



Recent increases in survival of western Steller sea lions in Alaska and implications for recovery

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ABSTRACT: Survival rates of endangered western stock Steller sea lions *Eumetopias jubatus* east of Samalga Pass (~170° W) have rebounded to nearly the same levels estimated for the 1970s prior to their decline in abundance. We estimated survival of sea lions hot-branded as pups (N = 1449) in 2000–2005 using Cormack-Jolly-Seber mark-recapture models and sighting data collected through 2011. Survivorship to Age 7 yr was greater for females (range: 0.352–0.386) than males (0.228–0.275), but was similar for each sex across the study area. Survival was lowest in the first year and increased through Age 4+ yr for both sexes in the eastern Gulf of Alaska (144–150° W). However, to the west, first-year survivorship was greater or equal to that of Year 2, and the difference was generally greater for males than females. Regional differences in the pattern of early survival could reflect spatial variability in early life history (e.g. duration of maternal care, growth rate) or habitat characteristics (e.g. prey availability, rates of predation). Population models indicate that natality of the increasing population east of Samalga Pass in 2000–2012 may not be significantly different from rates estimated for the 1970s prior to the decline in overall western abundance. Given current information, western Steller sea lions may satisfy the stock-wide demographic down-listing (to threatened status) criterion by 2015. However, due to continued abundance declines west of Samalga Pass, where no survival data are currently available, it is less certain that the western stock's regional down-listing criteria will be achieved.

KEY WORDS: Steller sea lion · Alaska · Branding · Survival

INTRODUCTION

The Steller sea lion *Eumetopias jubatus* inhabits the North Pacific Ocean, breeding and giving birth on terrestrial rookery sites ranging from central California north and west through British Columbia, Alaska, and Russia, including the Aleutian and Kuril Islands, along the Kamchatka Peninsula, and in the Sea of Okhotsk (NMFS 1992, 2008, Burkanov & Loughlin 2005) (Fig. 1). The Steller sea lion is one of the most studied marine mammals of the past 20 yr (Ferrero & Fritz 2002), largely because of a steep decline in abundance in the 1980s, its listing as 'threat-

ened' under the US Endangered Species Act (ESA) in 1990, and the potential for competitive overlap with some of the largest fisheries in the USA to affect its recovery (Fritz et al. 1995, NMFS 2008, 2010). Genetic, distribution, and population trend data led the National Marine Fisheries Service (NMFS) to separate the species into 2 stocks for management purposes in 1997 (Bickham et al. 1996, Loughlin 1997). The eastern stock, which breeds on rookeries east of 144° W, retained its 'threatened' status under the ESA, but increased at >3% per year since the 1970s following the cessation of predator control and commercial harvesting activities, and was removed from

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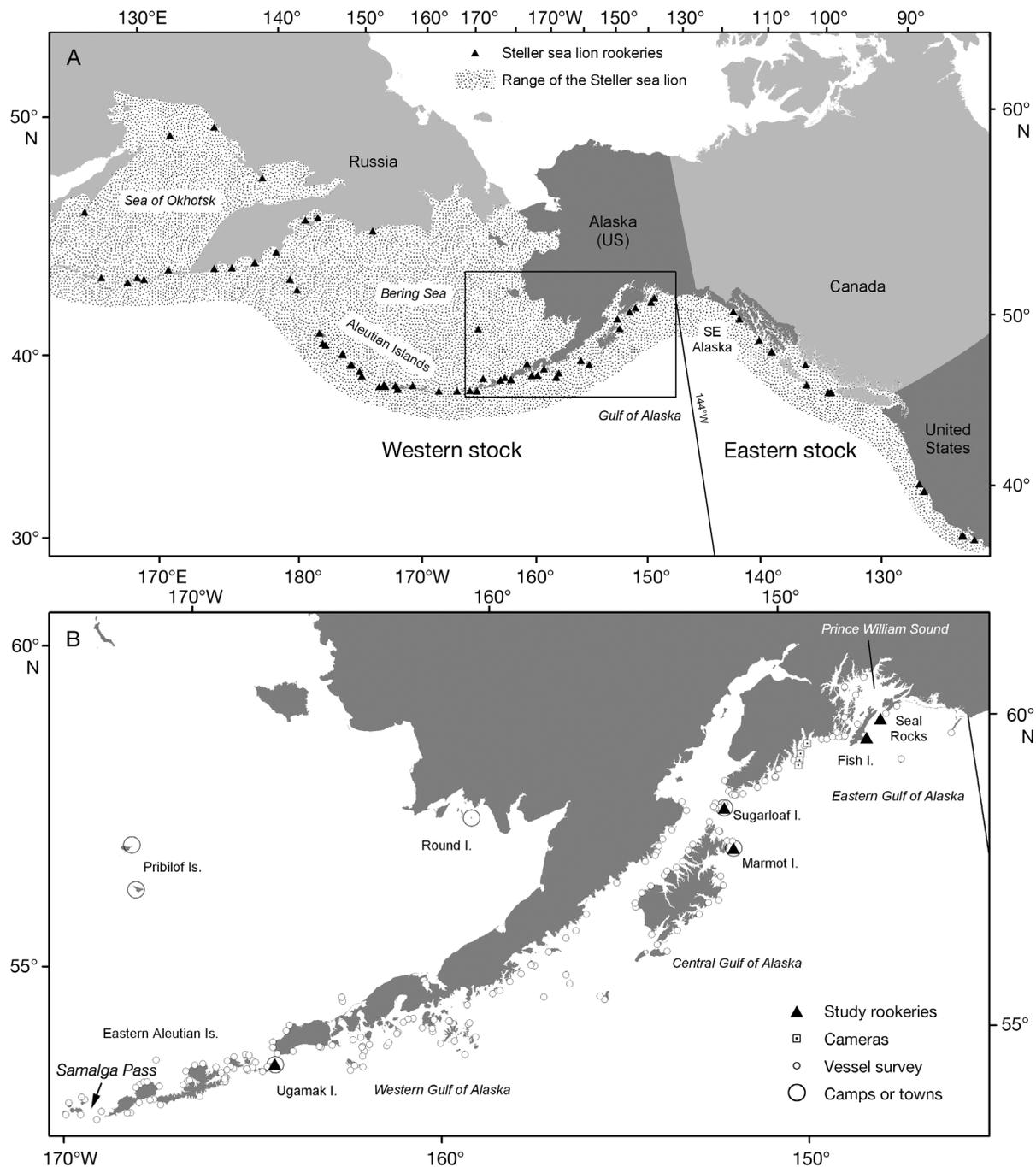


