

Article type : Article

LRH: MARINE MAMMAL SCIENCE, VOL. **, NO. *, ****

RRH: DELONG *ET AL.*: CALIFORNIA SEA LION SURVIVAL

Age- and sex-specific survival of California sea lions (*Zalophus californianus*) at San Miguel Island, California

ROBERT L. DELONG, **SHARON R. MELIN**,¹ **JEFFREY L. LAAKE**, NOAA Fisheries, Alaska Fisheries Science Center, Marine Mammal Laboratory, 7600 Sand Point Way N.E., Seattle, Washington 98115, U.S.A.; **PATRICIA MORRIS**, Año Nuevo Island Reserve, University of California, Santa Cruz, Long Marine Lab, 100 Shaffer Road, Santa Cruz, California 95060, U.S.A.; **ANTHONY J. ORR**, **JEFFREY D. HARRIS**, NOAA Fisheries, Alaska Fisheries Science Center, Marine Mammal Laboratory, 7600 Sand Point Way N.E., Seattle, Washington 98115, U.S.A.

ABSTRACT

We conducted a mark-recapture study of California sea lions (*Zalophus californianus*) using pups branded on San Miguel Island, California, from 1987-2014, and annual resightings from 1990 to 2015. We used the Burnham model (Burnham 1993), an extension of the Cormack-Jolly-Seber mark-recapture model, which includes recoveries of dead animals, to analyze age, sex, and

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/mms.12427](https://doi.org/10.1111/mms.12427)

This article is protected by copyright. All rights reserved

annual patterns in survival. Generally, females had higher survival than males. For female pups, the average annual survival was 0.600 and for male pups it was 0.574. Yearling survival was 0.758 and 0.757 for females and males, respectively. Peak annual survival was at age 5 and was 0.952 for females and 0.931 for males. Pups with larger mass at branding had higher survival as pups and yearlings, but the effect was relative within each cohort because of large between-cohort variability in survival. Annual variability in sea surface temperature (SST) affected survival. For each 1°C increase in SST, the odds of survival decreased by nearly 50% for pups and yearlings; negative SST anomalies yielded higher survival. Annual variation in male survival was partly explained by leptospirosis outbreaks. Our study provides a unique view of one demographic parameter that contributed to the successful recovery of the California sea lion population.

Key words: California sea lion, El Niño, leptospirosis, mark-recapture, survival, *Zalophus*.

Demographic models require estimates of survival, reproduction, and movement rates of individuals into and out of a population. Mark-recapture demographic studies of pinnipeds (seals and sea lions) have been limited because individuals of these species are long-lived, have extensive ranges, and spend most of their time at sea (Testa 1987, Huber *et al.* 1991, Hernández-Camacho *et al.* 2008). Consequently, population analysis has often been based on trends in indices such as annual counts of pups or adults, but the causal factors producing the trends are often unknown (Lowry *et al.* 1992, Fritz and Stinchcomb 2005, Towell *et al.* 2006). The annual variation in survival and natality rates derived from demographic studies

can provide insight into the underlying mechanisms for population trends, such as sex- or age-specific responses to population size, environmental changes, or disease (Fowler and Sinif 1992, Jorgenson *et al.* 1997, Coulson *et al.* 2000). Estimates of survival and natality can also be used to develop correction factors for population indices and to develop age-structured population models to estimate population growth rates (Wickens and York 1997, Holmes *et al.* 2007). For pinnipeds, estimates of life-history parameters can be obtained from cross-sectional samples from animals collected for research, during subsistence harvests, or incidental to fisheries (Lander 1981, Pitcher and Calkins 1981, Boyd 1985, York 1994, Bester 1995, Hammill and Gosselin 1995, Lima and Páez 1995) but these data are often biased toward specific sex or age classes and can lead to misleading inferences (Anderson *et al.* 1981, Messier 1990, Menkens and Boyce 1993). Mark-recapture studies of uniquely marked pinnipeds offer an alternative and often less biased method of estimating life-history parameters and have become a more common method to estimate vital rates (*e.g.*, Testa 1987, Huber *et al.* 1991, Boyd *et al.* 1995, Schwarz and Stobo 2000, Beauplet *et al.* 2006, McIntosh *et al.* 2006, Wilkinson *et al.* 2011).

California sea lions (*Zalophus californianus*; hereafter sea lions) are an abundant pinniped with an extensive range along the Pacific coast of North America, from Mexico to southeast Alaska. The U.S. sea lion population has been increasing since they were protected by the U.S. Marine Mammal Protection Act in 1972 (MMPA). In 2011 the population was estimated at 296,750 animals (Caretta *et al.* 2013). However, since 2009, the population has shown considerable variability in pup production

and pup survival due to anomalous local ocean conditions (Melin *et al.* 2010, 2012) and an Unusual Mortality Event (UME; 2012–2015) that greatly reduced pup births and survival for several consecutive years (Leising *et al.* 2015). In addition, the Pacific coast colonies are regularly impacted 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. Over the last 40 yr, El Niño conditions affected the California Current ecosystem in 1982–1983 (Arntz *et al.* 1991), 1992–1993 (Lynn *et al.* 1995), 1997–1998 (Lynn *et al.* 1998), 2002–2003 (Venrick *et al.* 2003), 2009–2010 (Bjorkstedt *et al.* 2010), and 2015–2016 (Leising *et al.* 2015). El Niño conditions produce strong depressions of the thermocline, high sea surface height anomalies, and warm sea surface temperature anomalies in the California Current. These oceanographic changes result in reduced biomass of phytoplankton and zooplankton, which lead to changes in the abundance or distribution of fishes and invertebrates (Bograd *et al.* 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 (Lowry *et al.* 1991, DeLong *et al.* 1991, Melin *et al.* 2008). Lactating 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 both pup production and survival (Boness *et al.* 1991, DeLong *et al.* 1991, Francis and Heath 1991, DeLong and Melin 2000, Melin *et al.* 2012). Declines in pup production result from the inability of pregnant females to find sufficient

food to support gestation and declines in pup survival result from the inability of lactating females to find enough food to support lactation, resulting in pup starvation.

In addition to environmental events that affect the population, sea lions also experience periodic outbreaks of leptospirosis, a disease caused by a spirochete bacterium (*Leptospira pamona*; Colagross-Schouten *et al.* 2002, Gulland *et al.* 1996), hookworm (*Uncinaria* sp.) disease (Lyons *et al.* 2001, Spraker *et al.* 2007), and domoic acid poisoning from a naturally occurring toxin (Scholin *et al.* 2000). Environmental and disease events may influence the dynamics of a population long after the immediate effects are observed in population trends (Jorgenson *et al.* 1997). Demographic studies allow the sex- and age-specific effects of environmental and disease events on population growth to be described and modeled, providing insights into the causes of changing population trends.

The only population growth model for California sea lions used survival and natality rates of the northern fur seal (*Callorhinus ursinus*) because there were no species-specific demographic data available (Lowry *et al.* 1991). In 1987 we initiated a long-term branding and resighting study at San Miguel Island, California, to estimate species-specific demographic parameters for use in population growth models of sea lions breeding on the California Channel Islands. Each summer, sea lions of all ages return to their primary breeding areas on the California Channel Islands off the coast of southern California. The breeding season offers a unique opportunity to observe all the age-classes and both sexes and to conduct longitudinal studies of uniquely marked individuals. Here, using data from branding and resightings of live animals,

and recoveries of dead animals from 1987 to 2015, we have estimated sex- and age-specific survival of sea lions at San Miguel Island, California, and evaluated the effects of environmental variation, disease, and individual variation in pup weight on survival rates.

METHODS

Study Site and Sea Lion Natural History

San Miguel Island (SMI) (34.03°N, 120.44°W), one of the California Channel Islands, is located 46 km off the California coast (Fig. 1). All age, sex, and reproductive classes of sea lions inhabit SMI at various times throughout the year, but the greatest number of animals at the colony occurs between late May and early August during the reproductive season (Peterson and Bartholomew 1967, Odell 1981, Heath 1989). Pupping occurs over a 6 wk period from late May to early July. Sea lion females give birth to a single pup and remain in constant attendance of the pup for 5–8 d postpartum. After this perinatal period, females begin a foraging-attendance cycle in which they alternate 2–4 d foraging trips at sea with 1–2 d nursing visits ashore until the pup is weaned at about 11 mo of age (Antonelis *et al.* 1990, Melin *et al.* 2000). Breeding occurs about four 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 from 1 d to 2 mo. 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.* 2004, Gearin *et al.* 2017). Juvenile (1-3 yr old) females and males are present at SMI throughout the year, but also frequent hauling areas and feed along the central California coast during the winter (Orr 2011).

Marking, Resighting, and Recovery Effort

Marking—From 1987 through 2014, we hot branded 3-5 mo old sea lion pups at SMI (180-500 each year). We branded between 1% and 4% of the pups born annually. The marking effort took between 2 and 5 d depending on the number of pups branded. Pups that weighed <12.0 kg or that appeared unhealthy (*e.g.*, labored breathing or lethargic) were separated from the main group of pups and were marked with tags on the foreflippers or their fur was clipped to avoid recapturing them during the subsequent days of the marking period. Although this resulted in a slightly biased sample of branded pups, typically fewer than a dozen pups (2%) were excluded in any year. We believe that the small or unhealthy pups were unlikely to survive and the stress of being captured might have further compromised their survival. From 1987 to 1992, we branded almost equal numbers of males and females but starting in 1993, we branded a larger number of females than males (*e.g.*, 2:1, 3:2) to increase the precision of female survival estimates and to provide a larger sample size for natality estimation.

Each day up to 150 pups were separated from large groups of sea lions hauled out on the beach. The animals were slowly herded to separate nonpups from the pups. Pups were herded into a 14.5 m² pen constructed of 1.2 m high urethane construction

fencing where they were held until they were marked. Small groups of 10-15 pups were moved as needed from the large pen for marking; each pup was weighed (to nearest 0.2 kg), sexed, and tagged on the foreflippers with uniquely numbered yellow roto tags (Dalton Ltd., Henley-on-Thames, England). The tags helped with detecting branded animals in large groups and also provided identification for animals found dead on beaches (decomposition often precluded identification by brand).

Each pup was restrained for branding using physical restraint or gas anesthesia methods. Gas anesthesia included isoflurane gas and oxygen delivered through a vaporizer with a cone or mask. Pups were branded on the left side (except right side in 1987) with a unique number and released. Branding on the left side allowed us to read brands as the animals moved down the south facing beaches during their morning migration to the water. Branding techniques are described in Merrick *et al.* (1996). Hot brands destroy the hair follicles leaving a dark brand mark that grows proportionally with the animal. Brands were completely healed 2 mo after application. Each brand digit was about 7.5 cm high and 5.0 cm wide at application. At adulthood for females, each digit was about 15.0 cm high and 8.0 cm wide. Brands of this size were easily observed from distances up to 500 m using binoculars, spotting scopes, or digital cameras.

Resighting—To obtain accurate estimates of sex- and age-specific survival, sea lions of all age and sex classes must be resighted after branding. Resighting all age and sex classes is complicated by the extensive range of sea lions. However, during the reproductive season, the range contracts primarily to the breeding islands and central California hauling sites. For this

analysis, we focused the resighting effort during the reproductive season to minimize the geographic areas surveyed each year and to maximize the number of branded sea lions available for resighting.

From 1990 through 2015, branded sea lions were resighted during the reproductive season, between 15 May and 15 August, at SMI. Observations were made from stationary blinds or from cliffs overlooking populated beaches. Branded animals were identified using binoculars, 20–60× zoom spotting scopes, and digital cameras, and were rarely disturbed. For each observation, the brand, date, area, and reproductive status (e.g., with pup, territorial) were recorded. Prior to 1994, observation effort was limited to SMI under the assumption that sea lions have high fidelity to their natal site. However, a study in 1994 indicated that many juveniles were hauling out at Año Nuevo Island (ANI; 37.01°N, 122.3°W) during the reproductive season, suggesting that observation effort confined to SMI would not be adequate to document juvenile survival. In 1996 the Farallon Islands (FAI; 37.7°N, 123.0°W), ANI, and haulouts in Monterey Bay were surveyed during the reproductive season (Fig. 1). The more extensive effort demonstrated that most juveniles could be observed at SMI, ANI, and to a lesser degree, FAI. We determined that juvenile survival could be estimated precisely with annual field resighting effort only at SMI and ANI because the sightings between FAI and ANI largely overlapped. From 1996 to 2015, surveys at ANI were conducted two to three times a week between May and August. In 1998 observation effort at the FAI was added to account for increased numbers of juveniles at the FAI because of El Niño conditions that resulted in a northward movement of juveniles. We obtained opportunistic observations

from the FAI in other years.

