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Research Article

Population Growth and Status of California Sea Lions

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ABSTRACT The California sea lion (*Zalophus californianus*) population in the United States has increased steadily since the early 1970s. The Marine Mammal Protection Act of 1972 (MMPA) established criteria for management of marine mammals based on the concept of managing populations within the optimal sustainable population (OSP), defined as a range of abundance from the maximum net productivity level (MNPL) to carrying capacity (*K*). Recent declines in California sea lion pup production and survival suggest that the population may have stopped growing, but the status of the population relative to OSP and MNPL is unknown. We used a time series of pup counts from 1975 to 2014 and a time series of mark-release-resight-recovery data from 1987 to 2015 for survival estimates to numerically reconstruct the population and evaluate the current population status relative to OSP using a generalized logistic model. We demonstrated that the population size in 2014 was above MNPL and within its OSP range. However, we also showed that population growth can be dramatically decreased by increasing sea surface temperature associated with El Niño events or similar regional ocean temperature anomalies. In this analysis we developed a critical tool for management of California sea lions that provides a better understanding of the population dynamics and a scientific foundation upon which to base management decisions related to complex resource issues involving this species. Published 2018. This article is a U.S.Government work and is in the public domain in the USA.

KEY WORDS birth rates, California sea lion, El Niño, generalized logistic, population growth, population status, survival, *Zalophus californianus*.

After centuries of exploitation of marine mammals, the Marine Mammal Protection Act of 1972 (MMPA) provided protection of all marine mammals in United States waters. The MMPA established criteria for management of marine mammals by the National Marine Fisheries Service (NMFS) and United States Fish and Wildlife Service (USFWS). The MMPA states that marine mammal populations "should not be permitted to diminish beyond the point at which they cease to be a significant functioning element in the ecosystem of which they are a part, and, consistent with this major objective, they should not be permitted to diminish below their optimum sustainable population" (16 U. S. C. 1361 Sec 2:5). The intent of the MMPA was to recover marine mammal populations to levels that ensured healthy and robust populations; however, translating the language into management actions presented numerous challenges.

The first challenge was defining optimum sustainable population (OSP). Eberhardt (1977) suggested that the OSP should be interpreted as the range of population sizes from the maximum size (*K*) to the size which gives maximum productivity or maximum sustainable yield (MSY). The NMFS adopted the definition for OSP as a population level between *K* and the population size that provided the maximum net productivity level (MNPL; i.e., greatest net change in the population; Federal Register, 21 Dec 1976, 41FR55536). A population can be designated as depleted under the MMPA if it is below the MNPL. Depleted populations are afforded more protection under the MMPA; consequently, determining OSP and MNPL is an important objective of agencies responsible for the management of marine mammals.

In practice, it is difficult to estimate MNPL for marine mammals because it requires substantial population data that

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are not available for most species (Gerrodette and DeMaster 1990, Ragen 1995), but it is thought to be between 50% and 80% of *K* (Read and Wade 2000). There are some examples in which MNPL and OSP has been estimated for marine mammals. Jeffries et al. (2003) and Brown et al. (2005) fitted generalized logistic models to the counts of harbor seal (*Phoca vitulina*) pups and non-pups on land during the pupping seasons. The OSP (MNPL/*K*) was 0.56 and 0.60 for Washington populations (Jeffries et al. 2003) and 0.61 for the Oregon population (Brown et al. 2005). For northern fur seals (*Callorhinus ursinus*), Ragen (1995) estimated that the mode of MNPL/K was 0.65 with a range of 0.5–0.8. In an assessment of gray whales (*Eschrichtius robustus*), Punt and Wade (2010) integrated across the range of 0.4–0.8 for MNPL, with a resulting MNPL point estimate in their baseline analysis of 0.656. Similarly, in an assessment of spinner (*Stenella longirostris*) and spotted dolphins (*Stenella frontalis*), Wade et al. (2007) integrated across a prior distribution of 0.5–0.8 for MNPL in a generalized logistic model, although in that case there was not enough information in the data to update or change the prior distribution.

Following historical reductions in the population from harvesting and bounties, the California sea lion (*Zalophus californianus*) population in the United States has been steadily increasing since the early 1970s when it was protected under the MMPA (Carretta et al. 2016*b*). Although the growth of the population is a conservation success, the status of the population relative to the MMPA criteria has not been determined. As the population has increased and expanded its range, California sea lions have increasingly been involved in resource conflicts with humans and endangered fish along the west coast of the United States that have resulted in some controversial management actions (e.g., lethal removal of adult male sea lions that feed on endangered salmonids at the Bonneville Dam on the Columbia River, Oregon; Weise and Harvey 2005, Wright et al. 2010). Determination of the status of the population relative to the MMPA criteria will provide support for management decisions that address these complex resource conflicts.

For the United States population of California sea lions (Carretta et al. 2016*b*), pup production (Lowry et al. 2017), and survival (DeLong et al. 2017) have recently declined, suggesting that the population may have stopped growing. For California sea lions, only counts of pups are available for a sufficient period (1975–2014) to evaluate population growth, MNPL, and OSP (Lowry et al. 2017). Berkson and DeMaster (1985) determined that pup counts alone could be used to assess a population status relative to OSP, but they did not consider situations in which the production of pups varied widely from density-independent factors like El Niño events, which can result in low numbers of births and high mortality of pups (DeLong et al. 1991). When pup counts fluctuate widely because of increased pre-census pup mortality or reduced birth rates, the number of pups does not immediately reflect the same magnitude change in the population size. Thus, an analysis based solely on pup counts could be misleading with large reductions in pup numbers at the end of the time series. However, in lieu of a better method, the status of California sea lions is currently determined by a correction factor applied to annual pup counts (Carretta et al. 2016*b*).

As an alternative to assessing the status of the population from pup counts, we developed a model that numerically reconstructs the California sea lion population by integrating multiple data sources and that accounts for variability in birth rates. Our primary objectives were to assess the population growth of California sea lions since the mid-1970s, evaluate the current population status relative to MNPL, and describe environmental and density-dependent impacts on survival, population growth rate, and realized at-census birth rates.

STUDY AREA

Five genetically distinct populations of California sea lions have been identified and include the United States population (U.S. or Pacific Temperate), which breeds on offshore islands in California; the western Baja California population, which breeds offshore along the west coast of Baja California, Mexico; and 3 populations (southern, central, and northern) that breed in the Gulf of California, Mexico (Carretta et al. 2016*b*). Our study applies only to the U.S. population that inhabits coastal waters from the United States-Mexico border, along the west coasts of the United States, British Columbia, Canada, and southeast Alaska, USA (Fig. 1). During the breeding season from May through August each year, most of this population returns to offshore rookery islands along the California coast (Fig. 1). Most of the breeding (99.7%) occurs on 4 islands in the California Channel Islands: San Miguel, San Nicolas, Santa Barbara, and San Clemente. The data used in this study included summer pup censuses of the California Channel Islands and other offshore breeding areas, and survival estimates derived from a single colony at San Miguel Island, which represents about 45% of the United States population.

