A NONINVASIVE DEMOGRAPHIC ASSESSMENT OF SEA LIONS BASED ON STAGE-SPECIFIC ABUNDANCES

Jeffrey Wielgus,[1,3] Manuela Gonzalez-Suarez,[1] David Aurioles-Gamboa,[2] and Leah R. Gerber[1]

[1]*Ecology, Evolution, and Environmental Sciences, School of Life Sciences, Arizona State University, Tempe, Arizona 85287 USA*
[2]*CICIMAR-IPN, Avenida IPN s/n Col. Playa Palo de Santa Rita 23096, La Paz Baja, Baja California Sur, Mexico*

Abstract. A pressing need exists to develop new approaches for obtaining information on demographic rates without causing further threats to imperiled animal populations. In this paper, we illustrate and apply a data-fitting technique based on quadratic programming that uses stage-specific abundance data to estimate demographic rates and asymptotic population growth rates (λ). We used data from seven breeding colonies of California sea lions (*Zalophus californianus*) in the Gulf of California, Mexico. Estimates of λ were similar to those from previous studies relying on a diffusion approximation using trends in total abundance. On average, predicted abundances were within 24% of the observed value for the inverse estimation method and within 29% of the observed value for the diffusion approximation. Our results suggest that three of the seven populations are declining ($\lambda < 1$), but as many as six may be at risk. Elasticity and sensitivity analyses suggest that population management in most sites should focus on the protection of adults, whose survival generally contributes the most to λ. The quadratic programming approach is a promising noninvasive technique for estimating demographic rates and assessing the viability of populations of imperiled species.

Key words: abundance; California sea lion; demography; El Niño; Gulf of California; inverse estimation; marine mammals; noninvasive techniques; population viability analysis; quadratic programming; Zalophus californianus.

INTRODUCTION

A central challenge in the conservation of long-lived mammals is to understand patterns of extinction risk based on limited demographic data. Obtaining estimates of demographic rates for marine mammals is particularly challenging due to the difficulty of studying these animals in the field (Barlow and Boveng 1991, Caswell et al. 1998, Stolen and Barlow 2003). However, field data are essential to assessing the status of populations and to assigning conservation priority (Eberhardt 1977, Wade 1998, Gerber and DeMaster 1999, Read and Wade 2000).

A number of quantitative approaches are currently used to assess population status, differing in data requirements, assumptions, and analytical capabilities (Table 1). The simplest approaches have been classified as "count-based methods" (Morris and Doak 2002) and rely on estimates of total population abundance to estimate asymptotic population growth rates (λ). Because estimates of total abundance are often available for imperiled species, count-based methods have been applied to a variety of species (reviewed in Dennis et al.

1991, Gerber et al. 1999). However, count-based models treat all individuals as identical, a simplification that may not be appropriate for age-structured populations such as long-lived animals. In such populations, the contribution of different age groups or stages to population growth varies, and thus dynamics are best analyzed using methods that characterize age groups or stages explicitly (Caswell 2001). However, such methods require estimates of age- or stage-specific vital rates, which can be logistically and financially costly to obtain.

Traditionally, two approaches have been used to estimate age- or stage-specific demographic rates: constructing cohort life tables and estimating transition frequencies (Table 1). Both methods require permanently marking individuals. The construction of cohort life tables requires marking individuals belonging to the same stage and following them throughout their lifetime, whereas estimating transition frequencies involves marking individuals in all stages and following them for at least one transition into the next stage class. Marking marine mammals for scientific purposes also raises a number of logistical, ethical, and legal challenges. Plastic or metal tags are short lived in the marine environment. New alternatives, such as passive integrating transponder tags, require close scanning of animals, which is rarely feasible with marine wildlife. While a number of advances have been made in marking techniques for terrestrial mammals (Banks et al. 2003,

TABLE 1. Comparison of quantitative approaches used to assess population status.

Approach	Data needs	Analytical capability and metrics obtained	Strengths
Count-based methods (e.g., diffusion approximation)	abundance data over time; ≥10 abundance estimates recommended	population growth rates (including variation), probability of extinction	data relatively straightforward to obtain, causing relatively low disturbance; data frequently available for imperiled species; easy to compute
Demographic methods, following cohorts	demographic rates from marked individuals; ideally, data collected over the species' life span	population growth rates (including variation), probability of extinction, sensitivity, and elasticity analysis	PVA packages facilitate computation (e.g., INAMT, RAMAS)
Demographic methods, estimating transition frequencies	demographic rates from marked individuals; age- or stage-specific estimates of abundance; ≥2 transitions recommended	population growth rates (including variation), probability of extinction, sensitivity, and elasticity analysis	data can be obtained in few years; PVA packages facilitate computation (e.g., INAMT, RAMAS)
Demographic methods, inverse estimation methods	age- or stage-specific estimates of abundance	population growth rates (including variation), probability of extinction, sensitivity, and elasticity analysis	data relatively straightforward to obtain, causing relatively low disturbance; data frequently available for imperiled species

Beier et al. 2005, Meekan et al. 2006, Solberg et al. 2006), these methods have seldom been applied to marine mammals. Consequently, branding of animals is generally considered as the only viable method to permanently mark pinnipeds. However, branding has generated legal and ethical disputes (McMahon et al. 2006*a*, *b*). For instance, the Humane Society of the United States filed a lawsuit in 2005 that temporarily stopped Steller sea lion research in Alaska (Dalton 2006), and the Australian government indefinitely suspended an elephant-seal pup branding program due to public outrage (Jabour Green and Bradshaw 2004). The need to obtain demographic information for endangered populations, and the problems with the techniques that are currently available for this purpose, illustrate the importance of developing alternative methods to assess marine mammal populations.

In contrast to methods that allow estimation of demographic rates by following marked individuals in time, "inverse methods" are data-fitting techniques that estimate age- or stage-specific demographic rates and λ indirectly from changes in age- or stage-specific abundance (reviewed in Caswell 2001). Inverse methods are computer intensive, which may explain why they have seldom been applied to population assessments (but see Dennis et al. [1995] and Holmes and York [2003] who used a maximum likelihood approach and Gross et al.

[2002] who used Bayesian estimation). Because inverse methods are based on fitting data, their results may be less reliable than mark-based approaches. On the other hand, recent advances in computer technologies have made inverse methods more accessible, and their use may involve lower financial expenses than those of field-based methods. A further assessment of inverse methods as potential tools for population viability analysis is thus warranted.