Most capture-recapture models assume that "marks" are not lost and are recorded correctly. In comparison to flipper tags, which are often used on pinnipeds, brands have the distinct advantage of being permanent and cannot be "lost" unless the brand is obscured (e.g., bite scars) or illegible, which occurred infrequently in our study (~2% of 5,197 animals observed at least once after branding). However, brands can be misread or recorded incorrectly, which can bias survival estimates. Brand misreads are most problematic if a brand of a dead animal is incorrectly recorded as being seen and thus alive. In 2003 we began using field computers with an error checking program as part of the data entry process. After the brand was entered into the computer, the program notified the observer if the brand number was for a sea lion that was known to be dead, the opposite sex, or if the sea lion had not been seen for two or more years (which is not necessarily an error). This program allowed the observer to check the brand entry against the branded animal being observed while in the field, and correct the brand number recorded if an error was made. This reduced the number of misread brand entries. In addition to the error checking program, we only used a brand resight if the brand was recorded at least twice (typically on different days) in the same year or if the branded animal was photographed for verification. We believe these procedures resulted in negligible levels of brand misreading and produced unbiased parameter estimates.

Recovery of dead animals—During routine surveys at SMI, the tags on any dead sea lion were removed and the recovery date was recorded for that animal. In addition, we recorded any marked

sea lion that stranded on the mainland, alive or dead, that was reported to us by the public or one of the marine mammal care centers in the West Coast Region Stranding Network. Without intervention and care most if not all of the stranded sea lions would die. Thus, even though some of the stranded sea lions were rehabilitated and released, we treated them as dead at the time they were recovered from the beach.

Model Development

Survival probabilities (S) were estimated from the resighting and recovery data of branded sea lions using the Burnham model (Burnham 1993), an extension of the Cormack-Jolly-Seber (CJS) model that includes dead recoveries. For CJS type models, the initial capture and marking is a release event and only recaptures (*i.e.*, resightings) of the marked individuals at later sampling occasions are treated as data. In the Burnham model, recoveries of dead sea lions that occur after release and between resighting occasions are also included.

A branded cohort of pups was "released" each year from 1987 to 2014 and surviving pups were resighted in the following years during the reproductive season. We used resightings from 15 May to 15 August 1990–2015 (no resighting effort in 1988–1989) as the sampling occasions. This time frame encompassed pupping, breeding, and postbreeding and allowed us to balance an adequate sample size of all age and sex classes against the possibility of losses (deaths) during each sampling occasion because few nonpup animals die within the short 3 mo breeding season. Although we received reports of branded sea lions all along the U.S. West Coast and occasionally in Mexico and Canada, we restricted the analysis to resightings made on SMI, ANI and FAI, where we had experienced observers.

In our analysis, we have assumed that all observed branded animals survive during the 3 mo resighting period that we treat as an occasion and all mortality occurs between resighting occasions. Recoveries of dead or stranded sea lions were treated as having occurred during the prior year if recovered before 1 July and in the following year if recovered after 1 July. Annual survival for nonpups in year y represented survival from 1 July of year y to 1 July of year $y + 1$. For pups, observations of survival were for a partial year for the time period from branding to 1 July of the following year. The timing of branding varied across years from 20 September to 13 November (Table 1). Even if annual pup survival was constant, the estimates could vary due to variation in the length of time between marking and resighting. In presenting pup survival estimates, we have converted the estimate to an annual rate (S_i^{1/t_i}), where t_i is the proportion of the i th year between marking and resighting. For example, if the time interval between marking and 1 July was 6 mo and the estimated survival was 0.7 then the annual rate would be $0.49 = 0.7^2$. In doing so we assumed survival was constant within the first year.

Model Parameters

The probability that a sea lion is sighted at some occasion following release is a function of the probability that it survives (S) and the probability of resighting and reading the brand of a surviving sea lion (p). For an animal to be recovered, it must survive until an occasion, die during the interval between occasions, and then be recovered and reported (r). S , p , and r are the three primary parameters in the Burnham model. The fourth parameter F is the probability the released sea lion remains in the area where resighting occurs. The model

assumes that recovery of dead animals can occur throughout the animals' range including areas where resighting does not occur.

Survival probability (S)—We examined 16 different models for survival that included some combination of sex, age, year, and their interactions, and covariates of pup weight and temporal or environmental effects (Table 2). We used a logit link to model survival as a function of covariates (White and Burnham 1990). For example, if x is some covariate, survival can be represented as $S = \exp(\beta_0 + \beta_1 x) / [1 + \exp(\beta_0 + \beta_1 x)]$ and $\text{logit}(S) = \log[S/(1 - S)] = \beta_0 + \beta_1 x$ is the log of the odds of survival. We will describe the influence of covariates in terms of the reduction or increase in the odds of survival. If $\beta_1 > 0$, a unit increase in x would increase the odds of survival by $\exp(\beta_1)$, which is the ratio of the odds at covariate value x and odds at covariate value $x - 1$. If $\beta_1 < 0$, then the odds of survival decrease.

Age and sex—Sea lion age was specified as the number of years at their last birthday (specified as 1 July). Thus, pups were age 0, yearlings age 1, and so on. We used the following categories for age: 0 (*i.e.*, birth to age 1), 1, 2–3 (*i.e.*, survival from age 2 to 3 and age 3 to 4 were equal), 4–6, 7–9, 10–12, 13–16, and ≥ 17 . We used these categories to reduce the number of age-specific parameters and because they were relevant to sea lion life history. Sea lions < 3 yr old were not reproductive and we expected the greatest change in survival for juveniles so we estimated a separate survival for ages 0, 1, and 2–3. Females may become reproductive at age 3 (rarely) or 4 and most are reproductive by age 7 (Melin *et al.* 2012), so the 4–6 age group represented animals that were a mix of nonreproductive and reproductive. Males also can breed at 4 yr of age but few

do; the average age of territorial males is 12 yr old because they must achieve the size and behavior to successfully defend a territory and gain access to breeding females (SRM, unpublished data). Ages ≥ 7 were divided into four groups to examine changes in survival of reproductive animals of both sexes at older ages. The age intervals were wider for older animals because the sample size of live animals decreased with age. In addition we fitted smoothed models for age using a cubic spline (*bs* function in *splines* package in R; R Core Team 2015) rather than separate categories.

Pup weight—Pup weight affects postweaning survival in other otariids (Baker and Fowler 1992, Hastings *et al.* 2011) so we examined models in which pup weight affected pup and yearling survival (Hastings *et al.* 2011). The pup weight covariate was the deviation of the pup's weight from the sex-specific mean weight of pups at branding from 1987 to 2014. Pup weight (in kg) is an individual covariate but we binned the weight deviation into 10 intervals (< -4.5 , -4.5 to -3 , -3 to -2 , -2 to -1 , -1 to 0 , 0 to 1 , 1 to 2 , 2 to 3 , 3 to 5 , and > 5) to achieve roughly equal number of sea lions in each interval (956–1,284 per interval). Each weight interval was used to define a group of animals within a cohort and the mean weight deviation in the interval was used as the numeric covariate value for each sea lion in that group. For example, if the mean weight for the entire female sample was 17.0 kg, a female pup that weighed 17.5 kg would have an anomaly of 0.5 kg and the pup would be in the 0–1 interval. This discretized numeric version of the covariate provided much faster model fitting run times and allowed use of the median $c\text{-hat}$ (\hat{c}) approach for evaluating overdispersion (Cooch and White 2012). For pups and yearlings, we have reported

the effect of weight on the average annual survival based on the annual sex-specific mean weight of all pups including those that were not branded because they were too small.

Year—We expected that survival would vary by year because of natural variation in prey availability and oceanographic conditions such as ENSO. We expected more temporal variation in survival of younger sea lions due to their greater vulnerability (Gaillard *et al.* 2000). We also expected that our ability to detect temporal variation would decrease for older ages due to smaller sample sizes. Therefore, in posing alternative models, we fitted temporal variation that differed across age categories of pups, yearlings, ages 2–3, and ages ≥ 4 . In evaluating temporal variation, we used a separate value for each year after 1993 but we pooled (variable: time) years 1987–1991 and 1992 and 1993 because the resighting efforts in those years were either lacking (1988–1989) or the data were not sufficient to estimate a separate annual survival reliably. The years 1992–1993 were modeled separately from 1987–1991 because these were years affected by El Niño conditions and we expected survival to be lower than other years.

Adult females, pups, and yearlings remain in southern California year round, whereas juveniles (ages 2 and 3) tend to occur in central California. Males generally travel farther north than females in summer and winter, and older males (ages ≥ 4) travel farther than juveniles in the winter, traveling as far north as southeast Alaska (Odell 1981, Maniscalco *et al.* 2004). Consequently, males could experience different environmental and prey conditions than females of the same age. Thus, we considered models in which variation in time for males of ages ≥ 2 and ages ≥ 4 differed from females.

Environment—We evaluated models with annual survival varying as a result of local changes in sea surface temperature (SST) in combination with a linear (on the logit scale) temporal trend. Changes in local SST can be an indicator of ENSO conditions or other anomalous environmental conditions that could affect survival (DiLorenzo *et al.* 2010). We evaluated the effect of SST on survival using an average SST anomaly, which was measured at four NOAA data buoys (Stations: 46054, 46218, 46011, pslc1; NOAA National Data Buoy Center, <http://www.ndbc.noaa.gov>) located 26–128 km north of SMI in the area where females primarily forage (Melin and DeLong 2000, Melin *et al.* 2008). For pups, we used the average SST anomaly from 1 October to 30 June and for nonpups 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.

Disease—We evaluated the impact of leptospirosis on male sea lion survival for ages ≥ 2 because very few pups and yearlings strand from leptospirosis infections. In models including a disease effect, we replaced the annual variation in male survival ages ≥ 2 with a covariate that measured the annual number of males that stranded due to leptospirosis. Numbers of stranded female sea lions with leptospirosis were lower than males and too small to evaluate the effect of the disease on their survival. A preliminary analysis modeling the effect of domoic acid toxicity on female survival in a similar way as the leptospirosis modeling for males showed a small negative effect of domoic acid toxicity in the survival rates of females.

However, data were not available for the number of strandings due to domoic acid toxicity after 2010 and therefore we did not include this disease in the present analysis.

Resighting probability (p)—We fitted five different models for p (Table 2) that evaluated main effects of year (time), sex, and age, and two-way and three-way interactions. The models for required interactions because we modified survey coverage over time and area. Also different sex and age groups use different areas during the reproductive season. Initially we presumed a high level of fidelity to the branding site because we assumed that pups were born where they were captured for branding and that they would have fidelity to the area (e.g., Baker *et al.* 1995). Thus, we focused the resighting effort in the area where pups were branded. However, we observed branded pups in other rookery areas of SMI, within days of being branded. Sea lions also colonized new areas on SMI over the study period, and juveniles and nonterritorial males were primarily using other areas of the island during the reproductive season. Consequently, as the study progressed, we expanded the resighting survey areas on SMI to include all areas of the island. This meant that any sex, age, and spatial differences in resighting probability would change over time.

We expected p to vary by year because of changes in the annual level of survey effort. There were few resights in 1988 and 1989, so we excluded them and set $p = 0$ for those two years. We pooled the years 1990–1993 because survey effort was generally low and evaluating annual differences was not reliable.

Males are not restricted to SMI during the reproductive season so we expected their resighting probability to be lower.

We observed that young males were more likely to be seen farther north at ANI during the reproductive season and that reproductive males that were territorial had a higher resighting probability than younger males at SMI. Females do not typically breed until age 3 or give birth until age 4 (Melin *et al.* 2012). Once females had given birth they were reliably seen each year. Thus, we expected resighting probability to vary by age because younger sea lions might spend less time on land and they inhabit areas on SMI that were surveyed less frequently than the main pupping/breeding area. We pooled age into the following intervals for p for both sexes, expecting the age effect to lessen with age: 1, 2-3, 4-6, 7-12, and >12.

Recovery probability (r)—Recovery probability is the probability that a sea lion that died or stranded between sampling occasions was recovered and reported. We evaluated three models for recovery probability (Table 2). In all models we included a separate parameter for pups because pups do not typically wean until April the year after they are born (Melin *et al.* 2000, Harris 2016), and if they die in their first year it will likely be on SMI. We searched the island for any pups that died on SMI shortly after branding and then in the following January. Also, in each model we included an effect for the last year (1 July 2015 to 1 July 2016) because not all of the dead recoveries had been included when the analysis was done. In addition, we evaluated models that added a separate recovery rate for yearlings, which tend to be distributed closer to islands and coast line and more likely to be recovered. We evaluated a linear trend in r because there has been an increase in the number of marine mammal care centers that rehabilitate marine mammals and a concomitant increase in the recovery and

reporting of stranded marine mammals during the 29 yr of the study. We did not consider a model with separate time effects for recovery due to small sample sizes of recoveries.