Pupping occurs over 6 weeks from late May to early July on uninhabited sandy beaches, rocky coves, or rocky points. Sea lion females give birth to a single pup and remain in constant attendance of the pup for 5–8 days postpartum. After the perinatal period, females begin an attendance cycle in which they alternate 2- to 4-day foraging trips at sea with 1- to 2-day nursing visits ashore until the pup is weaned at about 11 months of age (Antonelis et al. 1990, Melin et al. 2000). Breeding occurs about 4 weeks postpartum, beginning in late June and ending in early August. Adult females are nonmigratory and visit the rookery regularly throughout the year, particularly if they have dependent pups (Melin et al. 2000). Adult males arrive at the rookery islands in May, but peak numbers occur in July during the peak of breeding. A small proportion of adult males establish and maintain reproductive territories for 1–60 days. Nonreproductive males haul out in areas outside of the breeding territories. After the reproductive season, adult males migrate from the rookery islands to foraging areas and hauling sites along the California, Oregon, and Washington coasts, the islands of British Columbia, Canada, and southeast Alaska (Maniscalco et al.

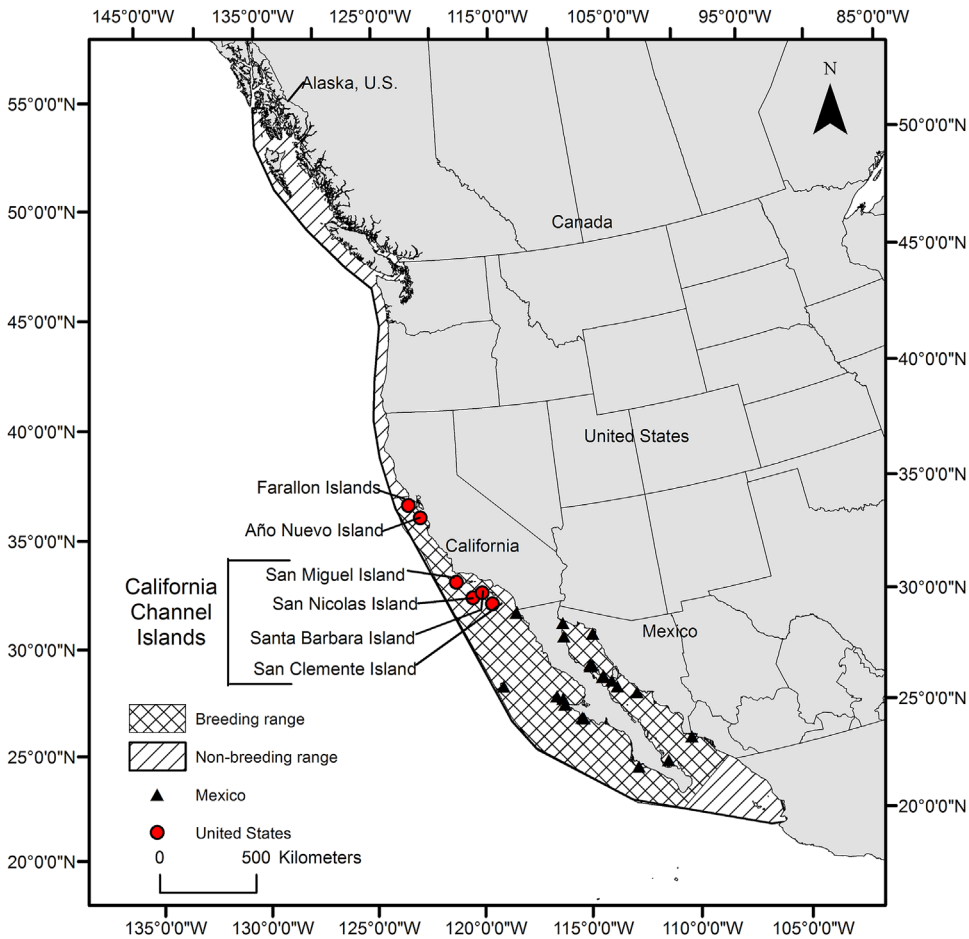

Figure 1. Range of male and female California sea lions and locations of breeding areas in the United States (circles) and Mexico (triangles). We used California sea lions branded at San Miguel Island, California between 1987 and 2014 to estimate survival rates.

2004). Juvenile (1–3 years old) females and males are present at the California Channel Islands throughout the year but also frequent hauling areas and feed along the central California coast during winter (Orr 2011).

California sea lion breeding colonies along the Pacific coast are regularly affected by the El Niño Southern Oscillation (ENSO), a global ocean-atmospheric pattern that consists of a warm El Niño phase followed by a cold La Niña phase. El Niño or La Niña conditions begin at the equator in the central Pacific ocean and then propagate northward along the west coasts of South America and North America dramatically affecting the productivity patterns of the California eastern boundary current (California Current) that the U.S. population of California sea lions relies on for food. El Niño conditions produce strong depressions of the thermocline, higher sea surface height anomalies, and warmer sea surface temperature anomalies in the California Current (King et al. 2011). These oceanographic changes result in reduced biomass of phytoplankton and zooplankton, which leads to changes in the abundance or distribution of fishes and invertebrates throughout the California Current (Bograd and Lynn, 2003). Sea lions feed on fishes and cephalopods, and during the El Niño phase of ENSO, these prey are redistributed northward or deeper in the water column in response to the warmer sea surface temperatures and the deepened thermocline. Consequently, prey become less available to sea lions, particularly nursing sea lions that are biologically tied to the colonies during the 11-month lactation period and have a limited foraging range (DeLong et al. 1991, Lowry et al. 1991, Melin et al. 2008). Pregnant and nursing sea lions travel farther and dive deeper during El Niño conditions, presumably in response to the changes in prey availability (Melin et al. 2008), resulting in significant declines in pup births and survival (Boness et al. 1991, DeLong et al. 1991, Francis and Heath 1991, DeLong and Melin 2000, Melin et al. 2012*a*).

METHODS

As an alternative to assessing the status of the population from pup counts, we numerically reconstructed the California sea lion population by integrating multiple data sources including 1) total pup counts for the U.S. population over a period from 1975 to 2014 (Lowry et al. 2017); 2) age- and sex-specific survival estimates derived from branding, resighting, and recovery data collected from 1987 to 2015 from a colony at San Miguel Island, California (DeLong et al. 2017); and 3) estimates of human-caused mortality (Carretta and Enriquez 2012; Carretta et al. 2016*a*, 2017).

We fitted a generalized logistic population growth curve to the annual reconstructed population sizes from which we could estimate MNPL and the status of the current population size relative to MNPL and OSP.

Our analysis involved 6 partially intertwined steps.

