



Survival rates of Steller sea lions from Oregon and California

BRYAN E. WRIGHT,* ROBIN F. BROWN, ROBERT L. DELONG, PATRICK J. GEARIN, SUSAN D. RIEMER,
JEFFREY L. LAAKE, AND JONATHAN J. SCORDINO

Marine Mammal Program, Oregon Department of Fish and Wildlife, 7118 N.E. Vandenberg Avenue, Corvallis, OR 97330, USA (BEW, RFB)

Marine Mammal Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 7600 Sand Point Way N.E., Seattle, WA 98115, USA (RLD, PJG, JLL)

Marine Mammal Program, Oregon Department of Fish and Wildlife, 1495 E. Gregory Road, Central Point, OR 97502, USA (SDR)

Marine Mammal Program, Makah Fisheries Management, Makah Tribe, P.O. Box 115, Neah Bay, WA 97357, USA (JJS)

* Correspondent: bryan.e.wright@state.or.us

Due to significant population declines in the 1970s and 1980s, Steller sea lions (*Eumetopias jubatus*) were listed as threatened under the U.S. Endangered Species Act in 1990, and subsequently partitioned in 1997 into an endangered western stock and a threatened eastern stock. We estimated survival rates from a mark-recapture study of 7 eastern stock cohorts marked as pups in California and Oregon from 2001 to 2009 ($n = 1,154$ pups) and resighted range-wide from 2002 to 2013. First-year survival rates were among the lowest found for Steller sea lions thus far, averaging 0.46 (range 0.21–0.72) for females and 0.44 (0.21–0.68) for males; yearling survival rates, however, were among the highest, averaging 0.85 for females and 0.81 for males. Low pup and high yearling rates offset each other, however, so that cumulative survival rates to age 4, averaging 0.33 for females and 0.27 for males, were similar to those found in studies from Alaska and Russia. While range-limit effects and environmental variation may be related to the low and variable pup survival rates we found, populations in Oregon and California nonetheless continued to grow, which contributed to delisting of the eastern stock in 2013. Continued monitoring and incorporation of new information on vital rates into regional population models will help inform post-delisting monitoring for the eastern stock of Steller sea lions.

Key words: California, *Eumetopias jubatus*, mark-recapture, Oregon, Steller sea lion, survival

Steller sea lions (*Eumetopias jubatus*) range across the northern Pacific Rim from California to northern Japan and were estimated to number between 240,000 and 300,000 animals in the 1950s (Loughlin 2002; National Marine Fisheries Service [NMFS] 2008). During the 1970s and 1980s, populations in western Alaska declined by up to 75%, prompting the species to be listed as threatened under the U.S. Endangered Species Act (ESA) in 1990 (U.S. Federal Register 1990). In 1997, NMFS recognized 2 Distinct Population Segments (hereafter referred to as “stocks”), separated east to west at 144°W longitude (Loughlin 1997). The western stock, due to persistent declines across much of its range, was re-classified as endangered under the ESA (U.S. Federal Register 1997). In contrast, the eastern stock, while initially retaining its classification as threatened, steadily increased in population size and was delisted in 2013 (NMFS 2013a; U.S. Federal Register 2013).

The cause or causes of the decline in the western stock have been the subject of much research and debate (e.g., see National

Research Council 2003; Berman 2008). Contrasting population dynamics between the stocks provide a unique opportunity to evaluate hypotheses regarding the underlying drivers of those dynamics. For example, one hypothesis for the decline in the western stock is chronic nutritional stress, caused in part by a predominantly low energetic density, gadid-rich diet (e.g., see Trites and Donnelly 2003). Fritz and Hinckley (2005), however, argued against that hypothesis, noting (among other things) that diets from many increasing eastern stock populations were also high in gadids (e.g., see Riemer et al. 2011). Another hypothesized factor in the western decline is decreased survival rates of juveniles (e.g., York 1994). Pendleton et al. (2006) compared survival rates from Alaskan rookeries in each stock from the 1980s and 1990s and found that survival rates of juveniles from the (increasing) eastern study population were indeed greater than survival rates from the (decreasing) western study population.

Recognizing the need for updated estimates of survival rates for Steller sea lions from throughout their range, multiple

research groups initiated mark-recapture programs based on the hot-branding of pups beginning in the late 1990s and early 2000s. These efforts were affirmed by a [National Research Council \(2003\)](#) review which noted that pup-branding programs were “essential for estimating pup and adult survival and would allow for the modernization of Steller sea lion demographics required for population models.” Results from these ongoing studies have now been published, including on eastern stock Steller sea lions from Alaska ([Hastings et al. 2011](#)) and western stock Steller sea lions from Alaska ([Fritz et al. 2014](#); [Maniscalco 2014](#); [Maniscalco et al. 2015](#)) and Russia ([Burdin et al. 2009](#); [Altukhov et al. 2015](#)). We report here on the survival of eastern stock Steller sea lions from southern Oregon and northern California. Our objectives were to estimate age- and sex-specific survival rates of Steller sea lions from the southern edge of the eastern stock range and to compare those with survival estimates from Alaska and Russia.

MATERIALS AND METHODS

Marking.—Steller sea lions are sexually dimorphic with a polygynous mating system and congregate seasonally at traditional breeding sites (rookeries) for pupping and mating. Pups are born between mid-May and late July and females breed approximately 10 days after parturition ([Pitcher et al. 2001](#)). We captured pups for marking at 2 rookeries: Pyramid Rock at Rogue Reef, Oregon during odd years from 2001 to 2009, and South Seal Rock at St. George Reef, California in 2002 and 2004 ([Table 1](#); [Fig. 1](#)). Total counts of live pups at Pyramid Rock and South Seal Rock during the study period ranged from approximately 600–900 and 350–450 pups, respectively. In addition, we routinely found 25–100 dead pups upon arriving at rookeries for branding work. With the exception of 2001, we limited our activity to a single day during the second or third week of July, at least several weeks after the median pupping date of June 15 for the Pyramid Rock rookery ([Pitcher et al. 2001](#)). In 2001, the initial year of the study, marking activities occurred over 3 days in late June and early July.