In this paper, we apply an inverse method to estimate stage-specific demographic rates and long-term population growth rates of seven breeding colonies of the California sea lion (*Zalophus californianus*; see Plate 1). California sea lions breed along the Pacific coast of California and Baja California, and throughout the Gulf of California. Non-breeding aggregations occur throughout a wider range along the eastern Pacific coast as far north as British Columbia (Peterson and Bartholomew 1967). California sea lions in the Gulf of California are considered to be fairly isolated genetically (Maldonado et al. 1995, Schramm-Urrutia 2002), and have declined in abundance >20% in the last decade (Szteren et al. 2006). Human-induced mortality is common in this area, and sea lion habitat is threatened by coastal habitat alteration, unregulated tourism, and pollution from agriculture and urban areas (Delgado-Estrella et al. 1994, Zavala-González and Mellink 1997,

TABLE 1. Extended.

Limitations	References
no age or stage structure limits detailed studies of population dynamics; does not allow estimation of demographic rates	Dennis et al. (1991), Morris et al. (1999), Morris and Doak (2002)
long-term data generally not available for long-lived and imperiled species; permanent marking of individuals may be invasive; computation and demographic rate estimation may be complicated	Ferson (1990), Ferson and Akçakaya (1990), Mills and Smouse (1994), Brook et al. (2000), Caswell (2001), Williams et al. (2001)
permanent marking of individuals from all stages may not be feasible for some species and may be invasive; assumes stable age distribution in sampled population(s); computation may be complicated	Ferson (1990), Ferson and Akçakaya (1990), Morris et al. (1999), Caswell (2001)
computer-intensive; validation of demographic rates obtained from this approach has been limited	Dennis et al. (1995), Morris et al. (1999), Caswell (2001), Gross et al. (2002), Morris and Doak (2002), Holmes and York (2003), Gerber et al. (2007), Wielgus et al. (2007)

Brusca et al. 2005). Therefore, effective management of the sea lion population in the Gulf of California is critical.

The inverse estimation method that we used is based on quadratic programming. Although the method was first proposed a decade ago (Wood 1997), it was applied only recently to empirical data (Wielgus et al. 2007). Similar to inverse estimation using a Bayesian approach (Gross et al. 2002), quadratic programming makes it possible to constrain the estimated demographic rates to a range of values that are considered realistic for the species (see *Methods*). The use of parameter constraints is particularly useful when dealing with species of conservation concern, in which case the values can be restricted to precautionary values. Another advantage of quadratic programming is the relative ease with which it can be implemented using software for numerical analysis. Model algorithms and computer code for quadratic programming are widely available (e.g., Byrne 1984, Caswell et al. 2001, Lau 2007), and the input required for the estimations are simply (1) a matrix containing abundance data and (2) a vector containing the constraints for the parameter values (see *Methods*). In addition, no assumptions are required about the types of distributions of the demographic rates, in contrast to Bayesian and maximum likelihood approaches.

METHODS

Field methods

We studied seven breeding colonies of the California sea lion (Fig. 1). Animals at each island were counted during June, July, or August. This period coincides with the reproductive season for California sea lions (Peterson and Bartholomew 1967). The reproductive season is an ideal time for counting individuals because at this time the majority (>77%) of animals remain on land, adult males defending territories and adult females giving birth and nursing the young (Bonnell and Ford 1987). In addition, >84% of pups are born from the end of May to the end of June (García-Aguilar and Aurioles-Gamboa 2003), so our census periods includes most of the individuals born during the year's reproductive season.

Population counts were conducted between 07:00 hours and 19:00 hours each day by circumnavigating the island in a small fiberglass boat with an outboard engine, at a distance ≤50 m from the shoreline (Aurioles-Gamboa and Zavala-González 1994, Zavala-González and Mellink 1997, Bester et al. 2001, Szteren et al. 2006). One trained observer recorded the total number of individuals classified into three stages distinguished by their morphology and size (Le Boeuf et al. 1983): pups, juveniles, and adults. Pups are young of the year, less than 1 m long, with dark brown pelage. Juveniles are individuals 1–4 years old, 1–1.3 m long, with gray or light-brown pelage. Adults are individuals
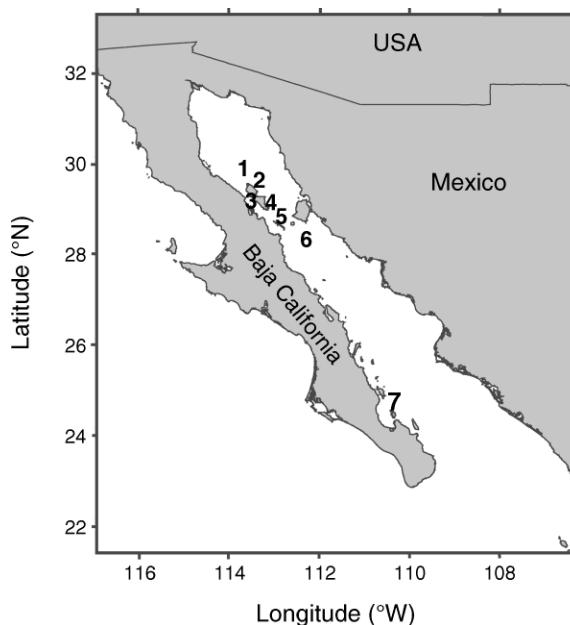