1. We imputed any missing values from available pup count data to construct an entire time series of annual pup counts for the United States population for 1975–2014.
2. We derived sex- and age-specific estimates of annual survival for 1975–2013.
3. With an initial population structure based on a stable age-distribution and the annual pup counts, we projected the abundances using survival estimates to reconstruct the age- and sex-specific population structure and total annual population size for 1975–2014.
4. We estimated annual sea lion bycatch from the halibut (*Paralichthys californicus*) set net fishery data as a minimal estimate of human-caused mortality for 1975–2014.
5. Using the bycatch estimates, we fit a generalized logistic growth curve to the time series of population size each year to estimate MNPL, K, and the status of the population in 2014 (N_{2014}/MNPL).
6. We conducted an analysis of realized birth rates derived from the sex- and age-specific population reconstruction.

These steps were partially recursive because we estimated missing survival rates using a density-dependence term derived from the population reconstruction that was, in part, based upon the survival estimates. This required a few iterations for convergence. Likewise, the analysis of birth rates contained a density-dependence term that was also derived from the generalized logistic fit. As described later, we propagated errors in the survival estimation and imputation of missing pup counts through each step using a bootstrap analysis.

Pup Counts

Pup counts for the entire United States population were available for 1975–1977, 1981–2008, and 2011–2014 using counts from Lowry et al. (2017) and for San Nicolas Island during 1985–1989 from previous reports (Bonnell et al. 1980, Stewart et al. 1993, Lowry and Maravilla-Chavez 2005). To accomplish the population reconstruction, we needed complete pup counts for each year (P_y). For missing years, we imputed values for 1978–1980 from predictions of a temporal trend using linear regression of the log of counts for 1975–2001. Lowry et al. (2017) describes how we imputed values for 2009–2010 from a complete ground count at San Miguel Island and a partial ground count at San Nicolas Island during those years. We assumed pup counts were known without error, but we propagated error from the missing imputed counts.

Age- and Sex-Specific Survival

Age- and sex-specific survival estimates from a mark-release-resight recovery model of branded California sea lions on San Miguel Island were available from 1987 to 2014 (DeLong et al. 2017). We used the annual survival estimates from the best model in DeLong et al. (2017). Pups were branded in fall at 3–4 months of age, but pup survival rates accounted for survival from the time of the pup counts in late July to branding by assuming a constant survival rate for that period as measured from 1 October to the following 1 July. Very early pup mortality can be higher, but it occurs before the pup count. Only pups were marked and released each year, so age-specific estimates were missing in year y for ages $a > y - 1987$ (e.g., only pup survival was available for 1987, only pup and yearling survival for 1988). Also, estimates of survival were not available for sea lions of any ages for 1975–1986. To provide estimates for these missing values, we fitted a linear mixed effects model to the logits (μ_{say}) of the set of survival estimates (S_{say}) for each sex ($s = m$ or f), age ($a = 0$–24), and year ($y = 1987$–2013), $\mu_{say} = log\left(S_{say}/\left(1 - S_{say}\right)\right)$. Predictive variables for fixed effects included sex, age, and annual covariates including average sea surface temperature (SST) anomaly, average pup weight, and N_y/K as a measure of density dependence in survival. For pup survival, we used the average SST anomaly from 1 October to 30 June and for juveniles and adults, we used the average SST anomaly from 1 July to 30 June to correspond to the survival periods in our models. In addition, for pup survival we also evaluated an average SST anomaly from 1 April to 30 September, which could affect pup weights at branding by affecting pregnant and lactating females. We used the local SST anomaly as a measure of environmental conditions during the study period and to identify years affected by El Niño conditions. Warmer SSTs are usually associated with lower productivity and prey availability, whereas cooler SSTs are associated with high productivity and good foraging conditions for sea lions. We used the average SST anomaly measured at 4 National Oceanic and Atmospheric Administration (NOAA) data buoys (stations: 46054, 46218, 46011, pslc1; NOAA National Data Buoy Center, http://www.ndbc.noaa.gov) located 26 km to 128 km north of San Miguel Island, California in the area where females from the colony primarily forage (Melin and DeLong 2000, Melin et al. 2008).

Annual estimates of pup and yearling survival were quite variable, so we included an annual random effect for those ages. From the fitted model, we predicted missing estimates of survival (e.g., for years <1987) with the fixed effect estimates, and where survival estimates were available from capture-recapture analysis (1987–2013), the estimated predictions included the fixed and random effect estimates.

The density-dependence term N_y/K in the mixed effects model for survival was only available after reconstructing the population and fitting the generalized logistic. Thus, we needed to iterate the model fitting for survival estimates, population reconstruction, and fitting of the logistic model. Carrying capacity in the mixed-effects model for survival primarily acts as a scalar for abundance N_y in N_y/K. With some reasonable starting values for N_y and K, we fitted the mixed-effects model, constructed the population size, predicted K, and repeated the process until the estimated parameters converged.

Human-Caused Mortality

To account partially for human-caused mortality in the population, we used data collected from the halibut set gillnet fishery, which is a primary cause of fishery entanglement and mortality for California sea lions (Carretta and Enriquez 2012). Total fishing effort data for the set gillnet fishery was available for 1981–2014 and the sea lion bycatch was observed in a sample of trips in 1990–1994, 1999–2000, 2006–2007, and 2010–2012 to estimate the average bycatch per unit effort. A gillnet closure area implemented in 1994 resulted in the halibut fishery being excluded from within 5.6 km of the southern California mainland. Consequently, we estimated 2 average bycatch rates: for years before and including 1994 and for years after 1994. We estimated the sea lion bycatch in a year (H_y) by multiplying the total annual fishing effort by the average bycatch rate for that year. The fishery was active from 1975 to 1980, but the amount of effort was not available, so we used a generalized additive model to predict the amount of fishing effort in those years using the log of fishing effort with a smoother across year.

Population Reconstruction

Population reconstruction for a set of years indexed by y is simply a series of estimates of the number of animals alive for each age a for females ($N_{f,a,y}$) and for males ($N_{m,a,y}$). The size of the total population in year y (N_y) is simply the sum of all the animals in each age for both sexes alive in that year, $N_y = \sum_{a=0}^{A} N_{f,a,y} + \sum_{a=0}^{A} N_{m,a,y}$, where A is the maximum age. From the number of pups in a year (P_y) and annual age- and sex-specific survival estimates ($S_{s,a,y}$) we can project forward to predict the number of animals in the population at each age over time for each sex. The population reconstruction assumes the population is geographically closed and only births add to the population. Assuming a 50:50 sex ratio of pups, $N_{f,0,y} = N_{m,0,y} = P_y/2$. For example, the expected number of yearling females in year $y+1$ is $N_{f,1,y+1} = N_{f,0,y} S_{f,0,y}$, where $S_{f,0,y}$ is female pup survival in year y and likewise for males using the male pup survival rate. In general, for any age and sex the equations are $N_{s,a+1,y+1} = N_{s,a,y} S_{s,a,y}$, where s is either f or m for females or males, respectively.