Pup capture and handling procedures evolved over time but after 2001 generally consisted of the following steps. First, an initial team of 4–6 researchers landed on the rookery as soon as possible after sunrise to carefully clear a portion of the rookery

of adults and herd up to 200 pups into a holding area. The work area at St. George Reef included a convenient pool that allowed pups to remain damp and cool during the holding period; at Rogue Reef, pups were kept cool with backpack water sprayers. The target sample size of 200 was based on a power analysis (conducted using simulated data and custom programming) indicating that 100 animals of each sex may be necessary to detect a 30–60% decline in survival from 0 to 4 years with 80% power, assuming a resight probability of 30–50%. The remainder of the research team (approximately 16–20 individuals, including 3–5 veterinarians) landed on the rookery to set up a work area consisting of 2–4 anesthesia stations, a pup-holding pen, a scale, and an area for hot-iron brands and a propane forge.

When ready for processing, batches of approximately 20 pups were separated from the larger group and herded into a holding pen. Pups were then removed from the pen and placed in hoop nets for weighing. Next, pups were anesthetized with isofluorane gas ([Heath et al. 1996](#)), sex was determined, measured (dorsal standard length and axillary girth), and tagged on the trailing edge of their fore-flippers with numbered Allflex global sheep tags. The left flanks of pups were then washed with seawater, dried with compressed air, and hot-branded ([Merrick et al. 1996](#)) with a unique alpha-numeric brand containing 1–3 numbers followed by a letter ([Table 1](#)). Lastly, pups were monitored for recovery from anesthesia and released back into or adjacent to the holding area. Staff rotated positions after each batch of approximately 20 animals. The total handling procedure lasted approximately 10 min per pup and the total disturbance to the rookery lasted approximately 10–12 h.

All methods conformed to American Society of Mammalogists guidelines for the use of wild mammals in research ([Sikes et al. 2016](#)). During the study period reported here there was no Institutional Animal Care and Use Committee (IACUC) overseeing our work but since 2011 identical methods have been approved by the IACUC of the Northwest and Alaska Fisheries Science Centers. In addition, all methods were approved under authority of U.S. Marine Mammal Protection Act/Endangered Species Act Permits 782-1446, 434-1669, 434-1892, and 14326, and U.S. Fish and Wildlife Service Special Use Permits OI-70151, OI-09-0007, OI-00075, and 13594-2-0046.

Table 1.—Number of Steller sea lion (*Eumetopias jubatus*) pups branded by year, rookery, and sex (F = female, M = male, NA = not available).

Year	Date (month/day)	Rogue Reef, Oregon		St. George Reef, California			Total	Brand sequence
		F	M	F	M	NA		
2001	6/28, 6/30, 7/1	80	100				180	1R–180R ^a
2002	7/13			74	65	1	140	1Y–140Y
2003	7/12	91	99				190	181R–370R
2004	7/12			75	76		151	141Y–291Y
2005	7/18	57	43				100	371R–470R
2007	7/16	93	100				193	471R–663R ^b
2009	7/12	102	98				200	664R–863R
Total		423	440	149	141	1	1,154	

^aBrand “91R” was branded instead as “901R.”

^bBrand “609R” was branded instead as “1606R.”

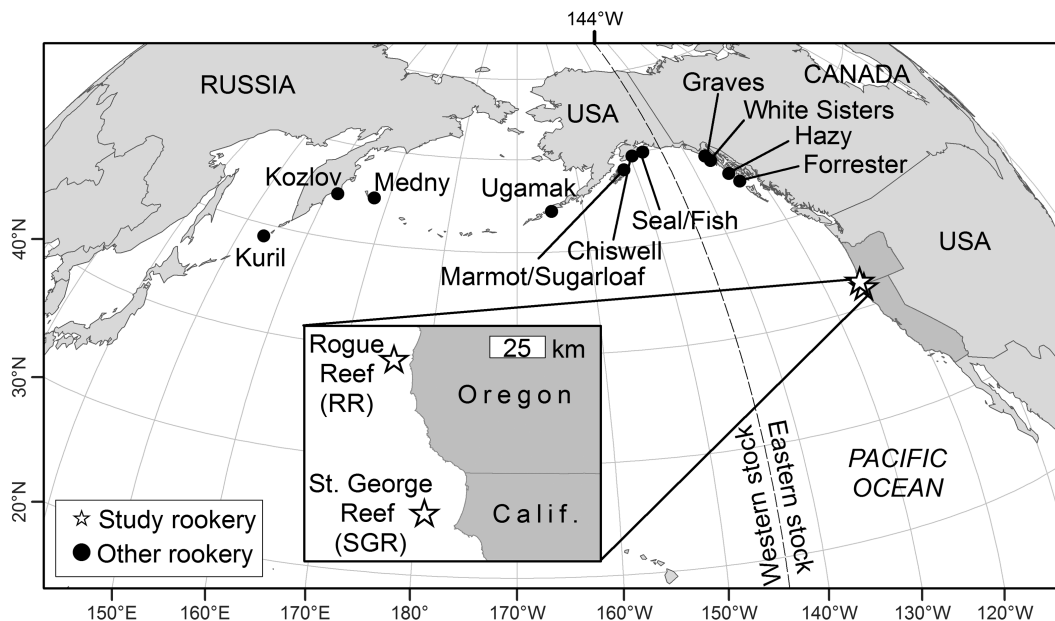


Fig. 1.—Steller sea lion (*Eumetopias jubatus*) range map showing stock boundary (144°W) and rookery locations where pup-branding has been conducted in recent decades. Site names and references are as follows: St. George Reef and Rogue Reef (this study; inset); Forrester, Hazy, White Sisters, and Graves (Hastings et al. 2011); Seal/Fish, Marmot/Sugarloaf, Ugamak (Fritz et al. 2014); Chiswell (Maniscalco 2014; Maniscalco et al. 2015); Forrester and Marmot (Pendleton et al. 2006); and Medny, Kozlov, and Kuril (Altukhov et al. 2015).

Resighting.—Pups were resighted from 2002 to 2013 using a variety of observation platforms and a network of observers from California to Alaska. Observation platforms included remotely operated video cameras, automated camera systems, vessel surveys, and shore-based surveys. We personally conducted resight surveys in northern California, Oregon, and Washington, whereas we relied on contractors, colleagues, and members of the public for resights in California, British Columbia, and Alaska. Nonetheless, spatiotemporal gaps in resight coverage were sometimes unavoidable due to limited resources.