FIG. 1. Map of the Gulf of California, Mexico, showing the location of the seven studied colonies of the California sea lion (*Zalophus californianus*): 1, Granito; 2, Los Cantiles; 3, Los Machos; 4, El Partido; 5, Rasito; 6, San Pedro Mártir; 7, Los Islotes.
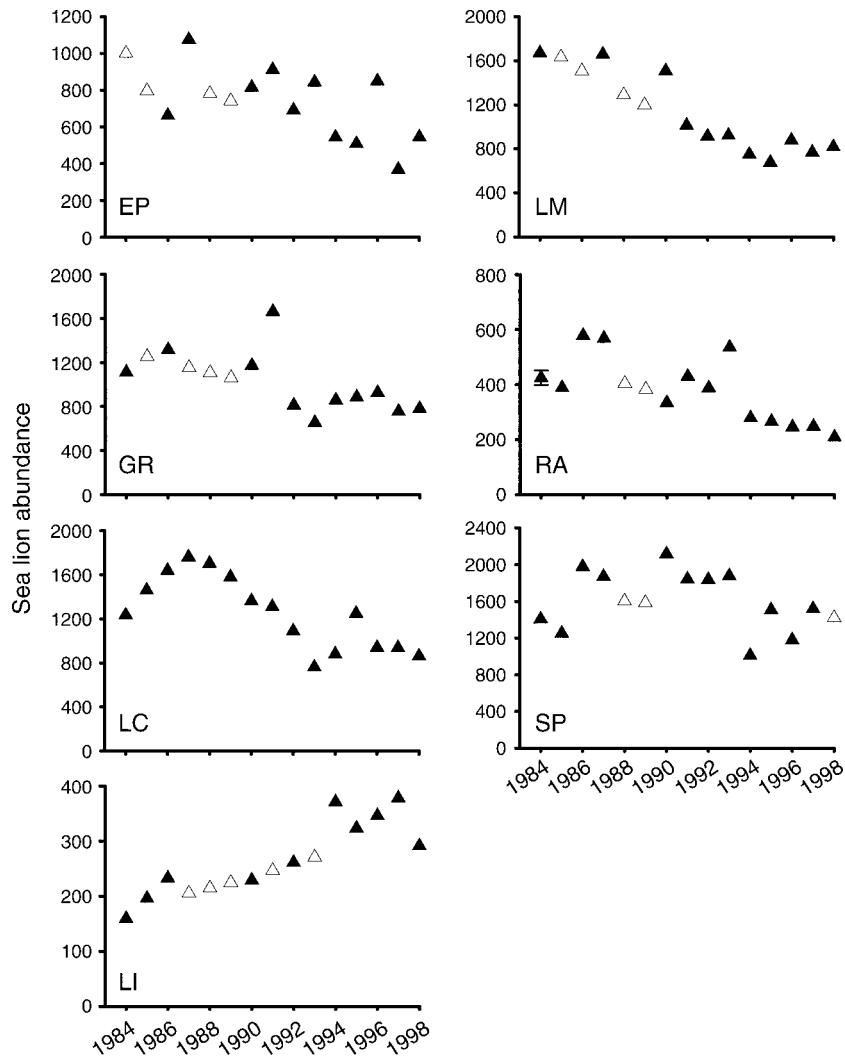
JEFFREY WIELGUS ET AL.

FIG. 2. Total abundances for seven California sea lion colonies in the Gulf of California, Mexico, for the period 1984–1998. Solid triangles represent survey data, and open triangles are estimated data points. The mean of four surveys (and SD) is shown for Rasito for 1984. Abbreviations are: El Partido (EP), Granito (GR), Los Cantiles (LC), Los Islotes (LI), Los Machos (LM), Rasito (RA), and San Pedro Mártir (SP).

larger than 1.4 m, with dark gray or brown pelage, and in the case of adult males, a pronounced sagittal crest (Le Boeuf et al. 1983). Observers used 7 × 32 binoculars as an aid in the identification of individuals during the counts.

Although California sea lions can travel long distances occasionally (Aurioles-Gamboa et al. 1983, Young et al. 2007), we assumed that each colony was a distinct reproductive unit because sea lion colonies in the Gulf of California are fairly genetically isolated.

Estimation of demographic rates

For our estimations, we used data for the period 1984–1998 because it contained the highest number of years in which censuses were conducted for all of the study sites. An uninterrupted time series was only

available for one breeding colony (Los Cantiles; Fig. 2). The maximum number of missing years for a colony was five (Los Islotes; Fig. 2), and the remaining colonies had between two and four missing years of data. Missing data were estimated by imputation: observed stage-specific abundances were log-transformed, and data for missing years were estimated by using the linear regression equation of observed abundances (dependent variable) and year (independent variable), and back-transforming the estimate. A previous study on California sea lions (Gonzalez-Suarez et al. 2006) found little evidence of bias associated with this estimation procedure.

Because some sea lions may be at sea (e.g., foraging) during surveys, four counts were made at the island of Rasito over a period of nine days (14–22 July 1984) to

test the precision of the census estimates (Morales-Vela 1985). Counts were made at different times each day (between 08:30 hours and 17:00 hours). The coefficient of variation (CV) for pups, juveniles, and adults was 7.2%, 10.8%, and 7.7%, respectively (see Fig. 2 for the SD of the mean count for the entire population), indicating a high precision in the counts and suggesting that the number of young and adult animals that were at sea at any one time was low. As expected, the juvenile stage had the highest CV. Juveniles probably have a higher tendency to spend time in the water, and thus to be miscounted. Unlike adults, juveniles do not guard territories on land (as adult males do), nor do they rely on land for nursing or birthing (as adult females do). Observer errors in adult counts have been associated with the dense aggregations of these animals (Le Boeuf et al. 1983, Lowry 1999), and errors in pup counts are likely linked to the difficulty of detecting pups that are concealed by rocks or larger animals.

Conflicting reports exist on the effects of El Niño/La Niña Southern Oscillation (ENSO) on California sea lion colonies. For instance, at San Nicolas Island in California, pup mortality increased during the 1982–1983 El Niño event compared to rates observed in the previous year (Ono et al. 1987). At Los Islotes in the Gulf of California, pup mortality rate did not differ between those same years (Aurioles-Gamboa and Le Boeuf 1991). ENSO has been linked to major changes in ecological processes in the subtropical Pacific Ocean (Karl et al. 1995), so we studied if a deterministic demographic model or a model that incorporated environmental variability due to ENSO was most appropriate for our estimations (Caswell 2001, Wielgus et al. 2007). We used the multivariate ENSO Index (MEI; Wolter and Timlin 1998) because it includes a wide range of environmental variables for the tropical Pacific: sea-level pressure, surface winds, sea surface temperature, surface air temperature, and cloudiness. We used the published bimonthly values of MEI for 1984–1998 to calculate a mean MEI value for each year and to classify each year as El Niño (mean MEI > 0) or La Niña (mean MEI < 0; index *available online*).[4] We considered values from January to July only, because we expected that food abundance during this period would have the largest effect in the size of the breeding population. Although no empirical evidence is available, it is likely that all sea lion stages experience high energy requirements during the first months of the year. At this time, adult females are completing gestation and often still nurse the young from the previous season. Adult males fast during the summer months while defending their territories, and must actively feed during the preceding months to accumulate enough energy reserves for the summer (Peterson and Bartholomew 1967). Finally, pups start feeding independently during this period.