However, to initiate the reconstruction in the initial year (i.e., 1975), we also needed estimates of $N_{f,a,y}$ and $N_{m,a,y}$ for yearlings and older animals ($1 \le a \le A$) to estimate the population size for years 1975 to 1975+A-1. To develop estimates of the sex- and age-specific population sizes in 1975, we used the stable age-distribution equations of Cole (1954) as described by Eberhardt (1985). Let c_a be the proportion at age a. Assuming an instantaneous constant growth rate r, the proportion at age a is $c_a = e^{-ra} l_a / B_a$, where $l_a = \prod_{a=0}^{a-1} S_a$ and $B_a = \sum_{a=0}^{A} e^{-ra} l_a$. We used a value of r derived from the slope of a linear regression from the log of the pup count from the first 7 years (1975–1981) and computed separate age-distributions (c_a) for each sex using the estimated survival rates for 1975. Using the pup count in 1975, we estimated the number of females and males in the population as $N_{f,1975} = P_{1975}/2/c_{f,0}$ and $N_{m,1975} = P_{1975}/2/c_{m,0}$, respectively. Then we estimated the number at each age from the age-distribution formula (e.g., $N_{f,a,1975} = c_{f,a} N_{f,1975}$).

Birth Rates

California sea lion birth rate estimates were only available for a few cohorts over a short time frame within the population reconstruction period (Melin et al. 2012*a*), so we could not include them in the model fitting, but we computed implied birth rates (B_y) at the census time from the population reconstruction values for females >4 years old (Melin et al. 2012*a*), $B_y = P_y/F_y$, where $F_y = \sum_{a=4}^{A} N_{f,a,y}$. These values will be lower and likely more variable than true birth rates because of early pup mortality prior to the pup count.

Previous studies reported that birth rates in the 1970s and possibly later were lower because of premature births associated with high levels of total dichlorodiphenyltrichloroethane (DDT) and polychlorinated biphenyl (PCB) concentrations in the blubber of reproductive females (DeLong et al. 1973, Gilmartin et al. 1976). Also, the birth rate is often lower during El Niño conditions (DeLong et al. 1991, Melin et al. 2012*a*, Lowry et al. 2017) and as the population increased density-dependent reductions in birth rates may have occurred. To examine these potential effects, we fitted models for B_y using covariates allowing for density-dependent effects in birth rate (N_y/K), El Niño conditions as reflected by the local SST anomaly from 1 July to 30 June (DeLong et al. 2017), and impacts of DDT concentrations (lipid weight ppm) that declined from the early 1970s to the present.

Values of DDT concentration from adult female blubber tissue samples were available for only a few years including 1970 and 1972 (DeLong et al. 1973, Gilmartin et al. 1976), 1991 (R. L. DeLong, NMFS, unpublished data), and 2001–2003 (Randhawa et al. 2015). Values in 1970, 1972, and 1991 were taken from fixed sample sizes of premature parturient and full-term parturient females but not in proportion to their occurrence in the population. Thus, we computed a weighted average of the 2 means based on the proportion of premature parturient and full-term females in the population (R. L. DeLong, unpublished data). An average of DDT concentration for a sample of females was available for 2001–2003 (Randhawa et al. 2015), so we used the single average with a year of 2002. We derived yearly values of the DDT concentration covariate with predictions from a linear regression of the log of observed DDT concentration values (273, 268, 10.5, and 10.8) over time (1970, 1972, 1991, and 2002). For the model fitting of birth rates (B_y), we assumed that B_y was approximately normal with mean μ_y and variance $\tilde{B}_y \times (1 - \tilde{B}_y) \times (e^{\gamma} + 1)$, where $\tilde{B}_y$ is the predicted birth rate and the parameter γ inflates the binomial variance ($\tilde{B}_y \times (1 - \tilde{B}_y)$) for over-dispersion. We

used linear combinations of the DDT, SST, and density-dependent (N_y/K) covariates to model μ_y with a logit link function. We estimated the parameters via maximum likelihood and selected from among models with various combinations of covariates based on Akaike's Information Criterion with small sample size correction (AIC_c).

Generalized Logistic Growth Model

In a discrete logistic model of population growth, $N_{y+1} = N_y[1 + R(1 - N_y/K)]$, where N_y is the population size in year y, R is the maximum growth rate, K is the carrying capacity of the population, and the derived value of MNPL is $K/2$. A generalized logistic model, $N_{y+1} = N_y[1 + R(1 - (N_y/K)^z))]$ has an additional exponent z with values >1, which allows MNPL/K to be >0.5 because MNPL/K is $(1+z)^{-(1/z)}$. To estimate K and MNPL of the California sea lion population, we used a generalized discrete logistic population growth curve fitted to the annual reconstructed population sizes (N_y). The basic equation for the growth curve is $N_{y+1} = N_y + N_y \times R \times (1 - (N_y/K)^z)) - H_y$, where R is the maximum rate of increase, K is carrying capacity, and H_y are the human-caused mortalities (bycatch) in year y. We expanded this equation to allow for variation in the population growth rate due to El Niño conditions as reflected by changes in the annual SST anomaly. Adding the SST anomaly in year y, the growth curve equation is $N_{y+1} = N_y + N_y \times (R + b \times SST_y)(1 - (N_y/K)^z) - H_y$, where b is an estimated slope for the effect of SST on the population growth rate and R is now the maximum rate of increase in years of average SST (anomaly = 0). We estimated the parameters (K, R, z, and b) using non-linear least squares with the function nls in R (R Core Team 2016). We used the reconstructed population size in 2014 divided by the estimate of MNPL as the measure of population status relative to OSP. If N_{2014}/MNPL >1, the population is within the OSP range.

To provide confidence intervals for parameter estimates and an evaluation of certainty about the population status relative to OSP, we used a parametric bootstrap approach with 1,000 bootstraps from which we computed 95% intervals, which were the 25th smallest and 975th largest value of the parameter estimates or derived statistics. We included all known sources of uncertainty including survival estimates derived from DeLong et al. (2017), imputed values of pup counts for missing values, estimates of human caused mortality, and DDT concentration values used in analysis of birth rates. For the latter 3 sources, we allowed the predictions to vary using the assumed error model in the regression or ratio estimation. For each bootstrap replicate, we completed 4 steps.

1. From the survival analysis, we assumed the logit of the sex- and age-specific survival estimates were distributed as a multi-variate normal with the mean vector computed from the estimated values and the variance-covariance matrix from the estimated model. The annual survival estimate for males >2 years old in 1996 was at a boundary of 1 with no valid variance estimate, which precluded evaluation of the multi-variate normal distribution, so we replaced it with the estimate from 1995 to allow the use of the parametric bootstrap. From the multi-variate distribution for the parameters, we drew a new sample of parameter estimates for the survival mode.
2. We generated a new set of imputed pup counts using the regression models described above and in Lowry et al. (2017).
3. We fitted the mixed-effects model to predict the complete set of age- and sex-specific survival estimates and reconstructed the population sizes from 1975 to 2014. In reconstructing the population size for the bootstraps, we used a binomial distribution to allow for stochastic variation in the proportion that survive from age a at time t to age $a+1$ at time $t+1$ rather than the deterministic equation.
4. After reconstructing the population over time, we fitted the logistic growth curve with one bootstrap set of human-caused mortality estimates and the fit of the model for birth rates using a bootstrap set of DDT concentration values.