Data collected for each resighted animal included brand, date, time, location, observer, a score indicating brand quality, an indicator for whether the left and right flipper tags were detected or read, an indicator for whether a photograph was taken, and a code indicating reproductive behavior. Resight effort occurred year-round but for this analysis the annual observation period was restricted to 15 May to 15 September, which was a trade-off between maximizing resight probabilities during the breeding season and minimizing parameter heterogeneity due to non-instantaneous sampling (see more on modeling assumptions below). Only resights that were verified by a photograph, or that were resighted > 1 day or by > 1 observer per season, were considered for inclusion in the analysis. Additional quality control checks included photo-confirming resights of animals with gaps of > 2 years between sightings and providing additional scrutiny to resights of difficult to read brands (e.g., due to scarring around brand digits).

Data analysis.—We used Cormack–Jolly–Seber (CJS) open-population models to estimate apparent survival (φ) and resight (p) probabilities (e.g., see Williams et al. 2002). CJS models estimate apparent or “local” survival, rather than true survival,

since the model cannot distinguish between permanent emigration and death. However, for brevity, and given that nearly the entire species range was subject to resighting effort, we hereafter simply refer to “survival.” It is important to note that since pups were marked at approximately 3 week of age, first-year survival, as well as cumulative survival to older ages, refers strictly to survival subsequent to age at capture and thus does not include neonate survival. We constructed annual encounter histories from resights beginning with the release year and continuing through 2013. Multiple resights of the same animal during the same annual observation period were collapsed into a single binary resighting event (i.e., “1” if release year or resighted at least once and “0” otherwise).

We used the R (R Core Team 2016) package RMark (Laake 2013) and program MARK (White and Burnham 1999) to develop CJS models for the hypothesized processes giving rise to the encounter history data. Explanatory variables hypothesized to affect survival probability included age (see below), sex (factor), natal rookery (factor), mass at capture (individual covariate), and year at branding (factor). Mass at capture was modeled as an interaction between an indicator variable for age 0 and mass (i.e., pup:mass) and was included because first-year survival was hypothesized to positively correlate with mass. Year at branding was modeled as an interaction between an indicator variable for age 0 and year (i.e., pup:year) and was included because first-year survival was hypothesized to be most sensitive to annual variation in environmental conditions. Explanatory variables hypothesized to affect resight probability included age (see below), sex (factor), year (factor), and rookery (factor). The age effect on survival was modeled 5 ways: age² = quadratic trend with age; age³ = 3 age classes (1, 2, 3+ years); age⁴ = 4 age classes (1, 2, 3, 4+ years); age⁵ = 5 age

classes (1, 2, 3, 4, 5+ years); and age6 = 6 age classes (1, 2, 3, 4, 5–10, 11+ years). The effect of age on resight probability was modeled 3 ways: age3, age4, and age5, as defined above for survival.

Explanatory variables were combined in a variety of additive and interaction models for survival (40 total) and resight probability (6 total), resulting in a grand total of 240 candidate CJS models (Table 2). We assessed goodness-of-fit of a global model using the median \hat{c} procedure in program MARK. Model selection proceeded by comparing Akaike's Information Criterion (AIC) corrected for small sample size for all combinations of survival and resight probability submodels. We used multi-model averaging across all models to derive final estimates of survival and resight probabilities (Burnham and Anderson 2002). Prior to CJS analysis, 1 animal of unknown sex was removed from the data set and the mass of 1 animal with a misrecorded value was replaced with the mean mass for its sex and cohort.

CJS model assumptions include: instantaneous sampling periods; homogeneity of resight and survival parameters; absence of tag loss or misidentification; permanent emigration; and independence of fate among animals (Williams et al. 2002). As noted above, a 4-month resight window is not "instantaneous" and thus would likely induce some parameter heterogeneity. Other sources of heterogeneity could result from incorrect sex determination of animals. Jamison et al. (2013) and Altukhov et al. (2015), for example, found that approximately 3% and 10–15% of the pups in selected samples of their respective studies had been assigned to the incorrect sex (or incorrectly recorded) at branding. Heterogeneous resight probabilities have been found to produce relatively small (typically negative) bias in survival estimates but the effects of heterogeneous survival on CJS survival estimates is less well known (Williams et al. 2002). For branding studies, tag loss can occur due to

Table 2.—List of candidate Cormack–Jolly–Seber (CJS) models for use in estimating apparent survival (φ) and resight (p) probabilities for Steller sea lions (*Eumetopias jubatus*) branded as pups at Rogue Reef, Oregon, and St. George Reef, California, 2001–2009. Each survival model was crossed with each resight model resulting in a total of 240 possible CJS models. CJS model used to test goodness-of-fit was $\varphi\{\text{sex} \times \text{age6} + \text{rookery}\} p\{\text{sex} \times \text{age5} + \text{time} + \text{rookery}\}$.

Survival models	Resight models
sex \times age ^a	sex \times age ^b + year
sex \times age ^a + rookery	sex \times age ^b + year + rookery
sex \times age ^a + pup:mass	
sex \times age ^a + pup:year	
sex \times age ^a + pup:mass + rookery	
sex \times age ^a + pup:year + rookery	
sex \times age ^a + pup:mass + pup:year	
sex \times age ^a + pup:mass + pup:year + rookery	

^aAge was modeled 5 ways for each φ model: Age² = quadratic trend with age, age3 = 3 age classes (1, 2, 3+ years), age4 = 4 age classes (1, 2, 3, 4+ years), age5 = 5 age classes (1, 2, 3, 4, 5+ years), and age6 = 6 age classes (1, 2, 3, 4, 5–10, 11+ years).

^bAge was modeled 3 ways for each p model: age3, age4, and age5, as defined for φ .

poor brand-iron application resulting in illegible or difficult to read brands (van den Hoff et al. 2004). Hastings et al. (2009), for example, found that approximately 3% of brand resights contained errors. Illegible brands would result in a negative bias in survival estimates. The assumption that all emigration is permanent would likely not be necessary since nearly the entire species range had some exposure to resight effort. Lastly, it is unknown to what extent fates of sea lions are independent but even if they were not, it would mostly affect the variance in survival estimates rather than the estimates themselves (Williams et al. 2002).