Fig. 1. (A) Location of study area (box; B) within the range of the western stock of Steller sea lion (*Eumetopias jubatus*) in Alaska, USA. Sea lions in the eastern and western stocks breed at rookeries (▲) east and west of 144° W, respectively. (B) Steller sea lion rookeries where pups were hot-branded, June–July 2000–2005, along with rookery and haul-out sites surveyed for branded animals in May–August 2001–2011 during vessel surveys, using *in situ* cameras, or by land-based observers at field camps or living in nearby towns

ESA protection in 2013 (Pitcher et al. 2007, NMFS 2013). The status of the western stock was changed to 'endangered' in 1997 because of persistent declines in counts of newborn pups and animals 1 yr and older (adults and juveniles, or non-pups; NMFS 2008).

Demographic analyses (York 1994, Holmes & York 2003, Fay & Punt 2006, Pendleton et al. 2006, Winship & Trites 2006, Holmes et al. 2007) have largely attributed the western stock decline in the 1980s to a steep, sudden drop in juvenile survival, but adult sur-

ivorship and natality (average annual probability that an adult female will give birth to a live pup) were also likely to have been negatively affected (Holmes & York 2003; Holmes et al. 2007). The decline was first noted in the late 1970s in the eastern Aleutian Islands (Braham et al. 1980; Fig. 1), but spread both east and west in the 1980s, when the steepest overall rates of decline ($\sim 15\% \text{ yr}^{-1}$) were observed (Loughlin et al. 1992). Coincident with the listing of the species under the ESA and the implementation of new regulations to reduce direct human-related mortality (Fritz et al. 1995), the rate of decline in the overall population slowed in the 1990s, but differences in regional trends emerged (York et al. 1996); the population stabilized in the center of its Alaska range (eastern Aleutian Islands and western Gulf of Alaska), but continued to decline at the ends of the range in the eastern-central Gulf of Alaska and western-central Aleutian Islands (Fritz et al. 2013). The western population in Alaska ceased declining in 2000, and a modest increase in abundance was observed through 2012, driven largely by increases east of Samalga Pass, while counts in most regions west of Samalga Pass continued to drop (Fritz et al. 2013).

Pitcher & Calkins (1981) provide a detailed description of the reproductive biology of the Steller sea lion. The breeding season (pupping and mating) of Steller sea lions is relatively short and synchronous, likely due to the strong seasonality of the environment in the Bering Sea and North Pacific Ocean and the need to balance aggregation for reproductive purposes with dispersion to avoid intra-specific competition for food resources (Bartholomew 1970). Adult males establish breeding territories on rookeries beginning in mid-late May, followed shortly by the arrival of adult females. Parturition usually occurs within days of arrival at the rookery (between late May and early July), with the mean birth dates varying between 9 and 14 June within the longitudinal range of this study ($147\text{--}165^\circ \text{ W}$; Pitcher et al. 2001). Pregnant females generally give birth to a single pup; twinning occurs, but is rare (Maniscalco & Parker 2009). Though biased slightly toward greater production of males, the sex ratio of pups at birth is approximately 1:1 (Pike & Maxwell 1958, Lowry et al. 1982).

The life history of a Steller sea lion through Age 11 yr is different for females and males. For females, Pitcher & Calkins (1981) reported mean ages of first ovulation and pregnancy of 4.6 and 4.9 yr, respectively, based on examination of collected (sacrificed) animals. Ovulation rates increased from 26% at 3 yr

to 100% at ≥ 6 yr, while pregnancy rates increased from 20% at 3 yr to 87% for females aged 8 to 20 yr. Sexual and social maturity in males is achieved at different ages, with sexual maturity occurring first (at 5–7 yr; Winship et al. 2001), followed by social maturity (at 9–13 yr; Thorsteinson & Lensink 1962, Winship et al. 2001, Raum-Suryan et al. 2002) once males have grown large enough to defend breeding territories.