This process provided 1,000 estimates of each parameter in the logistic growth curve, a ratio of predicted population size for 2014 divided by the MNPL estimate, and confidence intervals for the birth rate parameters. In the bootstrap process, we conducted model selection for the mixed-effects model of survival and the birth rate for each bootstrap to incorporate model selection uncertainty.

The research described in this paper was reviewed and approved by the National Atmospheric and Oceanic Administration, National Marine Fisheries Service, Alaska Fisheries Science Center/Northwest Fisheries Science Center Institutional Animal Care and Use Committee (IACUC) under approved protocol numbers A/NW 2010-7, A/NW 2013-5, and National Marine Fisheries Service MMPA Permit Numbers 717, 736, 782, 782-1812, 783-977, 1613, 16087, 16087-2 issued to the NMFS Alaska Fisheries Science Center, Marine Mammal Laboratory. The methods for marking and observing California sea lions for estimating survival are described in DeLong et al. (2017) and were approved under the permits and IACUC-approved protocols. Protocols for data collected prior to 2010 were not reviewed by the NMFS IACUC because the IACUC did not exist; however, protocols for pup censusing and the sea lion marking program have not changed since they began in the 1970s and 1980s. Research conducted by the NMFS Southwest Fisheries Science Center was authorized under MMPA Permit Numbers 347, 404, 684, 704, 774-1437, 774-1714, and 14097 and National Marine Sanctuary Permits GFNMS/MBNMS/CINMS-04-98, MULTI-2002-003, MULTI-2003-003, and MULTI-2008-003.

RESULTS

The California sea lion pup count in the United States population has increased steadily since 1975 except for

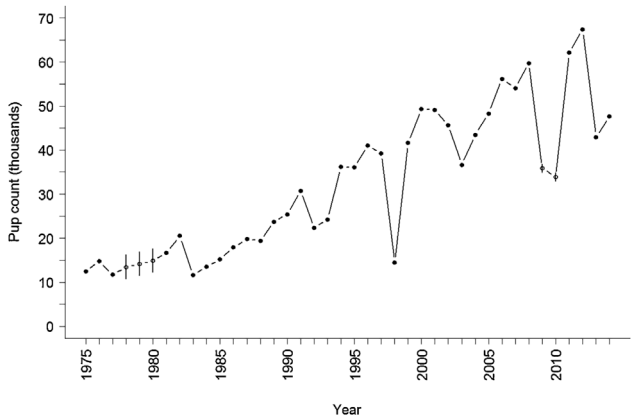

Figure 2. California sea lion population pup counts in the United States, 1975–2014. Open circles are imputed estimated values with vertical lines representing 95% bootstrap confidence intervals.

abrupt significant declines associated with El Niño events and recent declines in 2009, 2010, 2013, and 2014 (Fig. 2). These shifts in annual pup production are reflected throughout the age structure, which is dynamic over time (Fig. 3).

In addition to changes in the number of births, there has been significant annual variation in survival of pups and yearlings (DeLong et al. 2017). A recent decline in yearling and pup survival has resulted in low recruitment of females reaching age 2 and age 4 (Fig. 3). Even though the pup count in 2012 was the highest recorded (Fig. 2), the number of males and females reaching age 2 from this cohort was the lowest since the 1998 cohort (Fig. 3) when pup production was severely curtailed because of the strong 1997–1998 El Niño event.

The declines in pup births and juvenile survival from 2011 to 2014 have led to a leveling of the number of females $\geq$4 years old that comprise the reproductive age class (Fig. 4). This may have consequences for future population growth by depressing recruitment of reproductive females. Similar leveling occurred during other periods in the time series and followed the occurrence of El Niño events in 1982–1983 and 1997–1998 (Fig. 4). In each of these occasions, the high mortality of birth cohorts and poor survival of juveniles led to the leveling period, but each was followed by a period of strong population growth.

The reconstructed total population sizes (Fig. 5) are more variable over time than the reconstructed population sizes of females $\geq$4 years old (Fig. 4) because of the high degree of annual variability in pup and yearling numbers (Fig. 3). The sex- and age-partitioned population sizes (Table 1, Fig. 3) demonstrate the shifts in age structure with the number of sea lions <8 years old in recent years being lower than their peak abundance earlier in the time series and sea lions $\geq$8 years old being at their peak abundance. The sex- and age- partitioned population sizes also show the change in sex structure across age due to the sex-differential in survival at older ages (Tables S1 and S2, available online in Supporting Information). The abundance of males and females are similar up to age 8 but then diverge at older ages with females predominating because of lower survival of males of the same ages. From the population reconstruction values, we computed the multiplier that would be needed to derive the correct population size from the pup count in each year. The multiplier values ranged from 3.88 in 2000 to 10.06 in 1998 (Table 1). When the birth rate was >0.8 the average correction factor was 4.26, but the birth rate estimates were >0.8 in only 15% of the 39 years. For the remaining years, except 1999, the correction factor was >4.26.

The model-averaged estimates of parameters fitted to the annual birth rates computed from the reconstructed population sizes demonstrated a decline in birth rate from higher DDT concentrations in adult female blubber and

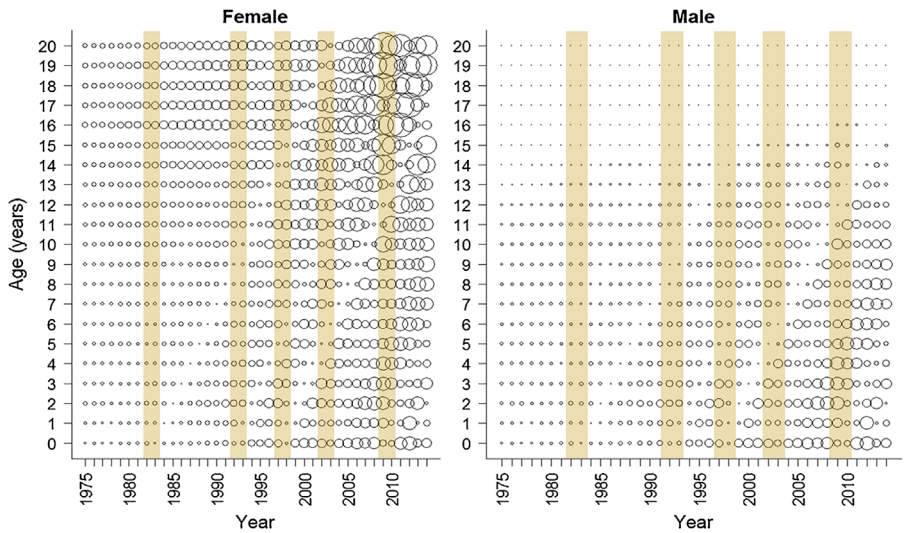

Figure 3. Relative abundance for female and male California sea lions in the United States, 1975–2014, for ages 0 to 20 years. Bubble size represents the proportion for age (a) in year (y) of females or males relative to the maximum number of animals (females+males) of age a among all years. Age axis is restricted to age 20 to improve visual for younger ages; most of the population (99.8%) was younger than age 21. Gold bars identify years affected by El Niño conditions.