RESULTS

Mark-resights.—We branded a total of 1,154 Steller sea lion pups between 2001 and 2009 (Table 1). We resighted 681 individuals (59% of 1,154) at least once from a total of 9,363 resights collected over the annual 4-month observation periods from 2002 to 2013 (Fig. 2). The majority of the resights were from Oregon (62.6% of 9,363), followed by British Columbia

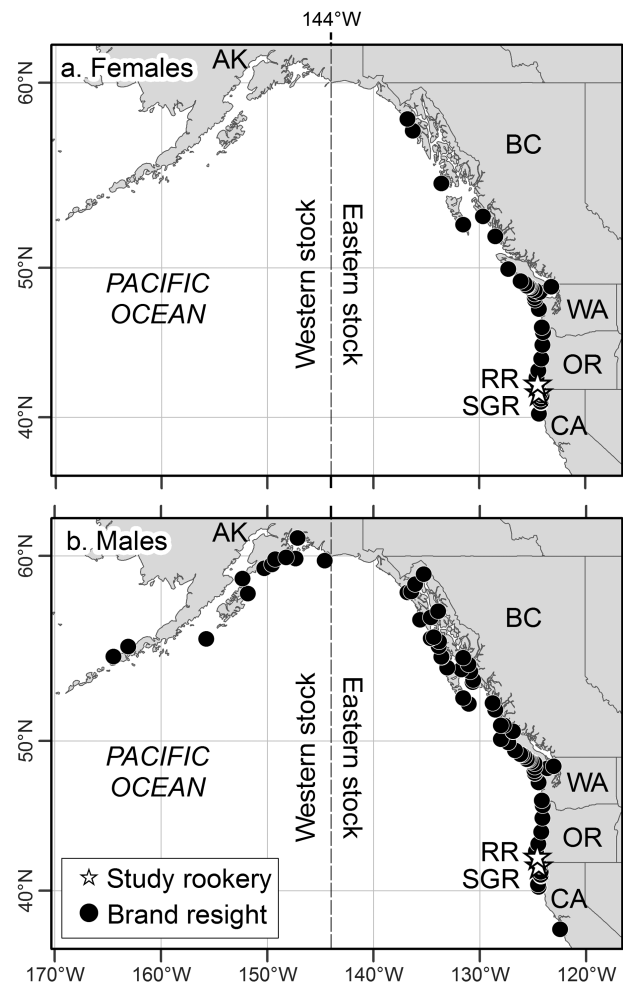


Fig. 2.—Brand resight locations for a) female and b) male Steller sea lions (*Eumetopias jubatus*) branded as pups at Rogue Reef (RR), Oregon, and St. George Reef (SGR), California, 2001–2009. Resights were from 15 May to 15 September from 2002 to 2013.

(20.1%), California (8.5%), Washington (7.6%), and Alaska (1.1%). Of the 681 resighted individuals, the majority were seen at least once in Oregon (85% of 681), followed by British Columbia (30%), Washington (28%), California (27%), and Alaska (7%); the total adds up to more than 100% because most animals were seen in more than one area. Males were resighted at greater distances from the natal rookeries than females. The northwesternmost and southeasternmost resights—both males—were at Unimak Island in Alaska (54.888°N, 164.558°W) and Año Nuevo Island, California (37.108°N, 122.337°W), respectively.

CJS models.—The overdispersion parameter based on the median \hat{c} procedure was estimated to be 1.17, indicating there was no evidence for lack of fit for the global model. Of the 240 possible candidate models (Table 2), the top 12 accounted for 99% of the cumulative weight of evidence (Table 3). Model averaging based on the entire set of 240 models was nonetheless used to derive all final estimates and their associated measures of uncertainty.

The top CJS models included just 2 of the 6 possible resight probability submodels, varying only by whether age was modeled with 4 (1, 2, 3, 4+ years) or 5 (1, 2, 3, 4, 5+ years) factor levels (Table 3). In general, resight probabilities were higher for females, older age classes, and for animals from Rogue Reef (Fig. 3; Supplementary Data SD1). Annual resight probabilities ranged from 0.18 to 0.88 for females and 0.14 to 0.77 for males.

The top CJS models included just 7 of the 40 possible survival probability submodels, varying only by how age was modeled and whether a rookery effect was included (Table 3). As with resight probabilities, survival probabilities were, in general, higher for females, older animals, and for animals from Rogue Reef (Fig. 4; Supplementary Data SD2). All of the top models included the pup:year interaction term, indicating that first-year survival varied by cohort. Pup (age 0–1) survival rates ranged from 0.21 to 0.72 for females and 0.21 to 0.68 for males. Yearling (age 1–2) survival rates averaged 0.85 for females and 0.81 for males. Annual survival rates plateaued for females by age 3 at approximately 0.93 and for males by age 4 at approximately 0.88.

Since all of the top models included the pup:mass interaction term, first-year survival estimates necessarily depended on a specific value of the mass covariate. We therefore calculated first-year survival estimates in Fig. 4 and Supplementary Data SD2 based on sex- and cohort-specific mean mass values rather than a single global average. However, to illustrate the general relationship between mass at capture and first-year survival, we plotted model-averaged predictions of first-year survival across the observed ranges of sex- and cohort-specific mass at capture values (Fig. 5). Mean masses of pups were similar in most years with the exception of 2001 when branding occurred 2–3 weeks earlier than other years. Mean masses for females and males in the 2001 cohort were 4.7 kg ($n = 80$) and 4.2 kg ($n = 100$) lighter, respectively, than pooled mean masses for subsequent cohorts, which were 25.7 kg for females ($n = 492$) and 29.3 kg for males ($n = 481$).

Lastly, we converted model-averaged annual survival rates to cumulative survival rates (Fig. 6; Supplementary Data SD3). While 4 of the 7 cohorts had similar survivorship curves (2002, 2003, 2005, and 2009), the 2 most extreme cohorts (2004 and 2001) varied by over a factor of 3. Compared to similar studies of Steller sea lions from Alaska and Russia, survival rates of pups from Oregon and California were generally lower and more variable than elsewhere (Fig. 7). First-year survival rates from our study averaged 0.46 for females compared to the range-wide average of 0.62; for males, the study average was 0.44 compared to the range-wide average of 0.60. By age 4, however, the differences across studies were less pronounced, with most estimates of cumulative survival from Oregon and California at or near the range-wide averages of 0.38 for females and 0.30 for males.

DISCUSSION

Several differences stand out when comparing the results of our study to similar studies of survival rates of Steller sea lions in Alaska (e.g., Hastings et al. 2011; Fritz et al. 2014; Maniscalco 2014) and Russia (e.g., Altukhov et al. 2015). First, survival estimates for pups (age 0 to 1) from all but our 2004 cohort were lower than those found elsewhere in the range,

Table 3.—Top Cormack–Jolly–Seber (CJS) model set (12 of 240) with 99% of the cumulative weight of evidence for estimating apparent survival (φ) and resight (p) probabilities for Steller sea lions (*Eumetopias jubatus*) branded as pups at Rogue Reef, Oregon, and St. George Reef, California, 2001–2009. AIC_c = Akaike’s Information Criterion corrected for small sample size.