Fidelity (F)—We have seen a small number (10) of branded adult females that immigrated to San Nicolas Island (about 130 km southeast of SMI) and reared pups there. However, we expected very high fidelity to SMI for reproductive adults and we surveyed at ANI to sight younger animals prior to their return to SMI for pupping and breeding, so we assumed a constant fidelity rate for all models.

Model Fitting and Selection

We used the R (R Core Team 2015) package *RMark* (Laake 2013) as an interface to MARK (White and Burnham 1999) to fit release-resight-recovery (Burnham) models to the data (see Appendix S1 for data, R code for fitted models).

We used Akaike's information criterion (AIC) and AIC adjusted for overdispersion (QAIC; Burnham and Anderson 2002) to select the best model(s). We used MARK to estimate overdispersion with the median \hat{c} approach (Cooch and White 2012) for a global model of (sexagetime), (sexagetime), (pup + yearling + time + last), and (constant). We used to compute QAIC and to inflate the estimated standard errors (SE) to reflect additional uncertainty resulting from overdispersion.

RESULTS

Marking and Resighting

From 1987 to 2014, 11,298 sea lion pups were branded (6,833 females and 4,465 males) between late September and mid-November (Table 1). During the annual sampling occasions (15 May to 15 August), 48.2% of female and 42.3% of male branded sea lions were sighted in one or more years following branding; however,

there were large differences among cohorts (Table 1). These were most notable for pup cohorts that were born in 1992, 1996, and 1997 because of poor survival during the 1992–1993 and 1997–1998 El Niño events, and unexplained high mortality of the 2012 cohort, which resulted in the declaration of an Unusual Mortality Event (UME) for sea lions under the U.S. Marine Mammal Protection Act. The UME continued into 2016. Although the 2013 cohort had average survival, the 2014 cohort had very poor survival due to excessively warm ocean conditions in fall 2014, and winter and spring of 2015.

A total of 472 branded sea lions were recovered dead ($n = 399$) or stranded and taken in for rehabilitation ($n = 73$). This represents 4.2% of the total number branded but the percentages of recoveries varied widely over the years and were highest from cohorts in 1992 and 1997 during El Niño events and from the 2012 and 2014 cohorts during the UME (Table 1). There were 206 pups, 127 yearlings and 139 older (ages ≥ 2) marked animals recovered dead or stranded. The percentages of those recovered at SMI were 64.6%, 25.2%, and 10.1% for pups, yearlings, and older animals, respectively.

In total, there were 124,721 resightings of which 86.7% were at SMI, 13.1% at ANI and the small remainder at FAI, which was only surveyed systematically for a few years. There were 91,953 resights of females and 32,768 of males. However, more females were branded than males so to examine differences across sex, age, and island we expressed the percentages in terms of the number of resightings for each sex (Fig. 2). ANI and FAI were used primarily by sea lions less than age 4, and primarily by age 2 males (Fig. 2). SMI was used primarily by older sea lions and mostly females (Fig. 2). The decline at ANI/FAI with

age was primarily due to sea lions maturing and moving back to SMI to participate in pupping and breeding whereas the decline at SMI for older ages reflects mortality.

Model Fitting

The estimated median \hat{c} overdispersion value for the global model was 1.03. Although it was close to 1, we used that value for calculations of QAIC for model selection. The two top models accounted for nearly all of the model weight and only differed in their treatment of survival for males of ages ≥ 2 (Table 2). The top model included different annual variation in survival for males and females at ages ≥ 2 . The second best model had the same structure as the top model except that annual variation of males ages ≥ 2 was replaced by the effect of leptospirosis. For the third best model $\Delta\text{QAIC} = 12.1$ and all of remaining models had weights < 0.002 , so we restricted model averaging for parameter estimates and results to the top two models.

Resighting Probability (p)

The best model for (model 1, Table 2) included main effects and two-way interactions for sex, age, and year. Resighting probability increased with age for males and females. Females typically had a higher p than males but that varied with year. For example, in 1997 and 2004, females of every age group had a higher p than males but in 2002, males had slightly higher or similar p to females (Fig. 3). Estimates of p ranged from < 0.1 to > 0.8 but in general were > 0.5 for most ages and years. Resighting probability increased from the early 1990s to the late 1990s due to changes in effort that impacted younger ages more than older ages. For example, p for 2-year-olds increased from 0.06 in the early 1990s to 0.55 in the late 1990s when resight effort was added at ANI (Fig. 4). In contrast, p for 7-

year-olds increased from 0.36 to 0.77 due largely to expanding the resight effort at SMI (Fig. 4).

Recovery Probability (r)

The best model for r (model 3, Table 2) included a differential recovery rate for pups, yearlings and an increasing trend over years. For pups, the recovery rate increased from 0.039 (95% CI: 0.030, 0.052) in 1987 to 0.086 (95% CI: 0.071, 0.105) in 2014. For yearlings, the recovery rate increased from 0.039 (95% CI: 0.028, 0.054) in 1988 to 0.084 (95% CI: 0.062, 0.112) in 2014. For sea lions ages ≥ 2 , the recovery rate increased from 0.019 (95% CI: 0.014, 0.025) in 1989 to 0.040 (95% CI: 0.032, 0.049) in 2014. All of the rates decreased by about 50% in 2015 because not all recoveries were available at the time the analysis was conducted.

Fidelity (F)

As expected, the constant F was at 0.987 (95% CI: 0.976, 0.993) suggesting that all but a small proportion of surviving sea lions visit ANI or SMI at some time.

Survival Probability (S)

The best model for survival (model 9, Table 2) described changes in age with a cubic spline, which was sex-specific. Generally, females had higher survival than males but the difference was very small for younger (pup and yearling) sea lions and it increased with age (Table 3). Peak annual survival for females at age 5 was 0.952 but it was nearly as high for ages 4-8. Survival dropped below 0.9 at age 11 and below 0.7 at age 17. For males, the peak annual survival of 0.931 was also at age 5 but was lower than that for females. Also, the decrease in survival with age occurred at younger ages for males compared to females. By age 8, male survival dropped below 0.9 and by age 12

it dropped below 0.7. Survival rates at older ages (≥ 18) were very imprecise for both sexes due to the small sample sizes alive at those ages. The increase in those rates was likely due to use of a cubic spline and with 95% confidence intervals spanning nearly 0 to 1, the point estimates are not useful after age 18. Only one female was observed at age 25 and no males were observed over 19 yr of age.

Pup weight at time of branding affected both pup and yearling survival with larger mass yielding higher survival. For each 1 kg above the long term mean at the time of branding, the survival odds increased by 1.12 (95% CI: 1.09–1.16) for pups and 1.11 (95% CI: 1.06–1.17) for yearlings. However, the impact of weight on survival depended on the year because there was substantial annual variation in both pup and yearling baseline survival (Fig. 5). The distribution of pup weights varied widely by cohort (Fig. 6) and cohorts with larger pups at branding did not always have higher annual survival (Table 4). For example, in 1998 pups in the smallest weight category had nearly the same survival rate as those in the largest weight category in 1996 because the 1996 cohort weaned at the onset of the 1997/98 El Niño, whereas the 1998 cohort weaned during La Niña conditions in 1999. Also, although the pups were at record high weights in 2004, this did not translate to higher first year survival.

Models describing annual variation in survival as a function of the local SST anomaly demonstrated significant decreases in survival with increasing SST anomalies; however, they were not among the top models, likely because survival is not solely affected by SST and a simple trend over time. The best model containing SST predicted that for each 1°C positive anomaly, the odds of survival decreased by nearly 50% for pups

and yearlings (pups: 0.526, 95% CI: 0.474, 0.583, yearlings: 0.454, 95% CI: 0.402, 0.513), declined by about 20% for ages 2 and 3 (0.793, 95% CI: 0.689, 0.912) and had no significant effect (0.944; 95% CI: 0.841, 1.059) on ages 4 and older. The same model suggested a temporal decline in survival for pups (slope: -0.048, 95% CI: -0.057, -0.038) and yearlings (slope: -0.025, 95% CI: -0.038, -0.011).

The second best *S* model included the effect of leptospirosis on male survival. The model estimates predicted that relative to a year with no stranded sea lions due to leptospirosis, for every 100 cases recorded, the odds of male survival for ages ≥ 2 decreased about 23% (odds ratio: 0.768, 95% CI: 0.642, 0.919). The annual observed number of stranded male sea lions due to leptospirosis over our study ranged from 0 to 223. The survival of age 5 males was at its lowest value when the number of stranded male sea lions due to leptospirosis was at its highest value in 2004 (Fig. 5).

DISCUSSION

Marking and Resighting

Over the 29 yr of this study, our design evolved as we learned more about the behavior and movements of sea lions and as the distribution of sea lions changed at SMI. We increased the resighting effort, increased the number of surveyed areas, and increased the number of female pups marked to increase the precision of survival estimates of the most critical component of the population. The increased effort and the expanded survey area increased the resighting probabilities of all the age groups and both sexes, and consequently, the precision of the survival estimates.

The reliability and readability of the marking technique

was equally important. Brands provided a permanent mark that was easily read at long distances with no disturbance to the colony. Between 1975 and 1986 various methods of tagging sea lions were undertaken (RLD, unpublished data) but yielded little resight data because of tag loss, tag unreadability, and the inability to approach animals to read tag numbers without disrupting the colony. With branded animals, we had a reliable permanent mark and were able to achieve resighting probabilities as high as 85%, which is not common in mark-recapture studies.

Model Assumptions

One of the central assumptions to mark-recapture studies is that marks are not lost, overlooked, or misread. Although brands cannot be lost, they must be read and recorded correctly and this process is prone to error. A brand may have been consistently misread due to poor brand quality, but this was rare. In a study of branding of New Zealand sea lions (*Phocarctos hookeri*), poor brands were uncommon and brands that were misread or unreadable were usually the result of scarring unrelated to the brand (Wilkinson *et al.* 2011). We found this to be true in our study as well and also that these individuals were uniquely identifiable due to the scarring, so the mark was not lost. We minimized the misread error by only including observations if the sea lion was observed two or more times in a year, unless a verifiable photograph of a single sighting was available. Some errors may have still occurred but our data filtering, field error checking protocols, and photographic verification of resights reduced or eliminated most reading or recording errors. The protocol of using sightings of animals that were seen twice in a sampling occasion or photographed may have introduced heterogeneity in the resighting probability. Sea

lions that hauled out less frequently or hauled out in areas that were surveyed less frequently would have a reduced chance of being sighted multiple times in a year relative to sea lions that hauled out more often or in areas frequently observed. Such behavior would increase the chance of a single sighting of the animal being discarded.

It is possible that other sources of heterogeneity remain that we currently have not or cannot model adequately. For example, over the years of the study, we received and made resightings of branded animals from San Nicolas Island, a colony about the size of SMI and located approximately 103 km southeast of SMI. Branded adult females with pups have been sighted in multiple years at San Nicolas Island indicating that a small level of emigration from SMI is occurring. These animals may occasionally be resighted at SMI but only intermittently, introducing heterogeneity into the resighting probability. Other examples of behaviors that may introduce heterogeneity into the resighting probabilities include nursing cycles of females and territorial behavior of males. Females with a nighttime nursing pattern may not be observed as frequently as females that nurse their pups during daytime. Similarly, males that hold territory in the water are less likely to be observed because their brand is only visible during low tide. However, these behaviors represent a small proportion of the large sample size of marked animals and it is unlikely that these behaviors significantly biased the survival estimates.

For CJS models, sampling occasions are assumed to be instantaneous events such that there are no deaths during the sampling period. Observations obtained over a 3 mo period are clearly not instantaneous and could lead to biased survival

estimates. However, O'Brien *et al.* (2005) showed that violating this assumption increases precision of survival estimates but does not increase bias in parameter estimates, particularly when survival and resighting rates are high. Our resighting probabilities were >0.40 in most years; therefore we believe the survival estimates were not affected significantly by the protracted resighting period.