Here we report estimates of juvenile (≤ 3 yr) and young adult (4–11 yr) survival rates based on observations of Steller sea lions hot-branded as pups on 5 western rookeries from 2000 through 2005. These are the first age-specific survival rates for western Steller sea lions born after the stock was listed as endangered in 1997 that were directly estimated from sightings of marked individuals. Our objective is to relate changes in survival to changes in abundance between the 1970s and 2000s, as well as discuss the relationship between vital rates (survivorship, natality, and movement) and regional abundance trends in the 2000s (Fritz et al. 2013, Johnson & Fritz 2014).

MATERIALS AND METHODS

Marking

Steller sea lion pups were individually marked (hot-branded) at 2–5 wk of age in late June or early July each year from 2000 through 2005 on 5 western rookeries in Alaska (Table 1, Fig. 1). Two of the rookeries (Seal Rocks and Fish Island) are located south of Prince William Sound in the eastern Gulf of Alaska, 2 (Marmot and Sugarloaf Islands) are in the central Gulf of Alaska near Kodiak Island, and 1 (Ugamak Island) is in the eastern Aleutian Islands. Mean sea lion birth dates range between 9 June (at Marmot Island) and 14 June (at Fish Island) at the study rookeries (Pitcher et al. 2001), and branding dates ranged from 24 June to 6 July. Pups were marked by hot-branding a letter corresponding to the natal rookery (J, Seal Rocks; E, Fish; X, Sugarloaf; T, Marmot; A, Ugamak) followed by a unique 1- to 3-digit number starting on the left shoulder and extending down the left side (Fig. 2A) using the methods of Merrick et al. (1996). All pups were weighed, measured (length), and immobilized using gas (isoflurane) anesthesia prior to branding. A minimum pup weight of 20 kg was established to avoid branding a very young animal shortly after birth. Since we do not know birth dates, setting a minimum weight for branding could

Table 1. Number of Steller sea lion pups branded by cohort, sex, rookery and region. Gaps indicate 0 pups branded

Rookery	Region	Cohort and sex														
		2000		2001		2002		2003		2004		2005		Totals		
		F	M	F	M	F	M	F	M	F	M	F	M	F	M	Total
Seal Rocks	Eastern Gulf			34	41			44	56			34	46	112	143	255
Fish Isl.	Eastern Gulf			17	15									17	15	32
Sugarloaf Isl.	Central Gulf	78	73			43	62			51	59			172	194	366
Marmot Isl.	Central Gulf	48	59			50	39			37	38			135	136	271
Ugamak Isl.	Eastern Aleutians			79	96			70	80			90	110	239	286	525
Total	Total	126	132	130	152	93	101	114	136	88	97	124	156	675	774	1449

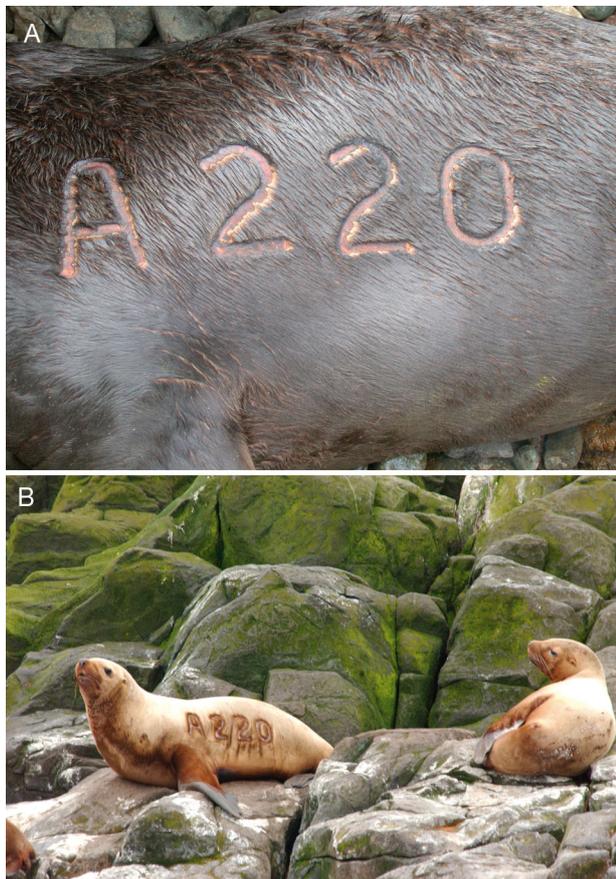


Fig. 2. (A) Brand 'A220' as applied on left side of ~1-mo-old male Steller sea lion on 24 June 2003, Ugamak Island. (B) 'A220' at ~11 mo old on 19 May 2004 at Clubbing Rocks, ~130 km east of Ugamak Island

bias our results toward those pups with greater birth weights and possibly higher survival (Hastings et al. 2009). We do not know the magnitude of this bias. The total duration that an individual pup was handled (measuring and branding) was approximately 5 min. The rookery was disturbed by human presence on land for between 6 and 9 h (see Wilson et al. 2012 for an analysis of the effects of the disturbance

caused by pup branding on adult and juvenile sea lions at the rookery). Other studies (e.g. Mellish et al. 2007, Hastings et al. 2009) have shown that branding has little to no measurable impact on health or short-term (12-wk) survival of juveniles or pups.