CJS model		No. parameters	ΔAIC_c	Weight
$\varphi\{\text{sex} \times \text{age}3 + \text{pup:mass} + \text{pup:year}\}$	$p\{\text{sex} \times \text{age}5 + \text{year} + \text{rookery}\}$	35	0.0	0.39
$\varphi\{\text{sex} \times \text{age}4 + \text{pup:mass} + \text{pup:year}\}$	$p\{\text{sex} \times \text{age}5 + \text{year} + \text{rookery}\}$	37	1.6	0.18
$\varphi\{\text{sex} \times \text{age}3 + \text{pup:mass} + \text{pup:year} + \text{rookery}\}$	$p\{\text{sex} \times \text{age}5 + \text{year} + \text{rookery}\}$	36	2.0	0.15
$\varphi\{\text{sex} \times \text{age}4 + \text{pup:mass} + \text{pup:year} + \text{rookery}\}$	$p\{\text{sex} \times \text{age}5 + \text{year} + \text{rookery}\}$	38	3.5	0.07
$\varphi\{\text{sex} \times \text{age}3 + \text{pup:mass} + \text{pup:year}\}$	$p\{\text{sex} \times \text{age}4 + \text{year} + \text{rookery}\}$	33	4.0	0.05
$\varphi\{\text{sex} \times \text{age}4 + \text{pup:mass} + \text{pup:year}\}$	$p\{\text{sex} \times \text{age}4 + \text{year} + \text{rookery}\}$	35	4.3	0.05
$\varphi\{\text{sex} \times \text{age}5 + \text{pup:mass} + \text{pup:year}\}$	$p\{\text{sex} \times \text{age}5 + \text{year} + \text{rookery}\}$	39	4.9	0.03
$\varphi\{\text{sex} \times \text{age}3 + \text{pup:mass} + \text{pup:year} + \text{rookery}\}$	$p\{\text{sex} \times \text{age}4 + \text{year} + \text{rookery}\}$	34	6.0	0.02
$\varphi\{\text{sex} \times \text{age}4 + \text{pup:mass} + \text{pup:year} + \text{rookery}\}$	$p\{\text{sex} \times \text{age}4 + \text{year} + \text{rookery}\}$	36	6.3	0.02
$\varphi\{\text{sex} \times \text{age}5 + \text{pup:mass} + \text{pup:year} + \text{rookery}\}$	$p\{\text{sex} \times \text{age}5 + \text{year} + \text{rookery}\}$	40	6.8	0.01
$\varphi\{\text{sex} \times \text{age}6 + \text{pup:mass} + \text{pup:year}\}$	$p\{\text{sex} \times \text{age}5 + \text{year} + \text{rookery}\}$	41	7.2	0.01
$\varphi\{\text{sex} \times \text{age}5 + \text{pup:mass} + \text{pup:year}\}$	$p\{\text{sex} \times \text{age}4 + \text{year} + \text{rookery}\}$	37	7.6	0.01

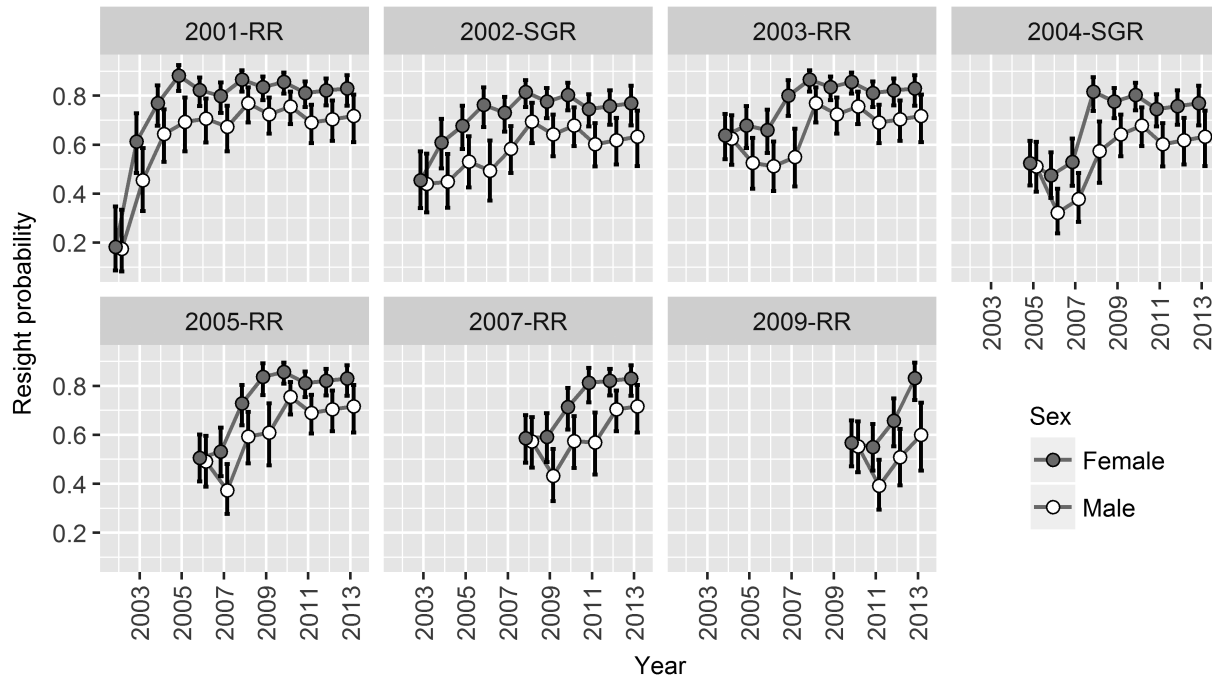


Fig. 3.—Model-averaged estimates and 95% CIs for annual resight probabilities (p) for Steller sea lions (*Eumetopias jubatus*) branded as pups at Rogue Reef (RR), Oregon, and St. George Reef (SGR), California, 2001–2009.