The long-term nature of our data set demonstrates the importance of the number of cohorts, the number of marked animals in each cohort, and the number of years of resighting effort to accurately describe sex- and age-specific survival patterns in a long-lived animal. In a demographic study of sea lions in the Gulf of California, Hernández-Camacho *et al.* (2008) used 23 yr of resight data from five cohorts (<200 animals branded total) to estimate survival; their small data set supported simple models that estimated sex- and age-specific survival for four age classes and demonstrated annual variation in pup survival. With the large variation in pup survival at the SMI colony, if we had only sampled five cohorts at some point in the time series, our view of the population's health would have been greatly influenced by the cohorts sampled. For example, between 2000 and 2004 or 2010 and 2014, pup survival rates were about 0.4, significantly lower than the survival rate that we obtained from our larger sample of 28 cohorts (0.60), and the results may have raised alarm at the population's health. The larger sample sizes and number of cohorts in our study allowed us to estimate separate survival rates for all ages and to detect differences in survival due to pup weight, environmental conditions, and disease outbreaks, providing more insight into which factors contribute most to the variation in survival and

the population dynamics.

Increasing the sample size of branded animals resulted in greater precision in estimating survival of the older ages. Even with these larger cohort sizes, the precision worsens at ages beyond 15 due to mortality reducing the sample size at older ages. This should improve somewhat as our larger cohorts from 2001 to 2006 age. However, we found that most of the survival dynamic is in juvenile sea lions from pups to age 3, which could be captured with smaller sample sizes, so we reduced the number of animals branded to 300 in 2007.

Effects of Age and Sex on Survival

Age-specific survival was lowest for the youngest and oldest sea lions. Pup and yearling survival was the most dynamic with three-fold changes in annual survival primarily due to environmental factors like El Niño conditions. Once animals reached 2 yr of age, their survival was higher than 0.9 for females aged 3–11 and exceeded 0.7 until age 17. Young males had survival rates exceeding 0.9 for ages 3–7 and greater than 0.7 until age 12. In a sexually dimorphic polygynous species like sea lions, it is expected that sex- and age-specific survival rates will differ for males and females (Clutton-Brock *et al.* 1985). Average survival to age 2 was nearly the same for male and female sea lions but in general male survival was lower, and it declined more rapidly with age than did female survival. Sea lion males must attain a large size to successfully compete for territories and gain access to breeding females. Thus, they require greater amounts of resources for survival compared to same aged females, which may compromise male survival. The mean age of territorial sea lion males is 12 yr, and we observed a decline in survival of males ages ≥ 12 that may be related to the

cost of the reproductive social system. Adult males fight and fast for days to weeks or months while holding territories (Peterson and Bartholomew 1967). The energetic drain and physical damage of such activities was reported to affect the survival of territorial northern fur seals (*Callorhinus ursinus*) (Johnson 1968) and apparently may also reduce the survival of sea lions.

Effects of Environmental Conditions on Survival

El Niño ocean conditions play a central role in the population dynamics of sea lions through lower survival of pups and lower natality rates at SMI (Melin and DeLong 2000, Melin et al. 2012). Our study spanned decades and included three El Niño periods as well as other shifts in oceanographic conditions that influenced survival of different age and sex classes. El Niño and other anomalous ocean conditions that increased the local SST more than 1°C from the long-term mean and persisted for several months or longer, had the greatest effect on survival of pups and yearlings, followed by 2–3 yr olds and then relatively minor declines in survival for ages ≥ 4 . In the California Current, during El Niño conditions, oceanographic changes temporarily reduce the availability of sea lion prey to nursing females and to juveniles that remain around the colony throughout the year. Nursing females have difficulty provisioning their pups and the result is high mortality of pups from starvation. Pups that do survive are smaller and our results showed that smaller pups have lower survival as pups but also as yearlings. Sea lions are almost a year old when they are weaned and if they wean at a lower weight and foraging conditions are poor, their survival as yearlings is compromised because they have smaller fat reserves and may have more

physiological limitations for diving and accessing food compared to fatter, larger pups. However, the impact of weight is more relative than absolute. For example, 80% of the pups in the 1996 cohort were average or larger than average but this cohort weaned in 1997 at the onset of a very strong El Niño and consequently had very poor yearling survival. In contrast, 80% of the pups in the 1998 cohort were smaller than average when branded but they were reared and weaned during strong La Niña conditions with plenty of food for nursing females and for newly weaned juveniles, and consequently had high pup and yearling survival rates. Older sea lions are able to travel farther and dive deeper and their foraging experience helps to buffer them from the effects of El Niño conditions in comparison to pups and yearlings. In contrast to our findings, studies of sea lions in the Gulf of California have shown that pup production is not impacted by El Niño (Aurioles *et al.* 1991) and survival was higher for cohorts born during or after El Niño conditions (Hernández-Camacho *et al.* 2008). The biological productivity in the Gulf of California is driven mostly by tidal patterns and local oceanographic features rather than by coastal upwelling. Consequently, El Niño does not impact the biological productivity of the Gulf of California as it does the Pacific waters of coastal California, and sea lions there do not experience significant effects from the events (Baumgartner and Christensen 1985, Arntz *et al.* 1991).

Effects of Disease on Survival

Outbreaks of diseases in pinniped populations can be devastating and are often age or sex specific (Kennedy *et al.* 2000, Härkönen *et al.* 2006). We found evidence for lower survival of subadult and adult males during outbreaks of

leptospirosis. The disease is characterized by periodic outbreaks with associated mortality of sea lions (Gulland *et al.* 1996) but our evidence is correlative and we cannot rule out the possibility that annual variability in other unknown factors is the cause of lower survival in those years. If the large decrease in survival detected in this study is solely from leptospirosis, then many infected individual males must die at sea because the number of strandings were far fewer than expected based on the estimated decrease in survival. Lower numbers of females strand from leptospirosis and outbreaks of the disease have not been observed on the breeding islands. Most of the sea lions infected with leptospirosis strand in central and northern California and farther north. It may be that the differential distribution of the two sexes during the nonbreeding season leads to males being more susceptible to the disease than females.

There are few other studies of sea lion or fur seal species that have estimated age-specific survival using longitudinal data over the lifetime of the animals. Our survival rates for male sea lions were similar to those reported for California sea lions in the Gulf of California but survival rates for female sea lions in the Gulf of California were lower than the SMI population (Hernández-Camacho *et al.* 2008). Survival rates from collections or mark-recapture studies of fur seals (*Arctocephalus* spp.), Steller sea lions (*Eumetopias jubatus*) and New Zealand sea lions indicate that our female pup and adult female survival rates are similar to species with similar life histories, which range between 0.452 and 0.828 for first year survival of females and between 0.889 and 0.953 for adult females (Wickens and York 1997; Beuplet *et al.* 2005, 2006;

Hastings *et al.* 2011; Wilkinson *et al.* 2011). We documented high peak survival rates for male and female sea lions and a distinct decline in survival for females after age 16 and males after age 12, though we had considerable uncertainty in the estimates at the oldest ages. The oldest female in our study was 25 yr old and no males were observed over 19 yr of age. These results are the similar to those reported for sea lions in the Gulf of California (Herrnández-Camacho *et al.* 2008), and likely represent the lifespan of California sea lions in the wild. The decline in survival with age is expected in a long-lived, slow-reproducing animal and recent studies have shown that this pattern can affect a population's viability over time (Jones *et al.* 2014, Robert *et al.* 2015), highlighting the importance of understanding age- and sex-specific survival rates for management and conservation of wild populations.

Longitudinal studies of long-lived species require a commitment to long-term studies with sufficient sample sizes of permanently marked animals and enough resighting effort to achieve precise estimates. With such a commitment, we were able to estimate sex- and age-specific survival and demonstrate individual variation in survival due to pup weight and annual variation in survival as a result of variation in environmental conditions and disease related strandings.

Ecological Implications

California sea lions were hunted in the late 1800s and early 1900s and the population was at historically low levels when it became protected under the MMPA in 1972 (Odell 1981). Since then, the U.S. California sea lion population has experienced steady growth over the past 45 yr. Our study encompasses much of that recovery period and provides a unique

view of the demographic patterns that contributed to the successful recovery of the California sea lion population. High juvenile and adult survival during much of the recovery period has resulted in robust growth of the population. The survival estimates reported here along with natality estimates previously obtained from the SMI branding study (Melin *et al.* 2012), provide a foundation for the first species-specific population growth model for California sea lions. The development of such a model is needed to inform management on a species that has been at the center of resource conflicts in parts of its range (*e.g.*, Weise and Harvey 2005, Wright *et al.* 2010) and also faces a challenging future. A marine environment with more frequent El Niño events (Cai *et al.* 2014) and overall ocean warming (Rykaczewski and Dunne 2010, King *et al.* 2011) in the future may lead to unpredictable changes in prey communities and marine disease outbreaks (Bossart 2011, Burge *et al.* 2014). Based on our findings, these changes are likely to affect survival patterns of sea lions and consequently, population trends. The SMI marking program will continue to provide invaluable information on how sea lions will respond to the changing marine environment.

ACKNOWLEDGMENTS

We thank Peter Boveng (then at SWFSC) and Jay Barlow of the Southwest Fisheries Science Center (SWFSC) who collaborated with us in a brand evaluation study in 1987 that provided a foundation for California sea lion demography studies. We thank the personnel at the NOAA Fisheries Marine Mammal Laboratory (MML), Alaska Fisheries Science Center (AFSC), SWFSC, Channel Islands National Park, Año Nuevo State Reserve, Point Reyes Bird Observatory, Point Blue, and all the volunteers who participated

in the annual branding, tagging, and resighting activities. We thank veterinary medical personnel from The Marine Mammal Center, Vancouver Aquarium, Sea World San Diego, and many independent wildlife veterinarians who administered anesthesia to pups during branding. We also thank M. Hester, Oikonos, and E. M. Burch, J. Elliot, University of California, Santa Cruz and G. Oliver for collecting data from Monterey Bay, the Farallon Islands, or Año Nuevo Island. The manuscript was improved with reviews by Paul Conn and Harriet Huber and the AFSC Publications Unit. Funding was provided by the West Coast Region of the National Marine Fisheries Service. We thank S. Wilkin of the West Coast Region of the National Marine Fisheries Service for collating the leptospirosis data from the stranding coordinators throughout California and providing them to us. More recent stranding data was kindly provided by K. Prager. We also thank Sue Pemberton of California Academy of Sciences, Shelbi Stoudt of The Marine Mammal Center, Lauren Palmer of The Marine Mammal Care Center at Fort MacArthur, Ruth Dover of the Channel Islands Marine & Wildlife Institute, Jonsie Ross of California Wildlife Center, Michele Hunter of Pacific Marine Mammal Center, and Jody Westberg of Sea World San Diego who provided reports of dead or stranded sea lions. Research activities were conducted under Marine Mammal Protection Act Permits 717, 977, 1613, and 16087 issued to MML and animal handling and care procedures were approved by the Alaska and Northwest Fisheries Science Centers' IACUC. This work was in part supported by the National Science Foundation (OCE-1335657). The findings and conclusions in the paper are those of the author(s) and do not necessarily represent the views of the National Marine Fisheries Service, NOAA. Reference to trade names does not imply endorsement by the

National Marine Fisheries Service, NOAA.

LITERATURE CITED

- Anderson, D. R., A. P. Wywialowski and K. P. Burnham. 1981. Tests of the assumptions underlying life table methods for estimating parameters from cohort data. *Ecology* 62:1121-1124.
- Antonelis, G. A., B. S. Stewart and W. F. Perryman. 1990. Foraging characteristics of female northern fur seals (*Callorhinus ursinus*) and California sea lions (*Zalophus californianus*). *Canadian Journal of Zoology* 68:150-158.
- Arntz, W., W. Pearcy and F. Trillmich. 1991. Biological consequences of the 1982-83 El Niño in the Eastern Pacific. Pages 22-42 in F. Trillmich and K. Ono, eds. *Pinnipeds and El Niño: Responses to environmental stress*. Springer-Verlag, Berlin, Germany.
- Aurioles, D., and B. J. Le Boeuf. 1991. Effects of the El Niño 1982-83 on the California sea lions in Mexico. Pages 112-118 in F. Trillmich and K. Ono, eds. *Pinnipeds and El Niño: Responses to environmental stress*. Springer-Verlag, Berlin, Germany.
- Baker, J. D., and C. W. Fowler. 1992. Pup weight and survival of northern fur seals *Callorhinus ursinus*. *Journal of Zoology* 227:231-238.
- Baker, J. D., G. A. Antonelis, C. W. Fowler and A. E. York. 1995. Natal site fidelity in northern fur seals, *Callorhinus ursinus*. *Animal Behaviour* 50:237-247.
- Baumgartner, T., and N. Christensen, Jr. 1985. Coupling of the Gulf of California to large-scale interannual climatic variability. *Journal of Marine Research* 43:825-848.
- Beauplet, G., C. Barbraud, M. Chambellant and C. Guinet. 2005.