Observation and identification of marked animals

Observations of branded animals made from 1 May through 31 August (2001–2011) were used in the analysis (Fig. 2B). Sightings during the remainder of the year were excluded in an effort to conform to the 'instantaneous' observation assumption of Cormack-Jolly-Seber (CJS) open population models used to estimate survival and sighting probabilities. We acknowledge that we have not entirely met this assumption, and that mortalities are likely to have occurred during our sighting period. For instance, 25% of the 12 Steller sea lion mortalities detected in 6 yr by Horning & Mellish (2012) using implanted 'life history transmitter' tags occurred in May–August. This would affect age-specific survival estimates during short studies with few years of sightings, but be mitigated in longer studies such as ours with 11 yr of sightings. Sighting effort consisted of: (1) small boat-based surveys lasting between 1 wk and 1 mo; (2) land-based observations by observers at field camps on Marmot and Ugamak Islands from late May through early August each year; (3) land-based opportunistic observations by northern fur seal (*Callorhinus ursinus*) researchers and residents of the Pribilof Islands; (4) land-based opportunistic observations by USFWS scientists on Round Island in Bristol Bay, eastern Bering Sea, or throughout the Aleutian Islands and Gulf of Alaska; (5) photographs or video taken by cameras operated by the Alaska Sea Life Center, Seward, AK (Maniscalco et al. 2010), mounted above 4 Steller sea lion haul-out and rookery sites (Fig. 1B); and (6) observations by collaborating scientists working in Russia and southeast Alaska

(Fig. 1A). In 2006, there was no field camp at Ugamak Island, the Marmot Island field camp was limited to the month of July, and there was reduced sighting effort expended overall in the USA because of a court-ordered injunction on most Steller sea lion research (Dalton 2005).

A branded animal must have been unambiguously identified to be included as a sighting in the recapture history. Observers recorded each brand character and a code indicating the quality of the identification and of the character/digit itself on the animal. A recapture of a marked animal was defined as a sighting only if each character or digit was clearly identified. Field identifications of marked animals were supported by high-resolution digital photographs in 99% of the individual sightings per year (Fig. 2B).

Estimation of sighting probability and survival rates

We used CJS open population mark-recapture models to estimate sighting probability (p) and apparent annual survival (Φ). Apparent annual survival is estimated and differs from true survival because death, mark loss, and permanent emigration from the study area cannot be distinguished from each other. However, for conciseness, we will use only 'survival' when discussing Φ . All analyses were conducted using the program MARK 4.3 (White & Burnham 1990); data input and model formulation were facilitated with the R statistical environment (R Development Core Team 2013) and the add-on package RMark (Laake & Rexstad 2007).

The factors age, sex, time (year), rookery, and region were used to model p ; age, sex, cohort (time; only for Φ in Year 1 as pup:time), rookery, and region were used to model Φ (see legend to Table 2 for explanation of model notation). Regions were used in the model because of differences in regional population trends and the strong similarity in trends at each of the 2 rookeries in the eastern and central Gulf of Alaska regions since the mid-1970s (York et al. 1996, Fritz et al. 2013). Pooled estimates by region could also yield more precise estimates of Φ .

Preliminary models were run to determine which factors and combinations were the most influential in estimating Φ and p . Initial runs were used to select the best p model (sex:time:region); this was then used to find the best combinations of factors to model Φ . All combinations of factors for Φ were run, along with several age bin schemes (e.g. 1, 2, 3, 4+ yr; 1, 2, 3, 4, 5, 6–7, 8+ yr; 1, 2, 3, 4–5, 6–7, 8+ yr; 1, 2, 3, 4,

5–7, 8+ yr). Preliminary Φ model runs revealed that survival generally increased during the first 3 yr, and then was relatively stable and high for Ages 4+ yr for both sexes. Once this age bin structure (1, 2, 3, 4+ yr) was selected, a total of 17 Φ models (using sex, age, region, rookery, and cohort) were run. Models were compared using Akaike's information criterion corrected for small sample size (AIC_c ; Burnham & Anderson 2002). Our estimate \hat{c} (over-dispersion parameter; Burnham & Anderson 2002) was less than 3, indicating that there were likely only minor violations of assumptions regarding independence and parameter homogeneity among individual marked animals. As such, AIC_c rather than quasi- AIC_c was used in model selection.

We developed an age-sex-structured population model (Leslie matrix) using current western regional survival (present study) and varying natality (see Holmes et al. 2007). We did this so we could estimate natality for the 2000–2012 period using current survival (from branding) and rates of population change (non-pup trends) from aerial surveys (Fritz et al. 2013, Johnson & Fritz 2014). Using the new survival estimates from this study, an initial age-specific reproductive rate array was adjusted with a tuning parameter so that the regional growth of the age-structured population would match current regional non-pup trends (Fritz et al. 2013, Johnson & Fritz 2014). To complete the survival schedule for Ages 12–31 yr, we matched the ratio of the survival decline in the schedule of the 1970s (stable) population in Appendix C of Holmes et al. (2007). That is to say, for age $a > 11$ yr, the following survival (Φ) was used:

$$\Phi_a = \Phi_{11} \left(\frac{\Phi_a^*}{\Phi_{11}^*} \right)$$

where Φ_a^* is the age a survival from the 1970s schedule (Holmes et al. 2007). The natality schedule was modeled as in Holmes et al. (2007), i.e.:

$$f_a = \min(1, \omega f_a^*)$$

where f_a is the natality at age a , f_a^* is the natality from the 1970s stable population (Holmes et al. 2007), and ω is a tuning parameter to vary in order to obtain the desired population growth of non-pups for the 2000–2012 period for the 3 regions (Table 1, Table S1 in the Supplement at www.int-res.com/articles/suppl/n026p013_supp.pdf). To obtain estimates of ω , we used the method of Conn et al. (2014) to create a simulated population of aerial surveys where ω is optimized to create trend estimates close to the observed trend estimates in each region using a sum-of-

squares objective function. In order to account for uncertainty in the observed trend estimates from Fritz et al. (2013) and Johnson & Fritz (2014), the same procedure was used to obtain ω values for the upper and lower 95% credible interval (CI) of the observed trend estimate. Thus, we have an approximate 95% CI for ω based on the posterior distribution of the observed trend estimates. If 1 is contained within the CI of ω for a region, then we would conclude that there is not strong evidence that 2000–2012 regional natality is different from that estimated for the 1970s central Gulf of Alaska population. We assumed a stable age distribution for the initial year (2000) for each regional model run, and closed regional populations. A combined eastern-central Gulf region was also formed because movement of branded animals during the breeding season from the central to the eastern region suggested that neither population was closed, and that movement may have affected regional trend estimates (Table S1 in the Supplement). Survival-at-age estimates for the combined eastern-central Gulf region were obtained by running a separate Φ [sex * age], p [sex:time:region] model using only data for pups branded on Seal Rocks, Fish, Marmot, and Sugarloaf (Table 1, Table S2 in the Supplement).

To obtain pooled estimates of survival-at-age by sex for the 4 southeast Alaska rookeries where Hastings et al. (2011) branded pups, we calculated a weighted average (without confidence bounds) based on individual rookery pup production in 2009 (Fritz et al. 2013) and assumed an even sex ratio (Pike & Maxwell 1958, Lowry et al. 1982). Using the weighted average survival-at-age values, we then estimated survivorship through Age 7 yr for both females and males for comparison with the western population.

RESULTS

Despite having the largest number of estimated parameters, the interactive models [sex:time:region] and [sex:age:region] provided the best combination of factors (had the lowest AIC_c and >90% of the weight of all models) to model p and Φ , respectively (Table 2). Using the simplest bin scheme (1, 2, 3, 4+ yr) rather than one that estimated more age-specific survivorships (e.g.: 1, 2, 3, 4, 5, 6–7, and 8–10 yr) greatly improved overall fits ($\Delta AIC_c = 15.9$ between top models) and revealed strong

sex:region interactions that were not evident with more fine-scale age bin structures. Interactive models for p and Φ allowed regional, temporal, and age- and sex-related effects to vary independently.

Sighting probability was generally higher for females than males, and increased from 2007 through 2011 for both sexes as the branded population matured and recruited to rookeries (Fig. S1 in the Supplement). Given that sightability generally increased with time, we thought age would be included as well, but it appears to have been overwhelmed by time and region in the best p model. Logistical and other factors (e.g. cruise schedules, weather) were chiefly responsible for the time:region effect on p , since they affected the specific sites visited each year. In addition, the effect of significantly reduced sighting effort led to low p values in 2006, particularly in the eastern Gulf of Alaska. Age was the most important factor used to model Φ , appearing in each of the top 15 models, followed by sex and region (Table 2). Cohort effects were not in any of the top 5 models (with >99% of the combined weight of all models), and rookery effects only appeared in the second highest rated model (with only 7.2% of the weight).

Regional effects on survival were largely expressed during the first 3 yr for both females and males (Table 3). Survival rates at Age 1 yr were lowest in the eastern Gulf of Alaska, and were not significantly different ($p > 0.05$) between females and males. Female survival at Age 1 yr was significantly greater ($p < 0.05$) in the central Gulf of Alaska and eastern Aleutian Islands than in the eastern Gulf of Alaska (Table 3, Fig. 3). In the central Gulf, female survival rates during each of the first 3 years were similar, ranging between 0.76 and 0.79, while for males, point estimates dipped from 0.79 at Age 1 yr to

Table 2. Top 5 models (with >99% of the weight of all models) used to estimate survival (Φ) and sightability (p) of branded western Steller sea lions in Alaska. Model 1 was used to estimate Φ and p . Weight: relative strength of model compared with all other models; ΔAIC_c : difference in AIC_c (Burnham & Anderson 2002) relative to the top-weighted model. Model factors: (:) interaction terms without main effects; (*) interaction terms with main effects; (+) additive main effects only

Model	Weight	ΔAIC_c	No. parameters
1. Φ (sex:age:region) p (sex:time:region)	0.909		86
2. Φ (age:rookery) p (sex:time:region)	0.072	5.1	82
3. Φ (age:region) p (sex:time:region)	0.004	10.8	74
4. Φ (sex * age) p (sex:time:region)	0.004	11.0	70
5. Φ (sex + age) p (sex:time:region)	0.003	11.2	67

Table 3. Age- and sex-specific survival estimates (Φ and 95% confidence interval, CI) of branded western Steller sea lions in Alaska by region, sex, and age. Average Φ was estimated for Ages 4+ yr