[4] ⟨http://www.cdc.noaa.gov/people/klaus.wolter/MEI/table.html⟩

We conducted ANOVA (two-way) to test for the effect of MEI (categorized as described above) and site on $r = \log(N_t/N_{t-1})$ for each stage. Because we did not observe an effect of MEI on r (see *Results*), and because our aim was not to estimate probabilities of extinction, which require stochastic modeling (Caswell 2001), we used a single, deterministic projection matrix:

$$\mathbf{L} = \begin{bmatrix} 0 & 0 & F \\ G_{\mathrm{p}} & S_{\mathrm{j}} & 0 \\ 0 & G_{\mathrm{j}} & S_{\mathrm{a}} \end{bmatrix}.$$

In this projection matrix, G_{p} is the probability of survival of pups from one year to the next (i.e., the probability of growing to juveniles), S_{j} is the probability of juveniles surviving and remaining in the juvenile stage, G_{j} is the proportion of juveniles that grow to adults, F is the average number of offspring produced per adult (fecundity), and S_{a} is the probability of survival of adults.

$\mathbf{L}$ can be expressed as a column vector $\mathbf{p}$ containing unknown values of the demographic rates. Changes in population size can be expressed as

$$\mathbf{N}_{(t+1)} = \mathbf{N}_{(t)}\mathbf{p}$$

where $\mathbf{N}$ is a matrix that contains abundance data for all of the studied stages in the population. If $\mathbf{N}_{(t)}$ and $\mathbf{N}_{(t+1)}$ are known (e.g., from yearly abundance data), the values of $\mathbf{p}$ can be estimated by minimizing the sum of squared deviations between $\mathbf{N}_{(t+1)}$ and $\mathbf{N}_{(t)}\mathbf{p}$. The problem can be expressed as the following minimization with respect to $\mathbf{p}$ (Wood 1997), where $\top$ represents the transpose of a matrix:

$$\text{minimize } ||\mathbf{N}_{(t+1)} - \mathbf{N}_{(t)}\mathbf{p}||^2$$

$$= (\mathbf{N}_{(t+1)} - \mathbf{N}_{(t)}\mathbf{p})^{\top} (\mathbf{N}_{(t+1)} - \mathbf{N}_{(t)}\mathbf{p})$$

or equivalently as

$$\text{minimize } [(\mathbf{N}_{(t+1)}{}^{\top}\mathbf{N}_{(t+1)}) - (\mathbf{N}_{(t+1)}{}^{\top}\mathbf{N}_{(t)}\mathbf{p})$$

$$- (\mathbf{p}^{\top}\mathbf{N}_{(t)}{}^{\top}\mathbf{N}_{(t+1)}) + (\mathbf{p}^{\top}\mathbf{N}_{(t)}{}^{\top}\mathbf{N}_{(t)}\mathbf{p})].$$

The first term is independent of $\mathbf{p}$ and can be ignored. The second two terms are identical, and the problem becomes:

$$\text{minimize } [\mathbf{p}^{\top}\mathbf{N}_{(t)}{}^{\top}\mathbf{N}_{(t)}\mathbf{p} - 2(\mathbf{N}_{(t+1)})^{\top}\mathbf{N}_{(t)}\mathbf{p})].$$

The objective function has a quadratic form. If the minimization problem has linear constraints, the problem is known as a quadratic program (Jensen and Bard 2003). We constrained all parameters to be positive and the sum of survival probabilities for each stage to be ≤1 (Caswell 2001), and used the quadratic programming tool of the optimization toolbox in MATLAB 7.0 (The Mathworks, Natick, Massachusetts, USA).

After estimating the stage-specific demographic rates for each colony, we calculated long-term asymptotic population growth rates (λ) as the dominant eigenvalue

TABLE 2. Estimated values (and bootstrap standard errors) of demographic rates for seven California sea lion (*Zalophus californianus*) colonies in the Gulf of California.

Island	G_p	S_j	G_j	F	S_a
El Partido	1.000 (0.015)	0.679 (0.083)	0.284 (0.150)	0.149 (0.021)	0.663 (0.123)
Granito	0.856 (0.163)	0.200 (0.158)	0.389 (0.317)	0.530 (0.071)	0.645 (0.173)
Los Cantiles	0.574 (0.115)	0.095 (0.163)	0.233 (0.395)	0.528 (0.025)	0.886 (0.145)
Los Islotes	0.437 (0.092)	0.147 (0.204)	0.478 (0.318)	0.456 (0.035)	0.950 (0.070)
Los Machos	0.505 (0.220)	0.461 (0.206)	0.539 (0.099)	0.307 (0.034)	0.743 (0.053)
Rasito	1.000 (0.025)	0.530 (0.117)	0.260 (0.245)	0.207 (0.032)	0.754 (0.133)
San Pedro Mártir	0.434 (0.171)	0.367 (0.235)	0.393 (0.139)	0.473 (0.036)	0.831 (0.048)

Notes: G_p is the probability of survival of pups from one year to the next (i.e., the probability of growing to juveniles), S_j is the probability of juveniles surviving and remaining in the juvenile stage, G_j is the probability of juveniles surviving and growing to adults, F is the average number of offspring produced per adult, and S_a is the probability of survival of adults. The asymptotic long-term population growth rate estimated from abundance data for 1984–1998 is given by λ (95% bootstrap confidence intervals in parentheses). For comparison, we also provide λ (λ_d) and 95% confidence intervals estimated with the diffusion approximation approach (Dennis et al. 1991). S_a^* is the value of S_a required to achieve $\lambda = 1$; for the empty cell, there is no relevant value as $\lambda > 1$ without any changes to S_a.

of each projection matrix (Caswell 2001). We resampled data from each observed time series 200 times to generate a set of bootstrap replicate time series, and we estimated projection matrix parameters from each replicate time series to obtain 95% bootstrap confidence intervals for the parameters and for λ (Efron and Tibshirani 1986).

Validation of the demographic results

We compared the estimates of λ obtained from the inverse estimation method to those obtained using the diffusion approximation (DA; Dennis et al. 1991), which is a widely used approach to estimate λ from total abundance (Dennis et al. 1991, Gerber et al. 1999, Morris et al. 1999, Buenau and Gerber 2004, Gonzalez-Suarez et al. 2006). We also compared total abundances estimated by both models (inverse estimation and DA) for the period 1999–2007 to the observed abundances in those years. For all sites except San Pedro Mártir (where the last year of data was 1997), 1998 was used as initial year. For the inverse estimation method, we predicted the entire trajectory of abundance after 1997 or 1998 using only data up to those years. We multiplied the vector of abundances for the initial year (1997 or 1998) by the projection matrix (L) to estimate abundances for the following years. For the DA, we used the equation

$$N_t = N_0 \times e^{(\mu + \sigma^2/2)t}$$

where N_0 is the initial year (1997 or 1998), μ is the population growth rate, and σ^2 is the variance estimated with the DA (Dennis et al. 1991). To gauge bias, we estimated the mean proportional error of the abundance predictions for each colony for all years after 1997 or 1998 during which counts were made as

$$\frac{\sum_{t=1}^{T} \dfrac{O_t - P_t}{O_t}}{T}$$

where O and P are, respectively, the observed and predicted abundance for year t, and T is the number of

predicted years. To gauge precision, for each estimation method we also calculated the absolute value of the total proportional error of the predictions as

$$\sum_{s=1}^{T}\sum_{t=1}^{T} \frac{|O_{ts} - P_{ts}|}{O_{ts}}$$

where O_{ts} and P_{ts} are, respectively, the observed and predicted abundances in year t and site s.