- Interannual variation in the post-weaning and juvenile survival of sub-Antarctic fur seals: Influence of pup sex, growth rate and oceanic conditions. *Journal of Animal Ecology* 74:1160-1172.
- Beauplet, G., C. Barbraud, W. Dabin, C. Kussener and C. Guinet. 2006. Age-specific survival and reproductive performances in fur seals: evidence of senescence and individual quality. *Oikos* 112:430-441.
- Bester, M. N. 1995. Reproduction in the female subantarctic fur seal, *Arctocephalus tropicalis*. *Marine Mammal Science* 11:362-375.
- Bjorkstedt, E. P., R. Goericke, S. McClatchie, et al. 2010. State of the California Current 2009--10: Regional variation persists through transition from La Niña to El Niño (and back?). *California Cooperative Oceanic Fisheries Investigations Report* 51:39-69.
- Bograd, S. J., and R. J. Lynn. 2003. Long-term variability in the southern California current system. *Deep Sea Research Part II* 50:2355-2370.
- Boness, D. J., O. T. Oftedal and K. A. Ono. 1991. The effect of El Niño on pup development in the California sea lion (*Zalophus californianus*) I. Early postnatal growth. Pages 173-179 in F. Trillmich and K. A. Ono, eds. *Pinnipeds and El Niño: Responses to environmental stress*. Springer-Verlag, Berlin, Germany.
- Bossart, G. D. 2011. Marine mammals as sentinel species for oceans and human health. *Veterinary Pathology* 48:676-690.
- Boyd, I. L. 1985. Pregnancy and ovulation rates in grey seals (*Halichoerus grypus*) on the British coast. *Journal of Zoology* 205:265-272.

- Boyd, I. L., J. P. Croxall, N. J. Lunn and K. Reid. 1995. Population demography of Antarctic fur seals: The costs of reproduction and implications for life-histories. *Journal of Animal Ecology* 64:505-518.
- Burge, C.A., C. M. Eakin, C. S. Friedman, *et al.* 2014. Climate change influences on marine infectious diseases: Implications for management and society. *Annual Review Marine Science* 6:249-277.
- Burnham, K. P. 1993. A theory for combined analysis of ring recovery and recapture data. Pages 199-213 in J.-D. Lebreton and P. M. North, eds. *Marked individuals in the study of bird populations*. Birkhauser-Verlag, Basel, Switzerland.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: A practical information-theoretic approach*. Springer, New York, NY.
- Cai, W., S. Borlace, M. Lengaigne, *et al.* 2014. Increasing frequency of extreme El Niño events due to greenhouse warming. *Nature Climate Change* 4:111-116.
- Caretta, J. V., E. Oleson, D. Weller, *et al.* 2013. U. S. Pacific marine mammal stock assessments: 2012. U.S. Department of Commerce, NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-504. 378 pp.
- Clutton-Brock, T. H., S. D. Albon and F. E. Guinness. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* 313:131-133.
- Colagross-Schouten, A. M., J. A. K. Mazet, F. M. D. Gulland, M. A. Miller and S. Hietala. 2002. Diagnosis and seroprevalence of leptospirosis in California sea lions from coastal California. *Journal of Wildlife Diseases* 38:7-

17.

- Cooch, E., and G. White. 2012. Program MARK: A gentle introduction. Available at <http://www.phidot.org/software/mark/docs/book/>.
- Coulson, T., E. J. Milner-Gulland and T. Clutton-Brock. 2000. The relative roles of density and climatic variation on population dynamics and fecundity rate in three contrasting ungulate species. *Proceedings of the Royal Society of London B* 267:1771-1779.
- DeLong, R. L., and S. R. Melin. 2000. Thirty years of pinniped research at San Miguel Island. Pages 401-406 in *Fifth California Channel Islands Symposium*. Santa Barbara Museum of Natural History, Santa Barbara, CA.
- DeLong, R., G. Antonelis, C. Oliver, B. Stewart, M. Lowry and P. Yochem. 1991. Effects of the 1982-83 El Niño on several population parameters and diet of California sea lions on the California Channel Islands. Pages 166-172 in F. Trillmich and K. A. Ono, eds. *Pinnipeds and El Niño: Responses to environmental stress*. Springer-Verlag, Berlin, Germany.
- DiLorenzo, E. D., K. M. Cobb, J. C. Furtado, *et al.* 2010. Central Pacific El Niño and decadal climate change in the North Pacific Ocean. *Nature Geoscience Letters*:762-765.
- Fowler, C. W., and D. B. Siniff. 1992. Determining population status and the use of biological indices in the management of marine mammals. Pages 1025-1037 in D. R. McCullough and R. H. Barrett, eds. *Wildlife 2001: Populations*. Elsevier Science Publishers, London, England.
- Francis, J., and C. Heath. 1991. Population abundance, pup mortality, and copulation frequency in the California sea

- lion in relation to the 1983 El Niño on San Nicolas Island. Pages 119–128 in F. Trillmich and K. Ono, eds. Pinnipeds and El Niño: Responses to environmental stress. Springer-Verlag, Berlin, Germany.
- Fritz, L. W., and C. Stinchcomb. 2005. Aerial, ship, and land-based surveys of the Steller sea lions (*Eumetopias jubatus*) in the Western stock in Alaska, June and July 2003 and 2004. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-68. 65 pp.
- Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* 31:367–393.
- Gearin, P. J., S. R. Melin, R. L. DeLong, M. E. Gosho and S. J. Jeffries. 2017. Migration patterns of adult male California sea lions (*Zalophus californianus*). U. S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-346. 27 pp.
- Gulland, F. M. D., M. Koski, L. J. Lowenstine, A. Colagross, L. Morgan and T. Spraker. 1996. Leptospirosis in California sea lions (*Zalophus californianus*) stranded along the central California coast, 1981–1994. *Journal of Wildlife Diseases* 32:572–580.
- Hammill, M. O., and J. F. Gosselin. 1995. Grey seal (*Halichoerus grypus*) from the northwest Atlantic: Female reproductive rates, age at first birth, and age of maturity in males. *Canadian Journal of Fisheries and Aquatic Sciences* 52:2757–2761.
- Hastings, K. K., L. A. Jemison, T. S. Gelatt, et al. 2011. Cohort effects and spatial variation in age-specific survival of Steller sea lions from southeastern Alaska.

- Ecosphere 2:1-21.
- Härkönen, T., R. Dietz, P. Reijnders, *et al.* 2006. A review of the 1988 and 2002 phocine distemper virus epidemics in European harbor seals. *Diseases of Aquatic Organisms* 68:115-130.
- Heath, C. B. 1989. The behavioral ecology of the California sea lion, *Zalophus californianus*. Ph.D. thesis, University of California, Santa Cruz, CA. 255 pp.
- Hernández-Camacho, C. J., D. Aurióles-Gamboa, J. Laake and L. R. Gerber. 2008. Survival rates of the California sea lion, *Zalophus californianus*, in Mexico. *Journal of Mammalogy* 89:1059-1066.
- Holmes, E. E., L. W. Fritz, A. E. York and K. Sweeney. 2007. Age-structured modeling reveals long-term declines in the natality of western Steller sea lions. *Ecological Applications* 17:2214-2232.
- Huber, H., A. Rovetta, L. A. Fry and S. Johnston. 1991. Age-specific natality of northern elephant seals at the South Farallon Islands, California. *Journal of Mammalogy* 72:525-534.
- Johnson, A. 1968. Annual mortality of territorial male fur seals and its management significance. *Journal of Wildlife Management* 32:94-99.
- Jones, O. R., A. Scheuerlein, R. Salguero-Gomez, *et al.* 2014. Diversity of ageing across the tree of life. *Nature* 505:169-173.
- Jorgenson, J. T., M. Festa-Bianchet, J.-M. Gaillard and W. D. Wishart. 1997. Effects of age, sex, disease, and density on survival of bighorn sheep. *Ecology* 78:1019-1032.
- Kennedy, S., T. Kuiken, P. D. Jepson, *et al.* 2000. Mass die-off

- of Caspian seals caused by canine distemper virus. *Emerging Infectious Diseases* 6:627-629.
- King, J. R., V. N. Agostini, C. J. Harvey, *et al.* 2011. Climate forcing and the California Current ecosystem. *ICES Journal of Marine Science* 68:1199-1216.
- Laake, J. 2013. RMark: An R Interface for analysis of capture-recapture data with MARK. NOAA Alaska Fisheries Science Center Processed Report AFSC-2013-01. 25 pp.
- Lander, R. H. 1981. A life table and biomass estimate for Alaskan fur seals. *Fisheries Research* 1:55-70.
- Leising, A. W., I. D. Schroeder, S. J. Bograd, *et al.* 2015. State of the California Current 2014-15: Impacts of the warm-water "Blob". *California Cooperative Ocean and Fisheries Investigations Reports* 56:31-68.
- Lima, M., and E. Páez. 1995. Growth and reproductive patterns in the South American fur seal. *Journal of Mammalogy* 76:1249-1255.
- Lowry, M. S., B. S. Stewart, C. B. Heath, P. K. Yochem and J. M. Francis. 1991. Seasonal and annual variability in the diet of California sea lions *Zalophus californianus* at San Nicolas Island, California, 1981-86. *Fishery Bulletin* 89:331-336.
- Lowry, M., P. Boveng, R. DeLong, C. Oliver, B. Stewart, H. DeAnda and J. Barlow, 1992. Status of the California sea lion (*Zalophus californianus californianus*) population in 1992. NOAA Southwest Fisheries Science Center Administrative Report. LJ-92-32. 34 pp. Available from Southwest Fisheries Science Center, PO Box 271, La Jolla, CA 92038.
- Lynn, R. J., F. B. Schwing and T. L. Hayward. 1995. The effect

- of the 1991-1993 ENSO on the California Current system. California Cooperative Oceanic Fisheries Investigations Report 36:57-71.
- Lynn, R. J., T. Baumgartner, J. Garcia, *et al.* 1998. The state of the California Current, 1997-1998: Transition to El Niño conditions. California Cooperative Oceanic Fisheries Investigations Report 39:25-49.
- Lyons, E. T., S. R. Melin, R. L. DeLong, A. J. Orr, F. M. Gulland and S. C. Tolliver. 2001. Current prevalence of adult *Uncinaria* spp. in northern fur seal (*Callorhinus ursinus*) and California sea lion (*Zalophus californianus*) pups on San Miguel Island, California, with notes on the biology of these hookworms. *Veterinary Parasitology* 97:309-318.
- Maniscalco, J. M., K. Wynne., K. W. Pitcher, M. B. Hanson, S. R. Melin and S. Atkinson. 2004. The occurrence of California sea lions in Alaska. *Aquatic Mammals* 30:427-433.
- McIntosh, R. R., P. D. Shaughnessy and S. D. Goldsworthy. 2006. Mark-recapture estimates of pup production for the Australian sea lion (*Neophoca cinerea*) at Seal Bay Conservation Park, South Australia. Pages 353-368 in A. W. Trites, S. K. Atkinson, D. P. Demaster, L. W. Fritz, T. S. Gelatt, L. D. Rea and K. M. Wynne, eds. *Sea lions of the world*. Alaska Sea Grant College Program, Fairbanks, AK.
- Melin, S. R., and R. L. DeLong. 2000. At-sea distribution and diving behavior of California sea lion females from San Miguel Island, California. Pages 407-412 in *Fifth California Channel Islands Symposium*. Santa Barbara Museum of Natural History, Santa Barbara, CA.
- Melin, S. R., R. L. DeLong, J. R. Thomason and G. R.

