems and greatly improve the detection of changes in survivorship and fecundity. We found that juvenile-fraction information allowed a change in vital rates to be detected within 1 year at a high significance level, whereas with only population and

newborn counts, at least 7 years of counts were required. The juvenile-fraction data also greatly decreased the uncertainly in the estimated vital rates and produced more stable estimates that were less sensitive to changes in the underlying model framework. In another recent study on the use of age-structure data, Doak and Morris (1999) used a comparison of the predicted stable age structure (from a current life table) to the actual age structure to detect environmental change affecting a slow-growing, long-lived species. Because transitory shifts in age structure occur after a perturbation and persist in long-lived species, this method can potentially reveal recent perturbations without long-term monitoring. Monson et al. (2000) used age-structure data to improve detection of the effects of the Exxon Valdez oil spill on sea otters (*Enhydra lutris*). Monson et al. used changes in the age distribution of sea otter carcasses to detect lingering increased mortality after the oil spill, which previous researchers, using more traditional methods and census data alone, had tried unsuccessfully to detect. These studies and ours indicate that, in certain situations, age-structure data can greatly improve the detection of demographic perturbation and of the demographic rates limiting a population's recovery. Such information is critical for developing management actions, setting research priorities, and establishing benchmarks for recovery.

Acknowledgments

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