Age (yr)	Eastern Gulf of Alaska				Eastern Aleutian Islands				Central Gulf of Alaska			
	Females		Males		Females		Males		Females		Males	
	Φ	95% CI	Φ	95% CI	Φ	95% CI	Φ	95% CI	Φ	95% CI	Φ	95% CI
1	0.555	0.450–0.656	0.6	0.476–0.713	0.785	0.682–0.861	0.873	0.700–0.953	0.779	0.697–0.844	0.789	0.688–0.863
2	0.913	0.645–0.984	0.67	0.498–0.806	0.738	0.626–0.826	0.574	0.465–0.677	0.757	0.646–0.841	0.692	0.563–0.797
3	0.935	0.712–0.988	0.834	0.621–0.939	0.945	0.795–0.987	0.899	0.739–0.965	0.788	0.684–0.865	0.726	0.597–0.826
4–10	0.95	0.905–0.974	0.913	0.838–0.955	0.896	0.859–0.924	0.883	0.845–0.913	0.938	0.913–0.956	0.871	0.834–0.901

0.69 and 0.72 at Ages 2 and 3 yr, respectively. In the eastern Aleutians, female survival rates at Ages 1 and 2 yr were similar, while male survival was significantly greater ($p < 0.05$) at Age 1 yr than at Age 2 yr (Table 3). At Age 3 yr in the eastern Aleutians, both female and male survival increased to rates that were not significantly different ($p > 0.05$) from those at Ages 4+ yr. Survival rates at Ages 4+ yr were generally the highest for both sexes and generally higher for females than males within each region.

Despite much lower Age 1 yr survival rates in the eastern Gulf (Table 3), survivorship of females to Age 4 and 8 yr (age of first birth and age at the beginning of the period with peak natality; Pitcher & Calkins 1981, Calkins & Pitcher 1982, Holmes et al. 2007) were similar between regions, ranging between 0.44–0.49 and 0.32–0.37, respectively (Fig. 3A). Similarly, survivorship of males to age of social maturity ranged between 0.17 and 0.21 (Fig. 3B), despite large regional differences in Ages 1–3 yr survival (Table 3).

Based on our Leslie matrix model, current (2000–2012) estimated natality in the eastern Gulf ($\omega = 0.97$, 95% credible interval of 0.68–1.34) is not significantly different from the 1970s baseline rate (Holmes et al. 2007), but remains low in the central Gulf ($\omega = 0.81$, 0.69–0.94). Combining these 2 regions yielded an estimate of ω (0.87, 0.72–1.03) that was 13% lower than, but not significantly different from, the 1970s. Estimated current natality in the eastern Aleutian Islands is 9% higher than that of the 1970s ($\omega = 1.09$, 0.92–1.28), but also not significantly different.

DISCUSSION

Pendleton et al. (2006) reported higher Age 1 yr than Age 2 yr survival rates in western Steller sea lions based on sightings of animals branded as pups on Marmot Island in the central Gulf of Alaska in 1987–1988. In contrast to our study, they found little difference in survival-at-age between the sexes, but this could be the result of a smaller sample size and lower overall sighting probability than in our study. We report that female western Steller sea lions in the western part of our study area have high Age 1 yr survival and no difference in survival between Ages 1 and 2 yr. Males in this same region also have high Age 1 yr survival but greater survival at Age 1 yr than Age 2 yr, with this difference being much larger to the west. However, western sea lions in the eastern part of our study area have a pattern of Age 1–2 yr survival that is similar to that of eastern stock sea

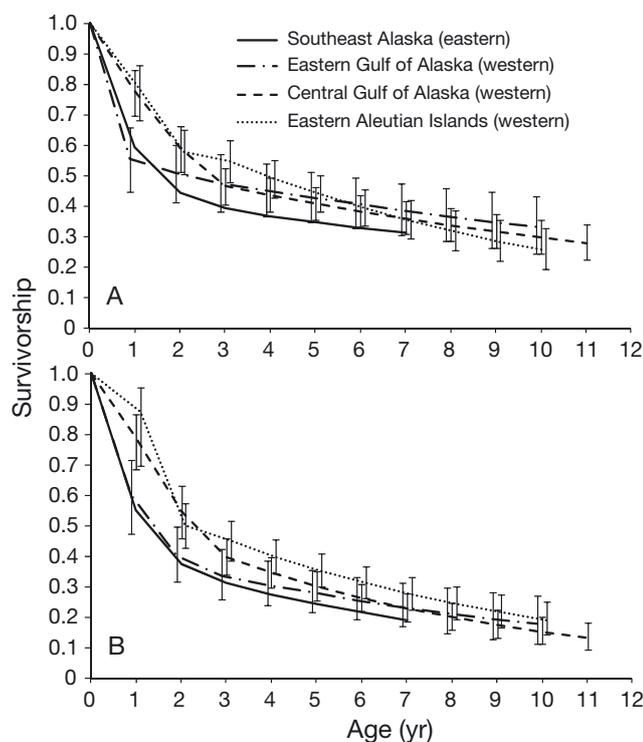


Fig. 3. Survivorship (proportion born surviving to age) of (A) female and (B) male Steller sea lions branded as pups at rookeries in Alaska: western stock (eastern and central Gulf of Alaska, and the eastern Aleutian Islands; present study) and eastern stock (southeast Alaska; Hastings et al. 2011). Legend in A also applies to B. Confidence bounds (95%) are plotted at Age -0.1 and $+0.1$ yr for the eastern Gulf of Alaska and eastern Aleutian Islands regions, respectively, and at the integer year for the central Gulf of Alaska

lions in southeast Alaska (Hastings et al. 2011) and other otariid pinnipeds (e.g. *Arctocephalus gazella*, Boyd et al. 1995; *A. pusillus pusillus*, Butterworth et al. 1995; *Zalophus californianus*, Hernandez-Camacho et al. 2008; *Callorhinus ursinus*, Lander 1981–1982) in which Φ is lowest during the first year and increases with age.