- VanBlaricom. 2000. Attendance patterns of California sea lion (*Zalophus californianus*) females and pups during the non-breeding season at San Miguel Island. *Marine Mammal Science* 16:169-185.
- Melin, S. R., R. L. DeLong and D. B. Siniff. 2008. The effects of El Niño on the foraging behavior of lactating California sea lions (*Zalophus californianus californianus*) during the nonbreeding season. *Canadian Journal of Zoology* 86:192-206.
- Melin, S. R., A. J. Orr, J. D. Harris, J. L. Laake, R. L. DeLong, F. M. D. Gulland and S. Stoudt. 2010. Unprecedented mortality of California sea lion pups associated with anomalous oceanographic conditions along the central California coast in 2009. *California Cooperative Ocean and Fisheries Investigations Reports* 51:182-194.
- Melin, S. R., J. L. Laake, R. L. DeLong and D. B. Siniff. 2012. Age-specific recruitment and natality of California sea lions at San Miguel Island, California. *Marine Mammal Science* 28:751-776.
- Menkens, G. E., Jr., and M. S. Boyce. 1993. Comments on the use of time-specific and cohort life tables. *Ecology* 74:2164-2168.
- Merrick, R. L., T. R. Loughlin and D. Calkins, 1996. Hot branding: A technique for long-term marking of pinnipeds. U.S. department of Commerce, NOAA Technical Memorandum NMFS-AFSC-68. 21 pp.
- Messier, F. 1990. Mammal life histories: Analyses among and within *Spermophilus columbianus* life tables—a comment. *Ecology* 71:822-824.
- O'Brien, S., B. Robert and H. Tiandry. 2005. Consequences of violating the recapture duration assumption of mark-

- recapture models: A test using simulated and empirical data from an endangered tortoise population. *Journal of Applied Ecology* 42:1096-1104.
- Odell, D. K., 1981. California sea lion *Zalophus californianus* (Lesson, 1828). Pages 67-97 in S. H. Ridgway and R. J. Harrison, eds. Handbook of marine mammals. Volume 1. The walrus, sea lions, fur seals and sea otter. Academic Press, London, England.
- Orr, A. 2011. Foraging ecology of immature California sea lions (*Zalophus californianus*). Ph.D. thesis, University of Washington, Seattle, WA. 201 pp.
- Peterson, R., and G. Bartholomew. 1967. The natural history and behavior of the California sea lion. Special Publication No. 1, The American Society of Mammalogists, Stillwater, OK.
- Pitcher, K. W., and D. G. Calkins. 1981. Reproductive biology of Steller sea lions in the Gulf of Alaska. *Journal of Mammalogy* 62:599-605.
- R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Robert, A., S. Chantepie, S. Pavard, F. Sarrazin and C. Teplitsky. 2015. Actuarial senescence can increase the risk of extinction of mammal populations. *Ecological Applications* 25:116-124.
- Rykaczewski, R. R., and J. P. Dunne. 2010. Enhanced nutrient supply to the California Current Ecosystem with global warming and increased stratification in an earth system model. *Geophysical Research Letters* 37:L21606.
- Scholin, C. A., F. Gulland, G. J. Doucette, et al. 2000.

- Mortality of sea lions along the central California coast linked to a toxic diatom bloom. *Nature* 403:80-84.
- Schwarz, C. J., and W. T. Stobo. 2000. Estimation of juvenile survival, adult survival, and age-specific pupping probabilities for the female grey seal (*Halichoerus grypus*) on Sable Island from capture-recapture data. *Canadian Journal of Fisheries and Aquatic Sciences* 57:247-253.
- Spraker, T. R., R. L. DeLong, E. T. Lyons and S. R. Melin. 2007. Hookworm enteritis with bacteremia in California sea lions on San Miguel Island. *Journal of Wildlife Diseases* 43:179-188.
- Testa, J. W. 1987. Juvenile survival and recruitment in a population of Weddell seals (*Leptonychotes weddelli*) in McMurdo Sound, Antarctica. *Canadian Journal of Zoology* 65:2993-2997.
- Towell, R. G., R. R. Ream and A. E. York. 2006. Decline in northern fur seal (*Callorhinus ursinus*) pup production on the Pribilof Islands. *Marine Mammal Science* 22:486-491.
- Venrick, E., R. Durazo, A. Huyer, *et al.* 2003. The state of the California Current, 2002-2003: Tropical and subarctic influences vie for dominance. *California Cooperative Oceanic Fisheries Investigations Report* 44:28-60.
- Weise, M. J., and J. T. Harvey. 2005. Impact of the California sea lion (*Zalophus californianus*) on salmon fisheries in Monterey Bay, California. *Fishery Bulletin* 103:685-696.
- White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46:120-139.
- Wickens, P., and A. E. York. 1997. Comparative population

- dynamics of fur seals. *Marine Mammal Science* 13:241-292.
- Wilkinson, I. S., B. L. Chilvers, P. J. Duignan and P. A. Pistorius. 2011. An evaluation of hot-iron branding as a permanent marking method for adult New Zealand sea lions, *Phocarctos hookeri*. *Wildlife Research* 38:51-60.
- Wright, B. E., M. J. Tennis and R. F. Brown. 2010. Movements of male California sea lions captured in the Columbia River. *Northwest Science* 84:60-72.
- York, A. E. 1994. The population dynamics of northern sea lions, 1975-1985. *Marine Mammal Science* 10:38-51.

Received: 12 September 2016

Accepted: 11 May 2017

Appendix S1. California sea lion data and R code used to generate age- and sex-specific survival estimates.

Figure 1. Breeding colonies in the United States (circles) and Mexico (triangles) and breeding and nonbreeding ranges of California sea lions. Marking of California sea lions took place at San Miguel Island, California, and resighting effort was conducted primarily at San Miguel Island and Año Nuevo Island, California, during the breeding season.

Figure 2. Resightings of California sea lions branded as pups at San Miguel Island, California. Branding occurred between 1987 and 2014. Resightings occurred between 1990 and 2015 and are by sex (F = female $n = 91,953$ resightings; M = male, $n = 32,768$ resightings), age, and island (SMI = San Miguel Island, ANI = Año Nuevo Island, FAI = Farallon Islands).

Figure 3. Examples of resighting probability estimates for female (circle) and male (triangle) California sea lions branded

as pups at San Miguel Island, California, showing resighting probabilities of each possible age in years 1997, 2002, and 2014.

Figure 4. Resighting probability of 2 yr old (2) and 7 yr old (7) California sea lion females branded as pups at San Miguel Island, California and resighted between 1989 and 2015.

Figure 5. Annual variation in survival rate for California sea lions branded as pups at San Miguel Island, California, between 1987 and 2014 (*S_i* for pups, yearlings, age 3 females, age 3 males, age 5 females, and age 5 males).

Figure 6. Proportions of each California sea lion pup cohort, 1987–2014, in each weight anomaly category at the time of branding at San Miguel Island, California, used in the analysis of pup weight effects on survival.

¹ Corresponding author: (e-mail: sharon.melin@noaa.gov).

Table 1. Number of female (F) and male (M) California sea lion pups branded on San Miguel Island, California, 1987–2014, the median branding date each year, the proportion resighted in at least one year after branding, and the proportion recovered dead or stranded alive.

Year	Median branding date	F	M	Proportion resighted	Proportion recovered
1987	21 Sep 1987	113	87	0.47	0.04
1988	22 Sep 1988	97	83	0.39	0.01
1989	22 Oct 1989	108	90	0.43	0.00
1990	2 Nov 1990	244	255	0.43	0.03
1991	21 Oct 1991	258	239	0.40	0.02
1992	13 Nov 1992	228	262	0.37	0.09

1993	20 Oct 1993	345	141	0.59	0.03
1994	3 Oct 1994	366	134	0.57	0.02
1995	30 Sep 1995	325	175	0.57	0.04
1996	27 Sep 1996	314	183	0.36	0.03
1997	25 Sep 1997	312	185	0.20	0.08
1998	23 Oct 1998	304	196	0.64	0.03
1999	28 Sep 1999	301	198	0.62	0.04
2000	28 Sep 2000	319	180	0.44	0.02
2001	27 Sep 2001	306	194	0.39	0.04
2002	27 Sep 2002	320	180	0.44	0.04
2003	28 Sep 2003	303	196	0.56	0.02
2004	13 Oct 2004	301	199	0.56	0.02
2005	19 Oct 2005	302	198	0.66	0.03
2006	22 Sep 2006	270	130	0.58	0.04
2007	20 Sep 2007	199	100	0.56	0.03
2008	20 Sep 2008	185	115	0.28	0.04
2009	24 Oct 2009	207	106	0.46	0.03
2010	26 Sep 2010	125	119	0.60	0.03
2011	23 Sep 2011	200	100	0.44	0.02
2012	26 Sep 2012	148	152	0.18	0.18
2013	25 Sep 2013	174	127	0.23	0.06
2014	23 Sep 2014	159	141	0.07	0.12
1987-2014		6,833	4,465	0.46	0.04

Table 2. Candidate models for survival (S), resighting probability (p), and recovery probability (r) fitted with the Burnham model to resighting and recovery data of California sea lions at San Miguel Island, California, 1987-2015. Sex is a factor variable with values M and F, whereas male and female are 0/1 indicator variables. Age S represents age bins for S and age p is age bins for p . The variables pup, yearling, twothree, and fourplus are 0/1 indicator variables for specific age groups.

Weight is the pup's weight at the time of branding expressed as an anomaly from the overall sex-specific mean. The term $bs(\text{Age})$ is a smooth cubic spline over age. The variable "time" represents time bins as described in the text for S and p . "Time" is a numeric variable to provide a linear trend over time. The variables $\text{ApriltoSeptSSTAnomalies}$, $\text{OcttoJuneSSTAnomalies}$, and $\text{JulytoJuneSSTAnomalies}$ are the average buoy sea surface temperature anomalies for the specified range of months. Variable leptom is the number of males that stranded during the year (July to following June) from leptospirosis. Variable "last" for recovery probability is 0 except for the last year when recovery data were incomplete. Models in bold were the top models.

Model	S (annual survival probability)
1	$\text{sex} * \text{AgeS}$
2	$\text{sex} * \text{AgeS} + \text{pup:weight} + \text{yearling:weight}$
3	$\text{sex} * bs(\text{Age}) + \text{pup:time} + \text{yearling:time} + \text{twothree:time} + \text{fourplus:time} + \text{pup:weight} + \text{yearling:weight}$
4	$\text{sex} * \text{AgeS} + \text{pup:time} + \text{yearling:time} + \text{twothree:time} + \text{fourplus:time} + \text{pup:weight} + \text{yearling:weight}$
5	$\text{sex} * bs(\text{Age}) + \text{pup:time} + \text{yearling:time} + \text{twothree:time} + \text{pup:weight} + \text{yearling:weight}$
6	$\text{sex} * \text{AgeS} + \text{pup:time} + \text{yearling:time} + \text{twothree:time} + \text{pup:weight} + \text{yearling:weight}$
7	$\text{sex} * bs(\text{Age}) + \text{pup:time} + \text{yearling:time} + \text{pup:weight} + \text{yearling:weight}$
8	$\text{sex} * \text{AgeS} + \text{pup:time} + \text{yearling:time} + \text{pup:weight} + \text{yearling:weight}$
9	$\text{sex} * bs(\text{Age}) + \text{pup:time} + \text{yearling:time} + \text{twothree:time} + \text{fourplus:time} + \text{male:twoplus:time} + \text{pup:weight} +$

yearling:weight

- 10 **sex * bs(Age) + pup:time + yearling:time +
female:twothree:time + female:fourplus:time +
male:twoplus:leptom + pup:weight + yearling:weight**
- 11 **sex * bs(Age) + pup:time + yearling:time +
female:twothree:time + female:fourplus:time +
male:twoplus:time + male:fourplus:time + pup:weight +
yearling:weight**
- 12 **sex * AgeS + pup:time + yearling:time + twothree:time +
fourplus:time + male:twoplus:time + pup:weight +
yearling:weight**
- 13 **sex * AgeS + pup:time + yearling:time +
female:twothree:time + female:fourplus:time +
male:twoplus:leptom + pup:weight + yearling:weight**
- 14 **sex * AgeS + pup:time + yearling:time +
female:twothree:time + female:fourplus:time +
male:twoplus:time + male:fourplus:time + pup:weight +
yearling:weight**
- 15 **sex * bs(Age) + ApriltoSeptSSTAnomalies:pup +
OcttoJuneSSTAnomalies:pup +
yearling:JulytoJuneSSTAnomalies +
twothree:JulytoJuneSSTAnomalies +
fourplus:JulytoJuneSSTAnomalies + pup:Time +
yearling:Time + twothree:Time + fourplus:Time +
pup:weight + yearling:weight**
- 16 **sex * AgeS + ApriltoSeptSSTAnomalies:pup +
OcttoJuneSSTAnomalies:pup +
yearling:JulytoJuneSSTAnomalies +
twothree:JulytoJuneSSTAnomalies +**

fourplus:JulytoJuneSSTAnomalies + pup:Time +
 yearling:Time + twothree:Time + fourplus:Time +
 pup:weight + yearling:weight

<i>p</i> (resighting probability)	
1	agep + male:agep + time + male:time + agep:time
2	time:sex:agep
3	agep * sex + sex:time
4	agep + male:agep + time + agep:time
5	agep * sex + time
<i>r</i> (recovery probability)	
1	pup + last
2	pup + yearling + last
3	pup + yearling + Time + last

Table 3. Age- and sex-specific annual survival of California sea lions at San Miguel Island, California. Estimates and confidence limits are averaged over years from the top model with cubic spline to describe age-effect. Ninety-five percent (95%) confidence interval (dashed lines) widens at older ages due to reduced sample sizes. The value *n* is number of sea lions resighted at the next age (e.g., for survival from age 0 to 1 it is the number of resightings of yearlings). A single female sea lion was sighted at age 25 but no male has been sighted past the age of 19.