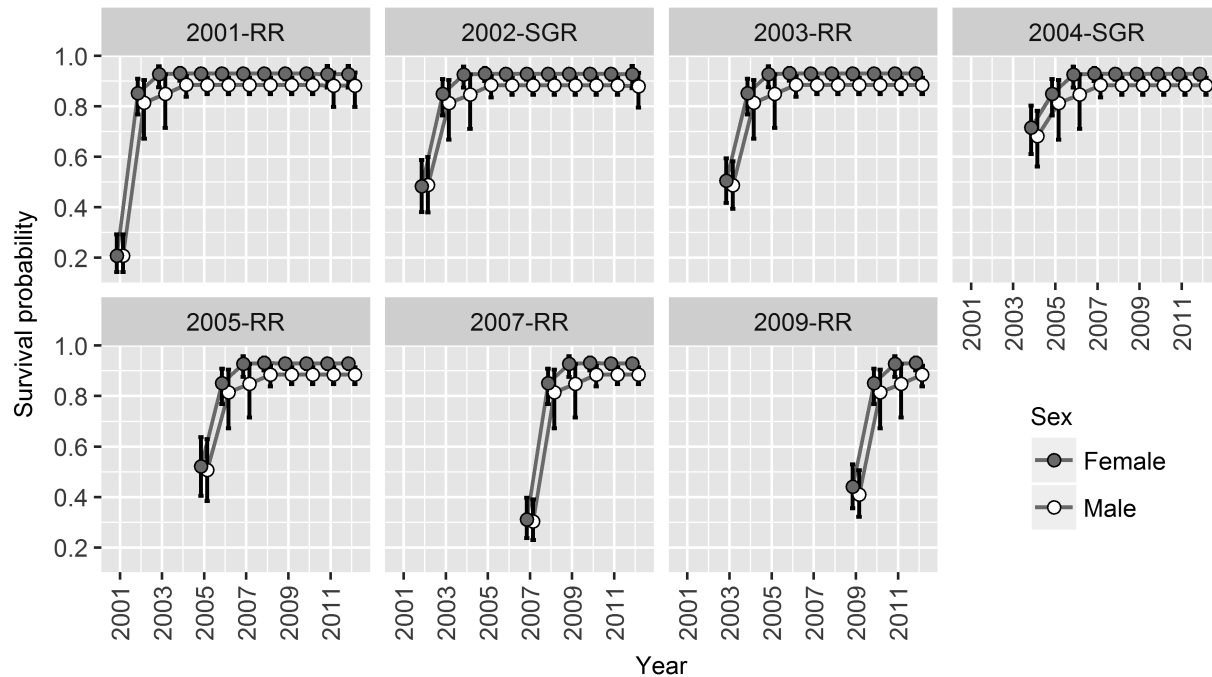


Fig. 4.—Model-averaged estimates and 95% CIs for annual survival probabilities (ϕ) for Steller sea lions (*Eumetopias jubatus*) branded as pups at Rogue Reef (RR), Oregon, and St. George Reef (SGR), California, 2001–2009.

particularly when compared to the western stock (Fig. 7). In the case of 2001, however, we suspect that this can at least partially be explained by methodological factors that made that year an outlier from the rest of our study. For instance, in 2001, we visited the rookery on 3 nearly consecutive days instead of on a single day as in subsequent years (Table 1). This may have potentially increased pup mortality relative to subsequent years due to repeated disturbance to the rookery. In addition,

we captured pups approximately 2 weeks earlier than in subsequent years. This consequently resulted in marking pups that were lighter than subsequent cohorts (Fig. 5). Since we and others (e.g., Hastings et al. 2011; Maniscalco 2014) found that survival of pups was positively associated with mass, early capture dates (and hence lower masses) therefore likely contributed to lower survival rates for the 2001 cohort. Concern over whether the 2001 cohort had undue influence on our overall modeling

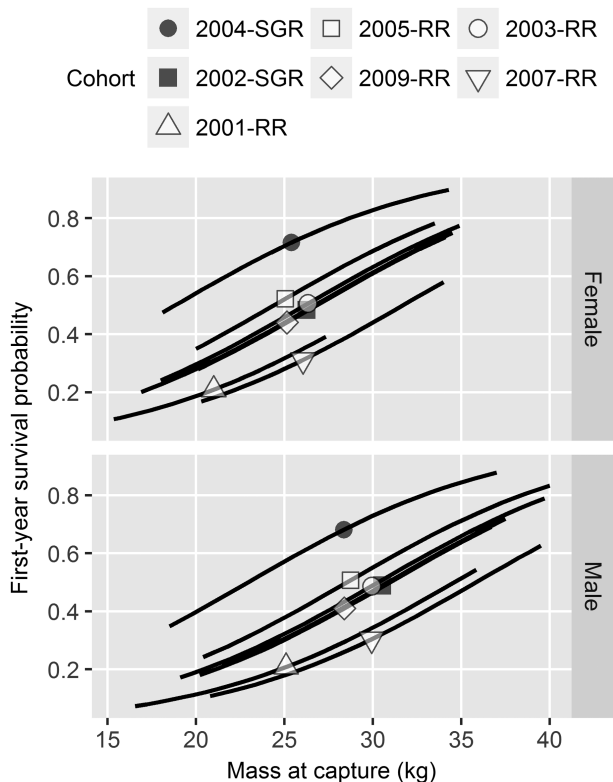


Fig. 5.—Predicted first-year survival probabilities as a function of mass at capture for Steller sea lions (*Eumetopias jubatus*) branded as pups at Rogue Reef (RR), Oregon, and St. George Reef (SGR), California, 2001–2009. Symbol location marks mean pup mass for each sex and cohort combination; cohorts in legend are sorted from highest to lowest survival probability.

results led us to reanalyze all our data without it. We found, however, that the list of top models in Table 3 was exactly the same without the 2001 cohort, albeit with some minor difference in the relative AIC rankings.

A second apparent difference between our study and some others was the significant annual variation we found in pup survival within rookeries (i.e., cohort effects) as expressed through the inclusion of the pup:year interaction term in all of our top models (Table 3). For example, estimated survival of female pups for the 2004 St. George Reef cohort was 1.5 times higher (absolute difference of 0.24) than the 2002 St. George Reef cohort (Fig. 6). Similarly, survival of female pups for the 2005 Rogue Reef cohort was 1.7 times higher (absolute difference of 0.21) than in 2007. In contrast, neither Burdin et al. (2009) nor Fritz et al. (2014) found evidence for cohort effects in their studies of survival rates of western stock Steller sea lions in Russia and Alaska, respectively. Hastings et al. (2011), however, did find evidence of cohort variation in eastern stock Steller sea lions (through age 2), but the effect was less pronounced with a maximum absolute difference of only 0.12 between cohorts.