Low sightability of the 2004 and 2005 branded western cohorts due to reduced effort in 2006 and heterogeneity in sighting probability of young branded sea lions could have affected the regional pattern of Age 1–2 yr survivorships. To test for the former, we ran Model 1 (Table 1) with only the 2000–2003 cohorts; the regional survivorship pattern was unchanged and the survival estimates were not significantly different ($p > 0.05$). However, heterogeneity in sighting probabilities may be contributing to this early survival pattern. Regions with relatively high Year 1 survival were also those where field camps were manned for several months each summer, increasing the likelihood that a branded juvenile would be seen if it were still not fully independent from its mother at Ages 1 and 2 yr. Conversely, less effort at rookeries in regions without field camps (eastern Gulf of Alaska) may have led to fewer observations of the same branded animal at both Ages 1 and 2 yr. As such, the model may have not been able to partition survival between the first 2 yr here compared with the more western regions, and this may be evidenced by the larger standard errors, particularly for Age 2 yr. However, where we may have our best sighting data, the pattern of survival during the first 2 yr appears to be different in the 2 stocks (Hastings et al. 2011), suggesting differences in Steller sea lion life history. High Age 1 yr survival in the west could be the result of longer average periods of maternal care, lower predation rates (see Horning & Mellish 2012), or a combination of these and other factors compared with the eastern stock. While our results suggest that the eastern Gulf of Alaska has a pattern more similar to that of southeast Alaska, heterogeneity and logistical issues related to sighting probability preclude this from being a firm conclusion at this point.

In general, our estimates of western Steller sea lion survival rates are higher than those estimated for eastern sea lions in southeast Alaska, particularly from the southern, larger, and older rookeries at Forrester and Hazy Islands (Hastings et al. 2011). Age 1 yr survival of pooled eastern females was nearly identical to western females in the eastern Gulf of Alaska, but was lower than western females in the central Gulf of Alaska and eastern Aleutian

Islands (Fig. 3A). Western female survivorships to Age 5 yr (range of 0.41 to 0.44 for the 3 regions) were similar and were all generally greater than the estimate for pooled eastern females (0.34; Fig. 3A). Western male survivorship to Age 5 yr was greater in the eastern Aleutian Islands (0.35) than in either of the other western regions (eastern and central Gulf of Alaska, 0.28 and 0.30, respectively) or southeast Alaska (eastern stock, 0.24; Fig. 3B).

A result common to all demographic modeling studies of the dynamics of the western Steller sea lion conducted since the mid-1990s (Pascual & Adkison 1994, York 1994, Holmes & York 2003, Fay & Punt 2006, Winship & Trites 2006, Holmes et al. 2007) is that the decline in abundance observed in the 1980s and early 1990s was associated with a large drop in the survival rate of juvenile sea lions. Empirical evidence from animals marked as pups in the central Gulf of Alaska in 1987–1988 supports these model results: juvenile survival rates were 21 % lower in the late 1980s and early 1990s than in the mid-1970s (York 1994, Pendleton et al. 2006), which is similar to demographic model estimates of juvenile female survival for this period reported by Holmes et al. (2007) (Fig. 4). The slower rate of population decline in the central Gulf observed in the 1990s and the population stability of the 2000s were associated with increases in juvenile survival (Holmes et al. 2007, Fritz et al. 2013). Our empirical results indicate that juvenile survival in the 2000s is higher than in the late 1980s and early 1990s (Pendleton et al. 2006, Holmes et al. 2007), but may still be slightly lower than in the 1970s (Calkins & Pitcher 1982, York 1994, Holmes et al. 2007).

There has been less agreement among model results in the magnitude of the changes that have occurred in adult survivorship and natality, though all models indicated declines in both for various lengths of time. Models that included data collected through the 1990s and early 2000s (Holmes & York 2003, Fay & Punt 2006, Winship & Trites 2006, Holmes et al. 2007) revealed that the steep population decline of the 1980s was associated with a large drop in juvenile survival and usually modest declines in both adult survival and natality. However, as the population decline slowed in the 1990s and increased slightly in the early 2000s, juvenile and adult survival improved, but results were mixed regarding changes (if any) in natality.

Holmes et al. (2007) observed a marked and continuous decline in natality in the central Gulf Steller sea lion population, and our Leslie model results support this conclusion if we too assume that this population