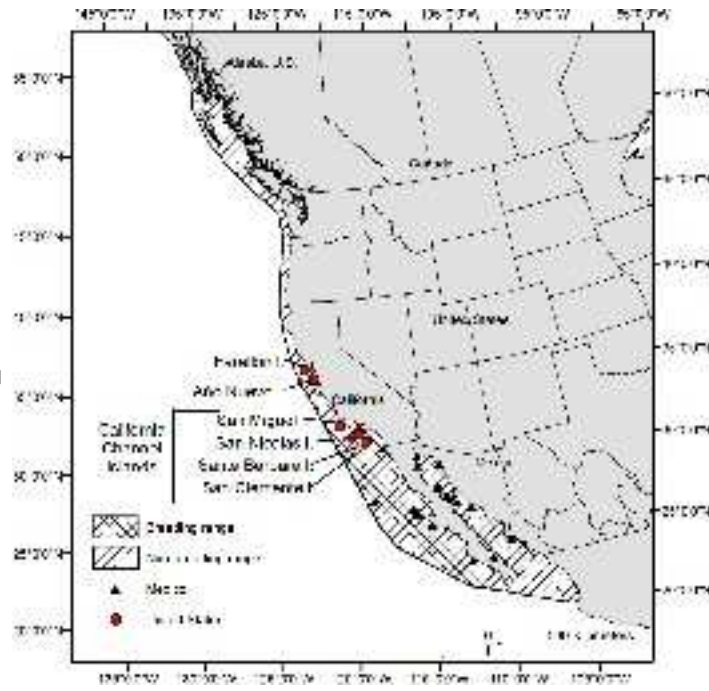
Age	Female			Male		
	Estimate	95% Confidence interval	<i>n</i>	Estimate	95% Confidence interval	<i>n</i>
0	0.600	0.559-0.641	1,814	0.574	0.530-0.617	986
1	0.758	0.720-0.792	2,052	0.757	0.713-0.795	1,047
2	0.903	0.884-0.920	2,030	0.858	0.832-0.880	1,119
3	0.920	0.902-0.935	2,100	0.892	0.869-0.912	1,108
4	0.951	0.941-0.960	2,034	0.927	0.912-0.940	1,046

5	0.952	0.943-0.961	1,938	0.931	0.919-0.941	937
6	0.950	0.940-0.958	1,837	0.923	0.911-0.934	879
7	0.944	0.934-0.952	1,687	0.908	0.895-0.921	774
8	0.933	0.923-0.943	1,559	0.887	0.871-0.901	696
9	0.921	0.909-0.931	1,364	0.856	0.838-0.873	613
10	0.901	0.888-0.913	1,128	0.804	0.779-0.827	488
11	0.877	0.862-0.890	1,009	0.744	0.713-0.773	368
12	0.845	0.828-0.861	794	0.669	0.631-0.706	252
13	0.812	0.791-0.832	616	0.586	0.533-0.637	167
14	0.772	0.747-0.795	529	0.512	0.435-0.587	91
15	0.734	0.704-0.762	392	0.440	0.331-0.554	58
16	0.705	0.667-0.741	286	0.383	0.239-0.552	30
17	0.680	0.627-0.728	187	0.354	0.170-0.595	11
18	0.656	0.581-0.724	129	0.350	0.120-0.681	10
19	0.651	0.546-0.743	78	0.366	0.082-0.787	0
20	0.664	0.521-0.783	41	0.407	0.058-0.885	0
21	0.692	0.501-0.833	23	0.472	0.040-0.951	0
22	0.722	0.472-0.883	9	0.585	0.031-0.984	0
23	0.808	0.512-0.944	4	0.736	0.030-0.996	0
24	0.864	0.522-0.974	1	0.867	0.040-0.999	0

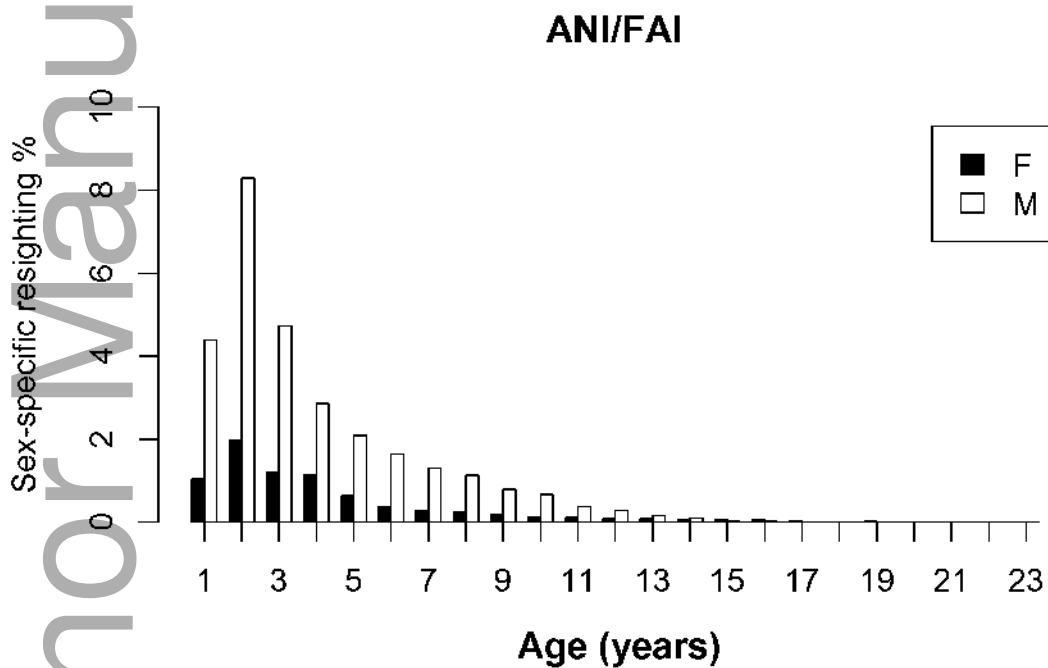
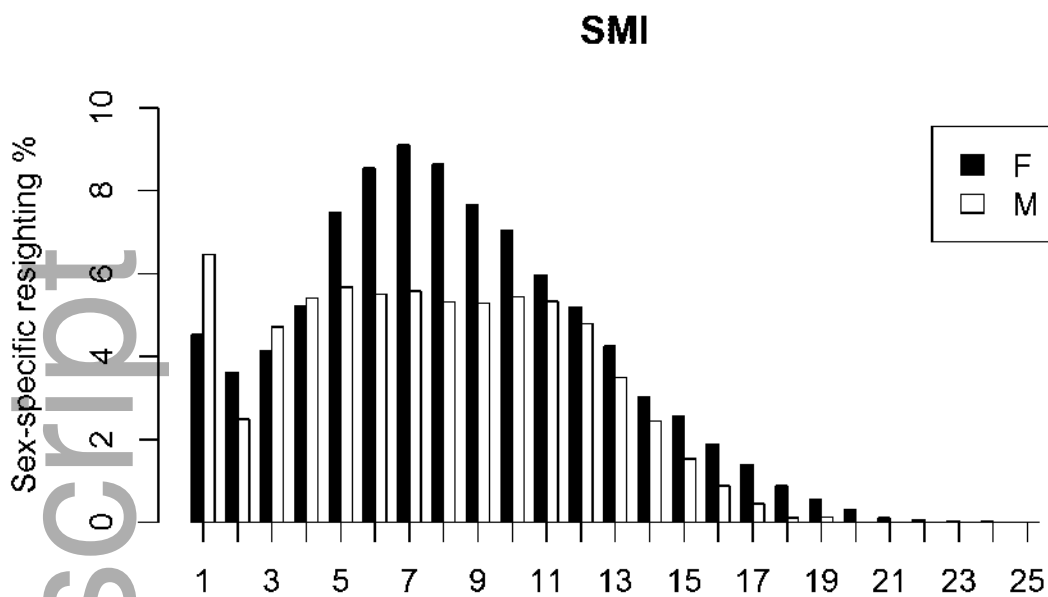
Table 4. Estimated annual female California sea lion pup survival rates for 1987, 1996, 1998, 2004, and 2012 for each weight anomaly bin based on a long-term average weight of 17.0 kg. Median weight anomaly for each year is shown in bold to demonstrate the annual variation in pup weights and its impact on survival.

Pup weight anomaly bin (kg)	Annual pup survival rates				
	1987	1996	1998	2004	2012
[<-4.5]	0.52	0.39	0.71	0.28	0.14
[-4.5, -3]	0.59	0.45	0.77	0.34	0.18

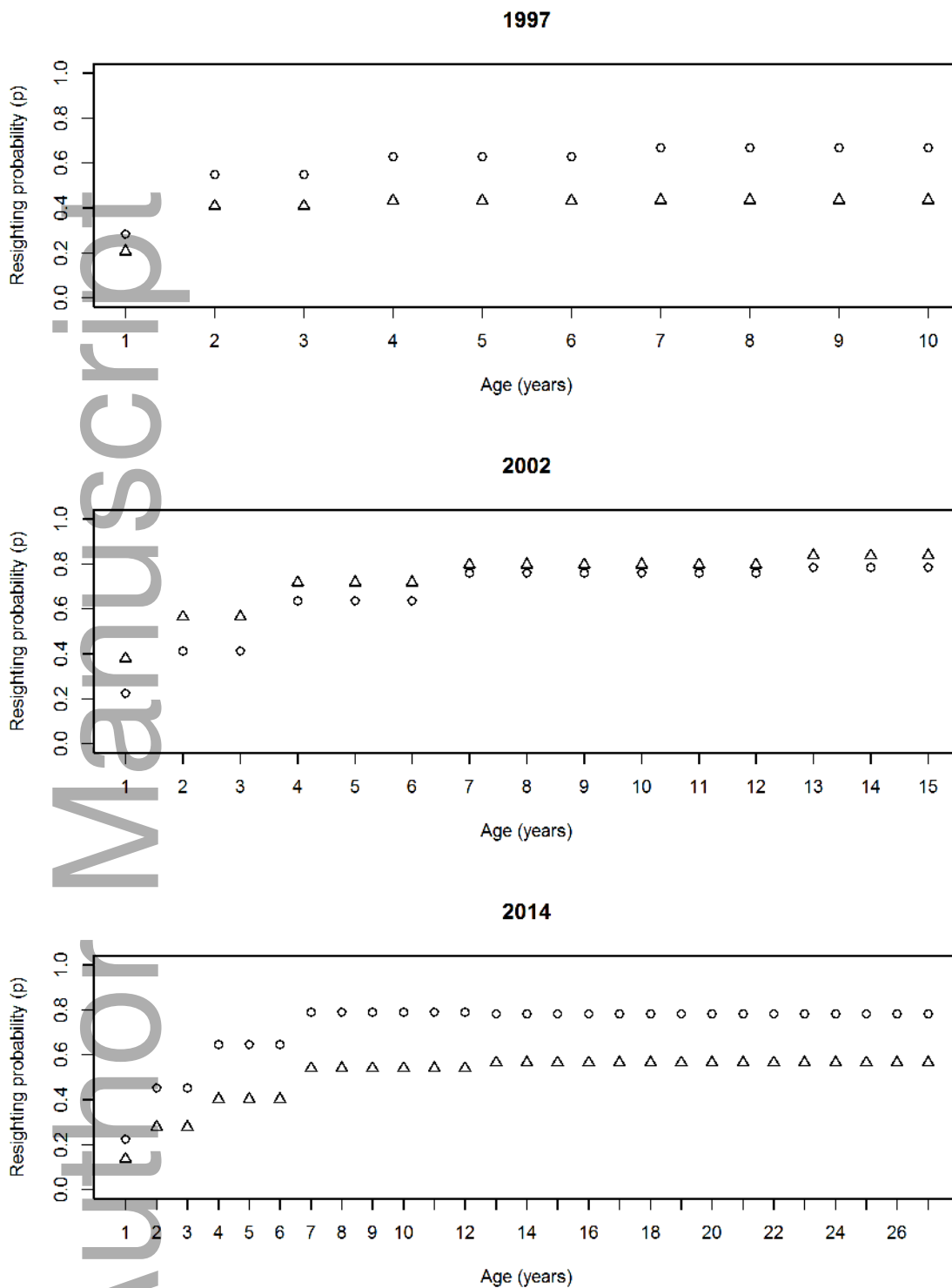
[-3, -2]	0.62	0.49	0.79	0.37	0.21
[-2, -1]	0.65	0.52	0.81	0.39	0.23
[-1, 0]	0.68	0.55	0.83	0.43	0.25
[0, 1]	0.70	0.58	0.84	0.46	0.28
[1, 2]	0.73	0.60	0.86	0.49	0.30
[2, 3]	0.75	0.64	0.87	0.52	0.34
[3, 5]	0.78	0.68	0.89	0.57	0.36
[>5]	0.82	0.73	0.93	0.67	0.27