A third and final difference we noted between our results and some others was in survival rates of yearlings (age 1–2). Nearly all other studies found survival rates of yearlings lower than the > 0.8 rates we found at St. George Reef and Rogue Reef for both sexes (Fig. 4). Maniscalco (2014) and Fritz et al. (2014),

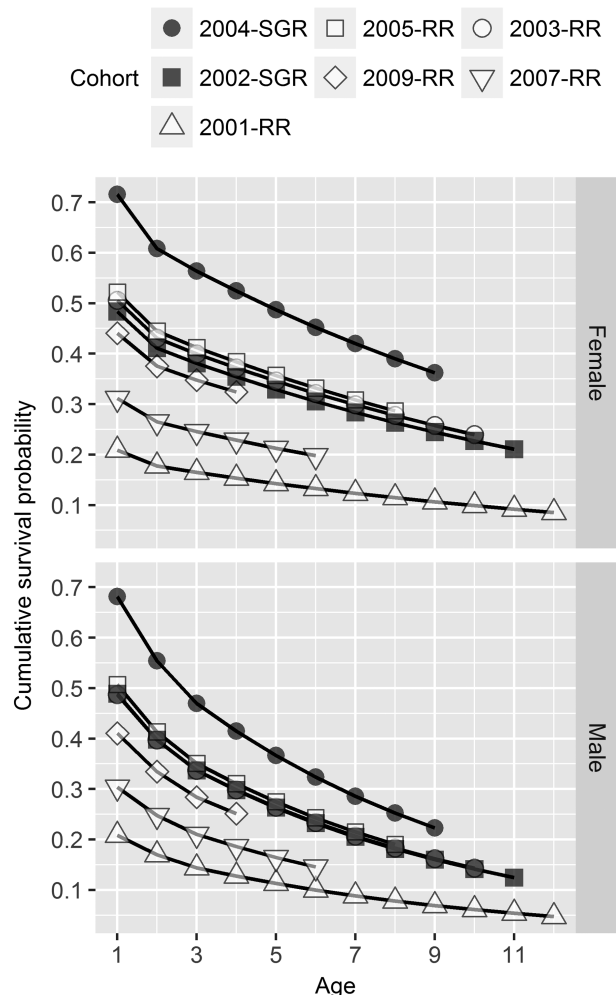


Fig. 6.—Model-averaged estimates of cumulative survival probabilities for Steller sea lions (*Eumetopias jubatus*) branded as pups at Rogue Reef (RR), Oregon, and St. George Reef (SGR), California, 2001–2009. Cohorts in legend are sorted from highest to lowest survival probability; survival estimates are plotted at the maximum of each age class (e.g., survival from age 0 to 1 is plotted at age 1).

for example, found survival rates of yearlings as low as 0.40 and 0.57, respectively, for western stock males. Hastings et al. (2011) found higher rates (> 0.70) for yearlings from the eastern stock in Alaska, but only 1 of their rookeries (Graves Rock) had survival rates that exceeded 0.8. There were thus 2 patterns in annual survival rates for ages 0–3 that emerged across studies, namely, whether survival increased monotonically with age, as in our study (Fig. 4) and others (e.g., Hastings et al. 2011; eastern Gulf of Alaska in Fritz et al. 2014; Kuril Islands in Altukhov et al. 2015), or whether it temporarily decreased due to higher survival rates for pups than yearlings (e.g., Maniscalco 2014; eastern Aleutian Islands and central Gulf of Alaska in Fritz et al. 2014; Medny Island and Kozlov Cape in Altukhov et al. 2015). As noted by Fritz et al. (2014), possible explanations for these 2 patterns could include differences in early life history such as duration of maternal care (e.g., see Maniscalco 2014), habitat characteristics such as varying predation rates (e.g., Horning and Mellish 2014) or prey availability, or heterogeneity in resight probabilities, which may have