Elasticity and sensitivity analyses

We studied the importance of each of the demographic rates in determining λ using two approaches: (1) the matrix **E** containing the elasticity values corresponding to each demographic rate (de Kroon et al. 1986), and (2) a variance-stabilized sensitivity (VSS; Link and Doherty 2002) which prevent some potentially misleading results of elasticity analysis (e.g., magnitude of survival elasticity > magnitude of mortality elasticity when survival > 0.5).

The matrix **E** was calculated as

$$\mathbf{E} = \frac{\delta ai}{\lambda} \times \frac{\delta \lambda}{\delta ai}$$

(Caswell 2001) where a refers to each of the i parameters of the population matrix. For islands with $\lambda < 1$, we also determined what increase in the value of the demographic rate that most contributed to λ would be required to make $\lambda = 1$ (i.e., the value required to achieve a sustainable population). VSS was calculated using the equation suggested for species that produce a single offspring per birth:

$$\text{VSS} = \frac{\sqrt{ai(1-ai)}}{\lambda} \times \frac{\delta \lambda}{\delta ai}.$$

RESULTS

Estimation of demographic rates and validation of the demographic results

The results of ANOVA indicated that MEI and site did not affect the growth rate (r) of any of the stages (all

TABLE 2. Extended.

λ (with 95% CI)	λ_d (with 95% CI)	S_a^*
0.890 (0.805–0.976)	1.081 (0.888–1.317)	0.868
0.915 (0.848–0.982)	1.020 (0.894–1.163)	0.779
0.969 (0.904–1.034)	0.992 (0.915–1.076)	0.922
1.050 (0.992–1.108)	1.058 (0.986–1.136)	
0.933 (0.865–1.002)	0.965 (0.895–1.040)	0.845
0.910 (0.832–0.988)	0.989 (0.875–1.117)	0.886
0.970 (0.933–1.007)	1.053 (0.922–1.202)	0.873

$F < 0.50$, all $P > 0.48$). Thus, a single, deterministic projection matrix was used to estimate demographic rates for the seven colonies (Table 2). For each colony, the asymptotic population growth rate (λ) calculated with the inverse estimation method was similar to the estimates obtained using the diffusion approximation, DA (Table 2). For individual sites, the mean of the proportional errors for the inverse estimation method was mostly positive (Fig. 3), indicating that, in contrast to the DA, this method tended to give conservative predictions of abundance. The absolute value of the total proportional error of the predictions of abundance was lower for the inverse estimation method (7.55) than for the DA (9.21). The total number of predicted years was 31, so on average each predicted abundance was within 24% of the observed value for the inverse estimation method and within 29% of the observed value for the DA. Results from the inverse estimation approach indicate that three of the seven populations are declining (point estimate of λ and upper 95% confidence interval <1), while another three populations may be at risk (point estimate of $\lambda < 1$, but upper 95% CI > 1; Table 2).

Elasticity and VSS analysis

Adult survival had the highest elasticity for all colonies except El Partido. For these colonies, elasticity of adult survival was between 2.4 and 10.6 times as high as the next most important parameter (Table 3). Juvenile survival has the highest elasticity value in El Partido (0.353), but the elasticity of adult survival was similar (0.320). VSS analysis yielded the same conclusions about relative parameter contributions as the sensitivity analysis except for El Partido, where fecundity had the highest VSS (Table 3). However, as in the sensitivity analysis, juvenile survival was more important than adult survival in El Partido. In order to reverse the population decline at each site (i.e., such that $\lambda \geq 1$), we found that adult survival would have to increase by factors of 1.04 at Los Cantiles, 1.05 at San Pedro Mártir, 1.14 at Los Machos, 1.18 at Rasito, 1.21 at Granito, and 1.31 at El Partido (Table 2). At El Partido, the declining trend could alternatively be reversed by increasing juvenile survival by a factor of 1.29 and maintaining the current rate of adult survival.

DISCUSSION

We have illustrated the application of a noninvasive method for estimating demographic rates for California sea lions in the Gulf of California. This "inverse" method uses a time series of stage-specific abundance data to estimate the parameters of the transition matrix by means of quadratic programming. Our estimates of long-term population growth rate (λ) were generally similar, although always lower, than those obtained using the DA method. The inverse estimation method also provided more precise predictions than the DA, and, by estimating stage-specific demographic rates, made it possible to analyze the importance of each demographic rate in determining the population growth rate. The inverse estimation approach underestimated abundances, and thus is a more precautionary predictive tool than the DA, which generally overestimated abundances.

The underestimation of abundances by inverse estimation may have resulted from the method's sensitivity to pronounced variations in abundance. For the five colonies in which the largest year-to-year change in abundance was a decrease (Fig. 2), the mean of the predictions was lower than the observed values, except for San Pedro Mártir (Fig. 3). Because the inverse estimation method uses abundance data for consecutive years to estimate the demographic rates, large changes in abundance may also make the estimation of demographic rates and λ difficult. Errors in sea lion counts may have contributed to the large year-to-year variations in abundance in some of the sites (Fig. 2). The predictions of abundance for El Partido and San Pedro Mártir, which are among the least studied sea lion colonies in the Gulf of California, were among the most
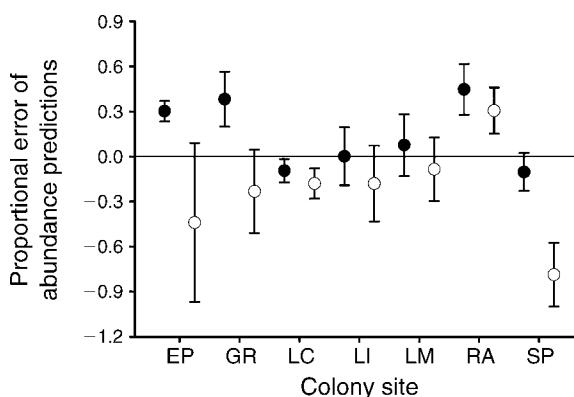