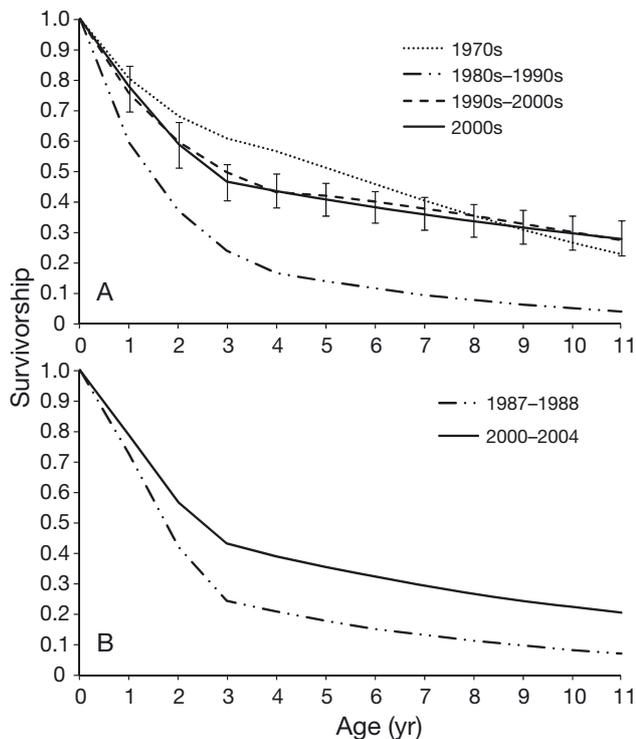


Fig. 4. Survivorship of Steller sea lions in the central Gulf of Alaska, 1970s through 2000s. (A) Females in the mid-1970s based on a life table (1970s; Calkins & Pitcher 1982, Holmes et al. 2007); modeled female populations in the late 1980s and early 1990s (1980s–1990s), and late 1990s and early 2000s (1990s–2000s; Holmes et al. 2007); and females branded as pups in 2000–2004 (2000s with 95% confidence bounds; present study). (B) Pooled females and males branded as pups in 1987–1988 (1987–1988; Pendleton et al. 2006); and pooled females and males branded as pups in 2000–2004 (2000–2004; present study)

is closed. However, the closed population assumption does not appear to be valid for the recent (since 2000) period (Fritz et al. 2013). When this region is combined with the eastern Gulf as the animal movement data suggest, the perception is that natality may only be slightly lower now in the combined region than in the 1970s. While it is not possible to determine whether movement from the central Gulf of Alaska to the eastern Gulf is a new phenomenon, perhaps in response to the severe decline experienced through the 1990s, the growth of the western Steller sea lion stock east of Samalga Pass may not be due to increased survival alone. However, there are several caveats to our analysis that preclude this from being a firm conclusion. First, survival estimates were treated as fixed and known in the Leslie model, and uncertainty in the survival values was not propagated to uncertainty in natality. Second, the overall shape of the natality curve was assumed to be the

same as the 1970s population (Holmes et al. 2007). If the actual shape of the schedule has changed (e.g. not as strong a drop in natality with age), the procedure employed here might increase the overall curve in an effort to increase natality in a particular part of the curve. Given that senescence has been observed in some (*A. pusillus pusillus*, Butterworth et al. 1995; *Z. californianus*, Hernandez-Camacho et al. 2008; *C. ursinus*, Lander 1981–1982) but not all (*Arctocephalus gazella*, Boyd et al. 1995) otariids, this assumption will be tested and empirical estimates of natality will be obtained as sightings of our study animals are obtained in subsequent years. Third, the age distribution used for the initial year in the model will affect the results. The assumption used here of a stable age distribution in 2000 may not be accurate given the large changes in abundance in the 2 previous decades (Fritz et al. 2013).

Our new empirical and model results for western Steller sea lion survival and natality indicate that where population trends are positive (east of Samalga Pass), vital rates have returned to nearly the same levels estimated for the mid-1970s prior to the steep decline in abundance. Increases in abundance in this area are responsible for the positive trend observed since 2000 in the western stock in Alaska overall (Fritz et al. 2013). The results of the Leslie matrix modeling undertaken in this study are not intended to be used to forecast regional population growth, but were simply used to compare natality schedules estimated for a 1970s stable population with those estimated for variably increasing populations, all east of Samalga Pass, in the period 2000–2012, as a follow-on to Holmes et al. (2007). There is no information, however, on Steller sea lion vital rates west of Samalga Pass where counts of pups and non-pups continued to decline through 2012 (Fay & Punt 2013, Fritz et al. 2013, Johnson & Fritz 2014).

There are 2 demographic criteria, along with the listing criteria, that must be met before NMFS considers changing the listing status of western Steller sea lions from ‘endangered’ to ‘threatened’ (NMFS 2008). The first is a statistically significant increase in abundance for the Alaska western stock as a whole over a 15 yr period beginning in 2000, when the lowest abundance count was made (NMFS 2008). The western stock appears to be on track to meet the first down-listing criterion by 2015 if abundance trends estimated through 2012 continue (Fritz et al. 2013, NMFS unpubl. data). The second demographic down-listing criterion states that trends in at least 5 of 7 western regions (6 in Alaska and 1 in Russia) must be ‘consistent’ with the overall stock trend, with the

added stipulation that trends cannot be declining in any 2 adjacent regions (NMFS 2008). Given trends observed in most of the Aleutian Islands (which include 2 of the 6 Alaska regions), it is unclear whether the western stock will meet the second criterion by 2015. Research will continue on understanding the possible causes of the continued decline west of Samalga Pass, which include nutritional stress related to environmental change or fisheries (NRC 1996, 2003, NMFS 2000, 2008, 2010, Malavear 2002, Trites & Donnelly 2003, Fritz & Hinckley 2005, Trites et al. 2007, Atkinson et al. 2008), predation by killer whales (Springer et al. 2003, Williams et al. 2004, Maniscalco et al. 2007, Horning & Mellish 2012), contaminants and disease that could impair reproduction (Burek et al. 2003, Atkinson et al. 2008, Castellini et al. 2012), and incidental and intentional takes in Russian fisheries (Burkanov et al. 2006).

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