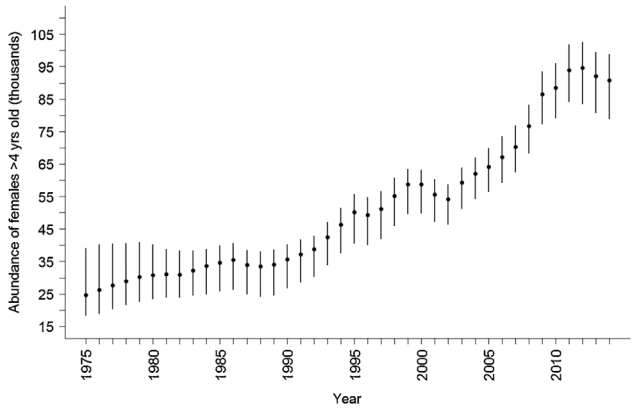

Figure 4. Predicted abundance of female California sea lions ages 4 and older in the United States population, 1975–2014, and 95% confidence intervals from parametric bootstrap.

higher SST anomalies associated with El Niño events and a possible density-dependent response in recent years (Table 2, Fig. 6). The birth rate odds $(B_y/(1-B_y))$ decline by 0.129 (95% CI = 0.004–0.563) for every 10 ppm DDT concentration increase, by 0.570 (95% CI = 0.491–0.702) for every 1°C of SST above normal, and by 0.155 (95% CI = 0.003–0.314) for each 0.1 N/K increase in abundance. The estimate of the SST effect was much more precise than either the DDT concentration or density-dependent responses.

For most of the period from 1974 to 2014, the estimated percentage of the California sea lion population killed as bycatch in the halibut set gillnet fishery was <2%, but during the period of highest fishing effort in the 1980s, it reached about 8.5%. In the past decade, it declined to <0.2%. Most of the bycaught California sea lions in the fishery were juveniles. If the bycatch is assumed to consist only of sea lions of age 0–3, those ages would represent a greater proportion of the total, but the pattern across time would be similar.

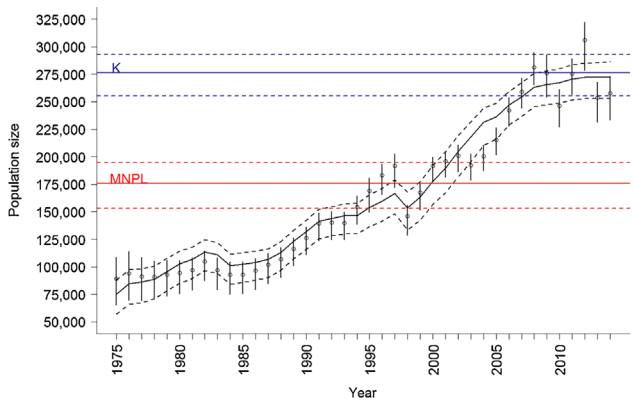

Figure 5. Fitted logistic growth curve (solid line) and 95% bootstrap intervals (dashed line) for reconstructed California sea lion annual population sizes in the United States, 1975–2014. Vertical lines are 95% bootstrap confidence intervals for reconstructed annual population sizes. We also present estimated carrying capacity (K; solid blue line) with 95% confidence intervals (dashed blue line) and maximum net productivity level (MNPL; red solid line) with 95% confidence intervals (dashed red line).

Table 1. Annual California sea lion pup counts from breeding areas in the United States and population sizes of female (F) and male (M) California sea lions from 1975 to 2014 estimated from a population reconstruction model. The multiplier is the correction factor for pup counts to derive the total population size.

		Population estimate			
Yr	Pup count	F	M	Total	Multiplier
1975	12,499	49,136	39,788	88,924	7.12
1976	14,749	51,944	42,226	94,170	6.39
1977	11,712	50,784	40,415	91,199	7.79
1978[a]	13,449	50,942	39,971	90,913	6.76
1979[a]	14,145	52,151	40,661	92,812	6.56
1980[a]	14,878	53,180	41,153	94,333	6.34
1981	16,701	54,748	42,249	96,997	5.81
1982	20,540	58,881	45,899	104,780	5.10
1983	11,595	55,342	41,465	96,807	8.35
1984	13,550	53,657	39,354	93,011	6.86
1985	15,224	53,753	39,259	93,012	6.11
1986	17,896	55,489	41,187	96,676	5.40
1987	19,796	58,017	43,827	101,844	5.14
1988	19,452	60,513	46,337	106,850	5.49
1989	23,757	65,162	51,021	116,183	4.89
1990	25,422	70,281	56,040	126,321	4.97
1991	30,747	76,840	62,383	139,223	4.53
1992	22,364	77,663	62,675	140,338	6.28
1993	24,274	77,681	62,178	139,859	5.76
1994	36,184	85,138	68,990	154,128	4.26
1995	36,073	93,031	76,067	169,098	4.69
1996	41,044	100,531	82,570	183,101	4.46
1997	39,245	105,432	86,367	191,799	4.89
1998	14,506	83,352	62,559	145,911	10.06
1999	41,695	94,426	72,932	167,358	4.01
2000	49,372	107,358	84,274	191,632	3.88
2001	49,078	110,679	85,126	195,805	3.99
2002	45,658	114,253	86,612	200,865	4.40
2003	36,659	110,691	81,384	192,075	5.24
2004	43,490	114,985	85,342	200,327	4.61
2005	48,331	122,423	92,825	215,248	4.45
2006	56,144	135,829	106,364	242,193	4.31
2007	54,088	144,443	114,561	259,004	4.79
2008	59,774	156,091	125,359	281,450	4.71
2009[a]	35,914	154,229	121,926	276,155	7.69
2010[a]	33,873	139,983	106,348	246,331	7.27
2011	62,109	155,174	120,315	275,489	4.44
2012	67,396	171,149	135,071	306,220	4.54
2013	42,913	146,010	107,652	253,662	5.91
2014	47,691	148,499	109,107	257,606	5.40

[a] Pup count estimated from imputed values from partial censuses or regression (Lowry et al. 2017).

From the fitted logistic growth model of the total reconstructed population size (Table 3, Fig. 5), the estimated maximum growth rate (R) for the California sea lion population was 0.07 under a normal SST regime. The California sea lion population size in 2014 (257,631) was estimated to be about 40% greater than MNPL (183,481) and the 95% confidence limit for N/MNPL (95% CI = 1.22–1.58) shows that the population is currently well within OSP (Table 3). Carrying capacity was estimated to be at 275,298 animals. Even with a substantial reduction in N, the population is expected to remain at OSP for the foreseeable future. However, an increase of 1° C SST was estimated to reduce the population growth rate by 0.07, thereby halting growth (Table 3). During strong El Niño events the SST anomaly can be ≥2° C resulting in a negative growth rate

Table 2. Model-averaged estimates of the logit of parameters for the California sea lion birth rate function computed from population reconstruction values for sea lions in the United States, 1975–2014. The 95% confidence intervals are from bootstrap replicates.