FIG. 3. Proportional errors (mean ± SD) of the predictions of abundance for seven California sea lion colonies in the Gulf of California, Mexico. Errors of the inverse estimation method are shown by solid dots, and errors of the diffusion approximation by open dots. Values above zero indicate that abundance was underestimated. The number of years predicted for each island was as follows: El Partido (EP), 4; Granito (GR), 6; Los Cantiles (LC), 4; Los Islotes (LI), 8; Los Machos (LM), 3; Rasito (RA), 4; and San Pedro Mártir (SP), 2.
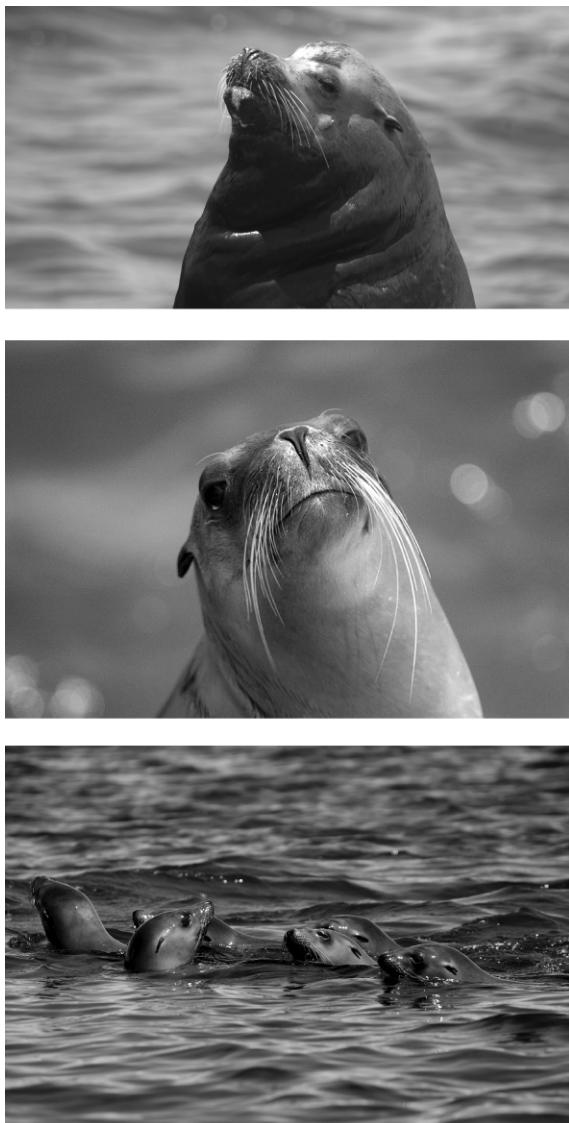
PLATE 1. (Top) Adult male, (middle) adult female, and (bottom) a group of juveniles of the California sea lion (*Zalophus californianus*) in the Gulf of California. Photo credits: M. Gonzalez-Suarez.

variable. In these colonies, the lack of familiarity of the observers with the sites may have resulted in inaccurate counts. In addition, sea lions may be more sensitive to the presence of humans in these sites that are seldom visited, and may engage in behaviors that make their counting more difficult (e.g., animals aggregating more densely; adults moving closer to pups to give protection).

We found that adult survival contributed most to λ at six out of seven sea lion colonies, whereas juvenile survival was the most important parameter in the remaining colony. The importance of adult survival may be explained by the number of age groups and the % of the population represented in this stage. The adult stage included approximately 16 age classes and on average represented 60% of population, while the pup and juvenile categories included only one and four age classes and represented 22% and 18% of the population, respectively. Therefore, it is perhaps not surprising that the adult stage contributed most to λ.

Our results suggest that effective conservation of California sea lion colonies in the Gulf of California could be achieved by focusing management efforts on improving adult survival. Adult survival in the studied area is affected by interactions with fisheries, which result in high rates of entanglement with fishing gear (Zavala-González and Mellink 1997, Aurioles-Gamboa et al. 2003), and may also result in competition for prey as some commercial species are also part of the sea lion's diet (García-Rodríguez and Aurioles-Gamboa 2004, Mellink and Romera-Saavedra 2005). Although California sea lions are affected by ENSO events in some areas of the Pacific Ocean (Ono et al. 1987), we found no evidence for an effect of ENSO on sea lion abundance in the Gulf of California. A previous study at Los Islotes (Aurioles-Gamboa and Le Boeuf 1991) also found that fecundity, the number of females in the colony, and pup mortality did not change during an El Niño year. In other areas or species in which ENSO (or other environmental phenomena) affect demography, it may be useful to estimate projection matrices that incorporate environmental stochasticity (e.g., Wielgus et al. 2007).

TABLE 3. Elasticities and variance-stabilized sensitivities (Link and Doherty 2002) for seven sea lion colonies in the Gulf of California, Mexico.

	G_p		S_j		G_j		F		S_a	
Island	Elasticity	Sensitivity	Elasticity	Sensitivity	Elasticity	Sensitivity	Elasticity	Sensitivity	Elasticity	Sensitivity
El Partido	0.109	0.000	0.353	0.242	0.109	0.174	0.109	0.261	0.320	0.228
Granito	0.177	0.072	0.049	0.099	0.177	0.221	0.177	0.166	0.421	0.313
Los Cantiles	0.073	0.063	0.008	0.024	0.073	0.132	0.073	0.069	0.774	0.278
Los Islotes	0.079	0.090	0.013	0.031	0.079	0.083	0.079	0.087	0.780	0.173
Los Machos	0.127	0.125	0.124	0.134	0.127	0.117	0.127	0.190	0.496	0.292
Rasito	0.108	0.000	0.151	0.142	0.108	0.183	0.108	0.212	0.524	0.299
San Pedro Mártir	0.104	0.119	0.063	0.083	0.104	0.129	0.104	0.110	0.625	0.282

Note: Parameter notation is given in Table 2.

The inverse estimation approach based on quadratic programming may offer a novel and useful solution to the problem of estimating demographic rates in marine mammals and imperiled species in general. Two clear advantages of the approach are that the data needed (1) can be collected using noninvasive field approaches and (2) are often available for imperiled species. The approach could be applied broadly for estimating demographic rates and assessing viability for populations of conservation concern. However, we suggest that caution be taken if abrupt changes in abundance occur, which may limit the predictive ability of this inverse estimation as discussed above. If doubts exist as to the reliability of the abundance data used in the estimations, robustness analyses similar to the ones that we illustrated here should be used to improve the reliability of management recommendations for endangered populations.