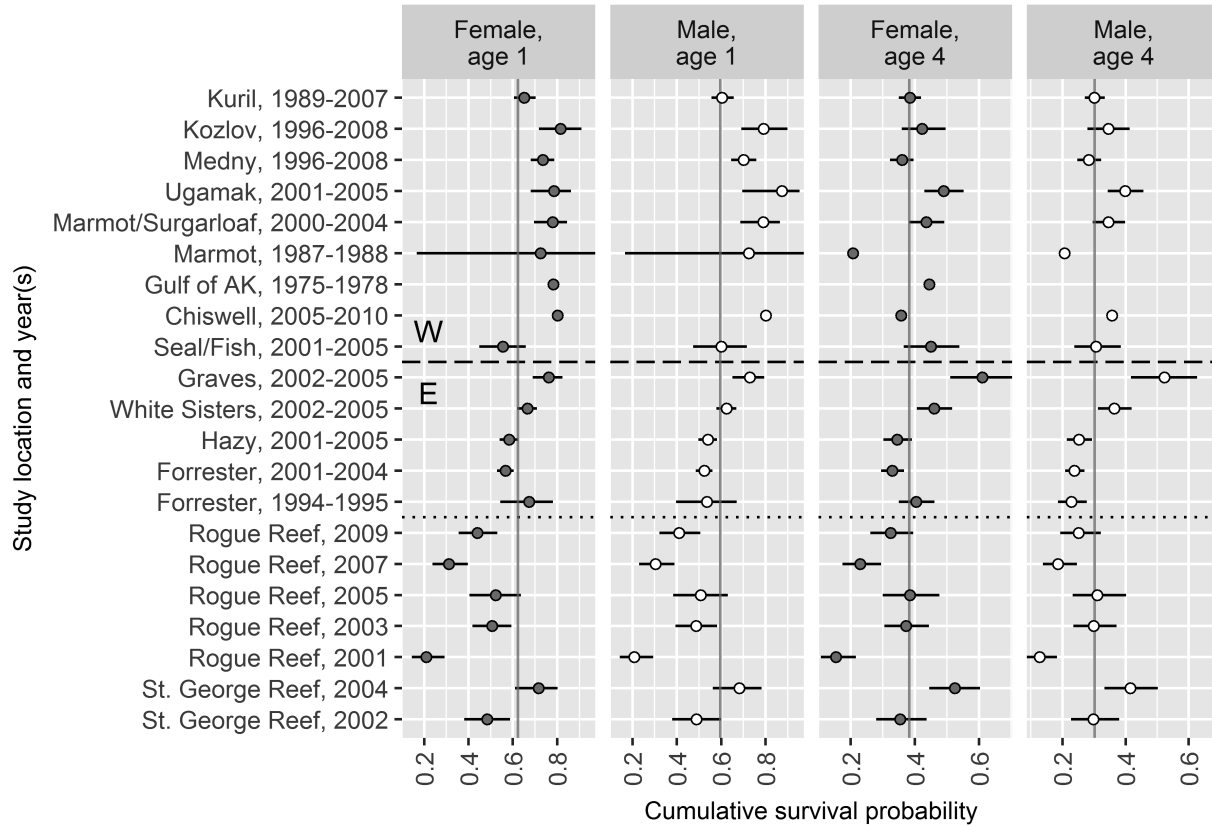


Fig. 7.—Comparison across studies of survival to ages 1 and 4 for female and male Steller sea lions (*Eumetopias jubatus*). Study populations on the y-axis are sorted spatially from southeast to northwest (see Fig. 1). Vertical, solid lines indicate mean survival rates across studies for each sex and age group. Horizontal, dashed line demarcates the east (E) and west (W) stock boundary; horizontal, dotted line demarcates this study from the rest of the eastern stock. Data sources were as follows: St. George Reef and Rogue Reef (this study); Gulf of Alaska, Marmot, Graves, White Sisters, Hazy, and Forrester (Hastings et al. 2011); Ugamak, Marmot/Sugarloaf, and Seal/Fish (Fritz et al. 2014); Chiswell (Maniscalco 2014); Medny, Kozlov, and Kuril (Altukhov et al. 2015). Point estimates and 95% CIs were not available for all combinations; some CIs were obtained via personal communication with study authors.

limited the ability to precisely partition survival rates among the first few years of life.

Other than for the 2001 cohort, it is not clear to us why we found such relatively low and variable survival rates for pups compared to other studies. One possibility may be related to the fact that the St. George and Rogue Reef rookeries are near the southern edge of the species' range, which has notably contracted over the last century due to hypothesized effects of anthropogenic disturbance, competition from California sea lions (*Zalophus californianus*), and environmental changes (Pitcher et al. 2007; NMFS 2008). Sexton et al. (2009), in their review of species range limits, found that peripheral populations are often at a species' environmental tolerance limits and thus exhibit temporal variability in population processes (e.g., survival) in years when environmental fluctuations exceed those tolerances. On the other hand, lower and more variable survival rates for younger age classes—and higher and more stable rates for adults—are a common feature of many large mammal species (e.g., Gaillard et al. 1998) so it is perhaps unsurprising that we found this pattern in our study. Furthermore, population growth for long-lived vertebrates is generally most influenced by survival rates of adult females rather than those of immature individuals (Eberhardt 2002) and, indeed, the St. George Reef

and Rogue Reef rookeries have shown sustained population growth for decades (e.g., Pitcher et al. 2007), despite the low and variable survival rates for pups that we found.

For sympatric California sea lions breeding in the California Channel Islands, there is a significant relationship between ocean warming during El Niño events and decreased survival rates of pups, which was most obvious during the strong El Niño of 1997–1998 (Carretta et al. 2016). During our study period, there were no strong El Niño events although there were relatively weak tropical El Niños in 2002–2003, 2004–2005, 2006–2007, and 2009–2010, though they did not generate strong oceanographic signals as far north as the California Current. There were, however, oceanographic anomalies in the northern California Current (Oregon and Washington) in 2005 (Peterson et al. 2006) and 2006 (Goericke et al. 2007), which were characterized by delayed onset of the spring upwelling season that resulted in low production of zooplankton and forage fishes, and resulted in reproductive failure of sea birds from central California's Farallon Islands north through Oregon. This was followed by strong La Niña conditions with cool ocean temperatures and increased productivity in 2007 (McClatchie et al. 2008). We would have expected that the 2007 cohort of Steller sea lion pups would have experienced good first-year survival

in response, yet this cohort experienced the lowest first-year survival recorded for any of the 7 cohorts other than 2001.

Clearly any relationship between ocean conditions and survival of Steller sea lion pups is more complex than that for California sea lions and will require further analysis once more data are available from additional marked cohorts. It is noteworthy, however, that the behavior of the 2 sea lion species that breed within the California Current is quite different. California sea lion pups are bound to the rookery of birth for most of their first year of life while the female exhibits central place foraging (Melin et al. 2000). In contrast, based on year-round brand resights, we found that female Steller sea lions leave the California and Oregon rookery rocks with their pups when they are approximately 2 months old and move northward to more productive coastal waters—as far as British Columbia—where the pups spend the remainder of their first year of life.

The decline of western stock Steller sea lions during the 1970s and 1980s precipitated a large investment in research by multiple government, academic, and nonprofit research groups (National Research Council 2003; Berman 2008), of which pup-branding programs such as ours is but one example. Importantly, all of the recent Steller sea lion pup-branding programs cooperated to some extent and employed similar field and data analysis methods, minimizing potentially confounding methodological differences when making cross-study comparisons. Moving forward, future studies should incorporate this new survival rate information into population models to better understand regional population dynamics in support of post-delisting monitoring efforts for eastern stock Steller sea lions (see NMFS 2013b). As Maniscalco et al. (2015) found for the western stock, we anticipate that continued monitoring of survival rates for eastern stock Steller sea lions at local levels will provide good indicators of broader population dynamics.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary data SD1.—Table of model-averaged estimates and 95% confidence intervals for annual resight probabilities (p) for Steller sea lions (*Eumetopias jubatus*) branded as pups at Rogue Reef (RR), Oregon, and St. George Reef (SGR), California, 2001–2009.

Supplementary data SD2.—Table of model-averaged estimates and 95% confidence intervals for annual survival probabilities (ϕ) for Steller sea lions (*Eumetopias jubatus*) branded as pups at Rogue Reef (RR), Oregon, and St. George Reef (SGR), California, 2001–2009.

Supplementary data SD3.—Table of model-averaged estimates and 95% confidence intervals for cumulative survival probabilities for Steller sea lions (*Eumetopias jubatus*) branded as pups at Rogue Reef (RR), Oregon, and St. George Reef (SGR), California, 2001–2009. Note that survival to age is listed at the maximum of each age class (e.g., survival from age 0 to 1 is listed as age 1).

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