Parameter[a]	Estimate	95% CI Lower limit	95% CI Upper limit
γ	8.02	7.88	8.61
Intercept	2.13	0.601	4.69
SST	−0.843	−1.21	−0.675
DDT	−0.0138	−0.0827	−0.000348
N/K	−1.68	−3.78	−0.0302

[a] γ is inflation value for binomial variance for over-dispersion, SST is sea surface temperature anomaly, DDT is concentration of dichlorodiphenyltrichloroethane in blubber of reproductive females, and *N*/K represents density dependence where *N* is abundance and *K* is carrying capacity.

Table 3. Logistic growth curve parameters used to estimate the size of the United States California sea lion population in 2014. The 95% confidence intervals are from 1,000 bootstrap replicates.

Parameter[a]	Estimate	95% CI Lower limit	95% CI Upper limit
z	3.93	2.09	7.79
R	0.0695	0.056	0.0947
N_{1975}	75,102	56,874	87,756
K	275,298	255,332	291,360
b	−0.0696	−0.101	−0.0493
MNPL	183,481	160,156	207,649
MNPL/K	0.666	0.583	0.756
N_{2014}	257,631	233,515	273,211
N_{2014}/MNPL	1.4	1.22	1.58

[a] N_y is population size in year y, K is the population carrying capacity, R is the maximum growth rate, z is the generalized logistic exponent, MNPL is maximum net productivity level, and b is the slope of the sea surface temperature covariate for growth rate.

from decreases in pup births and pup and juvenile survival. Thus, rapid declines in abundance could occur with persistent ocean warming.

DISCUSSION

We have proposed a conceptually simple population reconstruction approach to estimate the total population size and population growth of California sea lions in the United States, resulting in the first age- and sex- specific population growth model for the species. The method has a side benefit of providing complete sex- and age-structure of the population over time and provides derived estimates of birth rates. However, this approach does require a long-term data set with counts of pups and age- and sex-specific survival estimates. We used 39 years of pup counts and 28 years of survival estimates, which allowed us to identify factors contributing to the dynamic nature of the population.

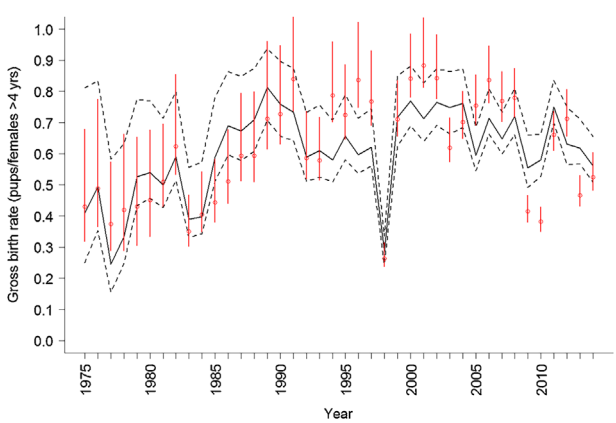

Figure 6. Model-averaged predicted birth rate function (solid line) for female California sea lions in the United States, 1975–2014, and 95% bootstrap confidence interval (dashed line). Model covariates included sea surface temperature anomaly in female foraging area, predicted dichlorodiphenyltrichloroethane (DDT) concentration in female blubber, and a density-dependence covariate (*N/K*) (abundance/carrying capacity). Points are the implicit gross birth rates computed from population reconstructions by dividing number of pups by number of females ≥4 years old. Error bars around points are 95% confidence intervals for birth rate computation from population reconstruction.

For this method, the population must be geographically closed with no immigration or emigration. Permanent emigration may be subsumed into the survival estimates so it was not a large concern. Immigration of California sea lions from Mexico's Pacific coast populations cannot be completely ruled out. If there is immigration, particularly of juvenile animals, then our estimates of population size derived from pup births will be too low in years when immigration occurred. Immigration that resulted in increased abundance of mature females not accounted for in our model could also affect our assessment of birth rates by making them higher than our model estimates.

Birth rates were very low during the first decade of the study in part because adult females suffered reproductive failure associated with high levels of DDT concentrations in their blubber (DeLong et al. 1973, Gilmartin et al. 1976). The effect of DDT concentrations on birth rates appeared to become less important after 1986, probably because of reduced levels of the contaminants in the southern California marine environment. Significant decreases in birth rates were clearly associated with warmer SSTs that occur during El Niño conditions, but elevated SSTs do occur outside El Niño events. Warmer SSTs negatively affect sea lion births because they are usually associated with other physical and biological oceanographic changes that occur in the California Current Ecosystem that lead to decreased prey availability to California sea lions (Chavez et al. 2002). The decreased prey availability leads to low pup growth rates, decreased birth rates, and higher mortality among sea lions (DeLong et al. 1991; Melin et al. 2010, 2012*a*,*b*). In some cases, the population response to warmer SSTs may span multiple years or may lag the event by months or years as indicated by the substantial variability in the abundance of pups and yearling age classes in our model. The relationships of SST, birth rates, and animal condition are sensitive to small- and large-scale changes in the marine environment and are likely not always a simple linear relationship nor the only environmental factor affecting changes in birth rates, animal condition, or survival. However, the strong relationship between warmer SSTs and changes in birth rates provides insight

into the potential impacts of warming oceans on sea lion population trends due to climate change.

The very large estimate of the parameter γ to allow for over-dispersion from binomial variance, suggests the birth rate model is incomplete and other factors not included in our model are causing additional variation in either the reconstructed population sizes or the true birth rates. One such factor is early pup mortality that occurs prior to the pup census in mid- to late July. The 2009 birth rate was far below the long-term average and the predicted value from the birth rate model because of high pup mortality prior to the pup census (Melin et al. 2010). Many reproductive females left the rookery early during the 2009 breeding season because foraging conditions were poor owing to an oceanographic upwelling relaxation along the central California coast during summer (Bjorkstedt et al. 2010). Consequently, reproductive females were either not impregnated, did not implant, or prematurely aborted leading to a similarly low birth rate value in 2010.

Even with the large data sets we used, they were still incomplete. In our application, we had only a partial set of age- and sex-specific survival rates limited to San Miguel Island from 1987 to 2014, but we devised a scheme to derive the missing estimates. Our approach assumes the survival estimates apply to the entire population of California sea lions breeding in the United States and the model for the derived survival estimates is unbiased. We also had to assume that the population had a stable age distribution in 1975 and we could accurately reconstruct it. By starting in 1975, any errors in the estimated age distribution would be largely diminished by 1990. Therefore, we do not believe that any possible problems are sufficient to invalidate our conclusion that the population has expanded past its MNPL and it is within the range of OSP. The location of MNPL relative to K (0.67) seems very sensible considering the assumed range of 0.5–0.8 that was used by Wade et al. (2007) and MNPL estimates for harbor seals (Jeffries et al. 2003, Brown et al. 2005). The California sea lion population growth model and the OSP conclusion were largely influenced by the data from the last 24 years when we had adequate survival estimates and accurate pup counts.