LITERATURE CITED

Aurioles-Gamboa, D., F. García-Rodríguez, M. Ramírez-Rodríguez, and C. J. Hernández-Camacho. 2003. Interaction between the California sea lion and the artisanal fisheries in La Paz Bay, Gulf of California, Mexico. Ciencias Marinas 29:357–370.

Aurioles-Gamboa, D., and B. J. Le Boeuf. 1991. Effects of the El Niño 1982–83 on California sea lions in Mexico. Pages 112–118 in F. Trillmich and K. A. Ono, editors. Pinnipeds and El Niño. Springer-Verlag, Berlin, Germany.

Aurioles-Gamboa, D., F. Sinsel, C. Fox, E. Alvarado, and O. Maravilla. 1983. Winter migration of subadult male California sea lions (Zalophus californianus) in the southern part of Baja California. Journal of Mammalogy 64:513–518.

Aurioles-Gamboa, D., and A. Zavala-González. 1994. Some ecological factors that determine the distribution and abundance of the sea lion Zalophus californianus in the Gulf of California. Ciencias Marinas 20:535–553. [In Spanish.]

Banks, S. C., S. D. Hoyle, A. Horsup, P. Sunnucks, and A. C. Taylor. 2003. Demographic monitoring of an entire species (the northern hairy-nosed wombat, Lasiorhinus krefftii) by genetic analysis of non-invasively collected material. Animal Conservation 6:101–107.

Barlow, J., and P. Boveng. 1991. Modeling age-specific mortality for marine mammal populations. Marine Mammal Science 7:50–65.

Beier, L. R., S. B. Lewis, R. W. Flynn, G. Pendleton, and T. V. Schumacher. 2005. From the field: a single-catch snare to collect brown bear hair for genetic mark–recapture studies. Wildlife Society Bulletin 33:766–773.

Bester, M. N., H. Moller, J. Wium, and B. Enslin. 2001. An update on the status of southern elephant seals at Gough Island. South African Journal of Wildlife Research 31:68–71.

Bonnell, M., and R. G. Ford. 1987. California sea lion distribution: a statistical analysis of aerial transect data. Journal of Wildlife Management 51:13–20.

Brook, B. W., J. J. O'Grady, A. P. Chapman, M. A. Burgman, H. R. Akcakaya, and R. Frankham. 2000. Predictive accuracy of population viability analysis in conservation biology. Nature 404:385–387.

Brusca, R. C., L. T. Findley, P. A. Hasting, M. E. Hendrickx, J. Torre Cosio, and A. M. van der Heiden. 2005. Macrofaunal diversity in the Gulf of California. Pages 179–203 in J. E. Cartron, G. Ceballos, and R. S. Felger, editors. Biodiversity, ecosystems, and conservation in northern Mexico. Oxford University Press, New York, New York, USA.

Buenau, K. E., and L. R. Gerber. 2004. Developing recovery and monitoring strategies for the endemic Mount Graham red squirrels (Tamiasciurus hudsonicus grahamensis) in Arizona. Animal Conservation 7:17–22.

Byrne, S. J. 1984. Solution of quadratic programming problems. New Zealand Journal of Operations Research 12:73–89.

Caswell, H. 2001. Matrix population models. Construction, analysis, and interpretation. Sinauer, Sunderland, Massachusetts, USA.

Caswell, W., S. Brault, A. J. Read, and T. D. Smith. 1998. Harbor porpoise and fisheries: an uncertainty analysis of incidental mortality. Ecological Applications 8:1226–1238.

Dalton, R. 2006. Sea-lion studies come to a halt after court judgment. Nature 441:677.

de Kroon, H., A. Plaisier, J. van Groenendael, and H. Caswell. 1986. Elasticity: the relative contribution of demographic rates to population growth rate. Ecology 67:1427–1431.

Delgado-Estrella, A., J. G. Ortega-Ortiz, and A. Sánchez-Ríos. 1994. Strandings of marine mammals during spring and autumn and their relationship with human activities in the northern Gulf of California. Serie Zoología 65:287–295. [In Spanish.]

Dennis, B., R. A. Desharnais, J. M. Cushing, and R. F. Costantino. 1995. Nonlinear demographic dynamics: mathematical models, statistical methods, and biological experiments. Ecological Monographs 65:261–281.

Dennis, B., P. L. Munholland, and J. M. Scott. 1991. Estimation of growth and extinction parameters for endangered species. Ecological Monographs 61:115–143.

Eberhardt, L. L. 1977. Optimal policies for conservation of large mammals, with special reference to marine ecosystems. Environmental Conservation 4:205–212.

Efron, B., and R. Tibshirani. 1986. Bootstrap methods for standard errors, confidence intervals, and other methods of statistical accuracy. Statistical Science 1:54–77.

Ferson, S. 1990. RAMAS/stage user manual: generalized stage-based modeling for population dynamics. Applied Biomathematics, New York, New York, USA.

Ferson, S., and H. R. Akçakaya. 1990. RAMAS/age user manual: modeling fluctuations in age-structured populations. Applied Biomathematics, New York, New York, USA.

García-Aguilar, M. C., and D. Aurioles-Gamboa. 2003. Breeding season of the California sea lion (Zalophus californianus) in the Gulf of California, Mexico. Aquatic Mammals 29:67–76.

García-Rodríguez, F. J., and D. Aurioles-Gamboa. 2004. Spatial and temporal variation in the diet of the California sea lion (Zalophus californianus) in the Gulf of California, Mexico. Fishery Bulletin 102:47–62.

Gerber, L. R., and D. P. DeMaster. 1999. An approach to endangered species act classification of long-lived vertebrates: a case study of north Pacific humpback whales. Conservation Biology 13:1203–1214.

Gerber, L. R., D. P. DeMaster, and P. M. Kareiva. 1999. Gray whales and the value of monitoring data in implementing the

US Endangered Species Act. Conservation Biology 13:1215–1219.

Gerber, L. R., J. Wielgus, and E. Sala. 2007. A decision framework for the adaptive management of an exploited species with implications for marine reserves. Conservation Biology 21:1594–1602.

Gonzalez-Suarez, M., K. E. McCluney, D. Aurioles-Gamboa, and L. R. Gerber. 2006. Incorporating uncertainty in spatial structure for viability predictions: a case study of California sea lions (*Zalophus californianus californianus*). Animal Conservation 9:219–227.