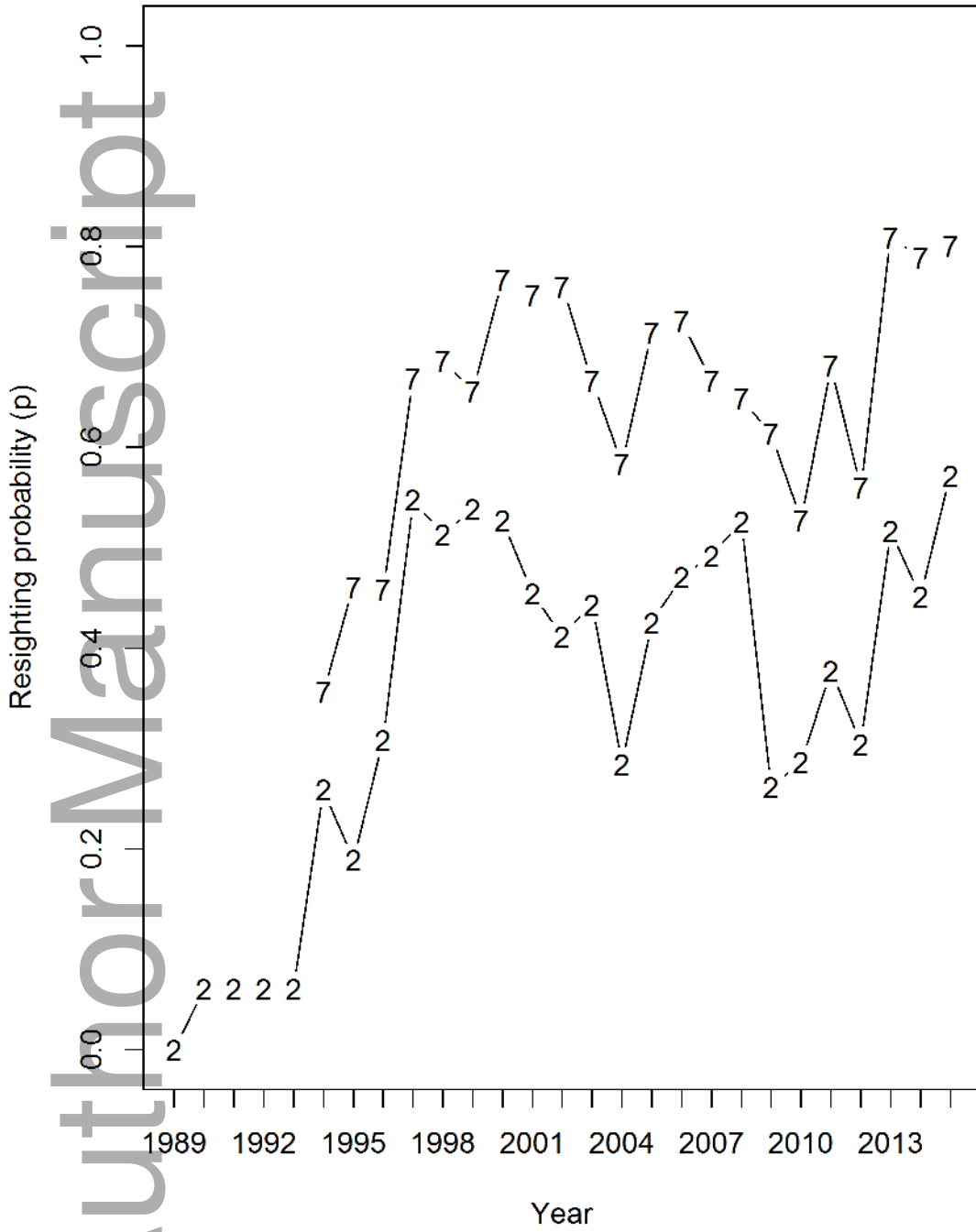
mms_12427_f1.tif



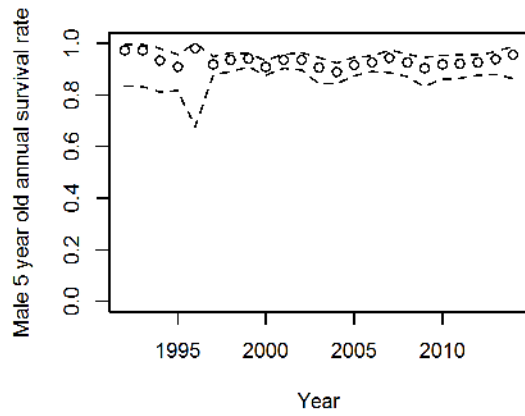
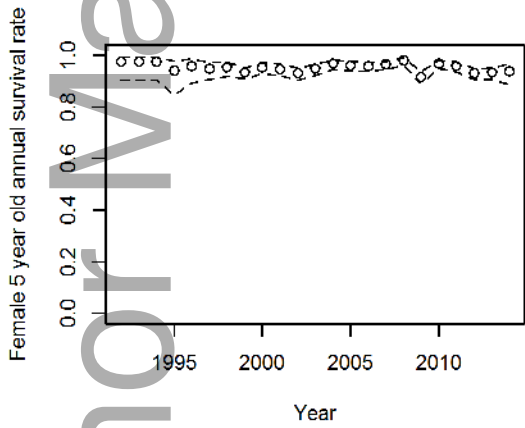
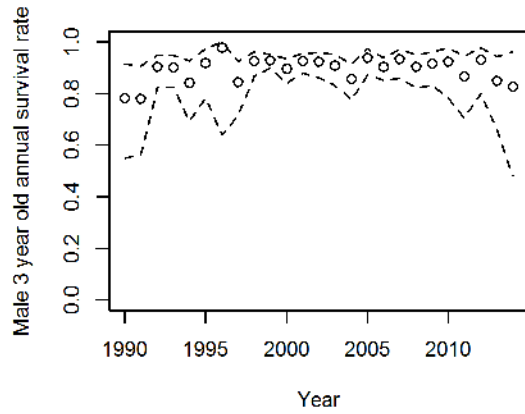
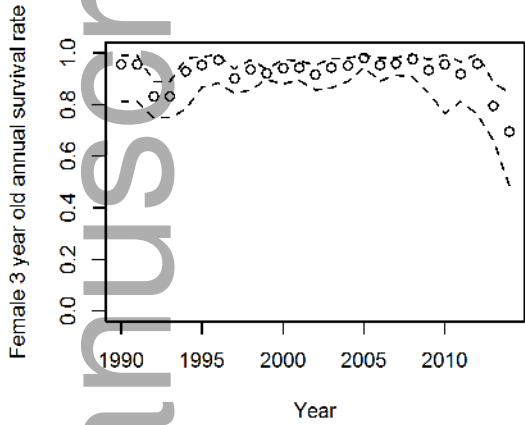
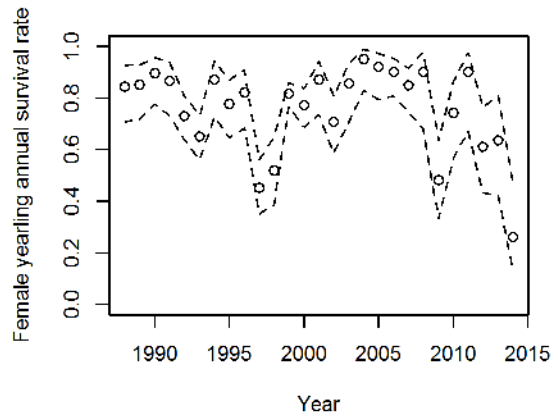
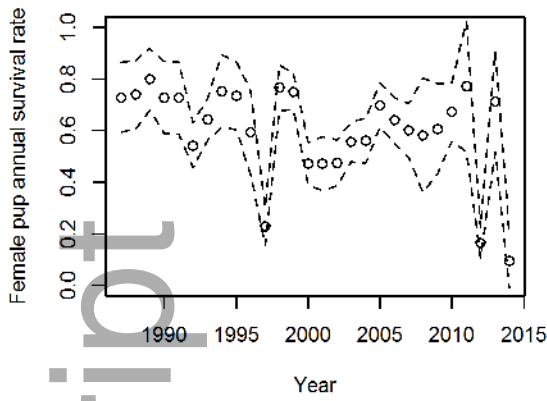
mms_12427_f2.tif



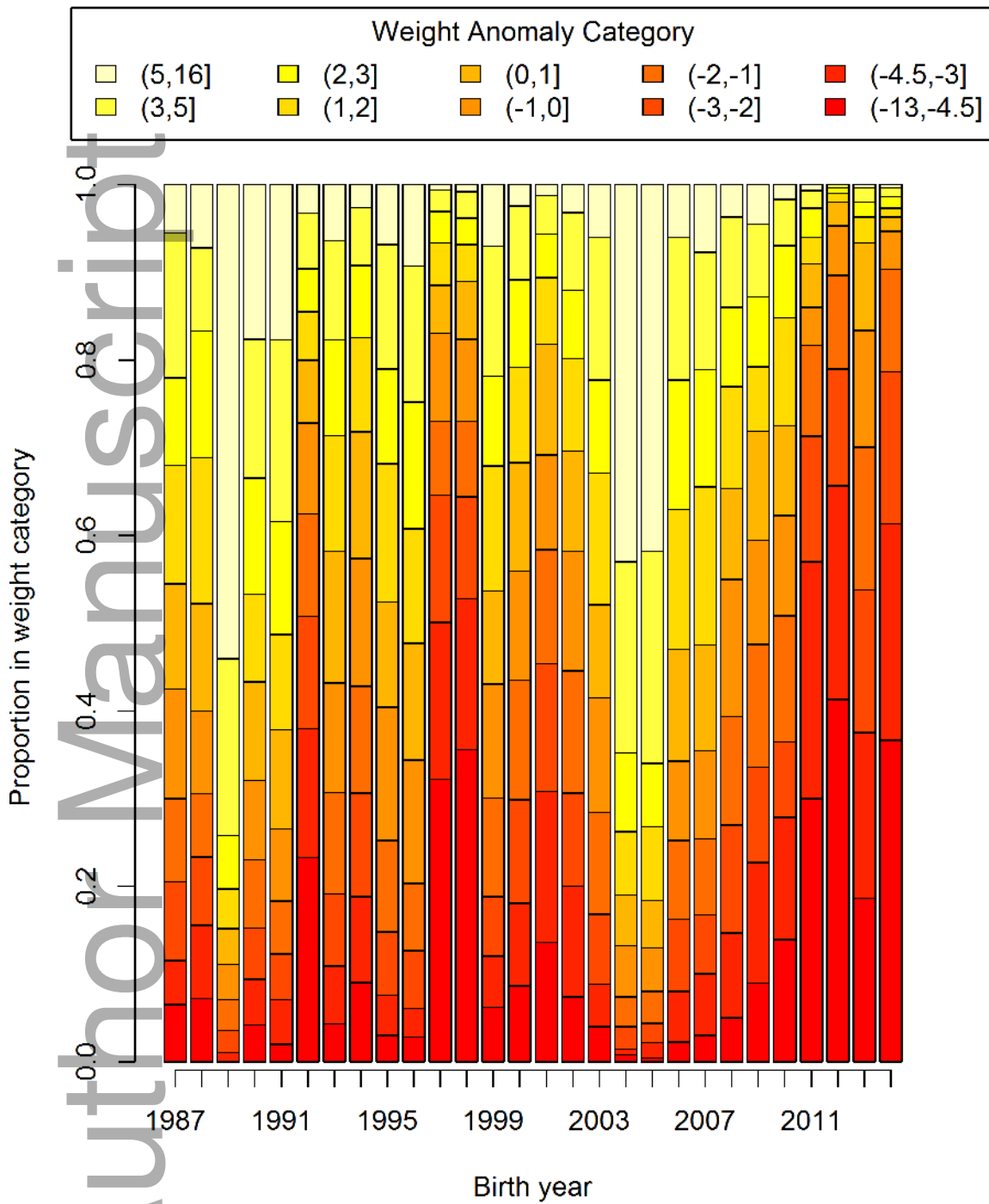
mms_12427_f3.tif



mms_12427_f4.tif



mms_12427_f5.tif



mms_12427_f6.tif