We cannot rule out the possibility that the population will increase again at some point in the future. If the California Current returns to a highly productive marine environment with ample prey for sea lions, the population will likely respond with higher survival and birth rates. However, what the population has experienced since 2009 is very different than what occurred in the late 1990s and early 2000s when the California Current was a productive ecosystem. The 1997–1998 El Niño event affected the birth cohorts of 1996–1998, resulting in a temporary leveling of population size, but it was short-lived because of the small number of cohorts affected. This was followed by a rapid growth period between 1999 and 2009. Decreases in the survival and birth rates since 2009 have been influenced by environmental anomalies in central and southern California (e.g., an oceanographic upwelling relaxation event in 2009 (Bjorkstedt et al. 2010), an El Niño in 2010 (Bjorkstedt et al. 2011), and an oceanic heat wave [i.e., The Blob] in 2013–2015 (Leising et al. 2015, McClatchie et al. 2016)) that have affected prey availability for juveniles and pregnant and lactating females that remain in the coastal California waters year round and influence population dynamics (Melin et al. 2010, 2012*b*). If the population had been much smaller during these events, like it was in the 1990s, *per capita* resources would have been greater, and the environmental effect may not have been as dramatic. Future monitoring of the population and its vital rates will allow a more robust assessment of whether density dependence is regulating growth of the population at current levels of population abundance.

All sources of mortality, including human-caused mortality, are reflected in the survival rates used in the model. We attempted to estimate human-caused mortality because the Potential Biological Removal (PBR) level is one of the criteria in the MMPA for determining a population's status. It is the maximum number of animals that can be removed from the population because of human-caused mortality while allowing the population to reach or maintain its OSP (Wade 1998). The default maximum rate of increase (R_{max}) for pinnipeds in the PBR scheme (Wade 1998) is 0.12; our R_{max} estimate was only 0.07 (95% CI = 0.06–0.09). Our estimate should not be treated as the potential maximum rate of increase for California sea lions because we have been able to include only a fraction of the human-caused mortality and because at the time that sea lions should have been increasing at their maximum (in the 1970s and 1980s), their reproductive rate was being hampered by the effects of DDT and PCB pollution (DeLong et al. 1973, Gilmartin et al. 1976). With respect to human-caused mortality of California sea lions, the largest estimates of mortality have historically been attributed to the halibut set gillnet fishery (Julian and Beeson 1998). However, this fishery represents only one source of human-caused mortality, and other sources include the swordfish (*Xiphias gladius*) and common thresher shark (*Alopias vulpinus*) large-mesh drift gillnet fishery (Carretta et al. 2017), fishery-related shootings (Greig et al. 2005), the ingestion of fishing hooks from recreational fisheries, and entrainment in power plant intake systems (Carretta et al. 2016*a*). Estimated bycatch in the California common thresher shark and swordfish drift gillnet fishery totaled approximately 1,400 animals between 1990 and 2015 (Carretta et al. 2017), a value that is less than some individual year bycatch estimates reported in the halibut set gillnet fishery by Julian and Beeson (1998). Hook-and-line fishery and shooting removals are based on opportunistic stranding reports, which represent minimum counts, because not all carcasses are documented and there is currently no way to correct for this bias. Greig et al. (2005) reported on the causes for 3,692 stranded sea lions over 10 years and concluded that 12% of the strandings were caused by human-induced trauma and 71% of those trauma cases resulted from gunshot wounds. If undocumented human-caused mortality is significant, then our estimates of maximum rates of increase for the population may be too low.

The dynamic age structure of the California sea lion population has implications for estimation of sea lion

abundance. In lieu of species-specific life-history parameters, a correction factor (multiplier) constructed from northern fur seal life-history parameters has been used to scale up the pup count to a total population estimate. For example, a value of 4.32 was used for the multiplier on the 2008 count of pups (Carretta et al. 2016*b*). However, our analysis shows that the multiplier could range from 3.88 to a maximum of 10.06 because of changes in pup production. Thus, constructing an estimate of abundance from the pup count with a constant multiplier is not a viable approach for California sea lions.

The challenges of maintaining a high-quality data set over multiple decades needed to reconstruct a population history are many and varied. Such studies for marine mammals are uncommon, largely because of the challenges associated with this long-lived group that spends very little time in view, ranges over vast expanses of ocean, and is costly to monitor (Bowen et al. 2010). However, the method we used here will be a useful tool for estimating the abundance of other MMPA pinniped species for which there are sufficient time series for abundance and vital rates. For example, the status of California and Eastern Pacific stocks of northern fur seals are currently computed using pup counts and a single life-history multiplier (Carretta et al. 2016*b*, Muto et al. 2017). A time series of pup counts and data on survival are available for both populations, so the approach we used here could be used to estimate abundance of the populations with some modification to allow for less complete time series.

MANAGEMENT IMPLICATIONS

The determination that the United States California sea lion population is at OSP has several important management implications. First, it indicates that the management objectives of the MMPA are being met for this species. Second, the determination that a population is at OSP provides the opportunity for individual states to request a transfer of the authority for management and conservation under the MMPA from NMFS to the state. In the case of California sea lions, the states of California, Oregon, and Washington could request this authority, but they must meet various criteria stipulated in the MMPA, including a state management program that is consistent with the purposes, policies, and goals of the MMPA and international treaty obligations.

The influence of changes in SST on the population growth of California sea lions needs to be considered in management of the species. If SST in the California Current increases 1°C in response to climate changes, our model predicts the annual growth rate would fall to zero and if the SST increased 2°C, the annual population growth rate would decline 7%. If this occurred, the population could rapidly fall below the range of OSP, potentially changing the population's status under the MMPA. This could lead to changes in management strategies and options.

Finally, in developing this analysis we have provided a critical tool for current and future management of California sea lions. Along the west coast of the United States, there are various resource conflicts involving this robust population of sea lions: fisheries interactions that lead to sea lion mortality and economic losses for the fisheries (Weise and Harvey 2005), interactions with people on public beaches and at marinas creating human safety concerns and inflicting property damage, and interactions with endangered fish possibly impeding the recovery of the fish populations (NMFS 1997, 2008). Perhaps the most high-profile management issue is at the Bonneville Dam on the Columbia River, where a controversial lethal removal program authorized under the MMPA, and managed by the states of Oregon and Washington, has been conducted in an attempt to alleviate sea lion predation pressure that may be impeding recovery of endangered salmonids (NMFS 2008). The model we presented here highlights the value of long-term research in support of management needs to meet MMPA mandates and the need to continue the research as the California sea lion population responds to environmental and anthropogenic changes that may alter its status. It is only through a long-term approach that managers will have a sufficient understanding of the dynamics of the California sea lion population on which to base future management decisions related to complex resource conflicts involving this species.

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