Gross, G., B. A. Craig, and W. D. Hutchison. 2002. Bayesian estimation of a demographic matrix model from stage-frequency data. Ecology 83:3285–3298.

Holmes, E. E., and A. E. York. 2003. Using age structure to detect impacts on threatened populations: a case study with Steller sea lions. Conservation Biology 17:1794–1806.

Jabour Green, J., and C. J. A. Bradshaw. 2004. The "capacity to reason" in conservation biology and policy: the southern elephant seal branding controversy. Journal for Nature Conservation 12:25–39.

Jensen, P. A., and J. F. Bard. 2003. Operations research: models and methods. John Wiley and Sons, New York, New York, USA.

Karl, D. M., R. Letelier, D. Hebel, L. Tupas, J. Dore, J. Christian, and C. Winn. 1995. Ecosystem changes in the North Pacific subtropical gyre attributed to the 1991–92 El Niño. Nature 373:230–234.

Lau, H. T. 2007. A Java library of graph algorithms and optimization. Chapman and Hall/CRC Press, Boca Raton, Florida, USA.

Le Boeuf, B. J., D. Aurioles-Gamboa, R. Condit, C. Fox, R. Gisiner, R. Romero, and F. Sinsel. 1983. Size and distribution of the California sea lion population in Mexico. Proceedings of the California Academy of Sciences 43:77–85.

Link, W. A., and P. F. Doherty, Jr. 2002. Scaling in sensitivity analysis. Ecology 83:3299–3305.

Lowry, M. S. 1999. Counts of California sea lion (*Zalophus californianus*) pups from aerial color photographs and from the ground: A comparison of two methods. Marine Mammal Science 15:143–158.

Maldonado, J. E., F. O. Dávila, B. S. Stewart, E. Geffen, and R. K. Wayne. 1995. Intraspecific genetic differentiation in California sea lions (*Zalophus californianus*) from Southern California and the Gulf of California. Marine Mammal Science 11:46–58.

McMahon, C. R., C. J. A. Bradshaw, and G. C. Hays. 2006a. Branding can be justified in vital conservation research. Nature 439:392.

McMahon, C. R., H. R. Burton, J. van den Hoff, R. Woods, and C. J. A. Bradshaw. 2006b. Assessing hot-iron and cryo-branding for permanently marking southern elephant seals. Journal of Wildlife Management 70:1484–1489.

Meekan, M. G., C. J. A. Bradshaw, M. Press, C. McLean, A. Richards, S. Quasnichka, and J. G. Taylor. 2006. Population size and structure of whale sharks *Rhincodon typus* at Ningaloo Reef, Western Australia. Marine Ecology Progress Series 319:275–285.

Mellink, E., and A. L. Romera-Saavedra. 2005. Diet of California sea lions, *Zalophus californianus*, at San Jorge Island, northern Gulf of California, Mexico, 1998–1999. Ciencias Marinas 31:369–377.

Mills, L. S., and P. E. Smouse. 1994. Demographic consequences of inbreeding in remnant populations. American Naturalist 144:412–431.

Morales-Vela, B. 1985. Aspects of the life cycle of the sea lion *Zalophus calfornianus* in Rasito Island, Gulf of California, Mexico. Thesis. Universidad Nacional Autónoma de México, Mexico City. [In Spanish.]

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology. Sinauer Associates, Sunderland, Massachusetts, USA.

Morris, D. W., D. F. Doak, M. Groom, P. Kareiva, J. Fieberg, L. R. Gerber, P. Murphy, and D. Thomson. 1999. A practical handbook for population viability analysis. The Nature Conservancy, Washington, D.C., USA.

Ono, K. A., D. J. Boness, and O. T. Oftedal. 1987. The effect of a natural environmental disturbance on maternal investment and pup behavior in the California sea lion. Behavioral Ecology and Sociobiology 21:109–118.

Peterson, R. S., and G. A. Bartholomew. 1967. The natural history and behavior of the California sea lion. American Society of Mammalogists, Shippensburg, Pennsylvania, USA.

Read, A. J., and P. R. Wade. 2000. Status of marine mammals in the United States. Conservation Biology 14:929–940.

Schramm-Urrutia, Y. 2002. Genetic and phylogeographic structure of the California sea lion (*Zalophus californianus californianus*) in waters adjacent to the Baja California Peninsula, Mexico. Facultad de Ciencias Marinas, Instituto de Investigaciones Oceanográficas. Universidad Autónoma de Baja California, Ensenada, Mexico. [In Spanish.]

Solberg, K. H., E. Bellemain, O. M. Drageset, P. Taberlet, and J. E. Swenson. 2006. An evaluation of field and non-invasive genetic methods to estimate brown bear (*Ursus arctos*) population size. Biological Conservation 128:158–168.

Stolen, M. K., and J. Barlow. 2003. A model life table for bottlenose dolphins (*Tursiops truncatus*) from the Indian River Lagoon System, Florida, USA. Marine Mammal Science 19:630–649.

Szteren, D., D. Aurioles-Gamboa, and L. R. Gerber. 2006. Population status and trends of the California sea lion (*Zalophus californianus californianus*) in the Gulf of California, México. Pages 369–384 *in* A. W. Trites, S. K. Atkinson, P. DeMaster, L. W. Fritz, T. S. Gelatt, L. D. Rea, and K. M. Wynne, editors. Sea lions of the world. Sea Grant College Program, Anchorage, Alaska, USA.

Wade, P. R. 1998. Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. Marine Mammal Science 14:1–37.

Wielgus, J., F. Ballantyne, E. Sala, and L. R. Gerber. 2007. Viability analysis of reef fish populations based on limited demographic information. Conservation Biology 21:447–454.

Williams, B., J. Nichols, and M. Conroy. 2001. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, San Diego, California, USA.

Wolter, K., and M. S. Timlin. 1998. Measuring the strength of ENSO: how does 1997/98 rank? Weather 53:315–324.

Wood, S. N. 1997. Inverse problems and structured-population dynamics. Pages 555–586 *in* S. Tuljapurkar and H. Caswell, editors. Structured-population models in marine, terrestrial, and freshwater systems. Chapman and Hall, New York, New York, USA.

Young, J. K., C. J. Hernández-Camacho, and L. R. Gerber. 2007. Long-distance movement of a pinniped neonate. Marine Mammal Science 23:926–930.

Zavala-González, A., and E. Mellink. 1997. Entanglement of California sea lions, *Zalophus californianus californianus* in fishing gear in the central-northern part of the Gulf of California, Mexico. Fishery Bulletin 95:180–184.